

Physiographical and historical effects on forest vegetation in central New England, USA

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Abstract

Aim Land-use history can be an important determinant of ecosystem characteristics, even in landscapes that outwardly appear ‘natural’. In New England, like much of the eastern United States, the natural reforestation of agricultural lands over the past 150 years has created a predominantly forested landscape. Understanding the physiographical and historical factors controlling forest structure and composition is a major challenge to ecologists, conservationists and land managers.

Location We studied the forest structure and composition of Petersham, Massachusetts, which is located in the Central Upland physiographical province of New England. Like much of New England, Petersham was largely cleared for agriculture by the mid-1800s, but most of the agricultural fields were abandoned and naturally reforested in the late-1800s and early 1900s. The modern landscape is > 90% forested by a mosaic of primary and secondary woodlands.

Methods At seventy-four randomly selected 0.04-ha plots, we measured the abundances of all vascular plants in the overstory and understory and nine physiographical and historical variables.

Results Species richness was primarily related to landform: species-rich communities occurred in poorly drained basins and species-poor communities occurred on well-drained glacial outwash. Distributions of the sixty-nine most common species were associated with (in order of importance) landform, past land use and elevation. Many species were restricted to specific physiographical conditions, but no species were restricted to specific past land uses. Nine plant associations identified by two-way indicator species analysis were associated with elevation, landform, soil texture and past land use. Ordination by canonical correspondence analysis indicated that the vegetation reflected two principal gradients: a physiographical gradient, defined by landform and soil texture, and a land-use gradient.

Main conclusions These analyses suggest the following ranking of factors controlling forest structure and composition in this landscape at this time: landform > agricultural history > elevation > hurricane = fire = logging. Even in this physically heterogeneous landscape, land-use history continues to play an important role in shaping forest vegetation 100–150 years after agricultural abandonment and reforestation.

Keywords

Eastern deciduous forest, human disturbance, landform, land-use history, natural disturbance, New England, physiography, vegetation.

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INTRODUCTION

Human alteration of the environment plays an important role in determining the structure and composition of biological communities. In landscapes with long histories of human activities, past land uses exert strong and enduring impacts on vegetation patterns and ecosystem processes. In Europe, which has a long history of human habitation, ecologists have distinguished primary woodlands, which remained forested throughout recorded history, from secondary woodlands, which were cleared previously for agricultural and other land uses (*sensu* Peterken, 1993). Primary woodlands support a more diverse woodland flora, including species that are restricted to these continually wooded sites (e.g. Hermy & Stieperaere, 1981; Peterken & Game, 1984; Dzwonko & Loster, 1992). Secondary woodlands, even those that have been forested > 500 years, remain depauperate of woodland species, especially those characterized by slow rates of dispersal or extreme sensitivity to disturbance. Consequently, primary woodlands serve as important refugia for woodland species and as sources of propagules for repopulating secondary woodlands (Peterken & Game, 1984).

Like Europe, New England and much of the eastern United States has been greatly altered by a history of deforestation and past land use (Raup & Carlson, 1941; Foster, 1992; Foster *et al.*, 1998). However, New England forests differ from their European counterparts in several important respects (cf. Rackham, 1986, 1990; Peterken, 1993). In New England, intensive agriculture generally lasted only 100–200 years and the predominant land use was pasture, rather than cultivation. During peak agricultural development, the residual woodland area was greater in New England and woodlands management consisted mostly of irregular patterns of selective- and clear-cutting. Today, much of Europe remains deforested and woodlands are fragmented by agricultural and urban development. Rural New England, in contrast, has become almost completely reforested during the past 100–150 years and the modern landscape is a mosaic of primary and secondary woodlands surrounding a few, isolated open areas.

These differences in landscape history may have profound implications for the ecology of woodlands in New England. In particular, a shorter, less intense history of agricultural land use may have resulted in a weaker imprint of land-use history on modern forest communities. Larger and more extensive populations of woodland species likely survived in the agricultural landscape and following reforestation, there were few spatial barriers to dispersal and colonization of woodland species into newly established secondary woodlands (see Bellemare *et al.*, 2002). Furthermore, the impacts of prior agricultural land uses may have been reduced by subsequent natural and human disturbances, including logging, the decimation of two important canopy species [*Castanea dentata* and *Fagus grandifolia*; vascular plant nomenclature follows Gleason & Cronquist (1991) throughout] by imported pathogens, and the 1938 New England hurricane, which destroyed > 70% of the standing

timber in Petersham (Raup & Carlson, 1941; Foster, 1988; Foster & Boose, 1992). Thus, it seems likely that George Peterken (1977, p. 231) would be correct in his assertion that under these conditions, 'secondary woodland would have quickly developed the plant and animal communities characteristic of primary woodland.'

Several studies have previously addressed the importance of agricultural history on forest vegetation in central New England (Whitney & Foster, 1988; Foster, 1992; Motzkin *et al.*, 1999). All of these studies found that land-use history was an important determinant of forest structure and composition 50–100 years after agricultural abandonment. However, these studies examined the effects of land-use history in landscapes that had been reforested < 100 years, or they only sampled small areas (< 400 ha) with a limited range of the regional physiography variation and emphasized more intensive land uses, especially cultivated land, which had a very limited distribution in New England. Their study site (Harvard Forest) was also managed intensively for forestry and includes > 100 ha of conifer plantations, which are not common elsewhere in this region. Thus, there remains a need to examine the effects of a broader range of physiological and historical factors on forest vegetation after 100–150 years of reforestation in central New England.

In this study, we examined the relative importance of physiography and history in controlling forest composition and structure in the town of Petersham, Massachusetts. Petersham covers an area of 9844 ha, has been largely reforested during the past 100–150 years and encompasses a wide range of physiological conditions and disturbance histories characteristic of central New England. These characteristics allowed us to examine an array of physiological factors (elevation, landform, soil texture and slope aspect) and the long-term effects of natural and human disturbances (hurricane, fire, logging and agricultural history). We addressed two general questions: (1) What is the relative importance of physiological and natural and human disturbances in determining the distribution and abundance of individual species? (2) Do distinct plant associations occur on sites characterized by different physiological conditions and disturbance histories? In addition, we addressed three specific questions concerning land-use history: (1) Was the spatial distribution of agricultural land uses determined by the underlying physiography? (2) Are the distribution and abundance of individual species still affected by agricultural land uses 100–150 years after reforestation? (3) Do sites with different land-use histories support distinct plant associations?

STUDY AREA

Petersham (42°30' N, 72°12' W) is located in the Central Upland physiological province of New England and is characterized by north–south ridges and valleys ranging in elevation from 160 m to 400 m a.s.l. (Taylor & Hotz, 1985). The nutrient-poor bedrock of highly metamorphosed schist and gneiss and intrusive granodiorite and tonalite is overlain by glacial till on uplands and glaciofluvial sediments along major drainages (Eschman, 1966). Soils are stony,

coarse-textured, moderately to strongly acidic Inceptisols and Spodosols, although poorly drained basins are filled by organic-rich, highly acidic Histosols. Depth to bedrock is variable but generally < 3 m and soils are locally underlain by an impermeable hardpan (Stout, 1952; Lyford *et al.*, 1963; Taylor & Hotz, 1985). The climate is transitional between moist continental and maritime climates with cold winters (mean January temperature = -7°C) and warm to hot summers (mean July temperature = 20°C) (Spurr, 1957). The annual frost-free season averages 137 days but varies considerably according to topographical position (range = 77–161 days). Mean annual precipitation is 108 cm and is evenly distributed throughout the year. Mean annual snowfall is 127 cm and snow cover persists through the winter months in most years.

The natural vegetation of Petersham is classified as transition hardwood-white pine-eastern hemlock forest (Westveld, 1956). Prior to European settlement in the early 1700s, the vegetation was dominated by mixed hardwoods and conifers (*Quercus*, *Betula*, *Fagus*, *Tsuga*, *Pinus* and *Picea*) (Whitney, 1793; Foster *et al.*, 1992; Foster & Zebryk, 1993). Native American populations in the Central Uplands were apparently small and likely had little impact on the vegetation (Foster *et al.*, 1998). Starting in 1740, European settlers began clearing the forests and agriculture peaked in the 1850s, when roughly 85% of the land was open (Fig. 1a). Arable land (< 10% of Petersham) was cultivated, but > 75% of the land was used as uncultivated pasture and meadow. Woodlands covered the remaining 15% and were grazed and logged repeatedly for fuel, timber and tanning bark (Raup & Carlson, 1941; Foster, 1992). Beginning in the mid-1800s, much of the agricultural land was abandoned and was naturally reforested by *Pinus strobus* and *Betula populifolia*. Many old-field pine stands were logged during 1890–1910 and were replaced by fast-growing hardwoods (especially *Acer rubrum*, *C. dentata* and *Quercus rubra*) and the shade-tolerant *Tsuga canadensis* (Spurr, 1956; Foster & O'Keefe, 2000). During 1913–16, *C. dentata*, an important overstory component, was decimated by the chestnut blight [*Cryphonectria parasitica* (Murr.) Barr], and the 1938 New England Hurricane destroyed 70% of the standing timber in Petersham, especially in exposed stands of *P. strobus* and other conifers (Foster, 1988; Foster & Boose, 1992). The modern landscape of Petersham is > 90% forested by a mosaic of primary and secondary woodlands (Fig. 1b).

