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PHYSIOGRAPHIC AND HISTORICAL INFLUENCES ON FOREST COMPOSITION IN CENTRAL NEW ENGLAND, U.S.A.

A Thesis Presented by

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To

The Graduate School of Arts and Sciences
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ABSTRACT

Forest composition and species distributions are largely controlled by a combination of deterministic and non-deterministic factors. Forest vegetation was examined to compare the relative influences of physiography and natural and human disturbances. The modern landscape of central New England is largely vegetated by a mosaic of continually forested and reforested woodlands. This unfragmented landscape belies an intensive and complex land-use history during the past 270 years.

In 70 randomly selected 0.04-ha forest plots, vegetation, physiography, and history were described. Abundance of all vascular species was recorded as the number and diameter for trees and percent cover and number for understory vegetation. Physiographic and historical variables described geographical location, physiography, soils, natural disturbances, forest management, and land-use history.

Multivariate analysis indicated that community composition reflects two pronounced gradients: a complex gradient of drainage, geomorphology, and landscape position and a gradient defined by intensity of land-use disturbance and age of secondary woodlands. Mean species richness shows significant relationships to geomorphology, landscape position, and drainage. Overstory type, identified by the dominant canopy species, is related to landscape position, past land use, and intensity of disturbance.

Distributions of 73 common species are associated with (ranked in order of importance) geomorphology, drainage, past land use, and landscape position. Logistic regression models identify landscape position, drainage, and land-use history as the best predictors of species distribution.

Although distributions of few species are strictly limited by land-use history, many species are restricted to specific habitats defined by physiographic conditions. The majority of these species are

associated with poorly-drained depositional basins and stream valleys; other species are associated with well-drained bedrock ridges. All analyses indicate that land-use history is more important for trees than for understory species. Distributions of most shrubs and ferns are not related to land-use history; instead, they are distributed along the physiographic gradient.

These analyses suggest the following ranking of influences on forest composition: PHYSIOGRAPHY > LAND-USE HISTORY > NATURAL DISTURBANCE = FOREST MANAGEMENT. The primary control on patterns of forest composition remains the physical environment defined by geomorphology and drainage. Although intensive land use and forest fragmentation diminished during the past 50-150 years, land-use history remains an important influence on forest composition. In contrast, more recent disturbances (windthrow, fire, and forestry) show little impact on forest composition. These results suggest that the effects of disturbances persist on different temporal scales: disturbances which completely remove forest cover persist longer than those which disturb but do not eliminate forest cover.

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PREFACE

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Different aspects of this study were greatly improved by discussions with certain individuals. Development of the appropriate study design and sampling techniques was made in collaboration with David Foster, Steve Hamburg, Cathy Mabry, and Gordon Whitney. Gary Carlton, Rich Lent, Cathy Mabry, and Gordon Whitney provided essential advice on statistics; and Emery Boose provided often timely help with computer hardware and software.

Rich Boone, Steve Hamburg, Kasey Keith, and Kathy Newkirk greatly improved my understanding of soils and soil processes; and together we developed the field key to land-use history based on soil characteristics. Information on the life history traits of individual species was provided by Cathy Mabry. My understanding of vegetation and land-use history was also greatly enhanced by discussions and field excursions with George Peterken both here and in Great Britain.

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I would also like to thank the many public and private landowners who allowed me to conduct field research on their property.

Dedication

This thesis and the effort that went into it are, in reality, the products of the thoughts and actions of the many people who have inspired and guided me through my life. None of this would be possible without my parents, Alvin and Sally Gerhardt, or the rest of my immediate family, Beth, Tom, and Anna Gerhardt.

Cathy Mabry was with me from the first trip to Pisgah through the final stages of writing and editing this thesis.

Many others have guided me through the journey of life and of learning (perhaps they are one and the same). I would include here not only my teachers, in both the formal and informal sense, but also the many close friends who have taught me through our life journeys and our intimate conversations. These people include, but are not limited to, Bill and Ruth Brooks, Bill Butler, Jack and Martha Carter, Kris Crossen, Vern Durkee, Ron Garrett, Ben Graham, and Jerry Tande.

And, of course, there is one final inspiration of great importance: that is the earth itself, which daily provides inspiration and insight (if only I would listen and learn). This thesis is dedicated to these people and the earth itself: MAY THE FOREST (OR PRAIRIE OR TUNDRA OR ...) BE WITH YOU.

"You have read and learned alot
and that's what college - and life - are all about."
Gary Ebersole

LITTLE GUY HAIKU
A rock underfoot
Suddenly it darts away
My little friend cat

INTRODUCTION

Vegetation composition reflects both the physical environment and natural and human disturbances. In fact, species distributions and overall plant composition integrate many ecological factors, and "no single factor account[s] for a large proportion of the variation in species' distribution" (Muller 1982). Past ecological research has focused on many of the important physiographic and historical processes controlling vegetation distribution and abundance. However, the relative importance of physiographic and historical factors varies considerably on both temporal and spatial scales, and it is of enormous interest to understand why physiography dominates in some situations and history in others.

Vegetation studies historically emphasized deterministic controls which explained vegetation patterns in terms of geology, physiography, soils, and climate (Whitney 1991). Gleason (1926) concluded that vegetation composition was determined by plant migration as mediated by fluctuating environmental conditions. Forest composition has been related to geomorphology, substrate, and topographic position (Spurr 1956; Hack and Goodlett 1960; Whitney 1991; Host and Pregitzer 1992). Hack and Goodlett (1960) suggested that tree and understory distribution were explained largely by geomorphological landforms and topographic position and that the principal mechanisms were nutrient and water availability.

Vegetation composition also varies in relation to soil morphology and chemistry. Soil drainage, which is primarily controlled by geomorphology and substrate, influences plant distribution. In central New England, xerophytic trees occur on sites underlain by permeable tills, and the distribution of most other trees depends on the depth to perched water tables on compacted tills (Stout 1952; Spurr 1956; Lyford et al. 1963; Walker 1975). Tree distribution and abundance has also been related to soil depth, pH, calcium, and magnesium (Walker 1975;

Farrell and Ware 1991).

Many studies have noted that the influence of physiography and soils is complicated by or less important than disturbance and successional history (Lyford et al. 1963; Walker 1975; Whitney 1991). Extreme historical events have major impacts on plant populations and consequently community composition (Austin and Williams 1988). Long-term changes in vegetation patterns are caused by climatic and tectonic processes and are examined by the disciplines of biogeography and paleoecology (Davis 1983; Jacobsen et al. 1987). Non-deterministic influences on vegetation patterns include both natural and human disturbances and result in more immediate and often dramatic changes in vegetation structure and composition.

Natural disturbances - which in New England include fire, windthrow, insects, and pathogens - can cause catastrophic changes in vegetation patterns. Both fire and windthrow have significant impacts on the age structure, size, density, and crown height of forest patches (Tande 1979; Foster and King 1986; Foster 1988; Foster and Boose 1992). In fact, many natural communities (grasslands, savannas, *Betula papyrifera* forests, and lichen woodlands) are maintained in a "dynamic equilibrium" by recurrent natural disturbances (Foster 1983; Foster and King 1986; Sprugel 1991).

Forest management and land-use history represent an anthropogenic counterpart to natural disturbance. Logging and overstory removal have varying impacts on forest composition. In northern New England, logging results in intense but short-lived changes in understory distribution and abundance, and the invasion of ruderal species immediately following overstory removal has little effect on the pre-existing species (Muller 1982; Hughes and Fahey 1991). In contrast, 45-87 year-old logged forests in the more diverse southern Appalachians do not recover the herbaceous cover or richness characteristic of undisturbed, old-growth forests (Duffy and Meier 1992).

Land-use has an important, if not overwhelming, influence on vegetation patterns and ecosystem processes (Raup and Carlson 1941; Peterken and Game 1984; Fuentes et al. 1989). The composition of forests remaining in the agricultural landscape largely resembles that of contiguous forests in undisturbed landscapes (Middleton and Merriam 1983). In fragmented landscapes, reforested agricultural lands remain depauperate of woodland species found in continually forested sites (Peterken and Game 1984; Dzwonko and Loster 1990). Intensive land use favors easily dispersed shade-intolerant species over more mesic shade-tolerant species (White et al. 1990).

Land-use legacies persist after cessation of intensive human activities, and recently reforested landscapes continue to show the impacts of land-use history (Spurr 1956; Foster 1992). In young secondary forests, stand age, land-use history, and disturbance history are the prevailing influences on both overstory structure and understory composition (Whitney and Foster 1988; Foster 1992; Mabry and Korsgren 1993). Ecosystem and soil processes also reflect the long-term influence of land-use history, and altered soil organic matter and nutrient pools persist long after agricultural abandonment (Daniels et al. 1983; Hamburg 1984).

Patterns of forest composition are complicated further by interactions between physiographic and historical factors. In particular, vegetation-site relationships are complicated by disturbance history (Lyford et al. 1963; Whitney 1991). Along environmental gradients, species are competitively superior within a limited range of site conditions (Drury and Nisbet 1973). Christensen and Peet (1984) concluded that species-site relations increase in importance during succession, because competition results in decreasing niche breadth and increasing site fidelity. Vegetative strata also respond differently to physiographic and historical factors: trees respond more directly to disturbances, but understory species are better indicators of physical site conditions (Whitney 1991).

