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# Vegetation patterns in heterogeneous landscapes: The importance of history and environment

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**Abstract.** Throughout the eastern United States, plant species distributions and community patterns have developed in response to heterogeneous environmental conditions and a wide range of historical factors, including complex histories of natural and anthropogenic disturbance. Despite increased recognition of the importance of disturbance in determining forest composition and structure, few studies have assessed the relative influence of current environment and historical factors on modern vegetation, in part because detailed knowledge of prior disturbance is often lacking. In the present study, we investigate modern and historical factors that control vegetation patterns at Harvard Forest in central Massachusetts, USA. Similar to the forested uplands throughout the northeastern United States, the site is physiographically heterogeneous and has a long and complex history of natural and anthropogenic disturbance. However, data on forest composition and disturbance history collected over the past > 90 years allow us to evaluate the importance of historical factors rigorously, which is rarely possible on other sites.

Soil analyses and historical sources document four categories of historical land use on areas that are all forested today: cultivated fields, improved pastures/mowings, unimproved pastures, and continuously forested woodlots. Ordination and logistic regressions indicate that although species have responded individually to a wide range of environmental and disturbance factors, many species are influenced by three factors: soil drainage, land use history, and C:N ratios. Few species vary in accordance with ionic gradients, damage from the 1938 hurricane, or a 1957 fire. Contrary to our expectation that the effects of disturbance will diminish over time, historical land use predicts 1992 vegetation composition better than 1937 composition, perhaps because historical woodlots have become increasingly differentiated from post-agricultural stands through the 20th century.

Interpretations of modern vegetation must consider the importance of historical factors in addition to current environmental conditions. However, because disturbances such as land use practices and wind damage are complex, it is often difficult to detect disturbance effects using multivariate approaches, even when the broad history of disturbance is known.

**Keywords:** Carbon:nitrogen ratio; Disturbance; Hurricane; Land use history; Matrix correlation; New England; Soil.

**Nomenclature:** Kartesz (1994), Anderson et al. (1990) and Stotler & Crandall-Stotler (1977).

## Introduction

A major goal of plant ecology is to determine the factors that control species distributions and community composition. Although forest patterns result in part from species-specific responses to edaphic conditions and resource availability, actual species distributions at any point in time differ from potential distributions as a result of several factors, especially biotic interactions and historical factors such as natural and human disturbance. Disturbance may influence community patterns by (1) directly altering the environment and resource distributions, (2) creating opportunities for the establishment of new species, or (3) reducing populations of established species. For instance, species with slow rates of dispersal or establishment may be absent from a site for decades or centuries, not because the site is inherently unsuitable, but simply because the species were removed by prior disturbance and have not had sufficient time to recolonize (Donohue et al. in press). A major challenge for ecological study is to evaluate the relative contribution of current environmental conditions and historical factors in determining observed vegetation patterns and dynamics.

The effects of historical factors on subsequent vegetation have been demonstrated for natural disturbances such as fire, wind storms, volcanoes, and pathogens, and these effects may persist for many hundreds of years (Grimm 1984; Foster & Zebryk 1993; Turner et al. 1997). Similarly, there is increasing recognition that previous human activity throughout Europe, the Caribbean, and North and South America continues to influence modern vegetation composition, structure, and function (Birks et al. 1988; Turner et al. 1990; Gomez-Pompa & Kaus 1992; Whitney 1994; Fuller et al. 1998). In eastern North America, 17th-18th century European settlement led to rapid forest clearing, with 60-85% of the land in agriculture by the mid-19th century. In contrast to Europe where considerable agricultural land remains, widespread farm abandonment in the eastern United States in the late 19th and early 20th centuries led to natural reforestation, such that 60-85% of the land is currently forested (Foster et al. 1998). Determining

the relative influence of human and natural disturbances and modern site conditions on community composition and dynamics in this landscape is complicated by (1) complex and intercorrelated environmental gradients, (2) a general lack of detailed information on long-term disturbance histories, and (3) the confounding of disturbance history with environmental variables. In order to address these problems and to determine the relative influence of environment and history on a range of modern forest types, we have adopted a number of approaches. A previous study (Motzkin et al. 1996) focussed on an environmentally homogeneous sand plain that allowed us to determine effects of disturbance history without the confounding effects of differing initial site conditions. The results confirmed the long-term influence of historical land use activities on modern vegetation patterns and identified several formerly widespread species that have not recolonized former agricultural lands in the nearly 100 years since agricultural abandonment. In an additional study testing the general applicability of these results, we documented that historical land use is a major determinant of modern vegetation patterns on sand plains across the region (Motzkin et al. 1999). Detailed studies of nutrient cycling and population demography were also conducted to determine the mechanisms by which historical factors exert persistent influence on current vegetation and ecosystem properties on these edaphically homogeneous sites (Compton et al. 1998; Donohue et al. in press).

In the current study, we extend these investigations to more complex upland areas where highly variable physiography coincides with a complex history of both natural and anthropogenic disturbance (Foster 1992). Our study site, the Prospect Hill Tract of Harvard Forest, is particularly appropriate for such investigations because, although it is representative of regional vegetation, site conditions, and land use history, 90 years of intensive research provide unusually detailed records of disturbance history (Raup & Carlson 1941; Spurr 1956; Foster 1992) and a rare opportunity to evaluate the influence of history and environment on modern vegetation. The site was extensively cleared for agriculture in the 18th and 19th centuries, with <15% remaining wooded by the mid-19th century (Foster 1992). Following agricultural abandonment beginning ca. 1850, natural and nearly complete reforestation occurred. Based on 1937 forest survey data, Foster (1992) determined that in the initial decades after agricultural abandonment, vegetation varied most strongly according to land use history and soil drainage. Many of the forested stands were subsequently damaged by a hurricane in 1938 and other disturbances. In order to determine whether historical land use activities continue to influence modern vegetation, even after an additional 60

years since agricultural abandonment and after more recent disturbances, we re-sampled the vegetation in 1992-1994. Whereas the 1937 survey focussed on trees, we sampled all vascular species as well as bryophytes, and we evaluate controls on the distribution and abundance of individual species, species assemblages, and life forms (i.e. trees, shrubs, herbs, and bryophytes).

Specific questions addressed in this study include:

1. What is the relative importance of environmental gradients versus disturbance history in controlling modern plant species distributions and vegetation patterns?
2. Do particular environmental and disturbance factors control the distribution of many different species, or do species vary widely in the factors that control their distributions?
3. Are the relationships between vegetation patterns, environment, and disturbance history consistent among different life forms?
4. Has the influence of historical land use activity on subsequent vegetation lessened with increasing time since agricultural abandonment and as a result of more recent disturbances?

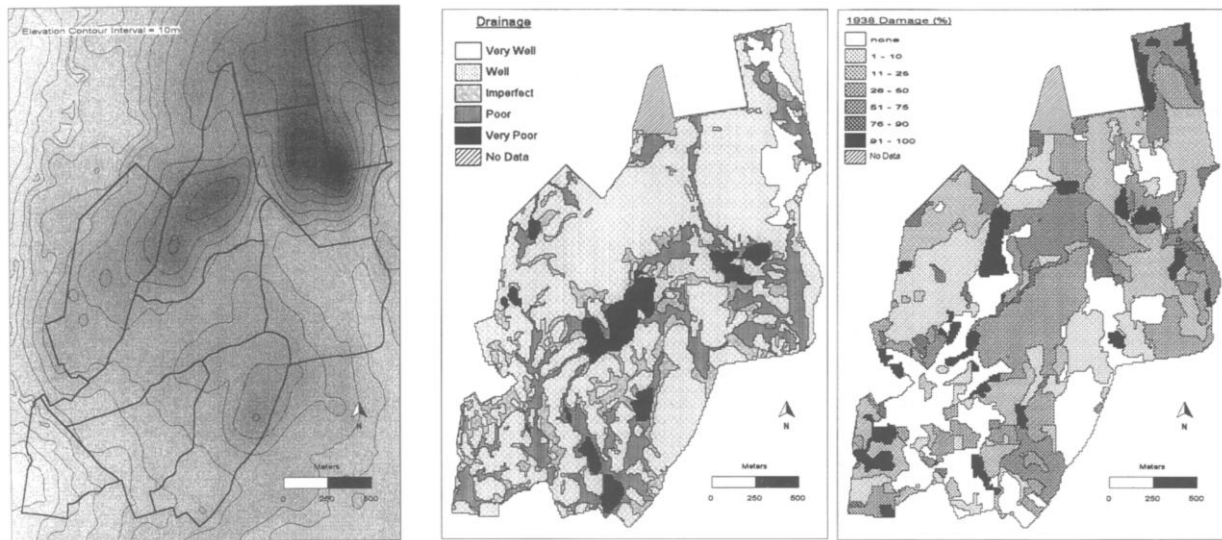
## Materials and Methods

### *Study site*

The 340-ha Prospect Hill Tract of Harvard Forest is located in the towns of Petersham and Phillipston in central Massachusetts, at 270 to 420 m a.s.l. (Fig. 1). Soils are largely acidic sandy loams that developed in glacial tills overlying gneiss and schist bedrock. Variability in relief, depth to bedrock, and the local presence of a hardpan (restrictive sub-soil horizon) create a highly variable pattern of soil drainage. The average annual temperature is 8.5°C, the frost-free period averages five months, and annual precipitation is well-distributed, averaging 105 cm, with 150 cm of snow (Rasche 1953). The vegetation is typical of the Transition Hardwoods-White Pine-Hemlock region (Westveld et al. 1956). The site is one of the oldest forest research sites in the United States, and has been intensively studied since its acquisition by Harvard University in 1907.

### *Vegetation, soils, and disturbance history*

In 1992, vascular vegetation was sampled on 269 plots that were 22.5 m × 22.5 m (0.125-acre), following the protocol for the 1937 forest census. Although the 1937 plots ( $N = 161$ ) were not permanently marked, the locations were indicated on detailed maps (scale 1" = 200'), enabling us to re-establish them. Because of the large size of the plots and the detail of the original maps, it is likely that our 1992 plots overlap the 1937 plots. In order to evaluate the full range of modern vegetation, we also established plots in stands that were not sampled



**Fig. 1.** The Prospect Hill Tract of Harvard Forest, indicating topography, soil drainage, and 1938 hurricane damage (percent of complete crown canopy damaged).

in 1937, including plantations and areas that were non-forested in 1937. The southwest corner of each 1992 plot was permanently marked with a numbered metal stake.