METHODS

Data collection

A total of 106 0.04-ha plots (20 × 20 m) were randomly selected from a 100-m grid overlaid on the 1 : 25,000-scale USGS topographical map of Petersham (Athol Quadrangle). Fifty-three plots were selected in each of two areas depicted as forested and non-forested on the 1830 map of Petersham (Lee & Lee, 1830) (Fig. 1a). Plots were located in the field by pacing mapped distances and compass bearings and locations were verified by topographical features. Thirty-two

plots were eliminated, because they occurred < 15 m from the forest edge, where canopy cover was < 75%, or where access was denied. Thus, data were collected and analysed from a total of seventy-four plots. Fifteen of these plots were moved 3–16 m to avoid physiographical or land-use boundaries or recent human disturbances (e.g. roads or excavations).

The vegetation in each plot was surveyed in early summer (May–July) and again in late summer (August–September) of 1992. All vascular plants were identified during each survey. Abundance of understory vegetation was estimated as percentage cover and as number of ramets grouped in ten classes (1, 2–5, 6–10, 11–25, 26–50, 51–100, 101–250, 251–500, 501–1000 and > 1000). Diameter at breast height (diameter 1.4 m above-ground) of standing live and dead trees (d.b.h. > 2.5 cm) was measured and used to calculate mean d.b.h., total free density and total basal area for each species. Tree regeneration (d.b.h. ≤ 2.5 cm) was counted as the numbers of saplings (height > 0.30 m) and seedlings (height 0.10–0.30 m).

Nine physiographical and historical variables were described for each plot (Table 1). Elevation, which served as a proxy for local climatic variation (Spurr, 1957), was measured from the USGS topographical map. Landform, which combined information on geomorphology, landscape position and soil drainage, was classified based on topography, surface features and soil profiles. Soil texture, represented by the proportion of sand by volume, was measured by the hydrometer method (Day, 1965). Slope aspect was calculated by a formula combining slope aspect and gradient (Frank & Lee, 1966): high values indicate steep, south-facing slopes; low values indicate steep, north-facing slopes. The occurrence of historical fires was based on the presence of macroscopic charcoal in the organic layers of the soil profile. Damage caused by the 1938 hurricane was ranked based on the presence and number of well-rotten boles and/or pit-and-mound topography orientated in a north-west direction. Recent logging history was measured as the number of cut stumps, which indicated the relative intensity of logging during approximately the past 50 years.

Past land use, classified as the most intensive past use (cropland, pasture, or woodland), was identified from historical maps and field evidence. Historical maps included the 1830 town plan (Lee & Lee, 1830), 1855 town map (Woodford, 1855), 1937–39 white pine blister rust maps (Harvard Forest Archives), 1938 land utilization map (Massachusetts State Planning Board, 1938) and 1951 and 1971 land use and vegetative cover maps (MacConnell, 1975). Field evidence included soil profiles, microtopography, surface rock cover and cultural artifacts such as stone walls (see Appendix 1 for details). Plots classified as woodland were forested on all historical maps and showed no evidence of human disturbance to the soil profile. Plots classified as pasture and cropland were depicted as non-forested on at least one historical map and had disturbed soil profiles. Cropland was identified by the presence of a distinct plough (Ap) horizon, which was absent from former pastures. When the maps and field evidence

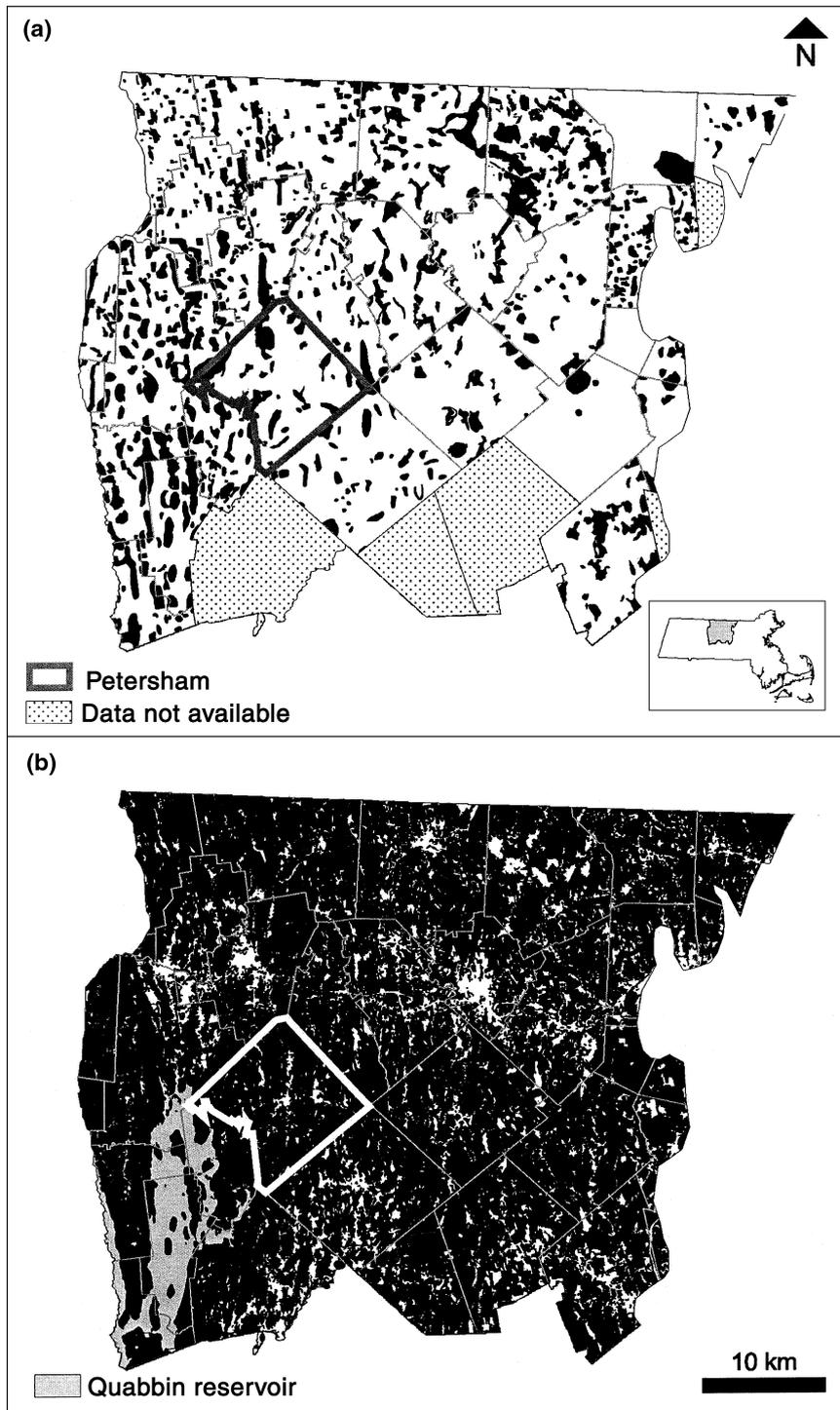


Figure 1 Forested (black) and open areas (white) in northcentral Massachusetts, USA, in (a) 1830 and (b) 1985. The 1830 town boundaries are shown on both maps.

disagreed, past land use was based on the relative clarity and strength of each line of evidence.

For pasture and cropland, date of abandonment was estimated from historical maps. In addition to the maps from 1830, 1855, 1937–39, 1938, 1951 and 1971, plots were classified as forested or non-forested in 1870 and 1900 by inferring forest cover at those dates based on the 1937–39

vegetation cover types [see Gerhardt (1993) for details]. These inferences were based on studies of forest succession following agricultural abandonment in central New England [especially Spurr (1956) and Foster (1992)]. Stands dominated by hardwoods alone or in combination with hemlock and white pine were identified as having been abandoned prior to 1870. Stands dominated by large white pine (d.b.h.