Natural disturbance frequency and intensity often vary in relation to local physiography and vegetation structure (Tande 1979; Foster 1985; Foster and King 1986; Foster and Boose 1992); and land-use patterns are largely defined by physiographic and soil factors (Iverson 1988; White et al. 1990). Previous studies of forest composition have examined interactions among physiography and land use (Hermy and Stieperaere 1981; Peterken and Game 1984; Glitzenstein et al. 1990; White et al. 1990); physiography, land use, and windthrow (Spurr 1956; Foster and Boose 1992); physiography and logging history (Muller 1982); and physiography, soils, and disturbance (Lyford et al. 1963; Walker 1975).

Vegetation studies that integrate both physiography and history are important in order to understand the ecology of vegetation in both 'natural' and anthropogenic landscapes. Central New England was fragmented historically by intensive land uses but has become almost completely reforested during the past 50-150 years to form a mosaic of continually forested and reforested lands. Following reforestation, the structure and composition of these forests were altered by logging of old-field *Pinus strobus*; the loss of *Castanea dentata*, a major forest component, to an imported pathogen; and the catastrophic devastation wrought by the Great Hurricane of 1938 (Raup and Carlson 1941; Spurr 1956; Foster and Boose 1992; Foster 1992).

This study examines the relative importance of physiographic and historical factors to forest composition in central New England, U.S.A. Three questions are addressed: 1) What are the patterns of species distribution and abundance and overall forest composition? 2) What are the important physiographic and historical factors influencing forest composition? 3) How do individual species and overall forest composition reflect the important physiographic and historical factors? Important factors considered include physiography, soils, natural disturbance, forest management, and land-use history.

It is important to note that this study does not determine causality, but rather identifies relationships among vegetation, physiography, and history. These relationships suggest mechanisms controlling forest composition and are intrepreted in terms of their ecological implications.

SITE DESCRIPTION

This study examines the ecological effects of physiography and history at the landscape level in forests not recently disturbed by intensive land-use or other human activities. The study area was defined as the town of Petersham, which covers 9844 hectares in northwestern Worcester County, Massachusetts, U.S.A. (Figure 1).

Physical Description

Petersham lies in the central upland physiographic province of southern New England (Taylor and Hotz 1985). Elevation ranges from 160 m at Quabbin Reservoir in western Petersham to 400 m on Prospect Hill in northern Petersham, but local topographic relief generally varies less than 60 m. The bedrock underlying Petersham consists mostly of highly metamorphosed schists and gneiss and intrusive granodiorites and tonalite (Harvard Forest Archives Map P2.8). The bedrock was eroded extensively during Pleistocene glaciation, and subsequent glacial melting left a mantle of glacial till on upland ridges and glaciofluvial deposits along major lowland drainages (Eschman 1966).

These glacial tills and outwash developed into stony, moderately to strongly acidic Inceptisols and Spodosols, classified as coarse-textured loams, sandy loams, and loamy sands. Low-lying basins and poorly-drained depressions are filled by deep, extremely acidic Histosols overlying glaciofluvial and lacustrine deposits. Depth to bedrock is variable but consistently shallow (0-10 m), and soils are locally underlain by a dense, impermeable hardpan extending 50-150 cm in

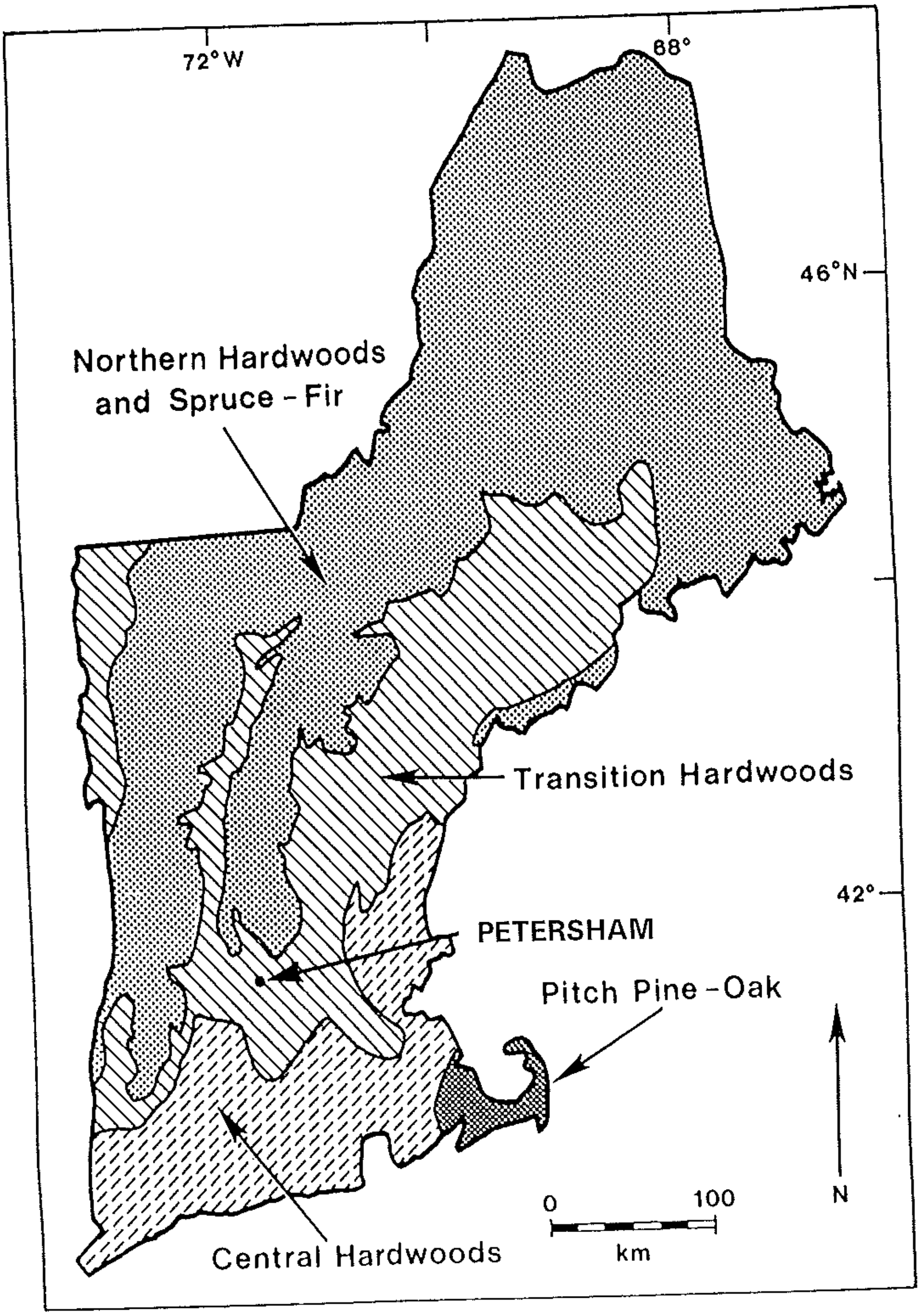

Figure 1. Location of the town of Petersham, Massachusetts on vegetation map of New England, U.S.A. [adapted from Foster (1992) and Westveld (1956)].

depth (Lyford et al. 1963; Taylor and Hotz 1985).

Central New England occupies a transitional zone between dry continental and moist maritime climates: winters are generally cold and summers moderately warm to hot. The mean January temperature is -7°C and the mean July temperature is 20°C. The annual frost-free season averages 137 days but ranges considerably according to topographic position (range: 77-161 days). Precipitation is evenly distributed throughout the year (monthly range: 75-108 mm), and mean annual rainfall is 110 cm. Mean annual snowfall is 127 cm, and snow cover persists through the winter months in some years (Spurr 1957).

Vegetation and Land-Use History

In Petersham, the Holocene was a period of little human activity and disturbance of forest cover. Following the end of Pleistocene glaciation (approximately 13,000 years B.P.), the treeless terrain was vegetated by graminoids, forbs, *Salix*, and *Alnus*. By 11,000 years B.P., this vegetation was replaced by cool-temperate successions of *Picea* and *Pinus* (probably *P. banksiana* and *P. strobus*). During the warm, dry hypsithermal interval beginning 8,350 years B.P., the spruce and pine forests were replaced by *Quercus* and *Tsuga*. However, *Tsuga* declined precipitously around 4,700 years B.P., and the forests became dominated by *Quercus*, *Betula*, and *Pinus* (Davis 1958; Zebryk 1991).

The modern forests of central New England developed approximately 2,000 years B.P., when *Castanea* became an important component of the deciduous forests consisting primarily of *Betula*, *Quercus*, *Pinus*, and *Tsuga*. During the early settlement period in the late 1700s, the vegetation of Petersham was dominated by central hardwoods (*Quercus* and *Castanea*) on the uplands and northern hardwoods (*Betula*, *Fagus*, *Acer*, *Fraxinus*, *Ulmus*, and *Tsuga*) in the swamps and lowlands. *Pinus strobus* was not mentioned as an important species, and "Walnut" (probably *Carya*) increased in importance following European settlement (Whitney 1793;

Raup and Carlson 1941; Foster 1992; Foster and Zebryk 1993).