At each plot, diameter at breast height (DBH) was measured for all trees >2.54 cm DBH and the abundance of each herb, shrub, and understory tree species (<2.54 cm DBH) was estimated using eight cover classes: (1) <1%; (2) 1-3%; (3) <5%; (4) 5-15%; (5) 16-25%; (6) 26-50%; (7) 51-75%; (8) >=75%. In 1994, we sampled all bryophyte species (epiphytes and terrestrial species) in the southwest one-quarter of 104 of the non-plantation plots, estimating abundance using three classes (present, abundant, very abundant). Species in the red oak (*Erythrobalanus*) group (*Quercus rubra*, *Q. velutina*, and *Q. coccinea*) were combined for all analyses.

Detailed soil descriptions and sampling were conducted according to a protocol developed and supervised by R. Boone (HF Archives 1995-26d). On all 269 plots, slope, aspect, and percent cover of rock were recorded, and soil drainage was determined following standard Soil Conservation Service methods (SCS; Anon. 1993). On each of 174 plots that were not in plantations or on wet sites with organic surface soils, three shallow soil pits were dug and profile descriptions prepared following SCS methods (Anon. 1993). Pits were randomly located and were dug into the B horizon (subsoil), to an average depth of 40 cm. Samples of the Oe- and Oa-horizons were taken under a 15 cm × 15 cm template, and 0-15 cm mineral soils were sampled with a 5 cm × 15 cm cylindrical steel corer. In the laboratory, samples were air-dried, sieved (< 2.0 mm for mineral

soil, <5.6 mm for Oe and Oa layers), and weighed for bulk density (BD). Subsamples were oven-dried at 105 °C to determine gravimetric water content and combusted at 550 °C to determine organic matter content (OM). Mineral soil samples were analyzed at the Natural Resources Conservation Service Soil Survey Lab in Lincoln, NE, using standard methods (Anon. 1992). Soil particle size distribution was determined by the pipet method, extractable cation concentrations were determined using ammonium acetate (pH 7.0) followed by atomic absorption spectrometry, and cation exchange capacity (CEC) was determined by displacement of ammonium by sodium chloride. Percent base saturation (BSAT) was calculated as the percentage of the CEC occupied by exchangeable bases, and sum of bases (SUMB) was the sum of exchangeable base cations. Mineral soil pH was measured in a 1:2 soil:water slurry and carbon (C) and nitrogen (N) concentrations were determined by a Fisons CN analyzer (Fisons Instruments, Beverly, MA).

The type and intensity of historical land use were determined as follows: a map of soil disturbance was developed for the entire tract through extensive examination of soils for presence/absence and depth of a plowed surface (Ap) horizon (Motzkin et al. 1996). The soil disturbance map was then compared with historical land use maps derived from archive records and field observations of stone walls and other artifacts (Raup & Carlson 1941; Spurr 1956; Foster 1992). In cases of apparent discrepancy between our map of disturbed soils and prior land use maps, we reviewed all historical records in order to map and assign each plot to one of the following

historical land use categories: (1) cultivated field, (2) improved pasture/mowing, (3) unimproved pasture, or (4) woodlot. Soil disturbance and land use maps depict the most intensive use for a site through time, not necessarily the most recent use. For instance, a site that was intensively cultivated and then grazed prior to agricultural abandonment would be classified as cultivated rather than pasture. This approach enabled us to determine land use patterns using independent soils and historical data. Unfortunately, data indicating the length of time that individual fields were cultivated do not exist, as is the case throughout most of the eastern U.S.

For each plot, 1938 hurricane damage was determined from a detailed survey that estimated damage for each stand (Rowlands 1939; Foster 1988). A detailed map of a 1957 fire that burned portions of the study area was used in conjunction with field observations to determine whether individual plots had burned. Additional information on the history of agriculture, timing of agricultural abandonment, and forest cutting activities were derived from extensive data in the Harvard Forest Archives (Raup & Carlson 1941; Foster 1992).

#### *Data analyses*

##### *Phytosociology and vegetation variation*

Species abundance data were classified and ordinated to identify the major assemblages of vascular plants and to determine site and disturbance factors that are related to the major axes of variation in the vegetation. In order to analyze overstory and understory data simultaneously, basal area data for trees >2.54 cm DBH were converted to abundance classes as follows: the maximum species basal area on any plot, which was 59 m<sup>2</sup>/ha for red pine, was assigned a value of 100%, and basal area classes corresponding to the eight cover-abundance classes were then calculated as a percentage of this maximum (Motzkin et al. 1996). Data for the herbs, shrubs, understory trees, and overstory trees were then combined into a matrix of 269 plots by 254 vascular plant species. Overstory and understory occurrences of the same species were treated as separate variables. Based on an agglomerative cluster analysis (AGGLOM; Orłóci 1967) of species abundance data for all plots, six vegetation types were identified. These data were also ordinated first using detrended correspondence analysis (DCA, Hill 1979), and then, using the DCA output as a starting point, by nonmetric multidimensional scaling (NMDS) of Bray-Curtis distances calculated from mid-points of cover classes for all vascular plants (Minchin 1987; Rohlf 1992). A similar ordination was conducted for the 230 non-plantation plots. NMDS ordinations using random starting points resulted in very similar ordinations to those that used the DCA output as a

starting point; results presented here are based on the DCA starting points. These NMDS ordinations were rotated onto their principle components so that Axis I corresponded to the direction of greatest variation. In order to interpret the ordination, multiple correlations were calculated between ordination axes and the abundances of tree species, and between the axes and each environmental or disturbance variable. These correlations serve the same function as a biplot and show the direction of increase for each variable in ordination space.

##### *Relationships of edaphic and disturbance variables*

The following soils variables had skewed distributions and were transformed into their natural logarithms: base saturation, sum of bases, calcium (Ca) and magnesium (Mg) concentrations, bulk density, cation exchange capacity, and nitrogen, carbon, and organic matter content. Correlations were calculated among all of the edaphic variables. Edaphic differences among the four historical land use categories were tested using Kruskal-Wallis tests. Topography, drainage, historical land use, 1938 hurricane damage, C:N ratio, and vegetation types were mapped to identify spatial patterns of variability.

##### *Environmental predictors of individual species distributions*

In order to investigate factors controlling individual species distributions, we modelled the occurrence of each species as a function of environmental and historical variables. These analyses were restricted to vascular species that occurred in >8% of the 174 non-plantation plots with soils data, and bryophytes that occurred in >10% of the 94 plots with bryophyte and soils data. Ubiquitous species (frequency of occurrence >90% for bryophytes, >92% for vascular species) were also excluded from these analyses. For each species, two logistic regressions were run using the LOGIT module of SYSTAT (Steinberg & Colla 1991): (1) a multiple logistic regression relating species presence/absence to drainage, pH, C:N ratio, intensity of historical land use, severity of 1938 hurricane damage, and presence/absence of 1957 fire; and (2) a single-step stepwise logistic regression to determine which of 13 edaphic and three disturbance variables (historical land use, 1938 hurricane, 1957 fire) was the single best predictor of species presence/absence. Categorical variables were ranked for these analyses. Percent silt and clay were not included because they were highly correlated with percent sand.

##### *Species richness*

In order to evaluate patterns of species richness among different life forms, we tallied the number of species of bryophytes, herbs, shrubs, understory trees, overstory

trees, and the total number of vascular species per plot, and tested for relationships using Spearman's rank correlations. Species richness of the different life forms were related to environmental and historical factors using correlations for continuous factors and Kruskal-Wallis tests for categories of historical land use.

#### *Correlations between life forms*

Matrix correlations were used to determine the degree of association between different life forms for the 104 plots in which all life forms were sampled. For each life form, we computed a dissimilarity matrix of Bray-Curtis distances between all pairs of the 104 plots (other metrics yielded similar results). Each dissimilarity matrix was then correlated against every other dissimilarity matrix, i.e., bryophytes by herbs, bryophytes by shrubs, bryophytes by understory trees, etc., in what is referred to as a Mantel test. A strong correlation, for instance, between the bryophyte dissimilarity matrix and the herb dissimilarity matrix would indicate that when two plots are dissimilar in terms of bryophytes they are also dissimilar in terms of herbs, or, conversely, when two plots are similar in terms of bryophytes they are similar in terms of herbs. Correlating the dissimilarity matrices is similar to comparing ordinations for the different life forms, but the matrix correlation is more fundamental since ordinations are derived from dissimilarity matrices.

The life-form matrices were also correlated against edaphic and disturbance matrices. The soils variables were standardized by subtracting the mean of each variable and dividing by the standard deviation. From these standardized data, a Euclidean dissimilarity matrix was computed, which was correlated against each plant matrix. In addition, based on ordination and logistic regression results, we selected two edaphic variables (soil drainage and C:N ratio) and two disturbance variables (historical land use and 1938 hurricane damage) to correlate individually against the vegetation dissimilarity matrices. For each of these four variables, a plot-by-plot matrix was computed. Euclidean distances were used for all except historical land use; the negative of the simple matching coefficient was used for land use because for this analysis land use was considered to be categorical and multinomial. The significance of our matrix correlations was determined by a randomization routine, and all computations were done in NTSYS (Rohlf 1992). The technique is further discussed by McCune & Antos (1981) and Leduc et al. (1992).

#### *Vegetation change: 1937 to 1992*

For 161 plots that were sampled in 1937 and 1992, we developed comparable data sets by grouping the 1992 DBH measurements into 1 inch (2.54 cm) classes.

For each plot, we calculated the change in total basal area and the basal area of the most common tree species (red maple, white pine, red oak, and hemlock). Changes in species composition were computed using the Bray-Curtis distance between the two samples based on relative dominance (species basal area divided by the plot basal area). These measures of change were correlated against soil drainage, pH, C:N ratio, intensity of historical land use, severity of 1938 hurricane damage, and presence/absence of 1957 fire.

In order to determine the relative strength of the relationship between overstory composition and historical land use in 1937 and 1992, we calculated three plot-by-plot dissimilarity matrices: one of Bray-Curtis dissimilarities of overstory data from 1937, one of Bray-Curtis dissimilarities of the 1992 overstory data, and one of the negative of the simple-matching coefficient of historical land use. Matrix correlations between the historical land use and the 1937 tree matrices, and between the historical land use and the 1992 tree matrices enabled us to quantify the extent to which the patterns of similarity or dissimilarity among plots for one data set correspond to the patterns for the other data set. A parallel analysis using Euclidean distances yielded very similar results.

