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ORIGINAL ARTICLE

Environmental causes and consequences of forest clearance and agricultural abandonment in central New York, USA

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ABSTRACT

Aim Climate, topography and soils drive many patterns of plant distribution and abundance across landscapes, but current plant communities may also reflect a legacy of past disturbance such as agricultural land use. To assess the relative influences of environmental conditions and disturbance history on vegetation, it is important to understand how these forces interact. This study relates the geographical distribution of land uses to variation in topography and soils; evaluates the consequences of land-use decisions for current forests; and examines the effects of agricultural land use on the chemical properties of forest soils.

Location Tompkins County occupies 1250 km^2 in central New York's Finger Lakes region. Like much of eastern North America, this area underwent forest clearance for agriculture during the 1800s and widespread field abandonment and forest recovery during the 1900s. The current landscape consists of a patchwork of forests that were never cleared, forests that developed on old fields and active agricultural lands.

Methods We investigated relationships among topography, soils and land-use decisions by gathering information about land-use history, slope, aspect, elevation, soil lime content, soil drainage and accessibility in a geographic information system (GIS). To assess the effects of agriculture on forest soil chemistry, we measured pH, organic matter content and extractable nutrient concentrations in field-collected soil samples from 47 post-agricultural and uncleared forests.

Results Steeper slopes, less accessible lands and lower-lime soils tended to remain forested, and farmers were more likely to abandon fields that were steeper, farther from roads, lower in lime and more poorly drained. Slope had by far the greatest impact on patterns of clearance and abandonment, and accessibility had a surprisingly strong influence on the distribution of land uses. The effects of other factors varied more, depending for example on location within the county. Current forest types differed accordingly in topography and soil attributes, particularly slope, but they also showed much overlap. Post-agricultural and uncleared forest soils had similar chemical properties. Forests on lands abandoned from agriculture 80–100 years before had slightly higher pH and nutrient concentrations than adjacent, uncleared forests, but these changes were small compared to environmental variation across the county.

Main conclusions Despite differential use of lands according to their topography and soils, the substantial influence of accessibility and the relatively small scale of land-use decisions allowed for broad similarity among forest types. Thus, the topography and soil differences created by land-use decisions probably contribute little to landscape-level patterns of diversity. Subtle changes in forest soil chemistry left from past agriculture may nevertheless affect plant distribution and abundance at finer scales.

Keywords

Agriculture, disturbance, forest history, geographic information system (GIS), land use, landscape, soil, spatial autocorrelation, topography.

INTRODUCTION

Broad-scale patterns in the distribution and abundance of organisms largely reflect variation in climate, topography and soils; documenting these connections has long been a central enterprise of biogeography in general and of plant ecology in particular. Disturbance, however, complicates the relationship between environment and vegetation, layering change in time over variation in space (e.g. Watt, 1947; Fig. 1). An interpretation of current landscapes must therefore take into account past disturbance as well as present environmental conditions, and it must take care to distinguish between them. Yet these two principal influences on plant distributions do not operate independently. Neither natural nor human disturbance falls on landscapes at random; fires, floods and windstorms affect certain communities more than others, and people tend to use different lands for different purposes. Disturbance may also cause persistent environmental changes that then continue to affect recovering vegetation. Specifying the interactions between disturbance and environment is thus critical to understanding why organisms live where they do.

Across landscapes throughout the world that support human habitation, agriculture has been a dominant form of disturbance shaping natural communities (Foster *et al.*, 1998). Many regions have experienced successive changes, with phases of forest clearance followed by agricultural abandonment and forest recovery (Whitney, 1994; Kirby & Watkins, 1998). This history of changing land use transformed continuously forested landscapes into discrete habitat patches: forests that were never cleared (primary forests), forests that developed on old fields (secondary forests) and active agricultural lands.

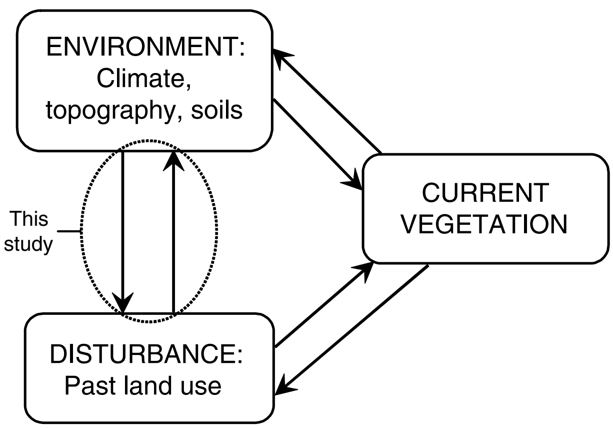

Figure 1 Conceptual diagram showing the reciprocal relationships among environmental conditions, disturbance and vegetation; and the focus of this study on the interactions among land use, topography and soils.

Since agriculture continues to influence the vegetation of many current landscapes, it is important to assess the full impact of this intense, pervasive and long-term disturbance on the geographical distribution of biological diversity. In temperate forests, recovery of species richness in the understorey is of particular interest because shade-tolerant perennial herbs represent the majority of plant diversity, and because their life-history traits likely make them sensitive to habitat fragmentation (Bierzychudek, 1982). Much work now documents differences in the understorey flora of forests with different land-use histories. Forest-herb communities of mature secondary forests show reduced species richness (e.g. Peterken & Game, 1984; Dzwonko & Loster, 1989; Matlack, 1994; Singleton *et al.*, 2001; Flinn & Marks, 2004) and altered species composition (e.g. Whitney & Foster, 1988; Wulf, 1997; Brunet & von Oheimb, 1998; Bossuyt *et al.*, 1999b; Vellend, 2005) compared with forest-herb communities of primary forests. The processes that create these patterns, however, are less well-known. Are these differences caused simply by the removal of vegetation, so that the recovery of diversity in secondary forests depends only on the arrival of seeds and spores? Or, do environmental conditions differ among forests of different history in ways that affect plant distributions? And, if forest types do differ in environment, were these differences imposed by initial decisions of which lands to use for what purposes, or were they created by the agricultural land use itself?

Few studies of understorey plant distributions have addressed the possible environmental differences between primary and secondary forests, while none has assessed the extent to which these might be due to prior conditions as opposed to land use. Yet agricultural land use clearly depends on environmental factors like physiographic position, slope and soil drainage (Foster, 1992; Matlack, 1997; Foster *et al.*, 1999). It is also clear that agriculture alters forest soils in predictable directions. In pastures, grazing animals churn and compact soils by trampling; in croplands, ploughing mixes soil horizons, levels microtopography, speeds decomposition and promotes erosion; and inputs of lime, fertilizer and manure raise pH and nutrient concentrations.