The post-settlement history of Petersham consisted of five major periods representing the predominant activities in the regional landscape (Foster 1992): speculation (1730-1750), low-intensity agriculture (1750-1790), commercial agriculture and small industry (1790-1850), farm abandonment and industrialization (1850-1920), and residential period (1920-1990). This 270-year history of human activity, which paralleled similar patterns in much of New England, resulted in the dramatic transformation of the Petersham landscape (Figure 2). In the late 1700s and early 1800s, forest cover decreased substantially as European settlers cleared land to develop subsistence and commercial agriculture. Maximum land clearance in Petersham occurred in the 1850s, when 85 percent of the land was cleared for agriculture and other land uses.

In the agricultural landscape, land resources were utilized for cropland, meadow, pasture, and woodland. Arable land, which accounted for <10 percent of the land in Petersham, was cultivated for hay, crops, and orchards. Cultivated lands lay fallow in some years or were cultivated for only a few years before being converted to other land uses. The majority (>75 percent) of the land in Petersham was cleared as uncultivated pasture or grassland. Isolated woodlands occupied the remaining 15 percent of the agricultural landscape in Petersham. These woodlands were harvested one or more times for firewood, timber, and tanning bark (especially *Castanea dentata*, *Quercus*, and *Tsuga canadensis*) and were either permanently, or at least occasionally, pastured (Raup and Carlson 1941; Foster 1992).

Beginning in the late 1800s, much of the agricultural land was abandoned, and became reforested by natural invasion of *Pinus strobus* and *Betula populifolia* (Figure 3). Many of the old-field pine stands were logged in 1890-1910 for the wooden box industry and were replaced by either fast-growing sprout hardwoods (especially *Acer rubrum* and

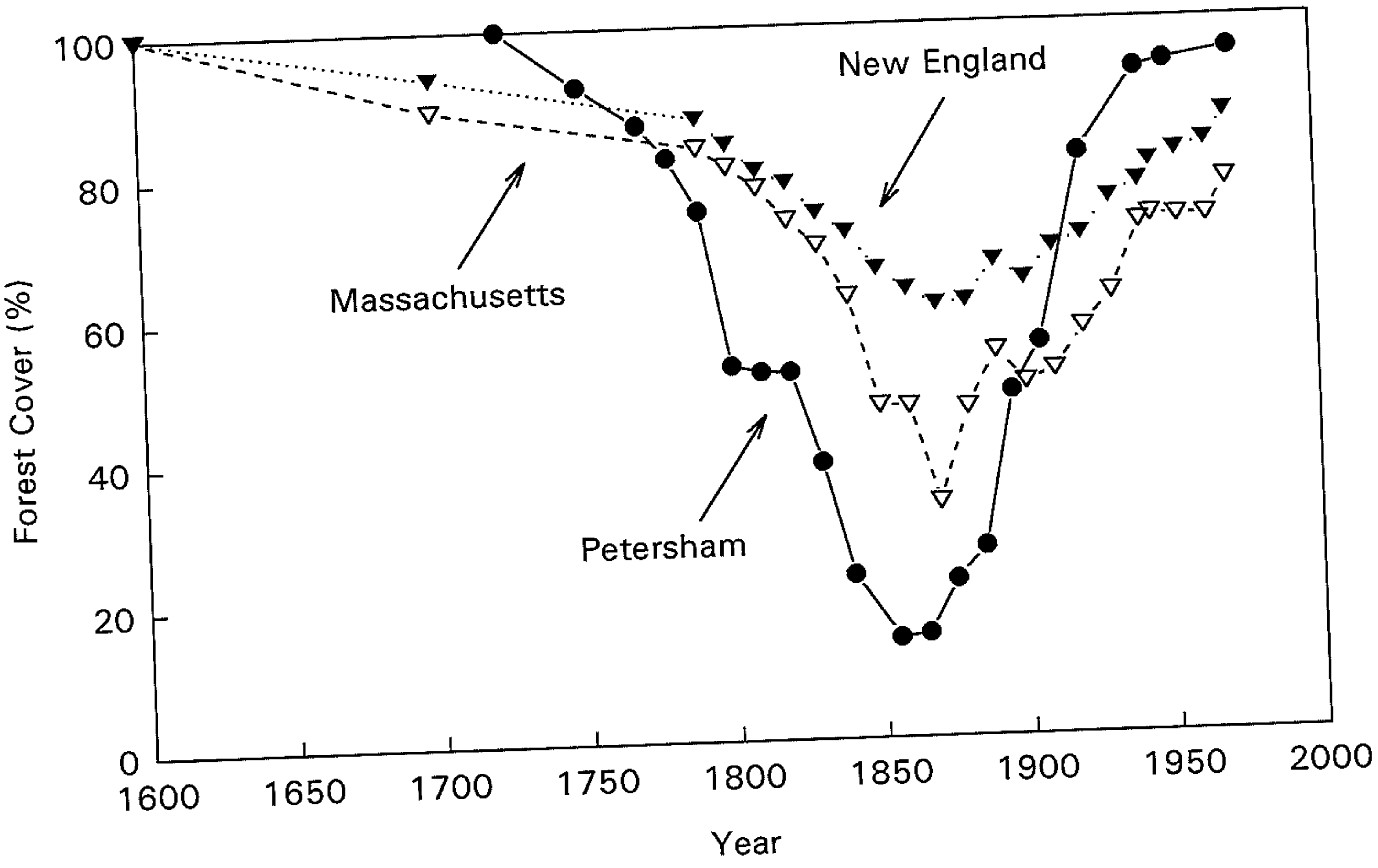

Figure 2. Change in forest cover during the period 1600-1980 in Petersham, Massachusetts, and New England, U.S.A. [adapted from Foster (1992)].

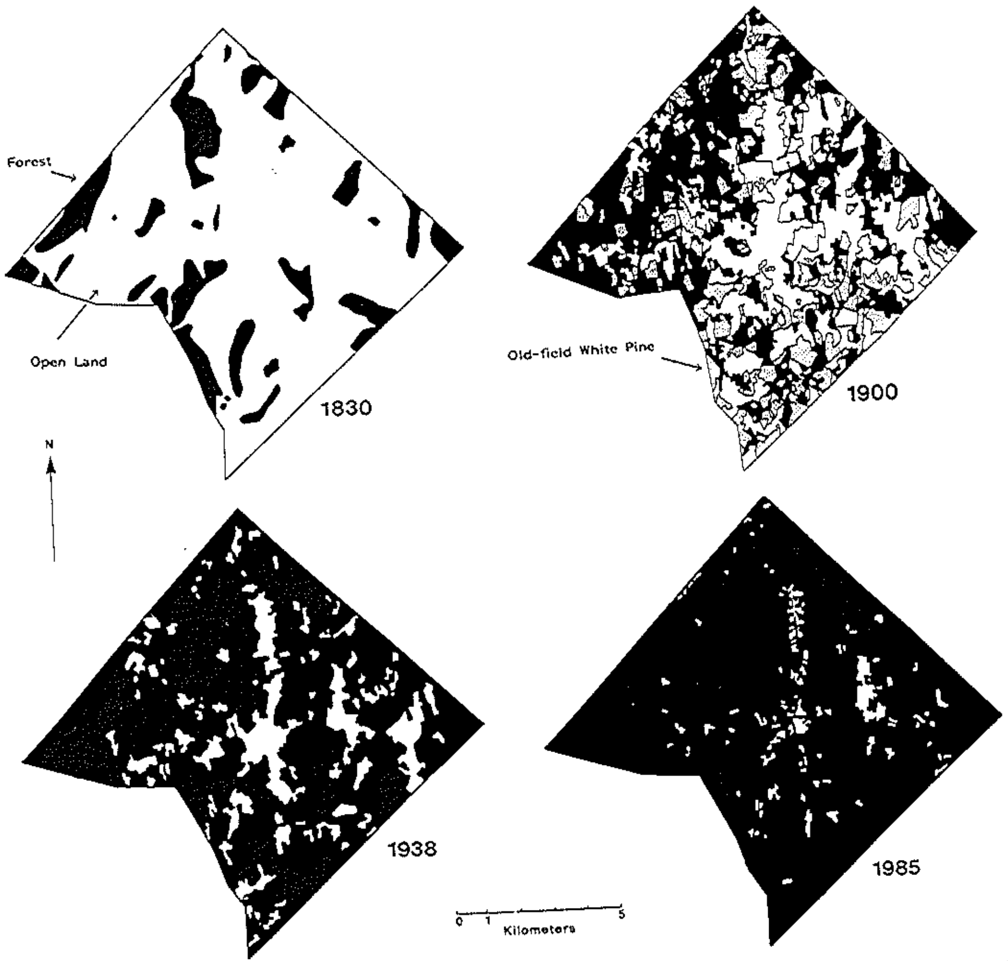

Figure 3. Sequence of forested and non-forested land during the past 160 years in Petersham, Massachusetts, U.S.A. The sequence represents Petersham prior to the peak of agriculture (1830), the transition to forest following agricultural abandonment (1900 and 1938), and the modern forested landscape (1985) [adapted from Foster (1992)].

Quercus borealis) or *Tsuga canadensis* (Raup and Carlson 1941; Spurr 1956).

Following reforestation, two disturbance events greatly altered forest structure and composition. During 1913-1916, *Castanea dentata*, an important forest overstory component, was eliminated from the forest canopy by the chestnut blight *Cryphonectria parasitica* (Murr.) Barr; and chestnut was replaced by *Tsuga* and hardwoods (Stout 1952; Westveld 1956; Foster 1992). The Great Hurricane of 1938 destroyed 9 x 10^6 m^3 of forest timber in a 150-km-wide path across central Connecticut and Massachusetts. Much of the damage was concentrated in exposed conifer stands dominated by *Pinus strobus*, *Tsuga canadensis*, and plantations (Foster and Boose 1992).