Table 1 Nine physiographical and historical variables measured at seventy-four forest plots in Petersham, Massachusetts, USA, during 1992

Variable	Categories or units of measure
Physiographical variables	
Elevation	Metres above sea level
Landform	Poorly drained glacial outwash, poorly drained basin, moderately well-drained stream drainage, moderately well- to well-drained bedrock ridge, well-drained marginal moraine, or well-drained glacial outwash
Soil texture	Percentage sand by volume
Slope aspect	Ratio of potential to maximum potential irradiation
Historical variables	
Hurricane damage	Undamaged, moderately damaged, or heavily damaged
Fire history	Presence or absence of charcoal
Logging history	Number of cut stumps
Past land use	Woodland, pasture, or cropland
Date of abandonment	Pre-1870 or post-1870

>15 cm) were identified as having been abandoned between 1870 and 1900. Stands dominated by grey birch or small white pine (d.b.h. <15 cm) were identified as having been abandoned between 1900 and 1937. For most analyses, secondary woodlands were divided into those abandoned before and after 1870.

Statistical analyses

Hurricane damage, past land use and date of abandonment were treated as ranked variables in some analyses. To determine whether there were significant associations among the measured environmental variables, all physiographical and historical variables were analysed by Pearson's correlation coefficient (ordinal variables), Spearman's ranked correlation coefficient (ranked variables), or the likelihood ratio *G*-statistic (nominal variables). These analyses also allowed

us to determine whether the spatial distribution of agricultural land uses was related to the underlying physiography. Relationships of species richness, mean d.b.h., total tree density, and total basal area with the physiographical and historical variables were analysed by fixed-effects analysis of variance (ANOVA) (nominal variables) or linear regression (ordinal and ranked variables). To determine the factors associated with the distributions (i.e. presence vs. absence) of individual species, the sixty-nine most common species (those occurring in ≥ 12 twelve plots) were analysed by contingency table analyses in relation to each of the nine physiographical and historical variables. Analyses of abundance data revealed similar patterns to those detected by analysing species distributions and are not presented here.

Vegetation data were classified into plant associations using two-way indicator species analysis (TWINSPLAN; Hill, 1979). Relationships of individual species with the plant associations were analysed by the likelihood ratio *G*-statistic (frequency) and fixed-effects ANOVA (abundance). Relationships of the physiographical and historical variables with the plant associations were analysed by the likelihood ratio *G*-statistic (nominal and ranked variables) or fixed-effects ANOVA (ordinal variables). The vegetation, physiographical and historical data were also analysed by ordination by canonical correspondence analysis (CCA) (PC-ORD; ter Braak, 1986, 1990). By restricting ordination axes to linear combinations of environmental variables, CCA identified floristic patterns directly explained by the measured physiographical and historical variables (ter Braak, 1986). For both community classification and ordination, all seventy-four plots and all 211 species were included. Species abundances were ranked in ten classes: trees were ranked by total basal area (species present only as saplings or seedlings were ranked in the lowest class); understory species were ranked in the ten classes for numbers of ramets described previously. Date of abandonment was not included in the CCA analysis, because it was only applicable to plots in secondary woodlands.

Values presented in the text are means ± 1 SD.

Table 2 Associations among nine physiographical and historical variables measured at seventy-four forest plots in Petersham, Massachusetts, USA, during 1992. Values are Pearson correlation coefficients (ordinal variables), Spearman's ranked correlation coefficients (ranked variables) and likelihood ratio *G*-statistics (nominal variables). The correlation between past land use and date of abandonment was not analysed, because the only applicable land use was former pasture

	Elevation	Landform	Soil	Slope	Hurricane	Fire	Logging
Elevation	1.000						
Landform	17.122	0.000					
Soil texture	-0.062	14.140	1.000				
Slope aspect	0.016	17.670	0.053	1.000			
Hurricane damage	0.010	16.207	0.105	0.094	1.000		
Fire history	1.136	12.491*	5.146	6.090*	1.732	0.000	
Logging history	-0.057	5.834	0.170	-0.027	-0.035	0.333	1.000
Past land use	1.083	7.663	1.563	0.357	4.657	0.022	1.785
Date of abandonment	2.980	4.001	0.403	0.320	11.515**	0.101	0.479

Significance levels are * $P < 0.05$ and ** $P < 0.01$.

RESULTS

Relationships among physiographical and historical variables

Few physiographical and historical variables were significantly associated and past land use was not associated with any other physiographical or historical variable (Table 2). Date of abandonment was associated with 1938 hurricane damage: damage was greater on agricultural lands abandoned prior to 1870 than those abandoned after 1870. Fire history was related to landform and slope aspect: historical fires occurred more commonly on well-drained marginal moraines and intermediate slope aspects.

Floristic composition and structure

We recorded 211 species of vascular plants, including thirty-one trees, thirty-two shrubs and woody vines, twenty-eight ferns and fern allies, twenty-three graminoids, and ninety-seven forbs. *Acer rubrum* was the only species that occurred in all seventy-four plots. Other species occurring in >75% of the plots (listed in order of frequency with number of plots in parentheses) were *Mitchella repens* (70), *Trientalis borealis* (70), *P. strobus* (66), *Maianthemum canadense* (65), *Q. rubra* (64), *Aralia nudicaulis* (62), *Vaccinium angustifolium* (59), *T. canadensis* (58), *Monotropa uniflora* (58), *Lycopodium obscurum* (56) and *Medeola virginiana* (56). Species richness (per 0.04-ha plot) averaged 38.4 ± 13.9 species but ranged from eight to seventy-eight species. Species richness was significantly related to landform but not to the other physiographical or historical variables (Table 3). Species richness was lowest on well-drained glacial outwash and highest in poorly drained basins (Table 4). Mean d.b.h., total tree density and total basal area were significantly related to only landform and slope aspect (Table 3). Total basal area was greatest on well-drained and poorly drained glacial outwash and least on moderately well- to well-

Table 4 Mean (± 1 SEM) species richness and total basal area on six landforms at seventy-four forest plots in Petersham, Massachusetts, USA, during 1992

Landform	Species richness (No. species plot ⁻¹)	Total basal area (m ² ha ⁻¹)
Well-drained glacial outwash (<i>n</i> = 8)	23.1 \pm 2.4	47.4 \pm 3.4
Marginal moraine (<i>n</i> = 12)	39.3 \pm 2.8	35.6 \pm 3.0
Bedrock ridge (<i>n</i> = 22)	35.7 \pm 1.6	32.4 \pm 1.5
Stream drainage (<i>n</i> = 10)	38.6 \pm 3.9	37.2 \pm 3.3
Basin (<i>n</i> = 10)	51.3 \pm 4.8	34.1 \pm 2.1
Poorly drained glacial outwash (<i>n</i> = 7)	37.0 \pm 5.8	44.3 \pm 3.8

Table 5 Numbers of species significantly associated (*P* < 0.05) with nine physiographical and historical variables at seventy-four forest plots in Petersham, Massachusetts, USA, during 1992

Variable	Trees	Shrubs	Ferns	Graminoids	Forbs	Total
Number of species	17	14	13	4	21	69
Physiographical variables						
Elevation	3	5	2	1	1	12
Landform	5	5	8	1	9	28
Soil texture	1	1	2	0	3	7
Slope aspect	0	0	0	0	0	0
Historical variables						
Hurricane damage	2	0	2	1	0	5
Fire history	0	1	0	0	3	4
Logging history	1	0	1	0	1	3
Past land use	6	3	1	1	7	18
Date of abandonment	1	0	1	0	2	4

drained bedrock ridges (Table 4). Total tree density was greater and mean d.b.h. was smaller on steep, south-facing slopes (data not presented).

Table 3 Associations of species richness, tree density, total basal area and mean d.b.h. with nine physiographical and historical variables at seventy-four forest plots in Petersham, Massachusetts, USA, during 1992. Significance was analysed by analysis of variance (nominal variables) or linear regression (ranked and ordinal variables)

Variable	d.f.	Species richness	Tree density	Total basal area	Mean d.b.h.
Physiographical variables					
Elevation	1,72	0.954	0.442	0.256	0.751
Landform	5,63	6.290***	1.623	4.707**	1.265
Soil texture	1,70	0.850	2.405	0.425	0.562
Slope aspect	1,72	0.171	5.715*	0.005	4.708*
Historical variables					
Hurricane damage	1,72	2.223	0.521	0.000	0.095
Fire history	1,72	1.127	0.015	3.104	2.056
Logging history	1,72	0.059	1.773	0.148	1.608
Past land use	1,56	1.055	0.004	2.958	1.617
Date of abandonment	1,26	1.014	2.258	0.245	0.177

Values are the *F*-statistics and significance levels are **P* < 0.05, ***P* < 0.01 and ****P* < 0.001.