#### *Inferential caveats*

A number of warnings are warranted. Many of our exploratory analyses seek to identify correlations between species distributions and environmental or historical factors. However, significant correlations do not necessarily indicate causation or identify mechanisms underlying correlations. Thus, although we refer to variables such as C:N ratio as 'predicting' the distribution of a species, they may actually be indicators of some other factors, such as available nitrogen, that directly affect plant performance. Specific limitations of our analyses include: 1. The plots are not spatially independent and many of the environmental and historical variables and species distributions are presumably spatially patterned, making it difficult to identify individual factors that control species distributions. Such patterning is, however, part of the complexity of site conditions to which plants must typically respond. 2. Although multiple logistic regression analyses allow us to evaluate the effect of one variable while holding others constant, variables that are not included in the models may also be biologically significant. In addition, these analyses assume that all effects are linear and additive, which is unlikely. 3. Precision in the quantification of variables varies. For instance, although we would like to be able to report whether the intensity of 19th century land use has a greater influence on modern species distributions than current edaphic conditions, we measured edaphic

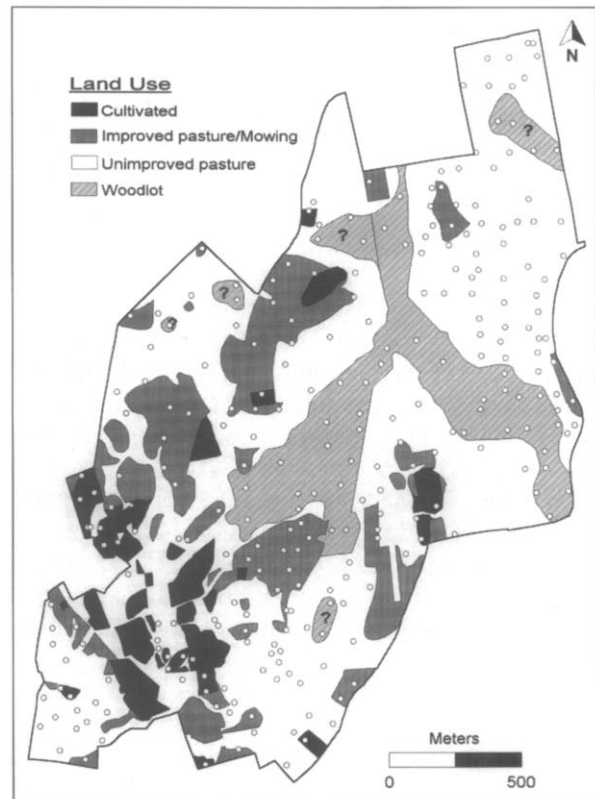
conditions better than land use history. Similarly, the plot-level intensities of disturbances such as the 1938 hurricane or the 1957 fire were coarsely estimated. 4. We have performed a large number of significance tests and are therefore likely to report a few significant results that are due to chance. We have chosen not to perform a Bonferroni adjustment for multiple tests (Rice 1989) in these exploratory analyses, accepting that some mistakes will be made while most of the conclusions should be sound.

## Results

### *Disturbance history*

The Prospect Hill Tract of the Harvard Forest, like much of central New England, has a varied and complex history of disturbance. Previous studies provide detailed information on the pattern of historical land use, including 18th and 19th century agriculture followed by farm abandonment and reforestation (Raup & Carlson 1941; Spurr 1956; Foster 1992). In the current study, extensive surveys of soil disturbance provide an independent and more ecologically relevant assessment of historical land use (Motzkin et al. 1996) in three soil-disturbance categories: 'undisturbed', 'deep', and 'shallow'. Undisturbed soils show no evidence of mixing by historical agriculture and are typically rocky, with black to dark brown, shallow (<5 cm) A-horizons, except on moist sites where they may be deeper. E-horizons  $\geq 1$  cm may occur, particularly beneath hemlock stands. Among the anthropogenically disturbed soils, areas with deep (>12 cm), well-developed plow (Ap) horizons with abrupt, smooth lower boundaries were distinguished from those with shallow (<12 cm) Ap-horizons with more gradual, wavy lower boundaries. Both shallow and deep Ap-horizons are lighter in color than undisturbed A-horizons, although dark A1-horizons that have developed since agricultural abandonment frequently occur at the top of these profiles. E-horizons are absent from disturbed soils.

Comparison of the soil disturbance map with land use maps developed by Raup & Carlson (1941), Spurr (1956), and Foster (1992) resulted in several important observations. Much of the area (77%) showed no evidence of soil disturbance, including unimproved pastures and continuously forested sites (Fig. 2). No field soil evidence enabled the separation of these two former land uses, although, where present, crude stone walls identify unimproved pastures. Many of the sites with soil disturbance were independently confirmed from historical records as having been cultivated. However, we identified several areas with plow layers that had not



**Fig. 2.** Historical land use map for the Prospect Hill Tract of Harvard Forest. Cultivated areas have deep (>12 cm), well-developed plow (Ap) horizons, improved pastures/mowings have shallow, more irregular Ap-horizons, and woodlots and unimproved pastures lack visible evidence of historical soil disturbance. Open circles indicate 269 sample plots.

been previously classified as cultivated, as well as a few sites previously mapped as cultivated where we found no evidence of plowing. In addition, using evidence for shallow plowing we were able to separate 'improved pasture/mowing' from unimproved pasture.

Based on these criteria, 7% of the area was previously cultivated, 16% was used as improved pasture or mowing, 61% was apparently used as unimproved pasture, and 16% has no soil disturbance and was continuously forested woodlot (Fig. 2).

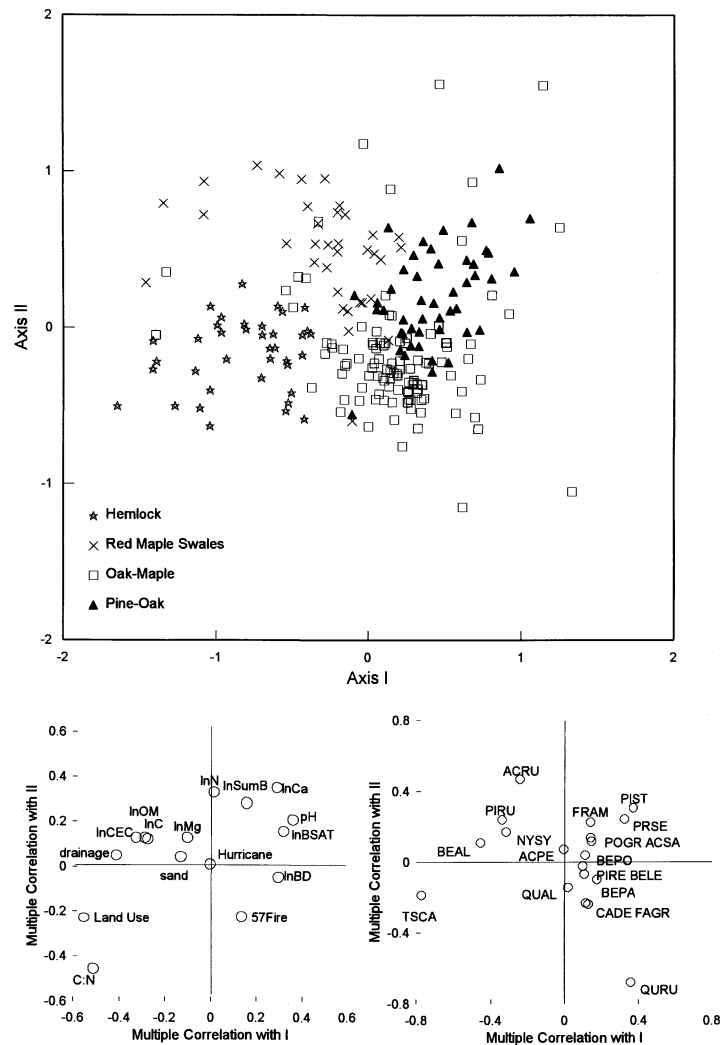
Several other disturbances have also affected the study area. Foster's (1992) cutting history of the area prior to acquisition by Harvard in 1907 indicates that nearly all of the merchantable second-growth timber was cut between 1885 and 1895. Since 1907, forest management established nearly 100 ha of conifer plantations, harvested white pine stands, and selectively cut hardwood and mixed stands (Gould 1960; Foster 1992). Beginning in 1913, the chestnut blight (*Endothia parasitica*) caused the elimination of tree-sized chestnut (*Castanea dentata*), which were formerly widespread

(Kittredge 1913; Foster 1992). Subsequently, the 1938 hurricane had variable impact, with 21% of the area sustaining >50% damage (i.e. loss of complete crown canopy), and 10% sustaining >75% damage (Fig. 1; HF Archives 1939-05). The 1957 fire affected ~ 9% of the area.

*Phytosociology and vegetation variation*

Cluster analysis of all 269 plots identified six vegetation types that differ in species composition and abundance (App. 1; www.opuluspress.se/jvs/arch.htm). 1. The Hemlock Type is dominated by *Tsuga canadensis*, with scattered large *Quercus rubra* and *Pinus strobus*, and occasional *Picea rubens*. The understory is generally sparse, but includes several shrubs, herbs, and liverworts that are less frequent in other types (App. 1). 2. The Red Maple Type is characterized by an overstory of *Acer rubrum*, *Fraxinus americana*, and *Betula alleghaniensis* and a dense understory of ferns and

shrubs characteristic of moist sites. Many bryophyte species occur with greatest frequency or abundance in this type. 3. The Oak-Maple Type is the most widespread vegetation and is dominated by *Quercus rubra* and *Acer rubrum*. Understory species include *Vaccinium pallidum*, *Gaultheria procumbens*, *Dennstaedtia punctilobula*, and *Lycopodium obscurum*. Few bryophyte species are more frequent in this type than in others. A few plots with high abundance of *Quercus alba*, *Fagus grandifolia*, or *Acer saccharum* might have been separated from the Oak-Maple Type had they been better represented within the study area. 4. The Pine-Oak Type is similar to the Oak-Maple Type, but has greater dominance by *Pinus strobus*. Characteristic understory taxa include *Crataegus* spp., *Cornus alternifolia*, *Maianthemum canadense*, and the liverwort *Nowelia curvifolia*, which frequently occurs on decaying pine logs. 5. Spruce Plantations have a canopy of introduced *Picea abies* and *P. glauca*, relatively few other trees, and a depauperate understory. 6. Red Pine Plantations have somewhat



**Fig. 3.** Ordination of 230 non-plantation plots by nonmetric multidimensional scaling of Bray-Curtis distances from midpoints of cover classes of all vascular species. The lower left-hand inset represents a scatter plot of Pearson's product moment correlation coefficients between axis scores and edaphic and disturbance variables, based on 174 plots for which soil data were gathered. The lower right-hand inset shows the correlations with abundances of canopy trees for all 230 plots. Species acronyms are as follows: *Acer pensylvanicum* (ACPE); *Acer rubrum* (ACRU); *Acer saccharum* (ACSA); *Betula alleghaniensis* (BEAL); *Betula lenta* (BELE); *Betula papyrifera* (BEPA); *Betula populifolia* (BEPO); *Castanea dentata* (CADE); *Fagus grandifolia* (FAGR); *Fraxinus americana* (FRAM); *Nyssa sylvatica* (NYSY); *Picea rubens* (PIRU); *Pinus resinosa* (PIRE); *Pinus strobus* (PIST); *Populus grandidentata* (POGR); *Prunus serotina* (PRSE); *Quercus rubra* (QURU).