The modern landscape of Petersham is >90 percent forested and represents a mosaic of continually forested and reforested land. Petersham and much of central New England is classified within the transition hardwoods-white pine-eastern hemlock zone (Westveld 1956). Important tree species include *Pinus strobus*, *Tsuga canadensis*, *Quercus rubra*, *Acer rubrum*, *Fraxinus americana*, *Betula lenta*, and *Acer saccharum*. The important deciduous species represent a transition between the central hardwoods (*Quercus alba*, *Quercus rubra*, and *Castanea dentata*) of southern New England and the northern hardwoods (*Acer saccharum*, *Fagus grandifolia*, and *Betula alleghaniensis*) of northern New England (Nichols 1935; Stout 1952; Spurr 1956).

METHODS

Study Design

The sampling strategy relied on randomly selected plots located on a 100-m by 100-m grid overlaid on the United States Geological Survey (USGS) 1:25,000-scale topographic map of Petersham (Figure 4). Each grid intersection (n=12,899) represented one potential sample plot, and 106 plots were selected by random numbers table. The 106 plots were

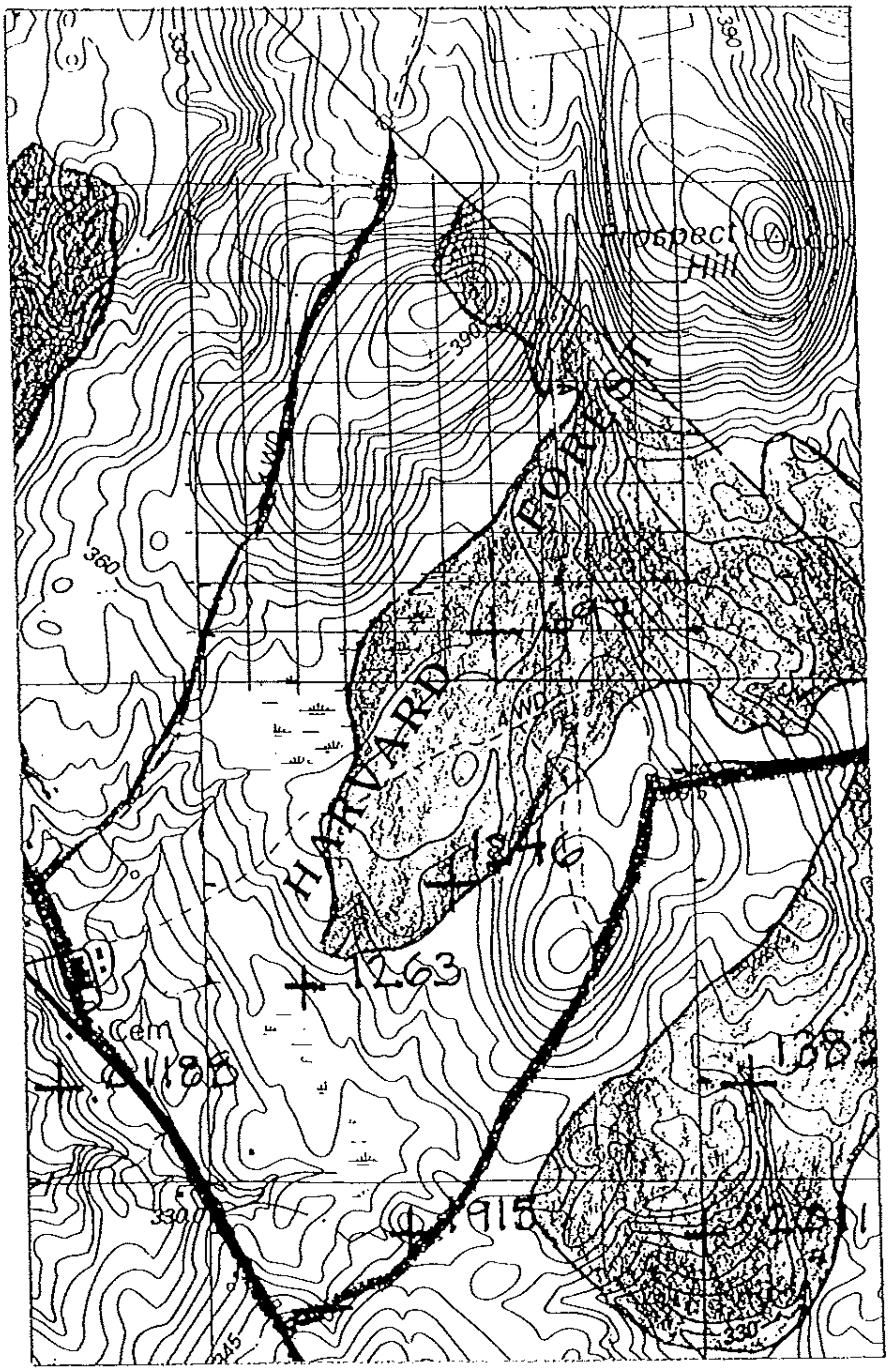

Figure 4. Section of the 100-m by 100-m grid overlaid on the USGS 1:25,000-scale topographic map of Petersham, Massachusetts, U.S.A. The numbered marks are selected sample points. Shaded areas were wooded in 1830; the remaining areas were cleared of forest [based on Lee and Lee (1830)].

selected equally (i.e. 53 plots each) from two strata defined as cleared and forested land on the 1830 land-use map of Petersham (Lee and Lee 1830).

Sample plots were located by standard orienteering techniques using measured distances and compass directions; locations were verified in the field by topographic features. Since this study was meant to sample closed-canopy forest, plots were eliminated when they occurred in non-forested areas, within 15 m of the forest edge, where crown cover was <75 percent, or where the landowner refused access. If necessary, plots were moved the minimal distance required to avoid physiographic and/or land-use boundaries (e.g. stone walls) or recent human disturbances (e.g. roads or excavations).

Square sample plots, measuring 20 m by 20 m (0.04 ha), were oriented with their diagonals aligned toward the four cardinal directions. Plot corners were located 14.14 m to the north, east, south, and west of the center point; and plots were squared by measuring the length of each side. The plot center and corners were marked by white PVC pipes, and the plot boundary was delineated by fluorescent pink tape.

Field Surveys

Field surveys were completed at 70 plots; the remaining 36 plots were eliminated for the reasons mentioned previously. To record seasonal variability and to ensure that all species were detected, vegetation in each plot was surveyed at least twice during the 1992 field season: once early in summer [May (n=14), June (n=28), July (n=26), or early August (n=2)] and once late in summer [August (n=59) or September (n=11)]. Two plots were surveyed three times during the 1992 field season (May, June, and September), and thirteen plots were also surveyed once prior to the principal field season [October (n=3) or November (n=10) 1991].

Physiographic and historical data were collected during the first survey of each sample plot, and soil description and sampling occurred during or on a separate visit after the second vegetation survey. Soil descriptions were completed at all 70 vegetation plots, but samples of organic and mineral horizons were collected at only 39 plots.

Vegetation Sampling

The procedures for sampling vegetation were modified from standard techniques for quantitative plots (Mueller-Dombois and Ellenberg 1974; Greig-Smith 1983). All vascular plants were identified to species, except those belonging to a few taxonomically difficult genera (e.g. *Amelanchier* and *Crataegus*). Nomenclature followed Gleason and Cronquist (1991). The presence of all species was recorded during each survey.

Two measures of abundance were collected for understory vegetation (shrubs and woody vines, ferns and fern allies, graminoids, and forbs): estimated percent cover and the counted or estimated number of stems grouped in 10 classes (1, 2-5, 6-10, 11-25, 26-50, 51-100, 101-250, 251-500, 501-1000, and >1000 stems). All standing live and dead trees (diameter >2.5 cm), including each stem of multiple-stemmed individuals, were measured by diameter 1.4 m aboveground. Each stem was assigned a crown position (dominant, co-dominant, intermediate, or suppressed; *sensu* Smith 1962). Tree reproduction (diameter ≤2.5 cm) was counted as the number of saplings (height >0.30 m) and seedlings (height <0.30 m excluding current-year seedlings).

Vegetation data were used to describe species distribution and abundance and overall forest composition. Species distribution, measured as frequency of occurrence, was simply the number of plots in which each species occurred, and species richness was the number of vascular species in each plot (# species/0.04 ha). Understory abundance was simply the separate field estimates of percent cover and number by class. Abundance of live trees was calculated as density (# stems/0.04

ha) and total basal area (m^2/0.04 ha) for each species. Overstory type was represented by the dominant canopy species with the highest importance value (sum of relative density and relative basal area).

Physiographic and Historical Factors

For each sample plot, physiographic and historical variables were examined in relationship to forest vegetation (Table 1). These variables included both numerical measurements and nominal classes and were treated as continuous, discrete, ranked, or nominal variables (*sensu* Sokal and Rohlf 1981).