Distributions of individual species

The distributions of the sixty-nine most common species were associated with (in order of importance) landform, past land use and elevation (Table 5). No species were associated with slope aspect. With the exception of past land use, few species were associated with variables describing natural and human disturbances. Individual species occurred more frequently on poorly drained basins (twelve species), woodlands and former pastures (nine species each), and intermediate elevations (six species). Landforms were associated with the distributions of eight ferns and fern allies; past land use was associated with six trees but few ferns or fern allies; and elevation was associated with five shrubs but few graminoids or forbs (Table 5). Fourteen species, occurring in anywhere from twelve to seventy-four quadrats, were not significantly associated with any

physiographical or historical variable (i.e. they occurred at similar frequencies across all classes of all measured variables): *A. rubrum*, *Carya ovata*, *P. strobus*, *Quercus velutina*, *Cornus alternifolia*, *Kalmia angustifolia*, *Nemopanthus mucronatus*, *V. angustifolium*, *Vaccinium corymbosum*, *Pteridium aquilinum*, *Brachyelytrum erectum*, *Epigaea repens*, *M. repens* and *Prenanthes* sp.

To illustrate the relationships between species distributions and the physiographical and historical variables, we present the significant associations with landform and past land use (Tables 6 and 7). Because cropland was clearly identified at only four plots, these analyses compared only pasture and woodland. Four patterns are apparent. First, the numbers of species occurring more frequently on different landforms differed greatly: twelve species were associated with poorly drained basins, but no species with

Table 6 Species significantly associated ($P < 0.05$) with landform at sixty-nine forest plots in Petersham, Massachusetts, USA, during 1992. Values are the percentages of plots in each landform in which each species occurred. Species are listed under the landform in which they occurred most frequently; no species occurred more frequently on well-drained glacial outwash or stream drainages. Frequency is the number of plots in which each species occurred. Significance was analysed by the likelihood ratio G -statistic (d.f. = 5 for all species)

Species (frequency)	Wd outwash ($n = 8$)	Marginal moraine ($n = 12$)	Bedrock ridge ($n = 22$)	Stream drainage ($n = 10$)	Basin ($n = 10$)	Pd outwash ($n = 7$)	G
Most frequent on marginal moraines							
<i>Castanea dentata</i> (34)	37	83	63	10	40	0	25.090***
<i>Corylus cornuta</i> (30)	12	66	54	30	30	14	11.393*
<i>Vaccinium pallidum</i> (14)	25	41	31	0	0	0	16.787**
<i>Viburnum acerifolium</i> (36)	12	83	59	40	30	42	13.793*
Most frequent on bedrock ridges							
<i>Betula lenta</i> (47)	62	66	90	50	40	42	13.011*
<i>Prunus serotina</i> (43)	25	33	81	60	70	57	12.816*
<i>Lycopodium clavatum</i> (23)	25	41	54	10	0	28	15.895**
<i>Monotropa uniflora</i> (56)	87	66	100	90	50	57	18.376**
Most frequent in basins							
<i>Betula alleghaniensis</i> (38)	25	41	40	80	90	57	14.156*
<i>Fraxinus americana</i> (26)	12	41	31	40	70	0	13.632*
<i>Ilex verticillata</i> (28)	0	25	36	40	90	42	20.507**
<i>Athyrium filix-femina</i> (14)	0	16	4	30	60	14	16.410**
<i>Dryopteris cristata</i> (11)	0	0	4	0	70	28	28.377***
<i>Dryopteris spinulosa</i> (35)	12	25	45	60	90	57	16.160**
<i>Onoclea sensibilis</i> (15)	0	8	4	20	80	28	26.195***
<i>Carex debilis</i> (15)	0	25	13	40	50	0	13.910*
<i>Arisaema triphyllum</i> (16)	0	16	4	20	80	28	24.914***
<i>Coptis trifolia</i> (30)	12	33	22	40	90	85	23.303***
<i>Rubus hispidus</i> (39)	0	66	68	30	90	42	23.865***
<i>Toxicodendron radicans</i> (14)	0	25	4	30	60	0	19.469**
Most frequent on poorly drained glacial outwash							
<i>Hamamelis virginiana</i> (27)	37	66	22	40	20	71	11.080*
<i>Thelypteris noveboracensis</i> (38)	0	50	45	80	80	85	22.233***
<i>Clintonia borealis</i> (30)	50	33	18	50	60	85	13.600*
Associated with multiple landforms							
<i>Lycopodium complanatum</i> (18)	12	8	45	0	20	42	14.251*
<i>Osmunda cinnamomea</i> (42)	25	50	36	80	100	100	28.708***
<i>Aster acuminatus</i> (20)	0	50	9	50	50	28	16.938**
<i>Aster divaricatus</i> (24)	12	58	22	60	40	0	15.007*
<i>Trientalis borealis</i> (68)	87	100	100	70	100	100	12.300*

Significance levels are * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

Table 7 Species significantly associated ($P < 0.05$) with past land use at fifty-eight forest plots in Petersham, Massachusetts, USA, during 1992. Values are the percentages of pasture and woodland in which each species occurred. Species are listed under the land use in which they occurred most frequently. Frequency is the number of plots in which each species occurred. Significance was analysed by the likelihood ratio G-statistic (d.f. = 1 for all species)

Species (frequency)	Pasture ($n = 33$)	Woodland ($n = 25$)	G
Most frequent on former pastures			
<i>Acer saccharum</i> (13)	36	4	10.064**
<i>Crataegus</i> sp. (12)	30	8	4.715*
<i>Prunus serotina</i> (35)	72	44	4.935*
<i>Quercus alba</i> (32)	66	40	4.123*
<i>Corylus cornuta</i> (21)	48	20	5.196*
<i>Ilex verticillata</i> (23)	51	24	4.633*
<i>Lycopodium complanatum</i> (12)	30	8	4.715*
<i>Maianthemum canadense</i> (50)	93	76	3.894*
<i>Toxicodendron radicans</i> (12)	30	8	4.715*
Most frequent in primary woodlands			
<i>Fagus grandifolia</i> (28)	36	64	4.403*
<i>Tsuga canadensis</i> (46)	63	100	15.877***
<i>Kalmia latifolia</i> (16)	15	44	5.956**
<i>Oryzopsis asperifolia</i> (9)	6	28	5.326*
<i>Clintonia borealis</i> (26)	21	76	18.124***
<i>Coptis trifolia</i> (27)	33	64	5.448*
<i>Gaultheria procumbens</i> (37)	51	80	5.196*
<i>Medeola virginiana</i> (44)	63	92	6.909**
<i>Trillium undulatum</i> (14)	9	44	9.707**

Significance levels are * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

either moderately well-drained stream drainages or well-drained glacial outwash. In contrast, equal numbers of species were associated with former pasture and woodland (nine species each). Secondly, individual species were often restricted to specific landforms. For example, ten species (most associated with poorly drained basins) did not occur on well-drained glacial outwash and six species did not occur on poorly drained glacial outwash. In contrast, no species were restricted to specific land uses (e.g. *Trillium undulatum* occurred in 44% of woodlands but also in 9% of former pastures). Thirdly, only one fern or fern ally (*Lycopodium complanatum*) was associated with past land use. In contrast, eight ferns or fern allies were associated with landform and five of these occurred more frequently in poorly drained basins or poorly drained glacial outwash. Finally, individual species were significantly associated with both landform and past land use. Two species associated with woodlands occurred more frequently on poorly drained basins (*Coptis trifolia*) or poorly drained glacial outwash (*Clintonia borealis*). In contrast, six species associated with former pastures also occurred more frequently on marginal moraines (*Quercus alba* and *Corylus cornuta*), bedrock ridges (*Prunus serotina* and

L. complanatum), or poorly drained basins (*Ilex verticillata* and *Toxicodendron radicans*).

The distributions of only four species were associated with date of abandonment. Three species (*T. undulatum*, *Thelypteris noveboracensis* and *Uvularia sessilifolia*) occurred more frequently on pastures abandoned prior to 1870; *B. populifolia* was the only species occurring more frequently on pastures abandoned after 1870.

Plant associations

Based on the TWINSpan analysis, the seventy-four plots were grouped into nine distinct plant associations. The nine associations shared many of the most common species (e.g. *A. rubrum*), but each type was characterized by a distinct subset of the remaining species. The nine plant associations differed in species richness and total basal area but not mean d.b.h. or total tree density (Table 8). The plant associations were also significantly associated with elevation, landform, soil texture and past land use (Table 8). In the descriptions that follow, the type name includes only those species that occurred in all plots of that type and at relatively high abundances ($\geq 5 \text{ m}^2 \text{ ha}^{-1}$ for trees and $\geq 2\%$ cover for understory species).