Many studies have documented consistent soil changes during early stages of forest succession on old fields. As trees regrow, soils typically gain acidity and lose base cations (Robertson & Vitousek, 1981; Thorne & Hamburg, 1985; Johnston *et al.*, 1986; Binkley *et al.*, 1989; Richter *et al.*, 1994; Ritter *et al.*, 2003). Bulk density decreases as organic matter (OM) accumulates (Billings, 1938; Coile, 1940; Jenkinson, 1971; Robertson & Vitousek, 1981), so that carbon, nitrogen and C:N ratio increase (Zak *et al.*, 1990; Post & Kwon, 2000; Hooker & Compton, 2003; Poulton *et al.*, 2003). As secondary forests mature, however, questions remain about the extent and persistence of these changes: how much does agriculture affect forest soils, and how long do these effects persist? Some cultivated soils recovered the acidity of ancient forests within 50 years of abandonment (Bossuyt *et al.*, 1999a), whereas in others physical and chemical changes induced by Roman agriculture remained after nearly 2000 years (Dupouey *et al.*, 2002). The degree and duration of the legacy of past agriculture in current forest soils seem highly site-specific, depending on both the initial conditions of the soil and the land use itself – its duration, intensity and specific practices. These may also interact if, for example, less fertile soils require more lime for adequate yields.

Here we address the causes and consequences of agricultural land use in Tompkins County, New York. First, we relate the geographical distribution of land uses to variation in topography and soils, asking whether people tended to clear or abandon pieces of land with certain features. Were farmers less likely to clear or more likely to abandon lands less favourable for agriculture – lands with steep slopes, north-facing aspects, high elevations, low-lime or poorly drained soils, or difficult access? Next, we evaluate the consequences of these decisions for current forests; if topography and soils influenced agricultural clearance and abandonment, then how do forests of different history differ in these same attributes? Finally, we assess the effects of agriculture on forest soils by comparing the chemical properties of field-collected soil samples from primary and secondary forests.

LOCATION

Climate, topography and soils

Tompkins County covers 1250 km^2 of land in the Finger Lakes region of central New York, USA. The region has a humid, continental climate, where the mean annual temperature is 7.7 °C, the mean frost-free season 146 days and the mean annual precipitation 90 cm, including 171 cm of snow (Northeast Regional Climate Center, 2004). Nearly all of Tompkins County lies on the glaciated Allegheny Plateau. The northern part of the county forms a relatively flat plain at 300–450 m asl, dissected by the deep Cayuga Lake valley and several creek drainages, whereas in the south, steep hills range from 120 to 640 m (Fig. 2a). Bedrock of Devonian age varies from limestone and calcareous shales and sandstones in the north to acid shales, sandstones and siltstones in the south (Williams *et al.*, 1909). Soils formed in glacial till, outwash and lake sediment, and most are fine silt loams (Neeley, 1965). Soil pH likewise ranges from circumneutral (6–7) in the north to strongly acid (4–5) in the south (Fig. 2b). The county thus comprises two distinct landscapes: the northern part, with relatively flat, lime-rich land, and the southern part, with rougher terrain and more acidic soils.

Vegetation and land-use history

Regional vegetation belongs to Braun's (1950) hemlock – white pine – northern hardwoods formation. Dominant species in local mesic, upland forests include sugar maple (*Acer saccharum* Marsh.) and beech (*Fagus grandifolia* Ehrh.; C.L. Mohler, P.L. Marks, S. Gardescu, unpubl. data). Old fields typically develop woody thickets within 30–40 years (Stover & Marks, 1998; Gardescu & Marks, 2004), and secondary forest canopies 80–100 years old consist of white pine (*Pinus strobus* L.), red maple (*A. rubrum* L.) and ash (*Fraxinus americana* L.).

Land-use patterns in Tompkins County changed drastically over the past 200 years. Although Iroquois inhabited the region in the eighteenth century, original land-survey records show that forest covered 99.7% of Tompkins County in 1790 (Marks & Gardescu, 1992). European settlement began during the 1790s, and clearance for agriculture proceeded throughout the 1800s. Open farmland reached its greatest extent around 1900, according to agricultural census data (Smith *et al.*, 1993; Fig. 2c). By the early twentieth century, many farmers began to abandon fields as they left for better farms or more profitable occupations elsewhere (Vaughan, 1928). Forests have since continued to recover, reaching 54% of the county's land area by 1995 (Table 1; Fig. 2d).

Although primary forests were never cleared for agriculture, most experienced selective cutting and cattle grazing during use as farm woodlots. Secondary forests grew on fields abandoned from a variety of agricultural uses, including croplands, pastures and hayfields.

METHODS

Effects of topography and soils on land-use decisions

Geographic information system analysis

To investigate the influence of variation in topography and soils on the geographical distribution of land uses, we assembled maps of land use, topography, soils and roads in a geographic information system (GIS; ArcMap 8.1, ESRI, 1999). For the land-use map, we scanned, georeferenced and digitized forest-history maps from Smith *et al.* (1993). These maps distinguished primary forests, which persisted through the time of maximum clearance in 1900, from secondary forests that developed on old fields between 1900 and 1938. To develop the maps, Smith *et al.* (1993) used 1936–38 aerial photographs (≥ 1 : 20,000) to identify primary and secondary