**Table 1.** Correlations among edaphic variables (top):  $|r| > 0.15$  are significant at  $P < 0.05$ . The bottom panel shows means (backtransformed when necessary) for the four historical land use categories. Data only for non-plantation plots that had sufficient drainage for soil analysis ( $N = 174$ ). Abbreviations and units of measurement are as follows: % base saturation (BSAT), sum of bases (SumB; [cmol(+)/kg]), calcium (Ca; [cmol(+)/kg]), % organic matter (OM), magnesium (Mg; [cmol(+)/kg]), total soil nitrogen (N; g/kg), total soil carbon (C; g/kg), bulk density (BD; g/cc), cation exchange capacity (CEC; [cmol(+)/kg]). Drainage classes range from 1 (somewhat excessively drained) to 6 (very poorly drained).

	Drainage	Sand	Silt	Clay	pH	C:N	ln BSAT	ln SumB	lnCa	lnOM	lnMg	lnN	lnC	lnBD	lnCEC
Drainage	1.00														
Sand	0.00	1.00													
Silt	-0.03	-0.97	1.00												
Clay	0.09	-0.71	0.53	1.00											
pH	-0.05	-0.11	0.12	0.04	1.00										
C:N	0.07	0.24	-0.21	-0.25	-0.35	1.00									
lnBSAT	-0.03	-0.10	0.04	0.25	0.28	-0.48	1.00								
lnSumB	0.23	-0.22	0.16	0.32	0.21	-0.48	0.83	1.00							
lnCa	0.15	-0.15	0.10	0.23	0.26	-0.53	0.79	0.83	1.00						
lnOM	0.43	-0.20	0.18	0.19	-0.03	-0.08	-0.10	0.39	0.18	1.00					
lnMg	0.38	-0.16	0.12	0.23	0.00	-0.09	0.32	0.59	0.37	0.47	1.00				
lnN	0.29	-0.27	0.24	0.26	0.14	-0.48	0.14	0.55	0.39	0.85	0.44	1.00			
lnC	0.40	-0.19	0.17	0.17	-0.01	-0.03	-0.10	0.38	0.16	0.94	0.46	0.88	1.00		
lnBD	-0.38	0.28	-0.27	-0.19	0.07	0.01	0.06	-0.32	-0.13	-0.76	-0.45	-0.65	-0.75	1.00	
lnCEC	0.47	-0.17	0.18	0.08	-0.14	0.02	-0.32	0.25	0.02	0.82	0.42	0.68	0.80	-0.65	1.00
Mean	2.85	60.62	32.73	6.66	4.24	21.65	1.13	-0.55	-1.64	2.34	-2.06	-3.73	-0.68	-0.38	2.96
s.d.	1.14	7.05	5.84	1.93	0.26	3.90	0.55	0.53	0.97	0.27	0.65	0.37	0.31	0.16	0.32
Mean back-transformed							3.10	0.58	0.19	10.34	0.13	0.02	0.51	0.69	19.28
Tilled $N = 16$	2.63	63.80	29.85	6.35	4.39	19.29	3.88	0.60	0.28	9.00	0.10	0.023	0.43	0.75	15.86
Improved $N = 21$	2.33	61.63	31.50	6.87	4.39	22.59	3.79	0.57	0.23	9.07	0.12	0.019	0.43	0.73	15.41
Pastured $N = 102$	2.79	59.09	34.02	6.88	4.25	20.58	3.24	0.61	0.21	10.42	0.13	0.025	0.52	0.68	19.69
Woodlot $N = 35$	3.43	63.01	31.00	6.00	4.07	25.30	2.20	0.48	0.11	11.63	0.14	0.024	0.59	0.14	0.02
Kruskal-Wallis	13.70**	17.79**	18.97**	6.54†	28.99**	45.05**	15.61**	5.87	11.35**	16.65**	5.17	11.99**	18.46**	13.95**	29.41**

† $P < 0.1$ ; \*\* $P < 0.01$ ; others not significant  $P > 0.1$ .

more varied tree regeneration than Spruce Plantations, but sparse herbaceous layers.

Cluster analysis and ordination of species abundance data (not shown) clearly distinguish the two plantation types from the other vegetation, with most understory species less frequent and less abundant in the plantations. In order to explore patterns of vegetation variation in the other types, we removed the plantation data and performed an ordination of species abundance data for the 230 remaining plots (Fig. 3). The Hemlock, Red Maple, and Pine-Oak Types defined by cluster analysis are relatively distinct on the ordination, whereas the Oak-Maple Type is more varied. The ordination is strongly influenced by the variation in abundance of hemlock, red maple, white pine, and red oak.

Continuous soil and disturbance variables (land use, hurricane damage, and fire) were correlated against the plot axis scores (Fig. 3, lower left) for the 174 plots for which we have soils data. Plots in the Hemlock Type are correlated with high C:N ratio and were continuously forested, whereas Pine-Oak and some Oak-Maple plots have low C:N ratios and were cleared for agriculture.

Plots with low values on Axis I (i.e. those in the Hemlock and Red Maple Types) typically have poor drainage, whereas most plots that burned in the 1957 fire currently support Oak-Maple stands. The ordination axes are not correlated with 1938 hurricane damage.

*Interrelationships of edaphic and disturbance variables*

Several of the edaphic variables are highly correlated (Table 1). Percent organic matter is positively correlated with carbon and nitrogen concentration and with CEC, and negatively correlated with bulk density. A somewhat weaker correlation exists between organic matter and soil drainage. pH does not vary widely (mean  $\pm$  SD:  $4.2 \pm 0.31$ ; range: 3.2-5.3) and has only a weak negative correlation with C:N ratio, and a weak positive correlation with base saturation and calcium concentration. C:N ratio is negatively correlated with base saturation, sum of bases, and calcium. The textural variables (sand, silt, and clay) are strongly correlated, but only moderately or weakly correlated with cation and nutrient levels.

Many of the edaphic factors differ with historical land use (Table 1). Continuously forested woodlots are generally more poorly drained than sites that were cleared for historical agriculture, and have higher organic matter content and C:N ratios, and lower pH, base saturation, and bulk density. Sites used intensively for historical agriculture (cultivated fields and improved pastures/mowings), are generally fairly well-drained, with low organic matter content and low C:N ratios.

#### *Environmental predictors of individual species distributions*

Logistic regression using environmental and historical variables identified significant predictors for nearly every species (Table 2). Soil drainage, C:N ratio, and historical land use were frequently selected as the best predictors of species occurrence, with some variation by life form. Drainage was the best predictor for approximately one-third of the bryophyte species, whereas C:N (or sometimes lnN) was more frequently the best predictor for herbs and shrubs. However, drainage, C:N ratio, and historical land use influence the occurrence of some species in each life form. The six-variable multiple logistic regressions indicate that for many species, one or more variables may have significant effects even while holding the others constant. For instance, for numerous species, land use history had a significant effect while C:N and drainage were held constant. For most environmental and disturbance variables, both positive and negative effects were detected, indicating varied and individualistic species response to particular gradients. Only a few species are positively associated with degree of damage from the 1938 hurricane (e.g. *Atrichum angustatum*, which was frequently found on old tip-up mounds) or the 1957 fire (e.g. *Betula papyrifera* and *B. populifolia*). The best predictor for the occurrence of a tree species in the overstory frequently differed from that for the species in the understory. Percent sand, lnC, lnOM, lnMg, lnCa, and pH were rarely the best predictors of individual species occurrence.

Several species are characteristic of sites that were never cleared for historical agriculture (Fig. 4). Whereas some species occur almost exclusively within low-lying sites that were continuously forested, others (e.g. *Brotherella recurvans*) occur in both continuously forested and former agricultural sites but are more abundant in historical woodlots.

#### *Species richness*

Species richness among all life forms is positively correlated (Table 3A), although the strength of the correlations vary. Bryophyte and herb species richness are

most strongly correlated, followed by herbs and shrubs, and herbs and understory trees. The weakest correlations occur between canopy trees and other life forms. Soil drainage is positively correlated with bryophyte species richness and more weakly with richness of herbs and shrubs (Table 3B). In contrast, overstory and understory tree species richness are negatively and weakly correlated with drainage. C:N ratios are negatively correlated with species richness of herbs and understory trees, and 1938 hurricane damage is not strongly correlated with species richness in any life form. Historical woodlots have fewer vascular plant species than sites that were cleared for agriculture, but bryophyte richness does not differ by historical land use (Table 3C).

#### *Matrix correlations between life forms*

Correlations of dissimilarity matrices for all life forms are positive and highly significant, with the strongest correlations between bryophytes and herbs, and between herbs and shrubs (Table 4). Correlations for bryophytes versus shrubs are somewhat lower, as are all matrix correlations involving trees.

Edaphic dissimilarities based on all soil variables are remarkably poor predictors of vegetation dissimilarities: none of the matrix correlations are significant (Table 4). Because this lack of overall relationship does not preclude the possibility that one or a few variables were of great importance, we compared dissimilarity matrices for four variables (soil drainage, C:N ratio, land use history, and 1938 hurricane damage) with the matrices for each life form (Table 4). The matrices of the four factors are largely independent: C:N is weakly correlated with land use ( $r_{\text{matrix}} = 0.14$ ), but all others are not significantly related. In contrast, the vegetation matrices are weakly but significantly correlated with C:N, drainage, and land use history. Drainage is more strongly correlated with bryophytes and herbs than woody plants, and land use is most strongly correlated with dissimilarities in mature trees. Hurricane damage is not significantly correlated with any of the life forms. In general, the edaphic and disturbance variables tested are not as strongly correlated with the plant matrices as the plant matrices are with each other.