Type 1 is *T. canadensis*-*P. strobus*-*A. rubrum*-*M. repens* forest. The overstory was characterized by the highest mean d.b.h. and total basal areas and high densities of *T. canadensis* ($989 \pm 166 \text{ stems ha}^{-1}$). This type occurred on sandier soils and past land use was always woodland.

Type 2 is *T. canadensis*-*A. rubrum* forest. The overstory was characterized by the highest tree densities, including *T. canadensis* ($1195 \pm 175 \text{ stems ha}^{-1}$), and the second highest total basal areas. Species richness was lowest in this type, and the understory cover was sparse (no understory species covered $> 2\%$ of the plots). This type occurred at lower elevations and primarily on pastures abandoned after 1870 that were subsequently heavily logged.

Type 3 is *T. canadensis*-*A. rubrum*-*Dennstaedtia punctilobula* forest. The overstory was characterized by high densities of *T. canadensis* ($606 \pm 218 \text{ stems ha}^{-1}$). Past land use was primarily woodland.

Type 4 is *T. canadensis*-*Hamamelis virginiana*-*V. angustifolium*-*Viburnum acerifolium*-*A. nudicaulis* forest. This type had the highest understory shrub cover. This type occurred at lower elevations on well-drained marginal moraines. This type also had the highest frequency of fire (50% of the plots) but suffered only moderate damage during the 1938 hurricane. Past land use was always woodland.

Type 5 is *P. strobus*-*A. rubrum*-*Q. rubra*-*M. canadense* forest. Species richness was moderately low. This type occurred on less sandy soils, and past land use was always pasture.

Type 6 is *A. rubrum*-*V. angustifolium* forest. This type occurred at higher elevations on moderately well to well-drained bedrock ridges with less sandy soils. Past land use was variable and this type showed little evidence of past logging.

Table 8 Relationships of four vegetation parameters and nine physiographical and historical variables with nine two-way indicator species analysis (TWINSPAN) – defined plant associations at seventy-four forest plots in Petersham, Massachusetts, USA, during 1992. Significance was analysed by analysis of variance (ordinal variables) or the likelihood ratio G-statistic (ranked and nominal variables). Values are mean ± 1 SEM or the categories representing > 66% of the plots in each type

Variable	Type 1 (n = 7)	Type 2 (n = 5)	Type 3 (n = 8)	Type 4 (n = 6)	Type 5 (n = 8)	Type 6 (n = 12)	Type 7 (n = 6)	Type 8 (n = 9)	Type 9 (n = 13)
Vegetation parameters									
Species richness**	32.9 ± 3.8	14.8 ± 2.9	36.3 ± 2.5	41.7 ± 1.9	28.9 ± 2.1	32.8 ± 1.6	33.2 ± 3.2	49.6 ± 2.3	55.9 ± 3.7
Tree density	1804 ± 336	2020 ± 279	1681 ± 250	1471 ± 101	1606 ± 171	1444 ± 138	1879 ± 173	1547 ± 141	1360 ± 86
Total basal area**	47.3 ± 4.1	45.8 ± 3.3	39.7 ± 4.4	35.9 ± 4.4	34.3 ± 3.0	34.1 ± 1.7	33.3 ± 3.8	30.5 ± 3.0	35.9 ± 1.6
Mean d.b.h.	19.6 ± 2.2	17.4 ± 1.2	18.0 ± 1.4	17.7 ± 1.5	16.6 ± 0.4	18.1 ± 1.2	15.3 ± 1.5	16.1 ± 1.2	18.7 ± 0.9
Physiographical variables									
Elevation***	290 ± 26	222 ± 10	294 ± 17	208 ± 7	246 ± 15	313 ± 12	264 ± 15	266 ± 15	272 ± 12
Landform***	-	-	-	Marginal moraines	-	Bedrock ridges	Bedrock ridges	-	Basins
Soil texture*	75.8 ± 2.5	4.6 ± 2.9	73.8 ± 1.4	75.0 ± 2.0	70.6 ± 1.9	68.0 ± 1.1	71.0 ± 2.2	72.1 ± 2.8	78.3 ± 2.2
Slope aspect	0.47 ± 0.01	0.48 ± 0.03	0.47 ± 0.01	0.47 ± 0.00	0.49 ± 0.01	0.47 ± 0.01	0.47 ± 0.01	0.48 ± 0.01	0.47 ± 0.01
Historical variables									
Hurricane damage	-	-	-	Moderate	-	-	-	None	-
Fire history	-	-	-	-	-	-	-	-	-
Logging history	1.4 ± 0.8	4.8 ± 1.5	2.0 ± 1.1	1.0 ± 0.7	1.5 ± 0.6	0.8 ± 0.3	1.8 ± 1.0	1.7 ± 0.5	1.9 ± 1.0
Past land use***	Woodland	Pasture	Woodland	Woodland	Pasture	-	Pasture	Pasture	Pasture
Date of abandonment	-	Post-1870	-	-	-	-	Post-1870	Pre-1870	Post-1870

Significance levels are *P < 0.05, **P < 0.01 and ***P < 0.001.

Type 7 is *A. rubrum*-*D. punctilobula*-*A. nudicaulis*-*M. canadense* forest. Mean d.b.h. was lowest in this type. This type occurred on moderately well to well-drained bedrock ridges and past land use was mostly pasture abandoned after 1870.

Type 8 is *P. strobus*-*A. rubrum*-*Q. rubra*-*V. angustifolium*-*V. corymbosum*-*L. obscurum*-*A. nudicaulis*-*Gaultheria procumbens*-*M. canadense*-*M. repens* forest. This type was characterized by the lowest total basal area, high species richness and the greatest cover of understory species, especially shrubs and ferns. This type was largely undamaged by the 1938 hurricane and occurred primarily on pastures abandoned prior to 1870.

Type 9 is *A. rubrum*-*Dryopteris spinulosa* forest. This type had the lowest total tree density and the highest species richness; total understory cover was also high, especially for shrubs and ferns. This type occurred in poorly drained basins with sandier soils. Past land use was primarily pasture abandoned after 1870.

Community ordination

Ordination by CCA indicated that the measured physiological and historical variables explained only 13.8% of the total variation in the species data along the first three axes (Table 9). Landform and soil texture were strongly associated with the first axis; past land use and landform,

Table 9 Canonical correspondence analysis eigenvalues, species-environment correlations and intraset correlations for nine physiological and historical variables and 211 vascular plant species at seventy-four forest plots in Petersham, Massachusetts, USA, during 1992. Intraset correlations indicate the relative importance of the environmental variables in explaining the variation in vegetation patterns along each axis. Date of abandonment was not included in this analysis, because it only applied to plots in secondary woodlands

Variable	Axis 1	Axis 2	Axis 3
Eigenvalues	0.279	0.122	0.089
Species-environment correlations	0.907	0.788	0.824
Variance in species data			
Percentage explained	7.9	3.4	2.5
Cumulative percentage explained	7.9	11.3	13.8
Physiographical variables			
Elevation	0.061	-0.229	-0.464
Landform			
Well-drained glacial outwash	-0.225	-0.246	0.029
Marginal moraine	-0.273	0.024	0.044
Bedrock ridge	-0.476	0.434	-0.017
Basin	0.892	0.103	0.245
Poorly drained glacial outwash	-0.001	-0.402	0.045
Soil texture	0.528	-0.064	-0.154
Slope aspect	-0.107	0.307	0.381
Historical variables			
Hurricane damage	-0.256	-0.093	0.296
Fire history	-0.089	0.056	-0.027
Logging history	0.106	-0.086	-0.273
Past land use	0.064	0.786	-0.410

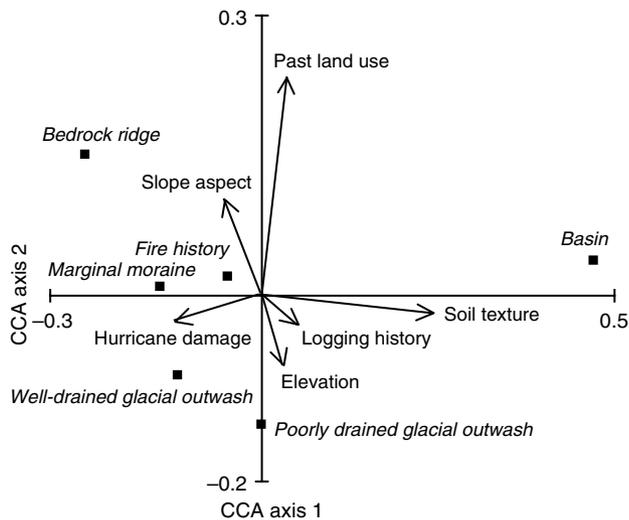


Figure 2 Relationships of eight physiographical and historical variables to the first and second canonical correspondence analysis axes derived from seventy-four forest plots in Petersham, Massachusetts, USA, during 1992. Squares and italicized labels indicate the centroids of nominal variables (landforms and fire history); arrows and unitalicized labels indicate the relative importance and direction of ranked and ordinal variables. The physiographical gradient extends from the upper left (bedrock ridges) to the lower right (basins) of the diagram, and the land-use gradient extends from the top (former pastures) to the bottom (primary woodland) of the diagram.