Physiography

Geographical location was measured from USGS 1:25,000-scale topographic maps. Latitude and longitude were measured on the Universal Transverse Mercator coordinate system (UTM Zone 18), and elevation was measured in meters above sea level. Bedrock geology (Hardwick tonalite, Monson gneiss, or Partridge schist) was identified from USGS bedrock geology field maps (Harvard Forest Archives Map P2.8). Surficial geology (exposed bedrock and unstratified till, unstratified till, stratified drift and outwash, organic deposits, or talus) and geomorphology (bedrock ridge, depositional basin, erosional stream valley, drumlin, glacial outwash, ice-contact stratified drift, marginal moraine, or talus) described parent material and landform and were classified in the field based on surface features and topography (*sensu* Davis 1983). Landscape position was assigned one of six ranked topographic positions within the local landform (ridge, upper slope, mid slope, terrace, lower slope, or bottom).

Slopes were characterized by gradient (mean percent slope measured by clinometer), aspect (one of 16 compass directions measured by magnetic compass), and shape (classified as planar, concave, convex, or undulating). Slope aspect was transformed to a numerical value by an

Table 1. Physiographic and historical variables analyzed in relation to forest composition in Petersham, Massachusetts, U.S.A. The values and formats of each variable are discussed in more detail in the text.

Variables	Value	Format
<u>Geographical Location</u>		
Latitude	Meters	Continuous
Longitude	Meters	Continuous
Elevation	Meters	Continuous
<u>Physiography</u>		
Bedrock geology	3 classes	Nominal
Surficial geology	5 classes	Nominal
Geomorphology	8 classes	Nominal
Landscape position	6 classes	Ranked
Slope shape	4 classes	Nominal
Slope aspect	16 classes	Nominal
Slope gradient	Degrees	Continuous
Solar irradiation	Index	Continuous
Microrelief	4 classes	Ranked
Surface rock cover	Percent	Continuous
Drainage	7 classes	Ranked
<u>Soils</u>		
Soil series	23 classes	Nominal
Soil texture	6 classes	Ranked
Soil rock content	Percent	Continuous
<u>Natural Disturbances</u>		
1938 hurricane damage	6 classes	Ranked
Evidence of fire	2 classes	Nominal
<u>Forest Management</u>		
Time since logging	3 classes	Ranked
Number of stumps	Number	Discrete
<u>Land-use History</u>		
Woodland history	2 classes	Nominal
Past land use	3 classes	Nominal
Intensity of disturbance	5 classes	Ranked
Age of secondary woodland	Year	Ranked
Distance to primary woodland	Meters	Continuous
Distance to primary woodland edge	Meters	Continuous
<u>Cultural Features</u>		
Distance to nearest building	Meters	Continuous
Distance to nearest road	Meters	Continuous
Distance to center of Petersham	Meters	Continuous

arc-cosine function (Beers et al. 1964). Potential solar irradiation (the ratio of the total annual potential insolation to the maximum potential insolation) was calculated from latitude, slope aspect, and slope gradient (*sensu* Frank and Lee 1966). Microrelief, which approximated habitat heterogeneity, was ranked in four classes (level, slight, moderate, and extreme) by the extent of local relief or microtopography. Surface rock cover was estimated as the percent of the ground surface covered by bedrock and boulders (diameter >25.6 cm; *sensu* Wentworth 1922).

Soils

Soil taxonomy was identified to soil series based on interim United States Department of Agriculture (USDA) 1:20,000-scale soil survey maps (USDA, unpublished). Additional data on soil characteristics were collected from a single soil pit (approximately 50 cm on a side and 50 cm deep) dug near the center of each plot. Each soil pit was described to characterize soil rock content [percent by volume of cobbles and boulders (diameter >6.4 cm; *sensu* Wentworth 1922)] and rooting depth (depth above which >95 percent of the roots occur). The occurrence of mottling was described by horizon and Munsell color. Soil drainage was assigned to one of seven ranked classes (very poor, poor, imperfect, moderately well, well, somewhat excessive, and excessive; *sensu* USDA 1981) based on mottling and examination of the soil profile. Depths to hardpan and water table were measured when encountered.

Each soil horizon was characterized by depth, thickness (mean and range), Munsell color, consistence, texture, percent of horizon occupied by rocks, and boundary definition and shape (*sensu* USDA 1981). Soil samples from both the organic and mineral horizons were collected within a 15 x 15 cm square: one sample combining all three organic layers (Oi, Oe, and Oa) and one sample from the top 15 cm of the mineral horizon(s).

Analysis of soil samples are not completed at this time.

Natural Disturbance

Natural disturbances were characterized by evidence indicating the occurrence of historical fires or windthrow. Damage inflicted by the 1938 hurricane was described in six ranked classes based on the presence and number of fallen boles and/or pit-and-mound topography of the proper age: undamaged (0 boles and mounds), slightly damaged 1 and 2 (<4 boles and mounds), moderately damaged 1 and 2 (<7 boles and mounds), and destroyed (≥7 boles and mounds). Evidence of historical fires, based on the presence of macroscopic charcoal, was recorded during examination of the soil profiles.

Forest Management

Human disturbances include both intensive agriculture and less intensive forest management activities occurring after reforestation. Forest management and tree harvesting were identified by the number of cut stumps; time elapsed since logging was ranked in three age classes based on the condition of stumps (very rotten, moderately rotten, and recent).

Land-use History

Land-use history was based on both documentary and field evidence. Documentary information included several historical maps: 1830 town plan (Lee and Lee 1830), 1855 town map of Petersham (Woodford 1855), 1937-1939 white pine blister rust maps (Harvard Forest Archives Map P3.2), 1938 land utilization map (Massachusetts State Planning Board 1938), and 1951 and 1971 land use and vegetative cover maps (MacConnell 1975). Sites were classified as forested or non-forested in 1870 and 1900 by extrapolation from the 1937-1939 vegetation types (Appendix 1).

Field verification of land-use history relied primarily on examination of disturbance to the soil profile (e.g. the presence of A_p or enriched A horizons). A dichotomous key was developed to classify land-use history based on soil profile characteristics (Appendix 2). Other field evidence included tree crown shape, multiple-stemmed sprouts, microtopography, surface rock cover, and cultural artifacts such as stone walls.

Land-use history was designated by woodland history, past land use, and intensity of disturbance. Past land use (cropland, pasture, or woodland) and intensity of disturbance (five ranked classes) were based solely on evidence of disturbance to the soil profile as interpreted in the dichotomous key (Appendix 2). Woodland history was defined as primary (sites that have always been forested) or secondary (sites that were previously cleared) woodland (*sensu* Peterken 1981). Woodland history was initially assigned separately based on documentary and soil evidence. Primary woodlands were forested on all historical maps and showed no evidence of human disturbance to the soil profile. Secondary woodlands, in contrast, showed either anthropogenic disturbance to the soil profile and/or were depicted as non-forested on at least one historical map. When documentary and soil information disagreed, woodland history was designated based on the relative strengths of the documentary and soil evidence.

The age of secondary woodlands was estimated from historical maps as the date of agricultural abandonment for each stand that was non-forested on at least one historical map. Because few historical maps are available, these estimates represent broad periods of time (e.g. abandoned between 1870 and 1900). For analysis, secondary woodlands were divided into those abandoned before and after 1870. Distance to the nearest primary woodland (secondary woodland plots) and distance to the edge of primary woodland (primary woodland plots) were measured in meters from a USGS 1:25,000-scale topographic map on which the 1830 land uses had been delineated (Harvard Forest Archives File 1991-13).

Distances to the nearest road, the nearest building, and the center of Petersham were measured in meters from the 1855 map of the cultural features of Petersham (Woodford 1855).

Selection of Important Variables

Based on preliminary data analysis, ten physiographic and historical variables were selected for further analysis. To represent the range of physiographic and historical processes, at least one variable was retained in each group of variables (except geographical location): physiography and soils, natural disturbance, forest management, and land-use history. The ten selected variables were geomorphology, landscape position, drainage, solar irradiation, number of stumps, hurricane damage, evidence of fire, past land use, intensity of disturbance, and age of secondary woodlands.

Although highly related, past land use and intensity of disturbance were retained for separate analyses, because they are nominal and ranked variables, respectively. Land-use history was ranked as intensity of disturbance for multivariate analysis and logistic regression, but past land use was used for univariate analyses of individual species distributions. Both past land use and intensity of disturbance were analyzed in relation to canopy dominance and species richness.

Geomorphology and surficial geology were integrated in a single variable describing both parent material and landform. Surface rock cover, soil rock content, soil texture, and microrelief describe different characteristics of the same physical substrate and were deleted. Water availability was described by drainage, which is controlled by surficial geology, geomorphology, landscape position, slope shape, slope gradient, soil texture, among other factors. Light availability was measured by potential annual solar irradiation, which integrated latitude, slope aspect, and slope gradient.

Other variables were dropped for several reasons: 1) they were related to other more meaningful variables [woodland history, distance to the edge of primary woodland, distances to cultural features (all related to past land use and intensity of disturbance), and time since logging (related to the number of stumps)]; 2) they represented a range of values which was insignificant in terms of plant biology [elevation (199 m), latitude (12.8 km), and longitude (14.0 km)]; 3) most samples represented a single value [bedrock geology (70 percent of the plots occurred on Hardwick tonalite)]; or 4) they were superseded by more site-specific variables [soil series (by soil texture)].

Data Analysis

Variable Correlations and Associations

In order to identify independent and related variables, relationships among the remaining physiographic and historical variables were calculated by Pearson's correlation coefficient (numerical variables), Spearman's ranked correlation coefficient (ranked variables), and the likelihood ratio G-statistic (nominal variables). For Spearman's correlations, numerical variables were ranked and analyzed in relation to the ranked variables. For contingency table analysis, both numerical and nominal variables were grouped into a few categories to ensure sufficient sample sizes. Type-I errors in the identification of highly correlated or associated variables were avoided by the Dunn-Sidak method (Sokal and Rohlf 1981).