#### *Amount of change since 1937*

In 1937, the average basal area in the sampled plots was 22.47 m<sup>2</sup>/ha. By 1992, the forest had more than recovered from the hurricane, with an average basal area of 26.66 m<sup>2</sup>/ha. Red oak (1.81 to 5.99 m<sup>2</sup>/ha) and hemlock (2.32 to 5.35 m<sup>2</sup>/ha) increased most, with a less pronounced increase in red maple (4.39 to 6.07 m<sup>2</sup>/ha).

**Table 2.** Exploratory logistic regressions characterizing the edaphic and historical correlates of occurrence for common but not ubiquitous plant species.  $f$  is the number of plots in which a species occurred. For vascular plants,  $N = 174$  plots; for bryophytes,  $N = 94$  plots. Vascular species that occurred in 15 or more plots and were absent from 15 or more plots were analyzed. Bryophytes that occurred in 10 or more plots and were absent from 10 or more were analyzed. Numbers under the variables are  $t$ -ratios.  $\rho^2$  is McFadden's  $\rho^2$ , which indicates the degree to which the six variable model explains presence or absence, though  $\rho^2$  is known to give much lower values than the familiar  $R^2$  of least-squares regression. The column on the far right shows the best single predictor variable from a series of 16 one-variable logistic regressions in which a species' occurrence was modeled as a function of drainage, percent sand, pH, C:N, lnBSAT, lnSumB, lnCa, lnOM, lnMg, lnN, lnC, lnBD, lnCEC, historical land use, 1937 hurricane damage, and whether or not the plot was burned in the 1957 fire. Species are ordered by their best predictor. Ranking for categorical variables is as follows: drainage (1 = somewhat excessively drained; 2 = well drained; 3 = moderately well drained; 4 = somewhat poorly drained; 5 = poorly drained; 6 = very poorly drained); land use (1 = cultivated field; 2 = improved pasture/mowing; 3 = unimproved pasture; 4 = woodlot); hurricane (loss of canopy cover: 0 = undamaged; 1 = 1-10%; 2 = 11-25%; 3 = 26-50%; 4 = 51-75%; 5 = 76-90%; 6 = 91-100%); 1957 fire (0 = no; 1 = yes).

	$f$	Drainage	pH	C:N	Land use	Hurricane	57 Fire	$\rho^2$	Best predictor
<b>Trees &gt;2.54 cm DBH</b>									
<i>Betula alleghaniensis</i>	(97)	4.16**	-1.20	0.72	2.15*	3.25**	0.24	0.22**	+Drainage**
<i>Betula papyrifera</i>	(92)	-2.89**	2.30*	1.14	0.32	2.16*	1.98*	0.11**	-Drainage**
<i>Fagus grandifolia</i>	(73)	-0.13	-0.94	1.71†	-1.11	0.29	0.44	0.02	+C:N†
<i>Acer saccharum</i>	(26)	-0.52	-0.78	-2.60**	-0.46	0.73	-0.61	0.07	-C:N**
<i>Prunus serotina</i>	(90)	-0.54	2.10*	-2.50**	0.10	1.69†	-1.75†	0.09**	-C:N**
<i>Tsuga canadensis</i>	(97)	1.13	-1.13	1.41	2.93**	1.76†	-2.38*	0.16**	+Land Use**
<i>Pinus strobus</i>	(138)	0.05	0.43	-0.68	-3.10**	-0.35	-2.49**	0.15**	-Land Use**
<i>Betula lenta</i>	(113)	-2.08*	-1.28	-1.54	2.92**	2.78**	1.77†	0.13**	+Hurricane**
<i>Betula populifolia</i>	(37)	-0.78	2.44**	3.58**	-1.93*	-2.73*	1.32	0.18**	-Hurricane**
<i>Acer pensylvanicum</i>	(43)	-1.93*	-1.24	-1.98*	0.54	1.19	1.62†	0.06*	+lnBD*
<i>Fraxinus americana</i>	(53)	2.51**	1.02	-4.22**	-0.08	1.87†	-1.39	0.18**	+lnN**
<i>Castanea dentata</i>	(51)	-1.06	0.81	1.30	-0.42	-1.15	0.82	0.03	-lnN†
<i>Quercus alba</i>	(33)	-1.72†	1.25	4.14**	-1.17	-0.75	2.09*	0.18**	-lnN**
<b>Trees &lt;2.54 cm DBH</b>									
<i>Betula alleghaniensis</i>	(63)	1.70†	1.02	-1.46	2.03*	1.52	0.40	0.05†	+Drainage*
<i>Acer pensylvanicum</i>	(91)	-2.99**	0.13	-3.46**	2.62**	1.71†	2.04*	0.13**	-Drainage**
<i>Acer saccharum</i>	(23)	1.90†	0.82	-2.93**	1.98*	0.02	-0.03	0.23**	-C:N**
<i>Betula lenta</i>	(82)	-1.49	-0.32	-3.01**	-0.17	-0.10	0.86	0.06*	-C:N**
<i>Fraxinus americana</i>	(56)	1.67†	-0.26	-3.53**	-2.95**	1.19	-1.22	0.16**	-C:N**
<i>Acer rubrum</i>	(147)	0.31	0.59	-0.42	-2.14*	-0.14	0.03	0.11**	-Land Use**
<i>Fagus grandifolia</i>	(117)	-0.59	1.07	0.10	-1.97*	1.17	-0.54	0.05†	-Land Use**
<i>Pinus strobus</i>	(125)	1.37	-0.47	-1.28	-4.52**	0.66	1.12	0.23**	-Land Use**
<i>Prunus serotina</i>	(127)	-1.42	-0.03	-2.22*	-3.99**	-0.09	-0.04	0.28**	-Land Use**
<i>Quercus rubra</i>	(158)	1.92*	-1.06	-0.43	-3.56**	-0.58	0.33	0.27**	-Land Use**
<i>Betula papyrifera</i>	(18)	-1.58	-1.89†	1.82†	-2.66**	1.04	3.27**	0.24**	+57 Fire**
<i>Betula populifolia</i>	(18)	-0.17	-0.38	1.50	-2.15*	-0.91	3.84**	0.20**	+57 Fire**
<i>Castanea dentata</i>	(83)	-2.40*	-0.68	1.70	-0.32	-0.95	2.31*	0.08**	+57 Fire**
<i>Quercus alba</i>	(49)	-1.78†	-0.54	2.48**	-3.95**	-0.52	1.07	0.15**	-lnCEC**
<i>Tsuga canadensis</i>	(111)	0.07	-0.84	2.76**	1.00	-0.72	-0.73	0.07**	-lnCa**
<b>Shrubs and vines</b>									
<i>Aralia nudicaulis</i>	(152)	2.12*	-0.08	-0.86	-0.51	2.00*	0.92	0.08	+Drainage†
<i>Ilex verticillata</i>	(40)	4.15**	1.19	-2.22*	-2.24*	0.01	0.55	0.18**	+Drainage**
<i>Rhododendron</i> spp.	(36)	2.49**	-0.58	2.33*	-1.17	-1.66†	-0.43	0.09**	+Drainage**
<i>Viburnum nudum</i>	(122)	2.77**	1.25	2.83**	-1.21	-0.90	1.70†	0.11**	+Drainage**
<i>Cornus canadensis</i>	(42)	-0.44	0.29	3.49**	-0.55	-0.22	0.71	0.08*	+C:N**
<i>Gaultheria procumbens</i>	(106)	0.43	-1.28	4.86**	-0.80	-0.77	0.86	0.18**	+C:N**
<i>Kalmia latifolia</i>	(20)	0.74	-0.22	2.94**	2.02*	0.46	-0.01	0.28**	+C:N**
<i>Mitchella repens</i>	(107)	0.52	0.21	3.88**	1.11	0.62	-0.17	0.12**	+C:N**
<i>Nemopanthus mucronatus</i>	(49)	0.56	-0.45	3.15**	-2.27*	-0.93	-0.81	0.07*	+C:N**
<i>Viburnum lantanoides</i>	(40)	-0.52	0.81	3.03**	2.79**	1.80†	0.72	0.19**	+C:N**
<i>Cornus alternifolia</i>	(31)	-0.68	0.87	-4.17**	-1.06	0.35	-0.03	0.27**	+C:N**
<i>Corylus cornuta</i>	(23)	-2.96**	-0.51	-3.73**	2.31*	1.72†	-0.03	0.26**	-C:N**
<i>Crataegus</i> spp.	(72)	-2.14*	0.14	-3.27**	1.26	-0.74	1.39	0.09**	-C:N**
<i>Rubus allegheniensis</i>	(23)	-2.76**	1.29	-3.77**	0.44	-0.44	0.10	0.29**	-C:N**
<i>Hamamelis virginiana</i>	(39)	1.86†	2.00*	2.93**	3.32**	0.40	-0.93	0.26**	+Land Use**
<i>Rubus</i> species	(68)	-0.17	0.22	0.65	-1.30	-1.19	0.70	0.02	-Land Use ns
<i>Vaccinium corymbosum</i>	(118)	1.53	2.02*	1.61	-2.74**	-0.55	1.34	0.10**	-Land Use**
<i>Aronia</i> spp.	(28)	2.32*	1.06	0.89	-1.86†	-1.91†	1.47	0.11**	-Hurricane*
<i>Spiraea alba</i>	(20)	1.61	1.43	-1.75†	-1.80†	-2.84**	0.08	0.29**	-Hurricane**
<i>Viburnum dentatum</i>	(61)	2.13*	0.10	-2.06*	-0.94	-3.04**	-1.28	0.12**	-Hurricane**
<i>Vaccinium pallidum</i>	(28)	-2.30*	0.09	3.03**	-1.70†	-2.15*	1.88†	0.18**	+57 Fire**
<i>Kalmia angustifolia</i>	(27)	1.66†	-0.64	2.05*	-1.76†	-1.33	-0.83	0.07†	+lnMg†
<i>Parthenocissus quinquefolia</i>	(16)	2.42*	0.94	-2.05*	-1.35	-0.96	-0.03	0.23**	+lnSumB**
<i>Toxicodendron radicans</i>	(23)	2.97**	-0.82	-2.57**	-2.52*	0.22	-0.03	0.21**	+lnBSAT**
<i>Vaccinium angustifolium</i>	(125)	-1.62	0.43	3.66**	-1.66†	-1.70†	0.03	0.15**	-lnN†
<i>Viburnum acerifolium</i>	(55)	-2.05*	2.31*	-0.63	1.41	0.38	0.12	0.05†	-Sand*

Table 2, cont.