with the second axis; and elevation and land use, with the third axis. Slope aspect, fire history, 1938 hurricane damage and logging history were not strongly associated with any of the first three axes. The ordination diagram reveals two pronounced gradients (Fig. 2). First, a physiographical gradient, defined by landform and soil texture, progresses from sandy basins and poorly drained glacial outwash across marginal moraines and well-drained glacial outwash to less sandy bedrock ridges. Secondly, a land-use gradient progresses from less-disturbed primary woodlands to more highly disturbed pastures and cropland. Trees, shrubs, graminoids and forbs are distributed across both the physiographical and land-use gradients (Fig. 3a,b,d). In contrast, ferns and fern allies are primarily associated with the physiographical gradient (Fig. 3c). When graphed along the first two CCA axes, the nine plant associations did not segregate neatly in ordination space (Fig. 4). In contrast, woodlands and former pastures did segregate in ordination space; however, there was no clear separation among pastures abandoned at different dates (Fig. 5).

DISCUSSION

In a heterogenous landscape that has been largely reforested 100–150 years, forest structure and composition were controlled primarily by physiography and agricultural history. Despite the broad heterogeneity and significant impact of physiography, agricultural land uses remained an important

factor affecting both individual species and the overall vegetation community. In contrast, more recent natural and human disturbances (the 1938 hurricane, wildfire and logging) had relatively little impact on the modern vegetation and had not erased the imprint of prior land uses. Thus, we suggest the following ranking of the long-term importance of physiographical and historical factors on forest structure and composition in this landscape: landform > agricultural history > elevation (local climate) > hurricane = fire = logging. Thus, these results suggest that land-use history may be less important in determining vegetation patterns in broadly heterogenous landscapes than has been suggested by studies focusing on more specific sites and vegetation types (e.g. Motzkin *et al.*, 1996; Bellemare *et al.*, 2002). Furthermore, this relative ranking of physiographical and historical factors will likely change over time. The impacts of past agricultural land uses will probably diminish, as has been true for other natural and human disturbances and future disturbances will have important, if short-lived, impacts when they recur. In the sections that follow, we discuss individual factors and groups of factors, their effects on forest vegetation and the ecological consequences of these effects.

Physiographical factors

Forest structure and composition were controlled by several physiographical factors (landform, soil texture and elevation). In this study, many species and plant associations were associated with or restricted to limited subsets of physiographical conditions. There are several possible explanations for these results. First, within these ranges of physiographical conditions, plants must occur within their physiological tolerances of soil and climate conditions and they must be able to acquire the resources necessary for germination, growth and survival. Both landform and soil texture are known to play important roles in controlling the physical and chemical properties of soils and nutrient and water availability (Buol *et al.*, 1980). In addition, local climatic conditions in Petersham vary greatly according to elevation and topographical position (Spurr, 1957). Secondly, the relationship between physical environment and species distributions may also reflect the life history characteristics of individual species. For example, ferns, which require free water for sexual reproduction, occurred more frequently in poorly drained basins than on well-drained sites. Thirdly, physiographical factors may play an important role in mediating the outcome of species interactions. For example, Grime (1973, 1979) proposed that competition should be less important in stressful environments. The association of many species and high species richness with poorly drained basins may reflect the inability of species to exclude one another under these harsh physical conditions (e.g. cold, saturated soils). Alternatively, these basins may offer greater microsite heterogeneity, especially in soil moisture and resource levels (F. Gerhardt, personal observation) and this broad range of microsites may favour the coexistence of a greater diversity of species (e.g. Beatty, 1984).

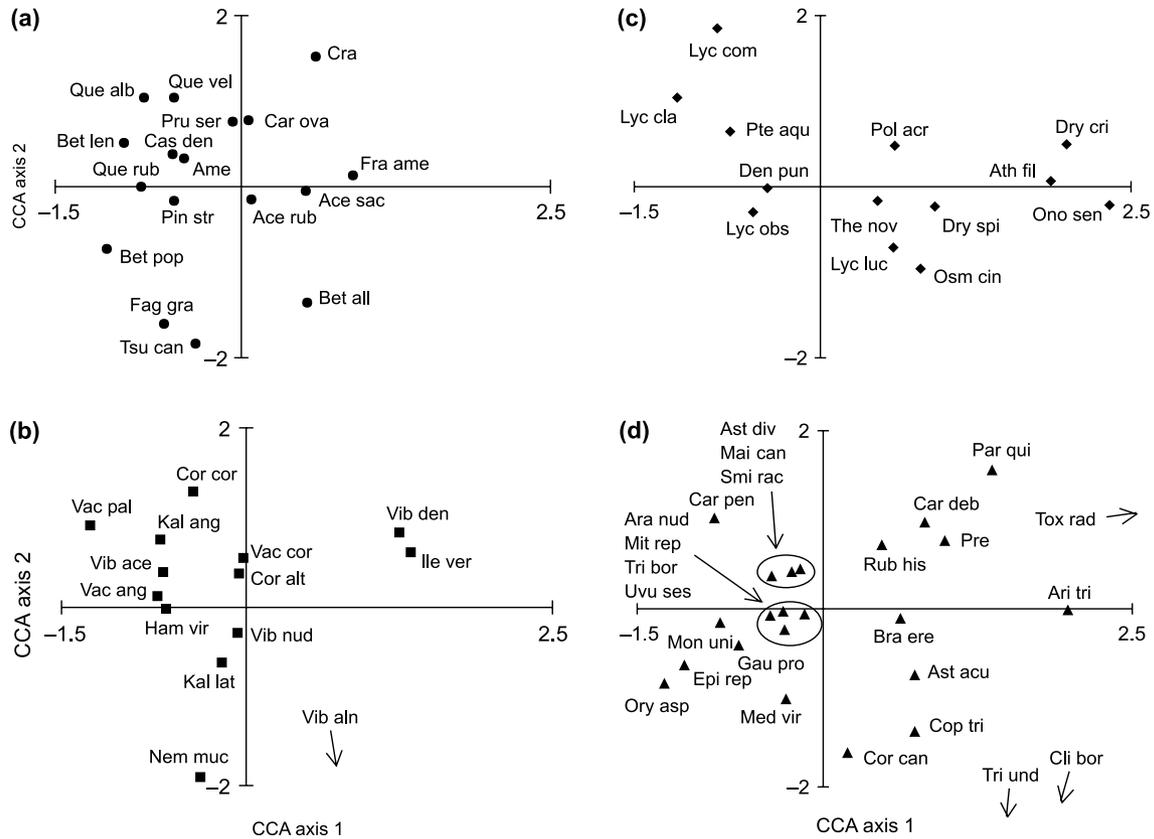


Figure 3 Species bi-plots for the first and second canonical correspondence analysis axes for the sixty-nine most common species occurring in seventy-four forest plots in Petersham, Massachusetts, USA, during 1992. Species are separated into four growth forms: (a) trees, (b) shrubs, (c) ferns and fern allies and (d) graminoids and forbs. Species abbreviations are the first three letters of the genus and species names. Trees include *Acer rubrum*, *A. saccharum*, *Amelanchier* sp., *Betula alleghaniensis*, *B. lenta*, *B. populifolia*, *Carya ovata*, *Castanea dentata*, *Crataegus* sp., *Fagus grandifolia*, *Fraxinus americana*, *Pinus strobus*, *Prunus serotina*, *Quercus alba*, *Q. rubra*, *Q. velutina* and *Tsuga canadensis*. Shrubs include *Cornus alternifolia*, *Corylus cornuta*, *Hamamelis virginiana*, *Ilex verticillata*, *Kalmia angustifolia*, *K. latifolia*, *Nemopanthus mucronatus*, *Vaccinium angustifolium*, *V. corymbosum*, *V. pallidum*, *Viburnum acerifolium*, *V. dentatum* and *V. nudum*. Ferns and fern allies include *Athyrium filix-femina*, *Dennstaedtia punctilobula*, *Dryopteris cristata*, *D. spinulosa*, *Lycopodium clavatum*, *L. complanatum*, *L. lucidulum*, *L. obscurum*, *Onoclea sensibilis*, *Osmunda cinnamomea*, *Polystichum acrostichoides*, *Pteridium aquilinum* and *Thelypteris noveboracensis*. Graminoids and forbs include *Aralia nudicaulis*, *Arisaema triphyllum*, *Aster acuminatus*, *A. divaricatus*, *Brachyelytrum erectum*, *Carex debilis*, *C. pennsylvanica*, *Clintonia borealis*, *Coptis trifolia*, *Cornus canadensis*, *Epigaea repens*, *Gaultheria procumbens*, *Maianthemum canadense*, *Medeola virginiana*, *Mitchella repens*, *Monotropa uniflora*, *Oryzopsis asperifolia*, *Parthenocissus quinquefolia*, *Prenanthes* sp., *Rubus hispidus*, *Smilacina racemosa*, *Toxicodendron radicans*, *Trientalis borealis*, *Trillium undulatum* and *Uvularia sessilifolia*.