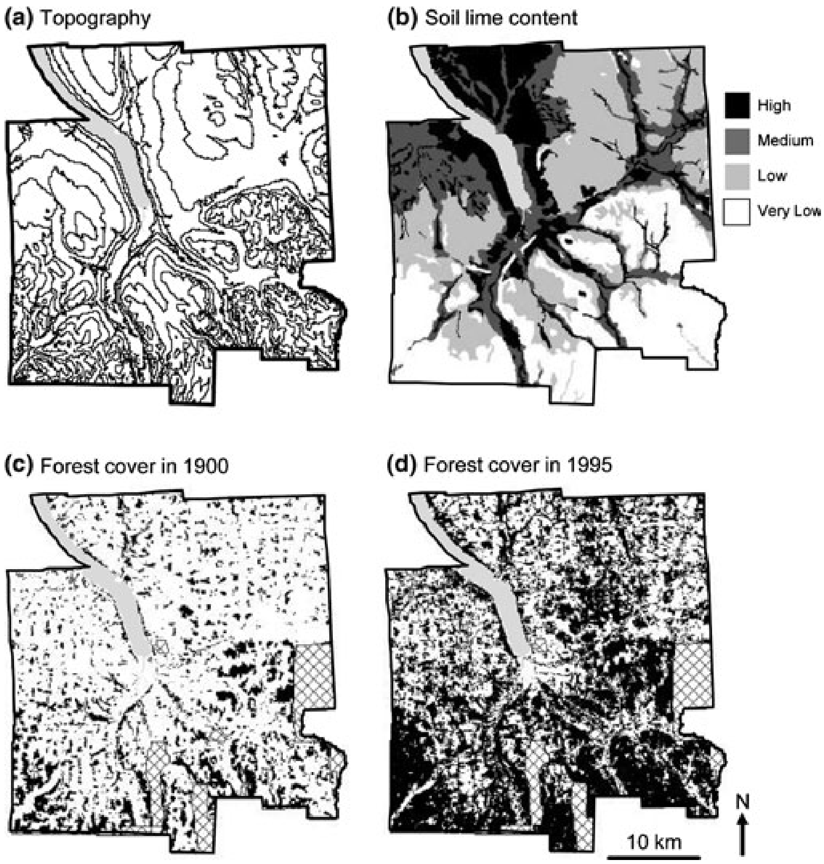

Figure 2 Maps of Tompkins County, New York, showing variation in topography [(a), 60-m contour lines], soil lime content (b), and forest cover in 1900 (c) and 1995 (d). Cross-hatching indicates places missed by 1936–38 aerial photographs (6% of the county's land area).

Table 1 Landscape composition of Tompkins County, New York in 1995, showing percentages of land area covered by forests of various history and agricultural lands. Forest cover totals include 'brushy' forests where history was unclear (1% of the county's land area)

Land use	Whole county	North	South
Primary forest present in 1900	17	11	25
Secondary forest that originated between 1900 and 1938	8.6	6.0	12
Secondary forest that originated between 1938 and 1995	27	23	31
All forest present in 1995	54	41	68
Agricultural fields active in 1995	31	41	20

forests based on tree height, crown size and uniformity of cover. They verified these designations by field checking all stands along a 1-km grid covering the entire county, a total distance of 2303 km, and every stand within one 7.5-min quadrangle (USGS, Reston, VA, USA). Marks & Gardescu (2001) discuss field evidence used to deduce forest history, and Smith *et al.* (1993) provide a full description of methods used to develop the forest-history maps. Small areas of 'brushy' forest where history was unclear (1% of the county's land area) we excluded from the analysis. We then combined the 1938 forest-history map with a land-use map based on 1995 aerial photographs (Tompkins County Planning Department, 2000a). This map added secondary forests that originated between 1938 and 1995 and agricultural lands that were active in 1995. Primary forests included deciduous, coniferous and mixed stands as well as wooded wetlands; secondary forests included conifer plantations and fields where trees and shrubs covered ≥ 80% of the area; and active agricultural lands included arable, pasture and fallow. The 2% of the county's land area where forest was cleared between 1938 and 1995 we excluded from the analysis. As the 1936–38 aerial photographs missed several places, the coincident area covered 94% of the county. The resulting land-use map represented all forests and fields present throughout Tompkins County in 1900, 1938 and 1995, allowing us to distinguish three current forest types: primary forest, secondary forest that originated between 1900 and 1938, and secondary forest that originated between 1938 and 1995.

To check the accuracy of the land-use map, we compared it against 1995 digital orthophotographs with 1-m ground resolution (New York Department of State, 2000). Since most discrepancies were < 35 m, we deleted the outer 35 m of each forest and field with the buffer function. We then converted the land-use map to a grid with 50 × 50-m cells. This cell size was the maximum appropriate for the small farm woodlots common in the region; the buffer and grid conversion excluded forests and fields of < 1 ha and ensured that those of ≥ 2 ha would be represented.

We constructed an elevation map for the county by merging 12 7.5-min digital elevation models (DEMs; USGS, 1998) with elevations in 10-m intervals for 10 × 10-m cells. In order to overlay the elevation map on the other maps, we projected it to the State Plane coordinate system for central New York (North American Datum 1983, feet) and converted it to the same 50-m grid. We extracted slope (°) and aspect (°) grids from the elevation map with the surface analysis function and converted aspect to degrees from north.

Soil information came from a digital map of soil associations (1 : 63,360; Tompkins County Planning Department, 2000b) we converted to the 50-m grid. We characterized the soil associations by two attributes particularly relevant to agricultural land-use decisions: lime content and drainage. Following verbal descriptions from the county soil survey (Neeley, 1965; Cline, 1970; Hutton, 1970) and USDA soil taxonomy (Soil Survey Division Staff, 1993), we grouped soils into four, ordered lime classes: high-, medium-, low- and very low-lime; and four, ordered drainage classes: well-, moderately well-, somewhat poorly and very poorly drained.

We also considered land accessibility, in order to compare the importance of this arbitrary, cultural factor to that of the environmental factors (Foster, 1992). To quantify access, we calculated the straight-line distance (m) from each 50 × 50-m cell to the nearest road, using the spatial analyst tool and a digital county road map (Tompkins County Planning Department, 1997). Roads in Tompkins County have changed little over the past 200 years, so that a modern road map effectively represents land accessibility during the entire period. Since people built most farmhouses and barns next to roads, this measure also likely describes distances relevant to working farmers. Distance to nearest road is largely independent of topography and soils, particularly in the northern part of the county where roads were laid along the compass lines of the original land survey.

In sum, GIS analysis resulted in a grid of 199,613 cells, each with information about past and present land use, slope, aspect, elevation, soil lime content, soil drainage and distance to nearest road.

Statistical analysis

We assessed the effects of topography (slope, aspect, elevation), soils (lime, drainage) and access (distance to nearest road) on land-use decisions with multiple logistic regression. Separate analyses examined three binary land-use decisions: whether or not to clear forests for agriculture by 1900; whether or not to abandon agricultural lands to forest between 1900 and 1938; and whether or not to abandon agricultural lands to forest between 1938 and 1995. Thus the first analysis compared primary forests to all lands once in agriculture (all secondary forests and active agricultural fields); the second compared secondary forests that originated between 1900 and 1938 to lands in agriculture at that time (secondary forests that originated between 1938 and 1995 and agricultural fields active in 1995); and the third compared secondary forests that originated between 1938 and 1995 to agricultural fields active in 1995. In order to capture meaningful differences between the landscapes of northern and southern Tompkins County, we performed each analysis for the whole county and for the northern and southern parts separately. We defined the boundary between north and south at 42°26′22″ N latitude, the base of Cayuga Lake (Fig. 2). To analyse the effect of aspect, we repeated all analyses with a subset of the data that included only slopes ≥ 5°, since aspect likely affects only lands with at least a slight slope.