Multivariate Analysis

Multivariate analysis defined community patterns based on species distribution and abundance and explained these patterns in relation to variation in physiographic and historical factors. Vegetation, physiographic, and historical data were ordinated by detrended correspondence analysis (DCA), canonical correspondence analysis (CCA), and detrended canonical correspondence analysis (DCCA) (CANOCO; Ter Braak 1986, 1990). These multivariate techniques rely on reciprocal averaging to extract continuous axes of variation in species data. By restricting ordination axes to linear combinations of environmental variables, CCA directly identifies the patterns in species and community variation which can be explained by known environmental variables (Ter Braak 1986).

All samples and all species were included in multivariate analyses. To investigate possible differences between overstory and understory vegetation, separate ordinations were performed for all vegetation data, trees only, and understory only. Species abundance was weighted on a 10-class scale. Tree species were ranked by total basal area. If only present as saplings or seedlings, tree abundance was automatically ranked in the lowest class. Abundance of understory species was ranked separately by stem number and percent cover, and the greater of the two ranked values was selected as the final abundance weight.

CCA eigenvalues measure the importance of each axis (scale: 0-1). Species-environment correlations, which measure the amount of variation in species data explained by the environmental variables, compare sample scores based on the weighted species scores and those derived from linear combinations of environmental variables. Cumulative percentages of variance measure the amount of variation in species data and in all species-environment relationships explained by the ordination axes.

Intraset correlations, which are relatively stable when collinearity is suspected, measure the magnitude of the relationships between environmental variables and the ordination axes derived from linear combinations of the environmental variables (Ter Braak 1986, 1990). Ordination diagrams illustrate environmental gradients and the patterns in species data and community composition as best explained by the environmental data. The location of the weighted average (or center of distribution) of each species perpendicular to the vector or centroid of each environmental variable indicates distribution of species along the environmental gradients (Ter Braak 1986).

Univariate Analyses

Species richness and canopy dominance were analyzed in relation to each other and to physiographic and historical variables. The relationship between species richness and canopy dominance was analyzed by analysis of variance (canopy dominance was the treatment and species richness was the response variable). Relationships between species richness and physiographic and historical variables were analyzed by analysis of variance (nominal variables) or linear regression (continuous or ranked variables). Relationships between canopy dominance and physiographic and historical variables were tested by the likelihood ratio G-statistic.

To evaluate their response to individual factors, distributions of the 73 most common species ($n \geq 10$ plots) were analyzed in relation to species richness, canopy dominance, and the selected physiographic and historical variables. Significant associations were identified by contingency table analysis and the likelihood ratio G-statistic. For each class of treatment variable, cell values were tabulated as the number of plots in which the species was present or absent. The likelihood ratio G-statistic tested the actual vs. expected cell frequencies for all classes of each variable. Species occurring in <10 plots were omitted to avoid problems associated with small sample sizes (Sokal and Rohlf, 1981).

Logistic Regression

To identify the most important variable(s) predicting individual species distributions, binomial logistic regression was used to model the occurrence of individual species as dependent on physiographic and historical variables (LOGIT; Steinberg and Colla 1991). For 73 species present in $\geq$10 plots, the variable(s) best predicting presence or absence of each species was selected by mixed stepwise logistic regression. Mixed stepping attempted to first eliminate and then to add variables to the regression model. Variables were added to the model only when the significance level of the score statistic was <0.05; variables were eliminated if the significance level of the Wald test statistic was >0.10. The selected regression models were used to calculate the prediction success, which represents the proportion of species presence and absence correctly predicted by the selected model.

RESULTS

Relationships among Variables

Many physiographic and historical variables are not significantly interrelated (Table 2). No significant relationships were detected for either solar irradiation or number of stumps. Significant relationships occur between 1) evidence of fire and geomorphology (marginal moraines have more evidence of fire than other geomorphological types), 2) hurricane damage and drainage and landscape position (hurricane damage increases with increasing drainage and slope position), and 3) landscape position and intensity of disturbance (more intensive land uses occur on higher slope positions).

Highly interrelated physiographic variables include geomorphology, landscape position, and drainage (Table 3). Drainage increases from poor to excessive as landscape position rises from bottoms to ridges. Depositional basins occur on poorly-drained bottoms; stratified outwash occurs on terraces; moderately- to well-drained mid and upper slopes are found on unstratified till on bedrock ridges; and marginal moraines are well- to excessively-drained.

Highly interrelated historical variables include past land use, intensity of disturbance, and age of secondary woodlands. By

Table 2. Pearson correlation coefficients (A), Spearman's ranked correlation coefficients (B), and likelihood ratio G-statistics (C) of physiographic and historical variables in study of forest vegetation in Petersham, Massachusetts, U.S.A. Significance levels are: * = < 0.05, ** = < 0.01, and *** = < 0.001.

A.

	Solar	Stumps
Solar irradiation	1.000	
Number of stumps	-0.021	1.000

B.

	Position	Damage	Drainage	Disturb	Age
Landscape position	1.000				
Hurricane damage	0.235*	1.000			
Drainage	0.453***	0.338*	1.000		
Intensity of disturbance	0.285*	-0.166	0.036	1.000	
Secondary woodland age	-0.110	0.238	0.018	-0.781***	1.000
Solar irradiation	-0.026	0.014	-0.057	0.160	-0.054
Number of stumps	0.027	-0.006	0.030	0.222	-0.121

C.

	Geomorph	Fire	Landuse
Geomorphology	0.000		
Evidence of fire	12.308*	0.000	
Past land use	7.415	0.018	0.000
Landscape position	62.186***	3.028	4.319
Solar irradiation	9.501	5.805	0.112
Drainage	50.565***	1.979	6.386
Hurricane damage	9.761	1.338	5.194
Number of stumps	3.187	0.264	2.243
Intensity of disturbance	20.509	1.621	65.028***
Secondary woodland age	13.133	0.160	32.912***

Table 3. Relationships among selected physiographic and historical variables in Petersham, Massachusetts, U.S.A. Values are the number and percentage (in parentheses) of the 70 plots sharing each combination of factors. Significance was analyzed by contingency tables and the likelihood ratio G-statistic.

	Landscape Position			
	Bottom	Lower	Mid	Upper
Geomorphology (df=12, G=62.186, p=0.000)				
Depositional basin	5 (7)	2 (3)	2 (3)	1 (1)
Stream valley		10 (14)		
Stratified outwash	8 (11)	4 (6)	1 (1)	2 (3)
Marginal moraine		6 (9)	3 (4)	3 (4)
Glacial drumlin				
Talus				
Bedrock ridge		2 (3)	7 (10)	12 (17)

	Drainage			
	Poor	Moderate	Well	Excessive
Geomorphology (df=12, G=50.565, p=0.000)				
Depositional basin	7 (10)	2 (3)	1 (1)	
Stream valley		6 (9)	4 (6)	
Stratified outwash	3 (4)	4 (6)	4 (6)	4 (6)
Marginal moraine			8 (11)	4 (6)
Glacial drumlin				
Talus				
Bedrock ridge		6 (9)	13 (19)	2 (3)
Landscape Position (df=9, G=31.067, p=0.000)				
Bottom and terrace	6 (9)	5 (7)		2 (3)
Lower slope	2 (3)	7 (10)	14 (16)	1 (1)
Mid slope	1 (1)	3 (4)	6 (9)	4 (6)
Upper slope and ridge		4 (6)	11 (16)	4 (6)

	Past Land Use		
	Woodland	Pasture	Cropland
Intensity of Disturbance (df=2, G=65.028, p=0.000)			
1 (least disturbed)	18 (26)		
2	6 (9)	3 (4)	
3		29 (41)	
4			4 (6)
5 (most disturbed)			
Age of Secondary Woodlands (df=4, G=76.486, p=0.000)			
Primary woodlands	24 (34)		
Pre-1870 secondary woodlands		6 (9)	1 (1)
Post-1870 secondary woodlands		15 (21)	

definition, past land use and intensity of disturbance are separate descriptions of the same historical land-use activities. Woodlands are less disturbed, and former pasture and cropland are more intensively disturbed. Past land use and intensity of disturbance are related to age of secondary woodlands: pre-1870 secondary woodlands occur on less disturbed sites, and post-1870 secondary woodlands occur on sites that were used more intensively as cropland and pasture.

Community Patterns

Multivariate Analysis

Ordinations by DCA, CCA, and DCCA yielded essentially the same results (Table 4). The higher DCA eigenvalues compared to the constrained CCA eigenvalues indicate that most, but not all, of the variation in species data is explained by the measured environmental data. The higher CCA and DCCA species-environment correlations suggest that the physiographic and historical variables explain major variation in species data. Based on the cumulative percentage variance, the first four axes consistently explain 17-24 percent of the variation in species data and >60 percent of the species-environment relationships. The lower DCCA eigenvalues and species-environment correlations indicate that detrending was unnecessary to prevent arching or to reveal dependent axes.

The intraset correlations indicate that the first four axes are clearly related to several physiographic and land-use history variables (Table 5). The first and second axes are correlated with geomorphology, drainage, and landscape position; and the third axis is related to intensity of disturbance and landscape position.