	<i>f</i>	Drainage	pH	C:N	Land use	Hurricane	57 Fire	$\rho^2$	Best predictor
<b>Herbs and ferns</b>									
<i>Coptis trifolia</i>	(69)	5.35**	-0.27	2.59**	-0.17	-0.24	-0.22	0.21**	+Drainage**
<i>Osmunda cinnamomea</i>	(102)	5.40**	-0.94	-1.05	1.19	0.90	-0.67	0.27**	+Drainage**
<i>Osmunda claytoniana</i>	(42)	3.71**	2.65**	-0.27	0.76	-1.12	-0.30	0.14**	+Drainage**
<i>Thelypteris noveboracensis</i>	(74)	4.16**	-0.07	-1.56	0.44	0.12	-0.99	0.11**	+Drainage**
<i>Carex pensylvanica</i>	(79)	-3.43**	0.22	-3.09**	-0.21	-0.54	2.66**	0.17**	-Drainage**
<i>Demnstaedtia punctilobula</i>	(150)	-2.55**	-1.45	-2.01*	0.55	1.13	0.55	0.10*	-Drainage**
<i>Lycopodium obscurum</i>	(138)	-1.69†	-0.28	0.59	-1.20	-0.20	0.99	0.04	-Drainage*
<i>Clintonia borealis</i>	(74)	2.32*	-0.50	3.52**	-0.64	1.65†	-1.08	0.12**	+C:N**
<i>Medeola virginiana</i>	(124)	0.66	0.51	4.12**	3.07**	-0.98	0.28	0.21**	+C:N**
<i>Trillium undulatum</i>	(31)	1.46	-0.60	3.95**	0.88	1.29	0.18	0.26*	+C:N**
<i>Brachyelytrum erectum</i>	(38)	2.23*	0.59	-4.53**	1.63†	1.78†	-0.70	0.21**	-C:N**
<i>Carex debilis</i>	(46)	1.22	0.69	-5.30**	-1.22	0.85	-0.84	0.32**	-C:N**
<i>Carex swanii</i>	(22)	-1.58	0.58	-3.13**	0.35	-1.09	-0.10	0.16**	-C:N**
<i>Polygonatum pubescens</i>	(38)	-2.81**	-2.43**	-3.26**	-1.92*	-0.97	-0.03	0.22**	-C:N**
<i>Maianthemum racemosum</i>	(39)	-1.29	-0.03	-4.89**	-0.97	0.62	-0.58	0.28**	-C:N**
<i>Solidago rugosa</i>	(23)	-1.12	1.78†	-2.88**	-0.03	-2.10*	-0.03	0.28**	-C:N**
<i>Uvularia sessilifolia</i>	(107)	1.15	-1.25	-2.32*	-1.88†	1.22	-0.71	0.06*	-C:N**
<i>Lycopodium clavatum</i>	(40)	-2.34*	-1.04	1.52	-3.68**	-1.05	-0.75	0.14**	-Land Use**
<i>Lycopodium complanatum</i>	(58)	-0.78	1.72†	1.18	-1.74†	-1.56	-0.21	0.06*	-Land Use**
<i>Maianthemum canadense</i>	(149)	-2.11*	0.18	-0.99	-2.87**	1.17	0.24	0.23**	-Land Use**
<i>Huperzia lucidula</i>	(21)	0.90	-0.74	-0.63	0.76	-1.90†	-0.03	0.08	-Hurricane†
<i>Arisaema triphyllum</i>	(15)	2.45**	1.47	-2.14*	1.30	1.80†	-0.03	0.22**	+lnSumB**
<i>Onoclea sensibilis</i>	(25)	3.40**	0.38	-3.61**	-0.69	0.34	-0.03	0.28**	+lnSumB**
<i>Monotropa uniflora</i>	(67)	-1.17	1.50	2.51**	0.84	-0.51	-0.01	0.04	-lnSumB**
<i>Aster</i> spp.	(17)	0.84	0.49	0.77	-1.04	0.64	1.38	0.04	+lnCa**
<i>Aster acuminatus</i>	(75)	1.46	0.19	-3.10**	1.10	0.73	0.52	0.06*	+lnBSAT**
<i>Aster divaricatus</i>	(33)	0.13	0.78	-2.50**	1.71†	0.78	0.66	0.06	-Sand**
<i>Athyrium filix-femina</i>	(24)	2.24*	-0.37	-4.12**	-1.38	0.62	-0.03	0.31**	+lnN**
<i>Dryopteris carthusiana</i>	(68)	2.22*	1.88†	-3.85**	0.11	3.76**	-2.08*	0.20**	+lnN**
<i>Cypripedium acaule</i>	(38)	-1.21	-0.56	2.84**	-2.61**	0.63	0.74	0.10**	-lnN**
<i>Pteridium aquilinum</i>	(97)	-1.09	-2.01*	1.51	-2.34*	-0.72	0.88	0.06*	-lnN**
<i>Monotropa hypopithys</i>	(20)	-2.03*	1.70†	1.18	-1.78†	-0.01	1.76†	0.18**	-lnCEC**
<i>Trientalis borealis</i>	(155)	0.65	-0.08	-0.52	-0.67	-0.01	0.03	0.04	-lnOM*
<b>Bryophytes</b>									
<i>Aulacomnium palustre</i>	(10)	3.19**	1.89†	0.42	-0.31	1.09	0.69	0.31**	+Drainage**
<i>Dicranum scoparium</i>	(43)	2.26*	0.38	0.44	0.67	-2.00*	-1.36	0.13**	+Drainage**
<i>Herzogiella striatella</i>	(15)	3.56**	0.97	0.63	0.23	-1.29	0.49	0.25**	+Drainage**
<i>Odontoschisma denudatum</i> <sup>2</sup>	(25)	2.12*	-1.66†	0.23	-0.01	-2.27*	0.45	0.15**	+Drainage*
<i>Sphagnum capillifolium</i>	(10)	3.00**	1.90†	-0.17	1.16	-0.08	1.04	0.29**	+Drainage**
<i>Sphagnum</i> sect. <i>Sphagnum</i>	(11)	3.46**	2.00†	0.17	1.24	0.13	1.14	0.41**	+Drainage**
<i>Thuidium delicatulum</i>	(27)	3.95**	0.87	-2.11*	0.86	0.44	-0.02	0.29**	+Drainage**
<i>Dicranella heteromalla</i>	(49)	-2.62**	1.00	-1.41	1.30	0.84	-1.19	0.10*	-Drainage**
<i>Schistidium apocarpum</i> <sup>3</sup>	(10)	-1.83†	-0.28	-1.21	0.30	-0.94	0.44	0.12	-Drainage†
<i>Pohlia nutans</i>	(16)	-1.96*	1.33	0.21	0.94	-0.14	1.25	0.10	-Drainage*
<i>Ptilidium</i> spp. <sup>2</sup>	(52)	-2.91**	1.34	1.52	-1.21	-2.16*	1.84†	0.17**	-Drainage**
<i>Dicranum fulvum</i> <sup>3</sup>	(70)	1.70†	-2.34*	-1.32	1.08	-0.59	0.69	0.14*	-pH**
<i>Bazzania trilobata</i>	(22)	1.45	1.10	2.25*	2.46**	-0.98	-0.17	0.37**	+C:N**
<i>Lepidozia reptans</i>	(17)	0.55	0.93	1.93*	2.69**	-1.41	-0.02	0.61**	+C:N**
<i>Polytrichum commune</i>	(59)	0.74	1.88†	2.40*	0.18	-1.16	-1.32	0.10*	+C:N†
<i>Tetraphis pellucida</i> <sup>2</sup>	(72)	2.50**	0.95	3.11**	1.11	2.79**	-2.91**	0.32**	+C:N**
<i>Callicladium haldanianum</i> <sup>2</sup>	(83)	0.90	0.00	-1.82†	-1.30	-1.59	0.13	0.25**	-C:N**
<i>Nowellia curvifolia</i> <sup>2</sup>	(31)	0.64	-1.74†	-1.89†	-0.13	0.89	-1.28	0.07	-C:N ns
<i>Brotherella recurvans</i>	(47)	2.32*	-0.29	0.94	1.99*	-1.23	-1.12	0.17**	+Land Use**
<i>Calypogeia fissa</i>	(31)	1.77†	1.22	0.50	2.77**	0.35	-1.02	0.20**	+Land Use**
<i>Leucobryum glaucum</i>	(59)	3.47**	2.70**	1.84†	3.45**	-0.89	-1.38	0.46**	+Land Use**
<i>Ulota crispa</i> <sup>1</sup>	(48)	-1.21	-0.24	-1.35	-2.38*	-2.34*	0.27	0.17**	-Land Use**
<i>Atrichum angustatum</i>	(20)	-1.26	1.30	-0.52	0.70	1.83	-1.01	0.09	+Hurricane†
<i>Cephaloziella</i> spp.	(14)	0.83	1.15	0.91	0.73	0.38	-0.12	0.04	sand ns
<i>Lophocolia</i> spp.	(65)	0.83	-0.30	0.91	-2.07*	1.41	0.02	0.12*	+Sand*
<i>Dicranum flagellare</i> <sup>2</sup>	(81)	1.59	1.79†	2.65**	0.99	2.08*	-1.94*	0.25**	-lnN**
<i>Diphyscium foliosum</i>	(19)	-0.63	-0.73	-1.10	1.83†	1.27	-0.72	0.09	-lnBD*
<i>Pallavicinia lyellii</i>	(11)	2.90**	2.35*	0.65	0.78	1.48	-0.02	0.35**	-lnBD**
<i>Frullania</i> spp. <sup>1</sup>	(53)	-0.49	0.98	0.34	-1.18	-1.99*	1.34	0.08	+lnBSAT**
<i>Platygyrium repens</i> <sup>1,2</sup>	(76)	0.19	-1.02	-0.91	-1.96*	-2.11*	0.72	0.15*	+lnBSAT
<i>Plagiothecium laetum</i>	(68)	0.80	0.03	1.00	0.40	-1.08	-1.15	0.06	+lnCEC†
<i>Steerecleus serrulatus</i>	(20)	-1.67†	1.58	1.36	-0.73	-1.70†	-0.58	0.12†	-lnOM*

†  $P < 0.1$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; all others  $P > 0.1$ ; <sup>1</sup> generally epiphytic; <sup>2</sup> lignicolous, often on rotting wood; <sup>3</sup> saxicolous; all other bryophytes occur frequently on soil.