Dividing the landscape into nearly 200,000 50 × 50-m cells created positive spatial autocorrelation, a tendency for similarity among cells close in space. This lack of independence among adjacent observations can produce false positive results in standard statistical analyses (Dale & Fortin, 2002; Diniz-Filho *et al.*, 2003). In order to avoid attributing land-use decisions to environmental factors when in fact they were influenced by land-use decisions on adjacent lands, we minimized the effect of spatial autocorrelation on the statistical tests by subsampling as follows. First, we randomly selected 1000 cells from each data set for preliminary logistic regression analysis. We characterized the spatial autocorrelation of the residuals from these models by calculating Moran's I (Moran, 1950; Diniz-Filho *et al.*, 2003) for 100-m distance intervals with code modified from Lichstein *et al.* (2002) in S+ SpatialStats (Kaluzny *et al.*, 1998). Since Moran's I was either non-significant ($P < 0.05$) or very low ($I < 0.2$) for cells ≥ 600 m apart, we created data sets free of spatial autocorrelation by sampling cells at least 600 m apart within east–west transects 600 m apart and one cell wide. These stratified-random samples were then used in the logistic regression analyses we report here. This subsampling procedure yielded ≤ 2438 cells per data set, representing only ≤ 1.2% of possible cells, so that the statistical tests are likely to be not only unaffected by spatial autocorrelation, but quite conservative as well.

Since we were primarily interested in the possible implications for present-day forest plant distributions, we also evaluated the consequences of past land-use decisions for current forests. Regardless of how forests differed from active agricultural lands in topography, soils and access, this analysis focused on differences among forests of different history. We compared the three forest types (primary, 1938 secondary and 1995 secondary) with multivariate analysis of variance of the same, subsampled data. We again performed the analysis for the whole county, the northern part and the southern part, and we repeated the analyses with only slopes ≥ 5° to analyse aspect. Both slope and distance to nearest road were square-root transformed to remedy positive skew. When forest types differed in the multivariate ANOVAS, we proceeded to specify the differences with univariate ANOVAS for individual environmental factors, using the sequential Bonferroni correction to limit overall error rate to $\alpha = 0.05$.

Effects of land use on chemical properties of forest soils

Site selection

We used two separate sets of field-collected soil samples to examine the effects of past agricultural land use on the chemical properties of current forest soils. Both data sets compared soils of primary forests to those of secondary forests that originated before 1938. The first, collected for a study of forest herb community diversity and genetic diversity, demography and performance of *Trillium grandiflorum* (Michx.) Salisb. (Vellend, 2005), included soil samples from 17 primary and 10 secondary forests. For this study, we chose secondary forests that contained *T. grandiflorum* and that were isolated in the landscape, bounded on all sides by either fields or younger secondary forests. We then chose primary forests to cover the same range of soil associations as the secondary forests (Neeley, 1965; Tompkins County Planning Department, 2000b) and to represent a wide range of areas (0.1–33 ha). As a result of these criteria, all sites were located in the northern part of Tompkins County, where both *T. grandiflorum* and isolated forests are far more common. All secondary forests also showed pit-and-mound microtopography that indicated they had never been ploughed, and thus they likely share a history of use as pasture (Marks & Gardescu, 2001). The presence of wire fence or barbed wire in many forest boundaries supported this conclusion. This set of soil samples we called the 'isolated' data set.

The second data set (hereafter, 'adjacent') comprised soil samples from 10 primary and 10 secondary forests that were paired in order to minimize underlying environmental differences between forest types and focus on the effects of the land use *per se*. The paired primary and secondary forests at each site not only adjoined one another, but also shared a similar slope, aspect, elevation and soil series (Neeley, 1965). We chose sites spread throughout the county that covered ≥ 1 ha. The secondary forests all lacked pits and mounds, and many had stonepiles, stone walls, stump fences or earthworks, indicating that they had been ploughed and used as arable fields (Marks & Gardescu, 2001).

Field sampling

We collected soil cores by removing intact litter from the forest floor and driving a steel pipe of 3-cm diameter to a depth of 10 cm. This depth likely includes the layers that most affect herbaceous plants. Within each forest, we took four samples along each of five transects, then thoroughly air-dried and combined the 20 samples into a composite.

For the isolated data set, where forests varied widely in area, we adapted the sampling design to sites of different sizes by collecting soil cores at random positions along transects spaced evenly across each site. For the adjacent data set, where all forests covered ≥ 1 ha, we used the same, regular sampling design at all sites, taking samples at even intervals along transects 50 m long, 25 m apart and at least 20 m from forest boundaries.

Laboratory analysis

Soil samples were analysed for pH, OM and extractable nutrient concentrations relevant to plant growth, including nitrate (NO_3^-), phosphorus (P), potassium (K), magnesium (Mg), calcium (Ca), iron (Fe), aluminium (Al), manganese (Mn), zinc (Zn) and copper (Cu). The Cornell Nutrient Analysis Laboratories (Cornell University, Ithaca, NY, USA) analysed the soils following standard methods. Soil pH was measured in a soil and water suspension (1 : 1 by volume) and OM by loss on ignition (550 °C for 2 h). Nutrients were extracted in Morgan's (1941) solution. Phosphorus concentration was measured colorimetrically by stannous chloride reduction, and other nutrient concentrations were determined by atomic absorption spectrophotometry.

Since NO_3^- concentrations in local forest soils generally fall below the limits of detection in Morgan's solution extractions, we also measured NO_3^- and ammonium (NH_4^+) concentrations with a more sensitive analysis for the adjacent data set only. They were extracted in potassium chloride and analysed colorimetrically by hydrazine reduction and phenate-hypochlorite methods, respectively.

Statistical analysis

Principal-components analyses summarized variation in the many, interrelated soil properties we measured. All except pH, OM and Cu we first natural-log transformed to improve normality, after adding 0.5 to P. We tested the effect of land-use history (primary or 1938 secondary forest) on site scores for the first three principal-component axes with multivariate analysis of variance.

For the adjacent data set, in which sites ranged across all of Tompkins County, we also included a factor to account for the known differences in pH and nutrient concentrations between the northern and southern parts of the county. In order to incorporate the paired design of this data set, we first tested for an effect of location in the county (northern or southern part) on the *difference* between primary and secondary forests at each site, with an intercept included in the model. The intercept term tested the main effect of land-use history, and the location term tested for an interaction between land use and location. We then tested for an effect of location on the *mean* of primary and secondary forests at each site, thus testing the main effect of location. When a factor showed significant effects in the multivariate ANOVAS, we tested its effects on individual soil properties with univariate ANOVAS corrected by the sequential Bonferroni method.