The ordination diagram reveals two pronounced gradients along the first and second axes (Figure 5): a complex physiographic gradient defined by drainage, geomorphology, and landscape position; and a land-use gradient representing intensity of disturbance and age of secondary

Table 4. Eigenvalues, species-environment correlations, and cumulative percentage variance of ordinations by detrended correspondence analysis (DCA), canonical correspondence analysis (CCA), and detrended canonical correspondence analysis (DCCA) of forest vegetation in Petersham, Massachusetts, U.S.A. CCA ordinations include data for all vegetation, trees only, and understory only.

	Axes			
	1	2	3	4
<u>Eigenvalues</u>				
DCA	0.344	0.226	0.116	0.091
CCA	0.269	0.222	0.128	0.084
CCA (trees only)	0.172	0.128	0.106	0.083
CCA (understory only)	0.293	0.233	0.136	0.092
DCCA	0.269	0.179	0.066	0.053
<u>Species-Environment Correlations</u>				
CCA	0.916	0.957	0.871	0.832
CCA (trees only)	0.873	0.865	0.770	0.782
CCA (understory only)	0.916	0.953	0.871	0.838
DCCA	0.907	0.888	0.842	0.835
<u>Cumulative Percentage Variance of Species Data</u>				
DCA	10.4	17.3	20.8	23.5
CCA	8.1	14.9	18.8	21.3
CCA (trees only)	8.3	14.6	19.7	23.8
CCA (understory only)	8.4	15.2	19.1	21.7
DCCA	8.1	13.6	15.5	17.1
<u>Cumulative Percentage Variance of Species-Environment Relation</u>				
CCA	24.1	44.1	55.6	63.1
CCA (trees only)	23.9	41.7	56.4	67.9
CCA (understory only)	25.1	45.1	56.8	64.7
DCCA	22.2	34.7		

Table 5. Intraset correlations of physiographic and historical variables from CCA ordination of forest vegetation data from Petersham, Massachusetts, U.S.A. The sign and magnitude of these correlations indicate their relative importance in explaining variation in community composition.

Variable	Axis 1	Axis 2	Axis 3	Axis 4
Bedrock ridge	-0.443	0.082	-0.191	0.066
Depositional basin	0.747	-0.288	-0.271	0.044
Stream valley	0.060	-0.022	0.141	-0.257
Drumlin	-0.119	0.026	-0.111	-0.063
Stratified outwash	-0.162	-0.166	0.303	-0.132
Marginal moraine	-0.235	0.029	0.021	0.252
Talus	0.271	0.869	0.218	0.015
Landscape position	-0.474	0.370	-0.468	0.164
Solar irradiation	-0.002	0.310	0.020	-0.067
Drainage	-0.579	0.461	-0.107	-0.335
Hurricane damage	-0.208	0.132	0.181	0.091
Evidence of fire	-0.123	0.046	-0.052	0.230
Number of stumps	0.056	-0.075	-0.018	-0.036
Intensity of disturbance	0.057	0.229	-0.562	0.086
Secondary woodland age	-0.189	-0.303	0.317	-0.014

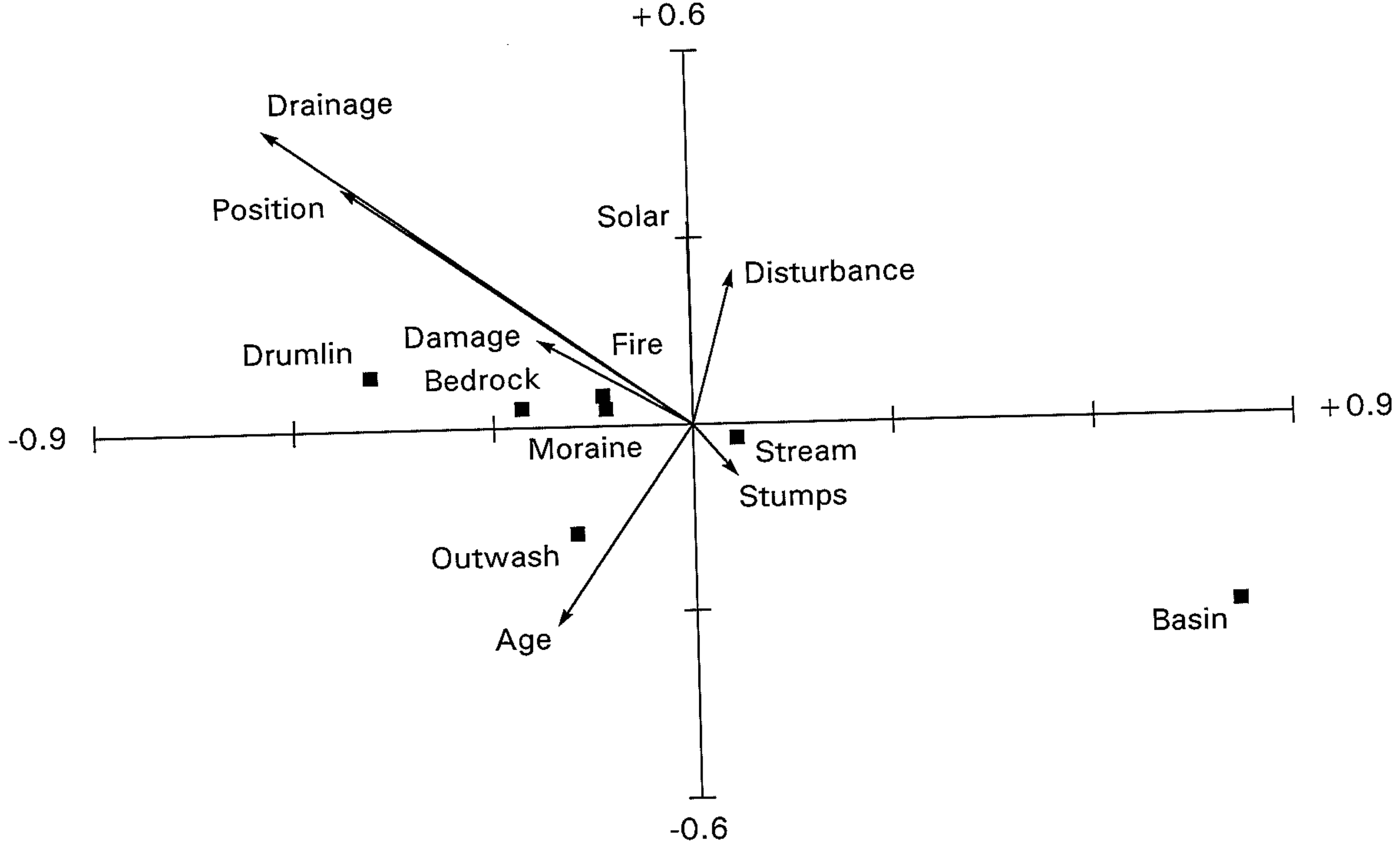

Figure 5. Relationship and importance of physiographic and historical variables on first and second CCA axes in study of forest composition in Petersham, Massachusetts, U.S.A. Environmental variables are indicated by large squares representing the centroids of nominal variables (evidence of fire and the different geomorphological types) and arrows representing the vectors of numerical variables (drainage, landscape position, intensity of disturbance, hurricane damage, number of stumps, and age of secondary woodlands).

woodlands. The physiographic gradient progresses from low poorly-drained basins across moderately well and well-drained outwash and moraines to excessively-drained bedrock ridges and upper slopes. Both hurricane damage and number of stumps parallel this gradient: increasing drainage and landscape position correspond with increasing hurricane damage but decreasing number of stumps.

Eigenvalues and species-environment correlations indicate that tree data are not explained as well by the measured physiographic and historical factors (Table 4). Because there is less variation in the tree data, the cumulative percentages of variance are higher. The important variables are nearly identical for all vegetation, for understory only, and for trees only (Table 6). The first and second axes relate to geomorphology, landscape position, and drainage. On the third axis, tree composition is explained not only by land-use history (both age of secondary woodland and intensity of disturbance) but also by hurricane damage.

Ordination diagrams depict the relationship of individual species to the environmental gradients (Figure 6). Trees, which are explained less well by the environmental data, largely cluster in the center of the two axes. However, peripheral species have affinities for wet basins and stream valleys (*Betula alleghaniensis*) or dry upper slopes and bedrock ridges (*Betula lenta*, *Betula populifolia*, and three species of *Quercus*). The land-use gradient is reflected by species associated with more intensive land uses (*Acer saccharum* and *Acer pensylvanicum*) and those found more frequently in less disturbed primary woodlands (*Betula alleghaniensis*, *Fagus grandifolia*, and *Tsuga canadensis*).

Shrubs primarily reflect the physiographic gradient: *Vaccinium pallidum* occurs on dry ridges, and *Viburnum dentatum* and *Ilex verticillata* occur in wet basins and stream valleys. Ferns also reflect the physiographic gradient: *Lycopodium complanatum*, *Lycopodium clavatum*, and *Pteridium aquilinum* occupy dry uplands; and *Dryopteris*

Table 6. Intraset correlations for the four most important variables on the first three CCA axes for all vegetation data, tree data only, and understory data only in study of forest vegetation in Petersham, Massachusetts, U.S.A.