**Table 3.** Analysis of species richness for bryophytes (BS), herbs (HS), shrubs (SS), understory trees (US), trees >2.5 cm DBH (TS), and all vascular species (VS).

A. Spearman's rank correlation <sup>1</sup> of species richness among life forms						
	BS	HS	SS	US	TS	Median
BS	1					17 <sup>2</sup>
HS	0.446**	1				14
SS	0.307**	0.378**	1			10
US	0.018 <sup>ns</sup>	0.350**	0.249**	1		8
TS	0.109 <sup>ns</sup>	0.252**	0.192**	0.227**	1	8
VS	0.406**					33

B. Spearman's correlations <sup>1</sup> with drainage class, C:N, and 1938 hurricane damage			
	Drainage	C:N	Hurricane
BS	0.434**	0.047 <sup>ns</sup>	-0.190*
HS	0.192**	-0.385**	-0.071 <sup>ns</sup>
SS	0.169**	0.103 <sup>ns</sup>	-0.102 <sup>ns</sup>
US	-0.259**	-0.288**	0.057 <sup>ns</sup>
TS	-0.194**	-0.030 <sup>ns</sup>	0.177*
VS	0.204**	-0.186*	-0.007 <sup>ns</sup>

C. Median species richness by land use <sup>3</sup>					
	Historical land use				Kruskal-Wallis
	tilled	impr. pasture/ mowing	unimpr. pasture	woodlot	
BS	16.0	15.0	18.0	18.0	5.67 <sup>ns</sup>
HS	14.5	12.0	14.0	11.5	24.72**
SS	11.0	9.5	10.5	8.0	7.01 <sup>†</sup>
US	9.0	9.0	8.0	5.0	72.33**
TS	8.0	7.5	8.0	7.0	8.96*
VS	37.0	33.0	35.0	28.0	30.30**

<sup>ns</sup>  $P > 0.1$ ; <sup>†</sup>  $P < 0.1$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ .

<sup>1</sup>Correlations are based on the smaller sample size of the two variables involved where  $N = 230$  for HS, SS, US, TS, and VS,  $N = 104$  for BS;  $N = 174$  for C:N, and  $N = 95$  for BS  $\times$  C:N.

<sup>2</sup>Bryophyte plots were one quarter of the vascular plant plots.

<sup>3</sup>Sample sizes for vascular plants:  $N = 20, 30, 130,$  and  $50,$  for the four historical land uses categories tabulated with vascular plants, and  $N = 13, 11, 55,$  and  $25$  when tabulated with bryophytes.

Of the major tree species, only white pine was reduced over the 55-year period, declining from an average of 10.14 to 4.35 m<sup>2</sup>/ha. Correlation of the amount of change from 1937 to 1992 with environmental and historical disturbance variables (Table 5) indicates that large increases in total basal area were associated with low hurricane damage, increases in red maple were greater when C:N ratio was low, and white pine decreased with increasing hurricane damage. Red oak increased on dry sites that had been heavily used during the agricultural era, whereas hemlock increased on historical woodlots. Overall dissimilarity in species composition (Bray-Curtis distance) between 1937 and 1992 increased with greater amounts of hurricane damage. All of these relationships are relatively weak trends, however, and allow for the possibility that other factors and processes may have been more important. Correlations of dissimilarity matrices indicate that land use was less strongly associated with 1937 overstory composition ( $r_{\text{matrix}} = 0.172$ ) than it was with 1992 overstory composition ( $r_{\text{matrix}} = 0.369$ ).

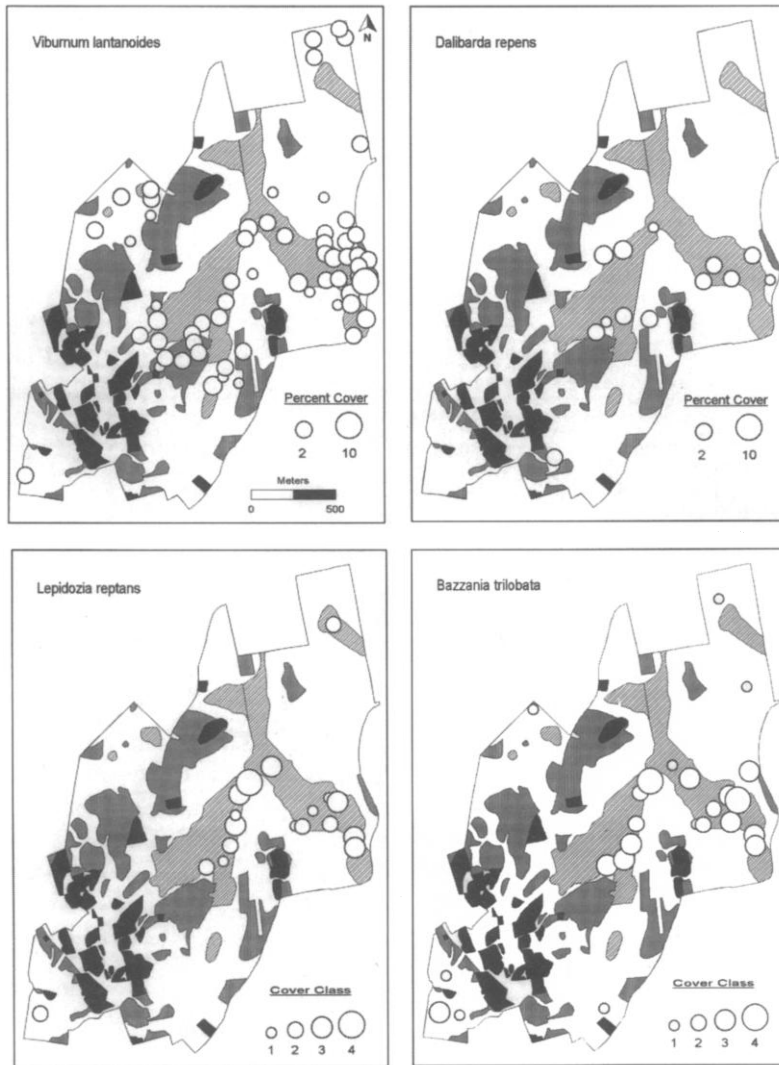
## Discussion

Our study site in central New England is representative of the heterogeneous landscape and forest history of much of the northeastern United States, differing primarily in the unusually detailed information on edaphic conditions and on human and natural disturbances. Results from our analyses suggest that in such landscapes, forest composition reflects complex interactions between species autecology, site conditions, and historical factors, and that some historical factors exert a long-lasting effect. We will first discuss the nature of modern plant assemblages on such sites. Then, we consider factors that influence species distributions and community patterns, and interpret the result that historical land use has more of an effect on current vegetation than it did in 1937. Finally, we will comment on the types of

**Table 4.** Correlations between dissimilarity matrices. These correlations quantify the degree to which pairwise dissimilarities between a set of 104 plots were the same for two life forms (top half-diagonal panel) or a life form and an environmental or disturbance variable (lower panel).

	Bryophytes	Herbs	Shrubs	Understory Trees	Trees >2.54 cm DBH
Herbs	0.50**				
Shrubs	0.35**	0.52**			
Understory trees	0.32**	0.43**	0.43**		
Trees > 2.54 cm DBH	0.32**	0.39**	0.38**	0.39**	
15 edaphic variables	0.01	0.07 <sup>†</sup>	0.01	0.05	0.01
Soil drainage	0.24**	0.19**	0.09**	0.05	0.10**
C:N ratio	0.08 <sup>†</sup>	0.16**	0.12*	0.19**	0.14**
Land use history	0.12**	0.14**	0.07*	0.19**	0.22**
Hurricane damage	-0.05	-0.03	-0.01	-0.06	0.05

<sup>†</sup>  $P < 0.1$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; all others  $P > 0.1$ .



**Fig. 4.** Distribution and abundance of species characteristic of continuously forested sites on the Prospect Hill Tract of Harvard Forest. Relative abundance is indicated by the size of the open circles. Historical land use is indicated as in Fig. 2.

relationships that standard community ecological studies are capable of detecting, and discuss some limitations that must be recognized in interpreting modern forest composition in complex landscapes.

#### *The community on Prospect Hill*

Several of our analyses indicate that plant assemblages are loosely organized, with species responding rather individually to complex historical and environmental factors (Gleason 1917; Whittaker 1967; Bratton 1975; del Moral & Watson 1978; Lee & LaRoi 1979; McCune & Antos 1981; Bradfield & Scagel 1984; Palmer 1986; Vitt & Chee 1990; see also Callaway 1997 for critique of the individualistic-continuum concept). For instance, in cluster analysis and ordination, relatively few species are restricted to one vegetation type and there is considerable overlap among types in species occurrence

and abundance, suggesting that the communities vary hyperdimensionally, with species responding to a wide range of gradients. In addition, although matrix correlations document significant relationships in compositional variation among all life forms, the strength of these relationships varies substantially between life forms. Bryophytes and herbs, and herbs and shrubs are most strongly correlated, whereas trees are less strongly correlated with other life forms. This suggests that overstory composition does not exert strong control over the composition of other strata, despite the observation that some tree species appear to strongly influence the distribution of individual species. For instance, several species (e.g., *Dalibarda repens* and the liverwort *Lepidozia reptans*) are largely restricted to hemlock stands in our study area, and a few epiphytic bryophytes are moderately-to-strongly host-specific (e.g. *Thelia hirtella* on *Quercus alba*). Comparisons of species richness among life forms indicate

**Table 5.** Correlations between environmental-historical factors and amount of increase in basal area of trees from 1937-1992 (sample sizes shown in parentheses).  $\Delta$  Total basal area combines all trees greater than 2" DBH. Bray-Curtis distances representing changes in species composition were calculated on proportions of the basal area in a plot at the time of sampling.