RESULTS

Effects of topography and soils on land-use decisions

Causes of past land-use decisions

All of the topography and soil attributes we considered affected land-use decisions at some time and place. Across all of Tompkins County, slope, accessibility and soil lime content most influenced decisions of whether or not to clear forests for agriculture before 1900 (81% of predicted values were concordant with observed values; Table 2). Steeper slopes, less accessible lands and lower-lime soils were more likely to remain forested. Soil drainage did not affect forest clearance. In the northern part of the county, accessibility had the greatest influence, and slope, elevation and lime content also affected the decision of whether to clear land. Lower elevations had higher odds of staying in forest. In the south, only slope and access mattered, with slope by far the most important.

Factors shaping forest clearance and field abandonment showed similar patterns. Between 1900 and 1938, decisions of whether or not to abandon fields across the county depended most on slope, accessibility, soil lime content and soil drainage (76% concordant; Table 2). Farmers tended to abandon fields that were steeper, farther from roads, lower in lime and more poorly drained. In the north, abandonment was sensitive to all these factors; accessibility was again most important, and lower elevations were more likely to be abandoned. Slope again had the greatest impact on decisions in the south, and lime content also had an influence.

Later abandonment decisions continued to reflect all factors we studied. Steeper slopes, more poorly drained and lower-lime soils, less accessible lands and lower elevations were more likely overall to be abandoned to forest between 1938 and 1995 (72% concordant; Table 2). Slope was most important in both the northern and southern parts of the county. Drainage also contributed substantially to decisions in the north, as well as lime content and elevation. In the south, only accessibility added to the effect of slope.

Aspect did not appear to affect most land-use decisions ($P \geq 0.1763$; $n \leq 680$; full results not shown). In one of nine analyses, it had a marginally significant effect on forest clearance before 1900: across the whole county, forests facing farther from north may have been more likely to be kept ($\chi^2 = 3.5076$, $P = 0.0611$; $n = 902$).

Consequences for current forests

Since past land-use decisions took into account variation in topography and soils, they produced differences among

Table 2 Effects of topography and soil attributes on land-use decisions in Tompkins County, New York

Factor	Whole county			North			South		
		χ^2	*P*-value		χ^2	*P*-value		χ^2	*P*-value
Odds of keeping forests in 1900*									
Slope	+	202.4	< 0.0001	+	51.78	< 0.0001	+	125.2	< 0.0001
Elevation	−	2.051	0.1522	−	12.40	0.0004	+	0.467	0.4943
Lime	−	4.707	0.0300	−	8.871	0.0029	−	0.243	0.6221
Drainage	−	0.075	0.7836	−	0.387	0.5339	+	0.002	0.9674
Distance	+	134.5	< 0.0001	+	58.96	< 0.0001	+	75.00	< 0.0001
Odds of abandoning fields between 1900 and 1938†									
Slope	+	67.56	< 0.0001	+	33.79	< 0.0001	+	25.85	< 0.0001
Elevation	+	0.218	0.6405	−	4.897	0.0269	+	2.590	0.1075
Lime	−	15.43	< 0.0001	−	10.37	0.0013	−	6.288	0.0122
Drainage	−	6.534	0.0106	−	25.50	< 0.0001	+	1.400	0.2367
Distance	+	22.01	< 0.0001	+	35.69	< 0.0001	+	1.595	0.2066
Odds of abandoning fields between 1938 and 1995‡									
Slope	+	182.3	< 0.0001	+	66.57	< 0.0001	+	66.14	< 0.0001
Elevation	−	8.502	0.0035	−	20.95	< 0.0001	−	0.147	0.7019
Lime	−	28.58	< 0.0001	−	28.51	< 0.0001	−	0.594	0.4410
Drainage	−	30.90	< 0.0001	−	39.68	< 0.0001	−	0.575	0.4482
Distance	+	8.610	0.0033	+	1.323	0.2501	+	9.229	0.0024

*$n = 2438$ For whole county; $n = 1295$ for north; $n = 1143$ for south.
†$n = 2095$ For whole county; $n = 1182$ for north; $n = 913$ for south.
‡$n = 1926$ For whole county; $n = 1129$ for north; $n = 797$ for south.
Results of multiple logistic regressions include the direction (+/−), magnitude (Wald chi-square) and significance of each effect on the odds ratio. Slope (°) and elevation (m) were continuous variables; soil lime content had four classes ordered from very low to high; soil drainage had four classes ordered from very poorly to well-drained; and distance to the nearest road (m) quantified accessibility.

Table 3 Differences in topography and soil attributes among forests of different history in Tompkins County, New York

	Whole county ($n = 1616$)			North ($n = 700$)			South ($n = 916$)		
Dependent variable(s)	F	d.f.	P-value	F	d.f.	P-value	F	d.f.	P-value
All	32.70	10, 3218	< 0.0001	10.99	10, 1386	< 0.0001	26.79	10, 1818	< 0.0001
Slope	81.36	2, 1613	< 0.0001	8.89	2, 697	0.0002	79.20	2, 913	< 0.0001
Elevation	12.22	2, 1613	< 0.0001	0.76	2, 697	0.4663	8.24	2, 913	0.0003
Lime	23.37	2, 1613	< 0.0001	1.77	2, 697	0.1706	18.06	2, 913	< 0.0001
Drainage	22.85	2, 1613	< 0.0001	4.98	2, 697	0.0071	17.64	2, 913	< 0.0001
Distance	82.12	2, 1613	< 0.0001	40.84	2, 697	< 0.0001	49.75	2, 913	< 0.0001

Analyses of variance compared three forest types: primary forests, secondary forests that originated between 1900 and 1938, and secondary forests that originated between 1938 and 1995. Slope (°) and elevation (m) were continuous variables; soil lime content had four classes ordered from very low to high; soil drainage had four classes ordered from very poorly to well-drained; and distance to the nearest road (m) quantified accessibility. Slope and distance to nearest road were square-root transformed.

current forest types in these attributes. Primary forests, secondary forests that originated between 1900 and 1938 and secondary forests that originated between 1938 and 1995 differed in topography and soils across the county and in the north and south separately (Table 3). For all of Tompkins County, primary forests had steeper slopes than 1938 secondary forests, and 1938 secondary forests had steeper slopes than 1995 secondary forests (Fig. 3). In the northern part of the county, slopes of primary forests were steeper than slopes of 1995 secondary forests, and 1938 secondary forests had slopes similar to both. In the south, primary forests had steeper slopes than either 1938 or 1995 secondary forests, which were similar. All slopes > 20° remained in primary forest (these occurred only in the south, and ranged up to 40°); all slopes > 12° were either never cleared or abandoned by 1995.