Agricultural history

In this study, agricultural history was not related to any physiological or historical variable, except hurricane damage. However, these analyses only compared woodlands and former pastures, as the sample size of croplands ($n = 4$) was too small to determine whether they occurred under a more restricted set of physiological conditions. These results indicate that the spatial distribution of woodlands and pastures was not determined by underlying physiography, as both woodlands and pastures occurred across the range of physiological conditions. Instead, the distribution of agricultural land uses may have been controlled by cultural features. For example, in Petersham, former pastures were located closer to roads and houses than were

primary woodlands (F. Gerhardt, unpublished data). In contrast to our study, the distribution of agricultural land uses in a smaller area of Petersham (< 400 ha) were related to soil drainage and texture as well as the location of property boundaries and proximity to houses and roads (Foster, 1992; Motzkin *et al.*, 1999). However, these studies sampled a higher proportion of cropland and a more limited range of the regional physiological variation than our study.

Our results clearly show that past land use remains an important factor controlling forest structure and composition in this landscape. Primary woodlands in Petersham supported several plant associations not found in secondary woodlands. All primary woodlands were dominated by *T. canadensis* either alone (Type 4) or in association with

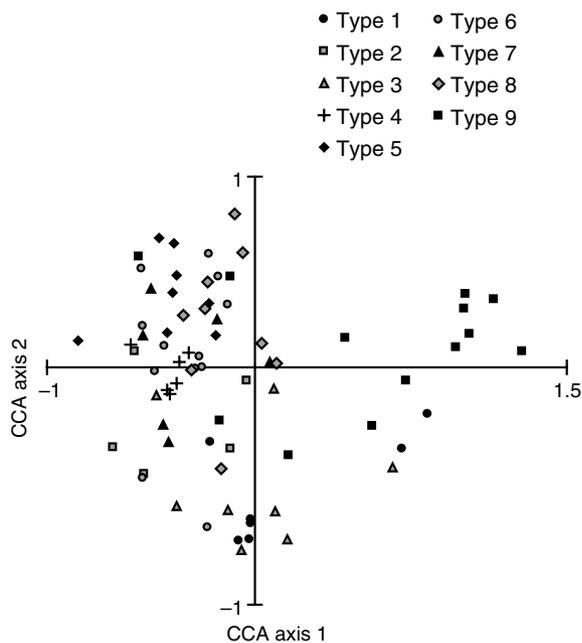


Figure 4 Distribution of nine two-way indicator species analysis – defined plant associations along the first and second canonical correspondence analysis axes derived from seventy-four forest plots in Petersham, Massachusetts, USA, during 1992. The nine types are described in the text.

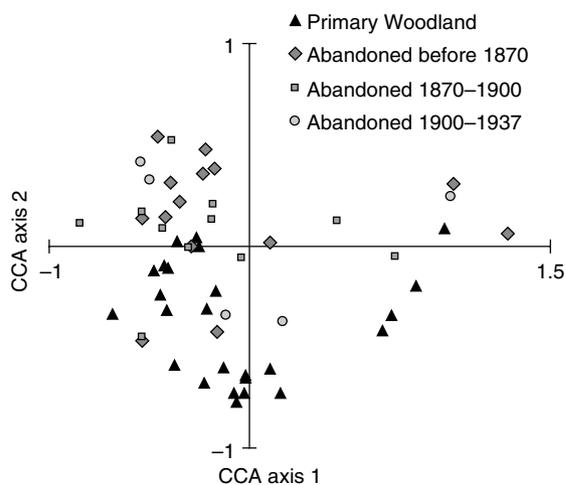


Figure 5 Distribution of primary and secondary woodlands of different ages along the first and second canonical correspondence analysis axes derived from seventy-four forest plots in Petersham, Massachusetts, USA, during 1992.

A. rubrum and *P. strobus* (Types 1 and 3). However, the convergence of primary woodlands to plant associations dominated by *T. canadensis* is likely to be the result of the combined effects of multiple natural and human disturbances, rather than autogenic succession following agricultural abandonment (McLachlan *et al.*, 2000). In contrast to primary woodlands, former pastures (Types 2 and 5–9)

were dominated by *A. rubrum* alone or in combination with other species. *Pinus strobus* and *Q. rubra* were important on pastures abandoned prior to 1870 (Type 8), and *T. canadensis* was important on pastures abandoned after 1870 that had been logged heavily (Type 2). *Acer rubrum*, which at the time of European settlement was abundant only on poorly drained sites (Spurr, 1956; Foster, 1992; Fuller *et al.*, 1998), is now a dominant species across a wide range of physiological and disturbance conditions, including well-drained sites. The widespread dominance of *A. rubrum* in these forests is echoed by other studies that show that this species has increased in importance throughout the northeastern forests (Abrams, 1998; Bürgi *et al.*, 2000). *Pinus strobus*, which is also more widespread today than in the presettlement forests, was more important during the late 1800s and early 1900s, when ‘old-field white pine’ was the dominant forest type on abandoned agricultural lands (Spurr, 1956; Foster, 1992). Its continued importance in the modern vegetation likely reflects its longevity and its emergence as an overstorey dominant in these forests.

In contrast to the plant associations, species richness was not related to past land use. Unlike many primary woodlands in Europe (e.g. Peterken & Game, 1984; Dzwonko & Loster, 1992), primary woodlands in Petersham were not associated with higher species richness. In fact, the plant associations with the highest species richnesses (Types 8 and 9) occurred primarily on former pastures. However, agricultural history remains an important factor controlling the distributions of many species. In this study, eighteen species showed significant associations with either primary woodland or former pasture. However, these associations were not as absolute as those observed in Europe, where some species are restricted solely to ancient or primary woodland (Peterken & Game, 1984; Dzwonko & Loster, 1992). The nine primary woodland species were generally more shade-tolerant species of the northern forests (e.g. *C. borealis*, *C. trifolia* and *T. canadensis*). In contrast, the nine species associated with former pasture included more shade-intolerant species characteristic of more southern forests (e.g. *P. serotina*, *Q. alba* and *T. radicans*). These differences may reflect the fact that primary woodlands were generally dominated by *T. canadensis* and secondary woodlands by *A. rubrum*. These differences in canopy dominants likely affected both understorey microclimate and soil chemistry and may also have affected the distribution of understorey species (e.g. Beatty, 1984; Whitney & Foster, 1988). Thus, the association of species such as *C. borealis*, *C. trifolia* and *T. undulatum* with primary woodlands may reflect the low light and cool, acidic soil conditions found under *T. canadensis*, rather than the direct effects of land-use history.

Although we detected no differences in the physiological characteristics of primary woodlands and former pastures, woodland species recolonizing former pastures face several other potential barriers. First, woodland species may be unable to disperse to secondary woodlands, whether isolated or contiguous to extant woodlands. Many woodland species are slow to colonize newly established woodlands, because they exhibit limited seed production, poorly

dispersed propagules and low rates of vegetative expansion (Peterken & Game, 1981, 1984; Dzwonko & Loster, 1992; Hughes, 1992; Matlack, 1994). However, the species associated with primary and secondary woodlands in this study showed no significant differences in vegetative reproduction, pollination syndrome, fruit morphology, or dispersal mode (F. Gerhardt, unpublished data; see also Mabry *et al.*, 2000). *Gaultheria procumbens*, which was found more frequently in primary woodlands in this study, has been shown to have limited seedling establishment and low population growth rates in secondary woodlands (Donohue *et al.*, 2000). In contrast, the widespread distribution of most ferns across all past land uses may reflect their ability to disperse widely and abundantly via small, wind-blown spores (but see Matlack, 1994). However, like Singleton *et al.* (2001), we found that *L. complanatum* did occur more frequently on former pastures than in primary woodlands. The occurrence of all primary woodland species in some plots on former pastures and the association of *T. undulatum* with both primary woodland and pastures abandoned prior to 1870 indicate that these species are slowly colonizing secondary woodlands (cf. Bellemare *et al.*, 2002).