	Soil drainage	Soil pH	C:N ratio	Historical land use	1938 hurricane	1957 fire damage
$\Delta$ Total basal area	0.10 (161)	-0.05 (131)	-0.02 (129)	0.11 (161)	-0.44** (161)	0.16* (161)
$\Delta$ <i>Acer rubrum</i>	0.06 (161)	-0.04 (131)	-0.31** (129)	-0.16† (161)	0.00 (161)	0.05 (161)
$\Delta$ <i>Pinus strobus</i>	0.15† (142)	0.04 (119)	-0.04 (117)	0.08 (142)	-0.47** (142)	0.12 (142)
$\Delta$ <i>Quercus rubra</i>	-0.26** (148)	0.09 (126)	-0.15 (124)	-0.21 (148)	-0.03 (148)	-0.09 (148)
$\Delta$ <i>Tsuga canadensis</i>	0.10 (97)	-0.28* (75)	0.45** (75)	0.47** (97)	-0.17† (97)	0.14 (97)
Bray-Curtis distance from proportions	-0.13 (161)	0.00 (131)	-0.06 (129)	-0.09 (161)	0.34** (161)	-0.17* (161)

† $P < 0.1$ ; \* $P < 0.05$ ; \*\* $P < 0.01$ ; all others  $P > 0.1$ .

similar results. Although species richness is positively correlated among all life forms, the strength of the correlations is strongest among bryophytes and herbs, and herbs and shrubs, and weakest among trees and all other life forms. Thus, correlation analyses of both life form composition and species richness suggest that communities are not tightly organized, the overstory does not exert strong control over the composition of other strata, and considerable variation results from individualistic patterns of species distribution in relationship to the environment and history.

#### Factors that explain variation in the vegetation

Ordination and logistic regression indicate that although species assemblages and individual species vary in the ways they are influenced by historical and environmental factors, soil drainage, land use history, and C:N ratio emerge as dominant gradients. Soil drainage generally influences vegetation (Curtis 1959; Peet & Christensen 1980; Pregitzer & Barnes 1982; Whitney 1991), and in our area, soils varied from very poorly drained organic soils in wetlands to somewhat excessively drained sandy loams in the uplands. Drainage appears to have a particularly strong influence on bryophyte composition and richness, whereas many tree species occur across a range of drainage classes.

Modern vegetation patterns strongly parallel historical land use, with the Hemlock Type largely restricted to continuously forested sites, the Red Maple Type primarily on former unimproved pastures or woodlots, the Oak-Maple Type on prior pastures and some cultivated fields, and the Pine-Oak and Plantation Types on former

pastures and plowed fields but generally not in woodlots. Some species are also clearly influenced by historical land use: *Pinus strobus*, *Lycopodium clavatum*, and *Maianthemum canadense* occur more frequently or with greater abundance on former agricultural fields than in continuously forested areas, whereas *Tsuga canadensis*, *Hamamelis virginiana*, *Calypogeia fissa*, and *Brotherella recurvans* are more frequent or abundant on continuously forested sites (Table 2). A few species are very infrequent or absent from the most intensively cultivated sites, although they occur on less-intensively used agricultural sites as well as in continuously forested areas (e.g. *Gaultheria procumbens*, *Medeola virginiana*, and others; R. Kern pers. comm.). Other studies have similarly identified species that are largely restricted to continuously forested sites and are very slow to recolonize after agricultural abandonment (Peterken & Game 1981, 1984; Whitney & Foster 1988; Glitzenstein et al. 1990; Brunet 1993; Hermy et al. 1993; Hermy 1994; Motzkin et al. 1996, 1999; Cooper-Ellis 1998). Several mechanisms may contribute to this pattern. For some species, restricted occurrence may result from dispersal, establishment, or other biological limitations to colonization of former agricultural lands (Peterken & Game 1984; Whitney & Foster 1988; Dzwonko & Loster 1990; Matlack 1994; Motzkin et al. 1996; Donohue et al. in press). In addition, the abundance of hemlock – a species that casts deep shade and deposits deep, acidic litter – in continuously forested sites and its absence from former agricultural sites, creates a distinctive understory microenvironment that apparently limits many species but is favorable to a few such as the bryophyte *Lepidozia reptans*.

Studies of the influence of land use on species richness have differed in their results. Whereas some have found that primary woodlands or old secondary woodlands adjacent to primary woodlands are species-rich relative to more recent and isolated secondary stands (Peterken & Game 1984; Hermy 1994; Matlack 1994), others have reported no effect or have found that more recently or intensely disturbed sites may actually support greater species richness (Motzkin et al. 1996; Koerner et al. 1997). In the current study, bryophyte species richness is similar among historical land uses but fewer vascular species occur in continuously forested stands, perhaps as a result of the inability of many species to tolerate low light and perhaps other resource limitations in dense hemlock stands. Thus, historical land use can have both direct and indirect (i.e. overstory-mediated) effects on species richness and composition.

Species assemblages and numerous individual species distribution patterns also varied with respect to C:N ratios, which are highest in continuously forested hemlock stands and lower in vegetation types on former agricultural sites. Because C:N ratios are negatively correlated with nitrogen concentrations but are not correlated with carbon, organic matter, or drainage (Table 1), we interpret variation in C:N ratios as representing primarily a nitrogen gradient. Support for this interpretation is found in the observation that several species (e.g. *Acer saccharum*, *Fraxinus americana*) that are negatively correlated with C:N ratios (i.e. most abundant on sites with low C:N ratios) are characteristic of rich sites (Whitney 1991). Moreover, for some species that are negatively correlated with C:N ratio, nitrogen levels are the single best predictors of their occurrence (e.g. *Athyrium filix-femina*; Table 2). C:N ratios are correlated negatively with calcium and pH, suggesting that the fertility gradient may result from a combination of nutrient levels and nutrient availability, which is strongly influenced by pH (Montes & Christensen 1979; Robertson 1982). In general, however, ionic gradients were not found to exert strong influence on distributions of many species within our study area, perhaps because soils developed from fairly uniform, acidic parent materials of well-mixed glacial till. These results differ from other studies (e.g. Peet & Christensen 1980; Balter & Loeb 1983; Cowell 1993) that were based on data from a broader range of parent materials and site conditions.

It is instructive to consider variables that were not closely associated with modern vegetation patterns. Despite dramatic effects on overstory composition and structure, in both our ordination analyses and in most logistic regression models of individual species occurrence, 1938 hurricane damage did not emerge as a primary factor influencing modern species distributions or vegetation patterns. Several factors may contribute to

these results: (1) understory patterns may be relatively independent of overstory composition and structure; (2) sufficient time may have passed since the hurricane to obscure initial effects (although see Jonsson & Esseen 1990); (3) hurricane damage may have been sufficiently widespread and varied that our stand-level data are inadequate to detect effects on the understory flora; (4) logging activity, which was widespread after the hurricane in both damaged and undamaged stands, may have obscured hurricane effects. We suspect that part of our inability to detect significant hurricane effects may be a common problem in ecological sampling: we are able to measure current environmental conditions and vegetation patterns, but we are not able to evaluate what the landscape would have been if the disturbance had not occurred. Thus, effects of widespread disturbances such as wind, logging, or pathogens, though important, may go undetected in correlative studies.

#### *Change since 1937*

Our results indicating that historical land use predicted overstory composition better in 1992 than in 1937 are counter-intuitive. We had expected that over time and with subsequent disturbances, this relationship would weaken. Two factors may contribute to these surprising results: (1) soon after agricultural abandonment, early successional tree species were widespread, and compositional differences between land use types were apparently less pronounced; and (2) historical woodlots became more distinct from post-agricultural sites in the 20th century as their hemlock-dominance increased as a result of the decline of chestnut and forest management activities that removed hardwoods and promoted hemlock (Harvard Forest Archives, unpubl. data; Foster et al. 1992). These results emphasize the observation that with long-lived species, historical land use activities may influence vegetation patterns for many decades or centuries after the disturbances have ceased, and even after additional major natural disturbances.

#### *Importance of history and modern environmental conditions*

We intentionally investigated a study area that is heterogeneous with respect to initial site conditions and that has a complex history of anthropogenic and natural disturbances, in part because such variability is characteristic of much of the eastern United States (Whitney 1994). Based on an evaluation of species assemblages, individual species distributions, and relationships among life forms, we determined that soil drainage, land use history, and C:N ratios are important gradients that influence the vegetation, and that although these variables



are partially correlated, they apparently also exert independent effects on vegetation patterns. In addition, we demonstrated that species distribution patterns are related to a wide range of environmental and historical factors, indicating highly individualistic responses to complex physical and historical factors. Some factors (e.g. 1938 hurricane damage) that we thought might be important are not correlated with the distributions of many species. Thus, while our results do not indicate a simple conclusion concerning the relative importance of environment versus history in determining modern vegetation patterns, they do document the influence of both environment and history.

It is significant that patterns of species assemblages and some individual species distributions continue to be influenced by historical land use activity. This is despite a century or more since abandonment of most agricultural sites, and intervening disturbances such as the 1938 hurricane, fire, pathogens, and 20th century forest management practices that could have obscured the effects of earlier land use practices. We conclude that modern assemblages and species distribution patterns are only partly the result of contemporary environmental conditions, and that for some species, modern distributions may be controlled more by historical factors than by variation in current resource conditions (Donohue et al. in press).

Our results have important implications for the use of standard community ecological data and multivariate analyses to interpret modern community composition and dynamics. Studies throughout the northeastern United States have documented the dramatic landscape transformations that have occurred historically as a result of changing land use practices and other disturbances (Kittredge 1913; Rowlands 1939; Foster & Boose 1992; Foster 1992; Foster et al. 1992, 1998; Fuller et al. 1998). At a stand-level, it is increasingly apparent that an understanding of such disturbances is critical to the interpretation of modern composition and structure (e.g. Foster et al. 1992), and we anticipated documenting similar historical effects in this study. However, despite the availability of detailed data on historical disturbances, our analyses suggest that historical land use and other disturbances only influence the modern distributions of some species. We do not interpret these results as indicating that history is only locally important in controlling modern vegetation. Rather, we suggest that historical disturbances have been sufficiently pervasive, varied, and complex as to preclude, in many instances, simple quantification. Despite our rigorous field and historical reconstructions, many of the details of historical land use will never be known (i.e. crops grown on particular fields, amendments applied, season and duration of cultivation, etc.; Foster 1992). In fact, we suspect

that the distribution and abundance of every species on the modern landscape has been significantly altered by historical disturbances. Our limited ability in complex landscapes to verify such influences results in part from the complexity of the disturbances and also from the limitations of quantitative analyses that enable us to measure current environmental conditions and vegetation patterns, but do not allow us to adequately evaluate what the landscape would have been if historical disturbances had not occurred. Thus, effects of widespread and complex disturbances such as hurricanes, fires, pathogens, and historical land use may go undetected, despite their strong and persistent influence on the landscape.

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