Elevations of primary and 1938 secondary forests were higher than those of 1995 secondary forests overall (Table 3; Fig. 3). This pattern appeared only in the southern part of the county; in the north, all forests had similar elevations. The highest places (610–635 m, hilltops in the south) were cleared initially but abandoned by 1938, and all elevations > 575 m (also in the south) were abandoned to forest by 1995.

Soil attributes also differed among the three forest types (Table 3). Primary and 1938 secondary forests had lower-lime soils than 1995 secondary forests across the whole county and in the south alone (Fig. 3). In the north, soil lime content was similar for all forest types: 28% of all forests had high-lime soils, 20% medium, 38% low and 14% very low. In the south, most primary (78%) and 1938 secondary forests (77%) occurred on very low-lime soils. While many 1995 secondary forests (56%) occurred on very low-lime soils as well, 23% fell on low- and 21% on high- or medium-lime soils.

Primary forest soils had better drainage than either 1938 or 1995 secondary forest soils in the whole county, the north and the south (Table 3; Fig. 3). Most primary forests (75%) in the north were well- or moderately well-drained, whereas the proportion in the better drainage classes dropped to 64% of 1938 and 1995 secondary forests. Nearly a third (29%) of 1938 secondary forests had very poorly drained soils. In the south, 83% of primary, 74% of 1938 secondary and 68% of 1995 secondary forests were well- or moderately well-drained, and only 3.7% of all forests fell in the worst drainage class.

Primary forests fell farther from roads than 1938 secondary forests, and 1938 secondary forests fell farther than 1995 secondary forests (Table 3; Figs 3 and 4). In the north, both primary and 1938 secondary forests were less accessible than 1995 secondary forests; in the south, primary forests were less accessible than both 1938 and 1995 secondary forests.

Current forest types did not differ in aspect ($P \geq 0.2190$; $n \leq 817$).

Effects of land use on chemical properties of forest soils

Principal-components analyses identified pH as the dominant gradient in chemical properties of the forest soils we sampled. The first principal-component axes for both data sets, which explained much of the variation (53–61%), correlated strongly with pH ($r = 0.96$–0.97; Figs 5a and 6a). Particularly in the adjacent data set, many other soil properties aligned with this axis as well: Al ($r = -0.96$), Fe (−0.94), Ca (0.92), Mn (−0.92), NH_4^+ (−0.85), Zn (−0.80), OM (−0.73), Mg (0.66), NO_3^- (0.63), and K (−0.61).

For isolated forests, past land use had no effect on current soil properties ($F = 0.75$, d.f. $= 3, 23$, $P = 0.5320$; Fig. 5). In the adjacent data set, however, primary forest soils differed significantly from soils of adjacent 1938 secondary forests ($F = 23.28$, d.f. $= 3, 6$, $P = 0.0011$). The secondary forests showed a slight elevation in pH and associated increases in nutrient concentrations (Table 4; Fig. 6b). Regardless of their history, forests in the northern and southern parts of the county differed dramatically along the same pH gradient ($F = 11.78$, d.f. $= 3, 6$, $P = 0.0063$; Table 4; Fig. 6c). Land-use history and location in the county did not interact ($F = 2.10$, d.f. $= 3, 6$, $P = 0.2023$).

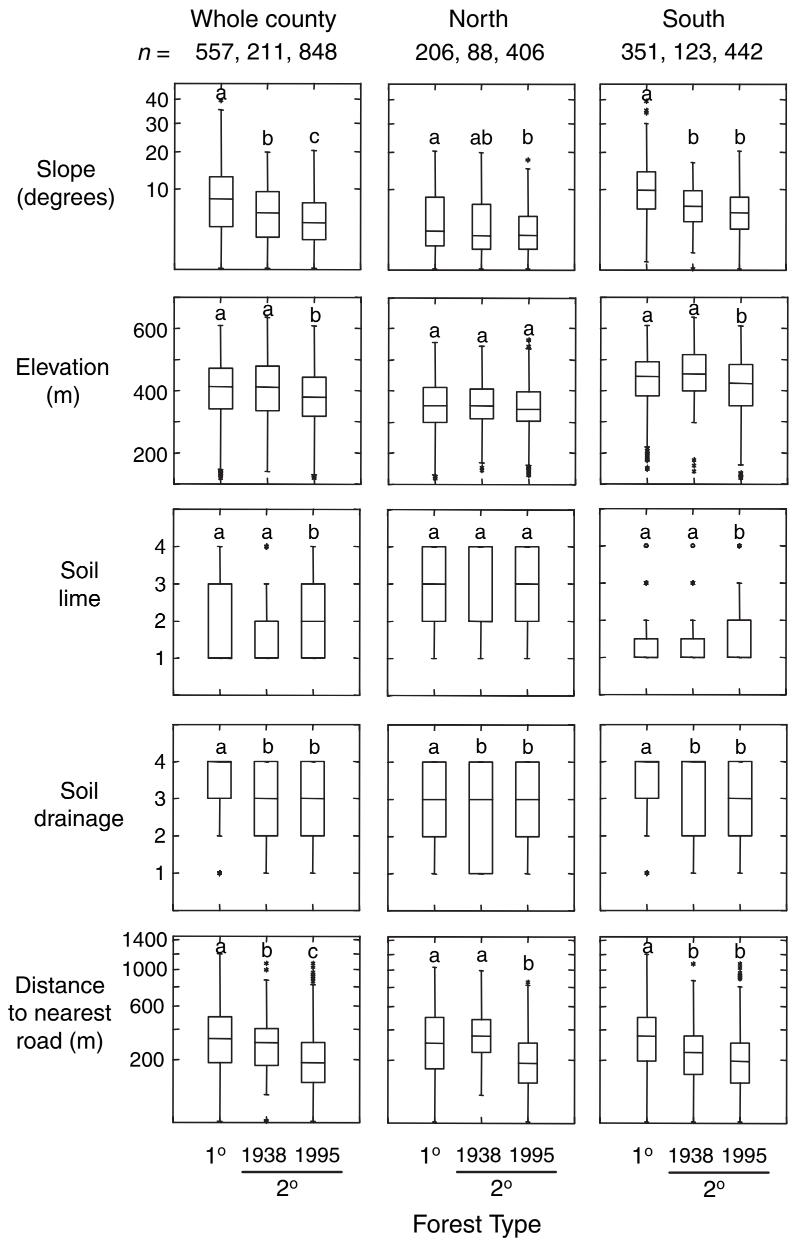

Figure 3 Boxplots of topography and soil attributes of forests in Tompkins County, New York, comparing primary forests, secondary forests that originated between 1900 and 1938, and secondary forests that originated between 1938 and 1995. Slope (°) and elevation (m) were continuous variables; soil lime content had four classes ordered from very low to high; soil drainage had four classes ordered from very poorly to well-drained; and distance to the nearest road (m) quantified accessibility. Slope and distance to nearest road were square-root transformed.