Woodland species may also be unable to tolerate the altered soil and nutrient conditions found on former agricultural lands. Agricultural land uses can have significant, long-term impacts on the physical and chemical properties of soils, including bulk density, pH, soil carbon and organic matter, nitrogen allocation and C:N ratios (Daniels *et al.*, 1983; Hamburg, 1984; Thorne & Hamburg, 1985; Kalisz, 1986; Compton *et al.*, 1998; Compton & Boone, 2000). Following agricultural abandonment and reforestation, at least some soil properties may return to their predisturbance levels; however, other properties may not approach levels found in undisturbed primary woodlands for at least 200 years (Hamburg, 1984; Peterken, 1993). In Petersham, former pastures were characterized by greater A horizon depth, soil pH, and organic matter content than primary woodlands (F. Gerhardt, unpublished data). However, it remains unclear how important these differences are in determining vegetation characteristics. At least for *G. procumbens*, differences in the physical and chemical characteristics of soils did not adversely affect demographic performance, and performance was actually greater on former agricultural lands than in primary woodlands (Donohue *et al.*, 2000).

Natural disturbance and logging history

Despite their immediate and dramatic impacts, the 1938 hurricane, fire and logging had surprisingly few long-term impacts on forest structure and composition. This result is similar to that reported by Motzkin *et al.* (1999), who found that neither the 1938 hurricane nor a 1957 fire had significant impacts on forest composition in the Harvard Forest. Although these types of disturbances can drastically alter overstory structure and composition, microclimate and the availability of soil and light resources (Carlton & Bazzaz, 1998), woodland species survive or quickly reestablish fol-

lowing all but the most severe disturbances (Muller, 1982; Foster, 1985; Hughes & Fahey, 1991; Hughes, 1992; Cooper-Ellis *et al.*, 1999). Other studies have shown that disturbed forests in New England converge in composition to those existing prior to hurricanes or logging in less than 50–60 years (Mabry & Korsgren, 1998; Ruben *et al.*, 1999). Forest fires, in contrast, were relatively uncommon in upland areas of central and northern New England historically (Patterson & Backman, 1988; Foster & Zebryk, 1993; Fuller *et al.*, 1998) and evidence of fire was found at only six of the seventy-four plots. This small sample size may have limited our ability to detect effects on forest structure and composition but accurately reflects the infrequent occurrence of fires in our study area.

Unexplained variation in vegetation characteristics

Interestingly, only 13.8% of the variance in the CCA analysis was explained by the measured physiographical and historical variables. The eight variables included in this analysis incorporate many of the acknowledged strong influences on forest vegetation in eastern North America. Thus, this result raises the question: what are the other important influences on forest vegetation in central New England? We suggest several possibilities. First, because we could not assign a date of abandonment to primary woodlands, this variable was not included in these analyses. However, our other analyses indicated that date of abandonment was relatively unimportant in explaining variation in community parameters or the distributions of individual species. Secondly, we did not include measures of soil fertility and chemistry in our analyses, in part because soil characteristics were likely affected by the other physiographical and historical factors as well as vegetation composition and structure. However, soil fertility and chemistry are known to have important effects on plant community structure and composition (cf. Bellemare *et al.*, 2002). Thirdly, some of the unexplained variation may be attributable to small-scale heterogeneity in the vegetation caused by microsite variation (e.g. Beatty, 1984). Because this heterogeneity occurred at a scale smaller than our sampling, it was not measured by our quadrats, although many species were patchily distributed within our quadrats (F. Gerhardt, personal observation). Fourthly, priority effects and chance events during colonization and succession may have important consequences for the structure and composition of forest communities (e.g. Egler, 1954; Drake, 1990, 1991; Drake *et al.*, 1993). However, we did not have detailed histories of the colonization and succession of the sites that we sampled, so that we were unable to evaluate the importance of these factors. Finally, biotic interactions not mediated by the measured physiographical and historical factors may explain substantial variation in forest structure and composition. Examples of these interactions include the effects of pathogens (e.g. chestnut blight) and herbivory [e.g. defoliation by gypsy moths (*Lymantria dispar* L.)], both of which have historically had important impacts on forest trees in central New England (Patterson & Backman, 1988). However, we did not have adequate records of the distribution

and degree of impacts of these pathogens and herbivore outbreaks to document their effects on forest composition and structure in Petersham. Additional research is required to evaluate the relative importance of all of these factors in explaining landscape-level variation in the forest vegetation of central New England.

Implications for secondary succession

Ecological theory suggests that vegetation–site relationships, which are initially obscured by disturbances, increase in importance during secondary succession (Christensen & Peet, 1984). Early successional species are thought to disperse widely and abundantly and to tolerate a greater range of environmental conditions, but they may be replaced by species exhibiting high degrees of habitat specificity (Grime, 1973, 1979; Muller, 1982; Bazzaz, 1987). In this study, physiography has replaced agricultural history and other natural and human disturbances as the dominant factor controlling forest structure and composition in the modern landscape. Thus, habitat specificity should be more important in determining forest structure and composition than species' life-history characteristics. However, comparing those species that were associated with both landform and past land use indicates that more species associated with former pastures ($n = 6$) than primary woodlands ($n = 2$) were associated with specific landforms. Thus, if anything, this study suggests that early successional species show greater habitat specificity than late successional species and that vegetation–site relationships may actually decrease in importance during succession.

The structure and function of disturbed and undisturbed communities are also thought to converge during secondary succession (Christensen & Peet, 1984). In this study, there was no evidence of convergence (or divergence) between primary and secondary woodlands. The ordination plot showing past land uses and dates of abandonment of the study plots (Fig. 5) shows no increase or decrease in similarity between primary and secondary woodlands of different ages. This lack of convergence may indicate that there has been insufficient time for convergence to occur or that these forests are developing in novel directions from those that existed previously. In this study, the oldest secondary woodlands have only been abandoned 120–150 years. Given the longevity of many forest trees, this represents a relatively short time period for forest development to occur and convergence might require a longer time frame (e.g. Foster *et al.*, 1998). For example, in the pre-European landscape, vegetation communities generally required 300–1200 years to revert back to their pre-disturbance structure and composition following the most severe disturbances (Foster & Zebryk, 1993). However, plant communities may also develop in novel directions following disturbances, especially in the face of chronic, large-scale disturbances caused by human activities. Opportunities for convergence may be limited by clear differences between historical and modern conditions, including marked differences in the soils on sites with different land-use histories, the decimation of several

important forest trees (e.g. *C. dentata* and *F. grandifolia*) by imported pathogens and chronic human activities such as continued logging, atmospheric pollution and global climate change. Consequently, other studies (e.g. Motzkin *et al.*, 1999; McLachlan *et al.*, 2000) have suggested that the structure and composition of primary and secondary woodlands may actually diverge, rather than converge, through time.

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Appendix I Dichotomous key for identifying land-use history from soil profile and other characteristics at forested plots in Petersham, Massachusetts, USA, during 1992. Land uses identified by this key represent the most intensive land use that occurred at each site. Unless otherwise stated, a site must meet all 'requirements' of the selected choice; 'indicators' provide supporting evidence but are not required for that choice. These criteria apply to soils in central New England that meet the following criteria: (1) upland glacial till, (2) not coarse-textured sands, (3) moderately well- to well-drained, (4) slope angle < 10° to minimize erosion and (5) no charcoal layer indicating severe fire. Numbers in parentheses following the land-use names indicate relative ranking from the least disturbed (1) to the most disturbed (5)

1a.	Profile meets two requirements	WOODLAND (1)
Requirements:	Oa depth ≥ 2.0 cm A depth < 3.0 cm E depth ≥ 1.0 cm	
Indicators:	A colour dark brown or black Bs and/or Bhs horizon present	
1b.	Profile does not meet two requirements	2
2a.	Profile meets one requirement	PASTURE OR WOODLAND (2)
Requirements:	A depth < 5.0 cm E depth < 1.0 cm	
Indicators:	Oa depth < 2.0 cm	
2b.	Profile does not meet one requirement	3
3a.	Profile meets all requirements	4
Requirements:	Homogenous A horizon Abrupt A/B boundary Gravels and boulders cover < 2% of surface Gravels in A horizon < 10%	
Indicators:	Wide stone walls or rock piles Small stones in stone walls or rock piles Level or slight microrelief	
3b.	Profile does not meet all requirements	PASTURE (3)
Indicators:	Narrow or no stone walls No small stones in stone walls	
4a.	Profile meets requirement	DEEP TILLAGE (5)
Requirements:	A depth ≥ 12.0 cm	
Indicators:	Gravels in A horizon < 2%	
4b.	Profile does not meet requirement	SHALLOW TILLAGE OR PASTURE (4)