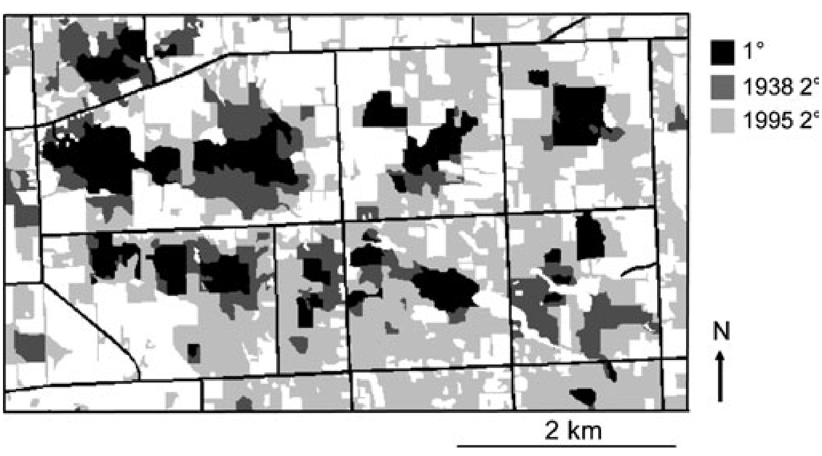

Figure 4 Map of a 25-km^2 tract of land in northern Tompkins County, New York, showing the geographical distribution of forests of different history in relation to roads.

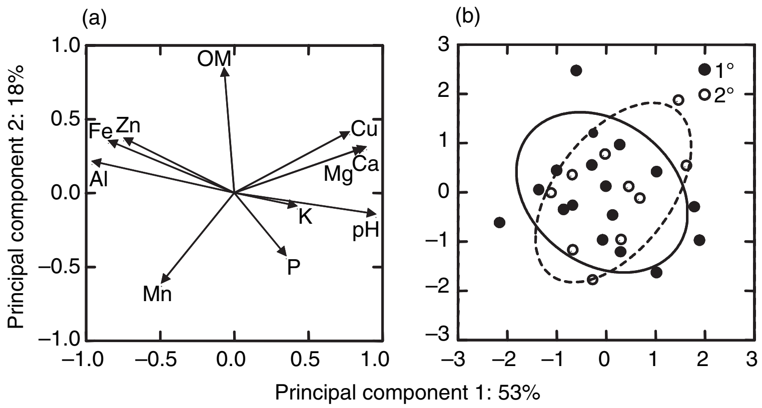

Figure 5 Soil properties of isolated primary and secondary forests in the northern part of Tompkins County, New York. Factor loadings (a) for principal components analysis of chemical properties show the correlation of each measured property with the first two axes and the proportion of variance the axes explain. A scatterplot (b) compares primary and secondary forests, with confidence ellipses ($P = 0.6830$) around the groups, a solid line around primary forests and a dashed line around secondary forests.

DISCUSSION

Agricultural land use in Tompkins County depended on topography and soil attributes in ways that showed farmers effectively avoided and abandoned lands less favourable for agriculture. Although social, political and economic factors presumably influenced land-use decisions as well, geographical patterns of land use were strongly associated with landscape characteristics. Slope had a dominant influence on both clearance and abandonment, affecting all decisions across the county and in the northern and southern parts separately. Overall and in the hillier south, slope consistently had a greater impact on land use than all other factors combined. Other factors varied in their effects on different decisions. Soil drainage, for example, affected field abandonment but not forest clearance, possibly because clearing and ploughing revealed or exacerbated drainage problems.

Factors affecting land use also varied across the county, suggesting that land-use decisions were sensitive not only to the characteristics of specific forests and fields, but also to the broader landscape context. For example, soil lime content affected all clearance and abandonment decisions in the northern part of the county, where the highest-lime soils occur, but only abandonment before 1938 in the south, where soils are generally more acidic. Similarly, soil drainage only affected decisions in the flatter, more swampy north. Lower elevations were more likely to remain forested and to be abandoned only in the north, where they represent lake shores and creek valleys.

Differential use of lands according to their topography and soils created predictable differences among forest types, particularly in slope. Despite these differences, however, current forest types also showed broad overlap in environmental attributes. In the north, for example, primary and secondary forests had similar soil lime content and drainage even though these factors influenced clearance and abandonment. This overlap among forest types likely results in part from the substantial component of arbitrary convenience in land-use decisions. Here, as elsewhere (Foster, 1992; Matlack, 1997; Foster *et al.*, 1999), accessibility had a surprisingly strong influence on the distribution of land uses. Particularly in the relatively homogenous landscape of the northern part of the county, access played as important a role as environmental variation in shaping clearance and abandonment decisions.

Another potential source of similarity among forest types is a difference in spatial scale between land use and environmental

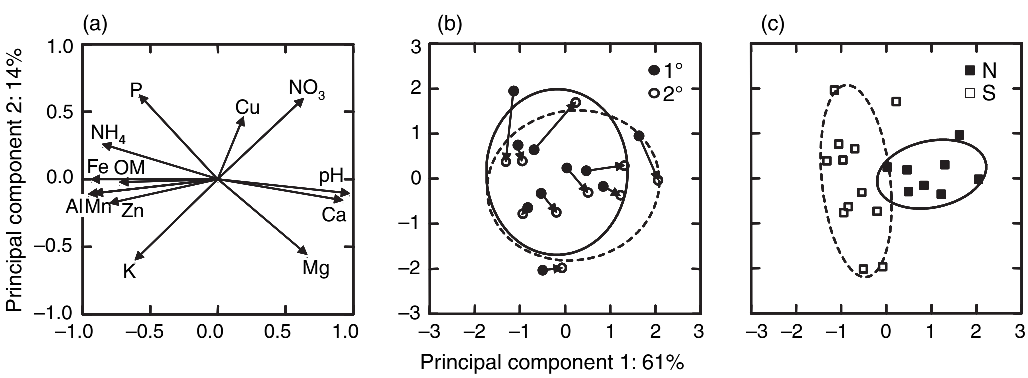

Figure 6 Soil properties of forests across Tompkins County, New York. Factor loadings (a) for principal components analysis of chemical properties show the correlation of each measured property with the first two axes and the proportion of variance the axes explain. Scatterplots show differences between pairs of adjacent primary and secondary forests (b) and between forests in the northern and southern parts of the county (c). Confidence ellipses ($P = 0.6830$) surround the groups. In (b), arrows connect adjacent pairs, a solid line surrounds primary forests and a dashed line secondary forests. In (c), a solid line surrounds forests in the northern part of the county and a dashed line those in the south.

Table 4 Chemical properties of forest soils in Tompkins County, New York, including pH, organic matter content (OM; percent by weight, measured by loss on ignition), and nutrient concentrations (mg kg^{-1})

	Mean ± SD				Analyses of variance			
					Primary vs. secondary		Northern vs. southern	
Soil property	Primary, northern ($n = 4$)	Primary, southern ($n = 6$)	Secondary, northern ($n = 4$)	Secondary, southern ($n = 6$)	F	P-value	F	P-value
pH	5.4 ± 0.5	4.4 ± 0.3	5.9 ± 0.6	4.7 ± 0.4	17.29	**0.0032**	14.53	0.0052
OM	9.9 ± 1.8	15.4 ± 2.5	8.7 ± 1.2	13.3 ± 4.5	4.23	0.0737	7.80	0.0235
P	0.1 ± 0.3	2.3 ± 2.3	0.0 ± 0.0	1.4 ± 1.9	4.36	0.0701	3.43	0.1012
K	68 ± 15	106 ± 30	71 ± 11	105 ± 20	0.23	0.6431	10.40	0.0122
Mg	162 ± 79	127 ± 75	195 ± 81	132 ± 88	3.32	0.1058	1.48	0.2590
Ca	1463 ± 722	752 ± 283	1790 ± 655	730 ± 232	1.43	0.2662	10.37	0.0122
Fe	34 ± 35	97 ± 46	17 ± 22	63 ± 30	13.31	0.0065	9.31	0.0158
Al	113 ± 64	255 ± 66	64 ± 34	223 ± 87	30.06	**0.0006**	11.93	0.0087
Mn	15 ± 3	42 ± 7	13 ± 4	34 ± 14	8.32	0.0204	31.05	**0.0005**
Zn	2.9 ± 1.1	7.4 ± 2.8	1.8 ± 0.8	6.2 ± 1.1	4.89	0.0579	30.96	**0.0005**
Cu	0.5 ± 0.3	0.7 ± 0.4	0.6 ± 0.2	0.5 ± 0.6	0.13	0.7306	0.00	0.9660
NO_3	4.4 ± 1.7	2.6 ± 0.6	3.7 ± 1.3	2.8 ± 1.1	0.30	0.5995	4.58	0.0647
NH_4	5.2 ± 0.8	7.6 ± 1.7	3.9 ± 0.6	7.9 ± 2.3	5.39	0.0489	15.77	**0.0041**

Analyses of variance compared primary forests to secondary forests that originated between 1900 and 1938; and forests in the northern part of the county to those in the south. Probabilities shown in bold type were considered significant according to the sequential Bonferroni correction ($\alpha = 0.05$).

gradients. Agricultural land-use decisions take place within and among individual farms, whereas topography and soils vary across larger areas as well. A typical farm in Tompkins County during the 1800s and early 1900s covered *c.* 100 acres or 0.4 km^2 (according to agricultural census records; Walrath, 1927). At this scale, topography and soils may vary little compared with the range of variation across the landscape. In addition to croplands and pastures, every farm needed a woodlot for fuelwood and sawtimber; if lands within the farm were similar, these uses may have been distributed somewhat arbitrarily. Even if people carefully selected the best lands available for each use, the scale of property ownership meant that one family might locate their woodlot on a piece of land that would make another farmer's best field.

Primary and secondary forests largely overlapped in soil chemical properties as well. Soils of mature secondary forests had slightly higher pH and nutrient concentrations than adjacent primary forests, but these differences were small in magnitude compared with landscape-scale environmental variation. Accordingly, primary and secondary forest soils were indistinguishable without adjacent pairs for comparison. The recovery of these soils from agriculture appears nearly complete after 80–100 years. This result agrees with several studies that have documented broad similarity between soils of primary and mature secondary forests (Kalisz, 1986; Bossuyt *et al.*, 1999a; Compton & Boone, 2000; Dzwonko, 2001; Graae *et al.*, 2003). It contrasts with other findings, often from less fertile sites, that a pronounced legacy of agriculture can persist in forest soils for over 100 years (Koerner *et al.*, 1997; Wilson *et al.*, 1997; Compton *et al.*, 1998; Verheyen *et al.*, 1999; Dupouey *et al.*, 2002). Although we could not directly address the effects of cultivation vs. pasturing with these data, our results are also consistent with the idea that cultivation has a much greater impact on soils, and that the most persistent soil changes result from ploughing and adding lime, fertilizer and other amendments (Koerner *et al.*, 1997; Wilson *et al.*, 1997; Compton & Boone, 2000). Our soil analyses captured the principal gradients in soil chemistry, but they were relatively coarse, leaving open the possibility that primary and secondary forest soils differ in other characteristics such as spatial heterogeneity, nutrient cycling rates and microbial communities.

Since primary and secondary forests mostly span the same range of environmental variation, the subtle differences we observed among forest types in topography and soils seem unlikely to explain broad-scale patterns of plant distribution across forests of different history. Rather, the recovery of diversity in secondary stands appears to depend primarily on the process of dispersal (Peterken & Game, 1984; Matlack, 1994; Vellend, 2003; Flinn & Marks, 2004). Environmental differences created by initial decisions and by land use itself may, however, affect patterns of plant colonization, establishment and persistence at more local scales. Even a small increase in pH and nutrient concentrations may differentially enhance the growth and reproduction of some species, potentially altering population performance, community composition and competitive interactions. Both environmental effects on land-use patterns and land-use effects on environmental conditions may thus have important implications for vegetation (Fig. 1). Yet in this landscape, it appears that the legacy of agriculture in forest soils has been relatively slight and ephemeral compared with the strong influence of topography and soils on agricultural land use.

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