Axis 1		Axis 2		Axis 3	
Variable	Correlation	Variable	Correlation	Variable	Correlation
<u>All Vegetation</u>					
Depositional basin	0.747	Talus	0.869	Disturbance	-0.562
Drainage	-0.579	Drainage	0.461	Landscape position	-0.468
Landscape position	-0.474	Landscape position	0.370	Woodland age	0.317
Bedrock ridge	-0.443	Solar irradiation	0.310	Unstratified outwash	0.303
<u>Trees Only</u>					
Talus	0.650	Drumlin	0.519	Woodland age	-0.456
Landscape position	0.486	Talus	-0.455	Hurricane damage	-0.447
Drainage	0.474	Landscape position	0.326	Disturbance	0.409
Solar irradiation	0.383	Depositional basin	-0.314	Depositional basin	0.388
<u>Understory Only</u>					
Depositional basin	0.746	Talus	0.869	Disturbance	-0.538
Drainage	-0.581	Drainage	0.449	Landscape position	-0.470
Landscape position	-0.482	Landscape position	0.355	Woodland age	0.297
Bedrock ridge	-0.456	Woodland age	-0.304	Depositional basin	-0.293

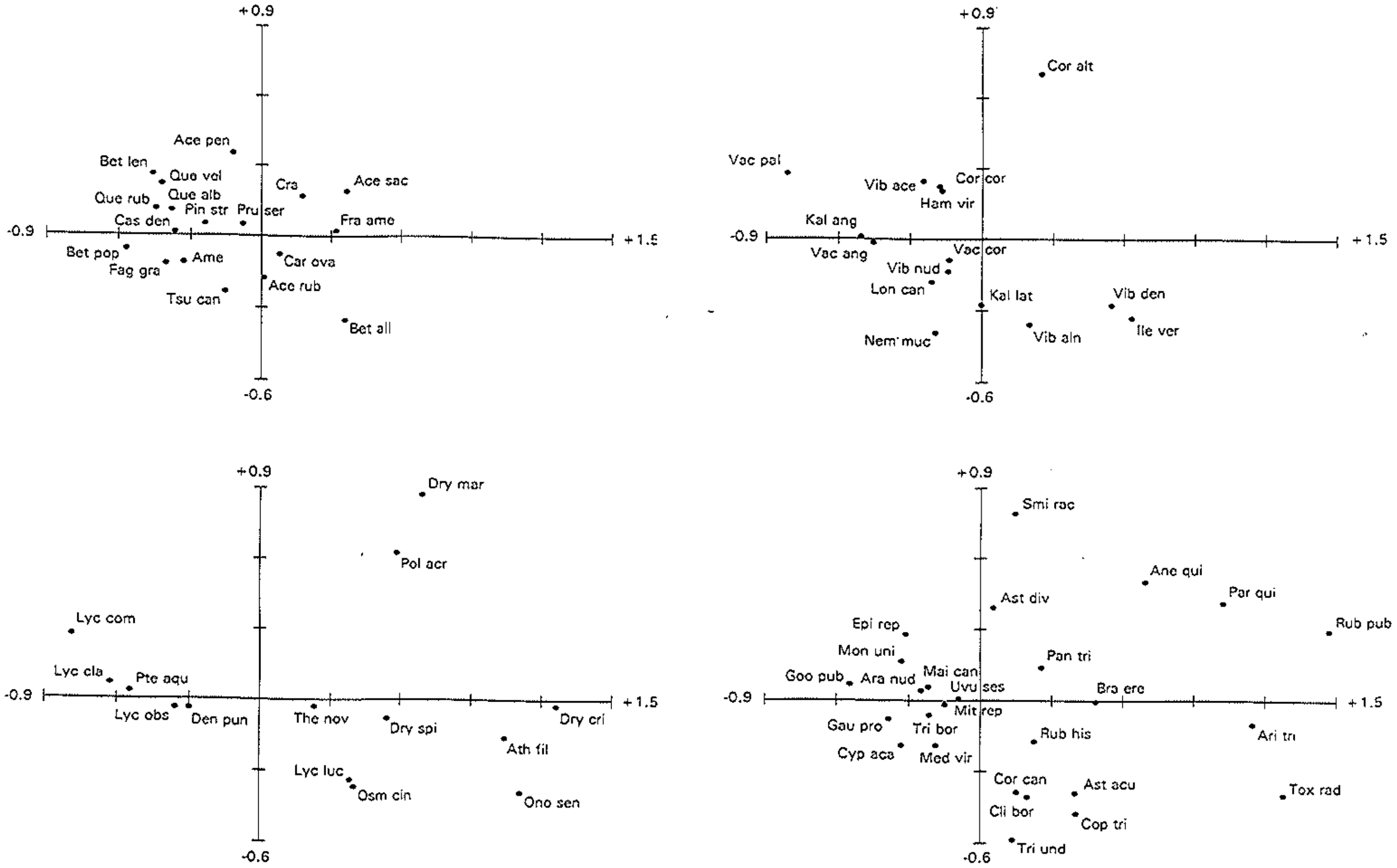

Figure 6. Distribution of A) trees, B) shrubs and woody vines, C) ferns and fern allies, and D) graminoids and forbs along the first and second axes of CCA ordination of forest vegetation data in Petersham, Massachusetts, U.S.A. The important environmental factors are illustrated in Figure 6; species abbreviations represent the first three letters of the generic and specific names which are listed in Table 11.

cristata, *Onoclea sensibilis*, and *Athyrium filix-femina* occupy wet basins. Two ferns are also associated with more intensive land-use history: *Dryopteris marginalis* and *Polystichum acrostichoides*.

Graminoids and forbs reflect the greatest variation along the physiographic and land-use gradients. Several forbs are associated with wet basins and streams: *Toxicodendron radicans*, *Rubus pubescens*, *Arisaema triphyllum*, and *Parthenocissus quinquefolia*. Forbs associated with land-use history include those in more intensively used secondary woodlands (*Smilacina racemosa*, *Aster divaricatus*, and *Parthenocissus quinquefolia*) and those in less disturbed primary woodlands (*Trillium undulatum*).

Based on species distributions along the ordination axes, the second axis, which was correlated with land-use history, may also represent a fertility gradient from nutrient-enriched sites characterized by *Acer saccharum*, *Fraxinus americana*, and *Polystichum acrostichoides*) to nutrient-poor sites characterized by *Amelanchier*, *Kalmia angustifolia*, *Kalmia latifolia*, and *Tsuga canadensis*.

Species Diversity

The vascular flora includes 174 species: 31 trees, 29 shrubs and woody vines, 26 ferns and fern allies, eight graminoids, and 80 forbs (Appendix 3). Mean species richness is 36.0 species/0.04 ha (S.E.=1.6) but ranges from 8-74 species/0.04 ha. Species richness is significantly related to canopy dominance, geomorphology, landscape position, and drainage (Table 7).

Species richness varies significantly with geomorphology (Table 8). Low species richness occurs on unstratified tills on bedrock ridges and on stratified outwash and contact drift; and high species richness occurs on depositional basins. Species richness decreases significantly with increasing landscape position: higher species richness occurs at lower slope positions (Figure 7). Species richness also decreases

Table 7. Significance of relationships among species richness, canopy dominance, and physiographic and historical variables in forest plots in Petersham, Massachusetts, U.S.A. Values are the degrees of freedom, test statistic, and the probability. Species richness was analyzed by analysis or variance (ranked or nominal variables) and linear regression (discrete or continuous variables); and canopy dominance, by the likelihood ratio G-statistic.

	Species Richness			Canopy Dominance		
Variable	df	F	P	df	G	P
<u>Physiography and Soils</u>						
Geomorphology	4	7.944	0.000	8	13.810	0.087
Landscape Position	1	4.829	0.031	6	16.028	0.014
Drainage	1	6.757	0.011	6	10.064	0.122
Solar irradiation	1	0.090	0.765	4	2.063	0.724
<u>Natural Disturbance History</u>						
Evidence of fire	1	1.310	0.195	2	3.405	0.182
Hurricane damage	1	2.204	0.142	4	2.469	0.650
<u>Forest Management</u>						
Number of stumps	1	0.250	0.618	4	3.176	0.529
<u>Land-use History</u>						
Past land use	2	0.568	0.570	2	7.470	0.024
Intensity of disturbance	1	1.242	0.269	6	29.634	0.000
Age of secondary woodland	1	0.160	0.692	2	0.010	0.995

Table 8. Species richness in relation to geomorphology and canopy dominant species in Petersham, Massachusetts, U.S.A. Values are the number of plots, mean species richness (# species/0.04 ha), and standard error of the mean. Statistical analysis of geomorphology did not include glacial drumlin or talus, and statistical analysis of canopy dominance only included *Acer rubrum*, *Pinus strobus*, and *Tsuga canadensis*.

	N	Mean Richness	S.E.
Mean	70	36.0	1.6
<u>Geomorphology</u>			
Depositional basin	10	52.3	4.9
Stream valley	10	36.6	3.7
Stratified outwash	15	28.1	3.1
Marginal moraine	12	37.2	2.7
Glacial drumlin	1	34.0	
Talus	1	63.0	
Bedrock ridge	21	31.8	1.8
<u>Canopy Dominance</u>			
Acer rubrum	18	40.2	2.8
Acer saccharum	1	42.0	
Betula alleghaniensis	1	74.0	
Betula lenta	2	34.5	3.5
Fagus grandifolia	3	26.0	3.2
Pinus strobus	12	41.7	4.7
Quercus rubra	6	36.3	4.6
Tsuga canadensis	27	30.2	2.1

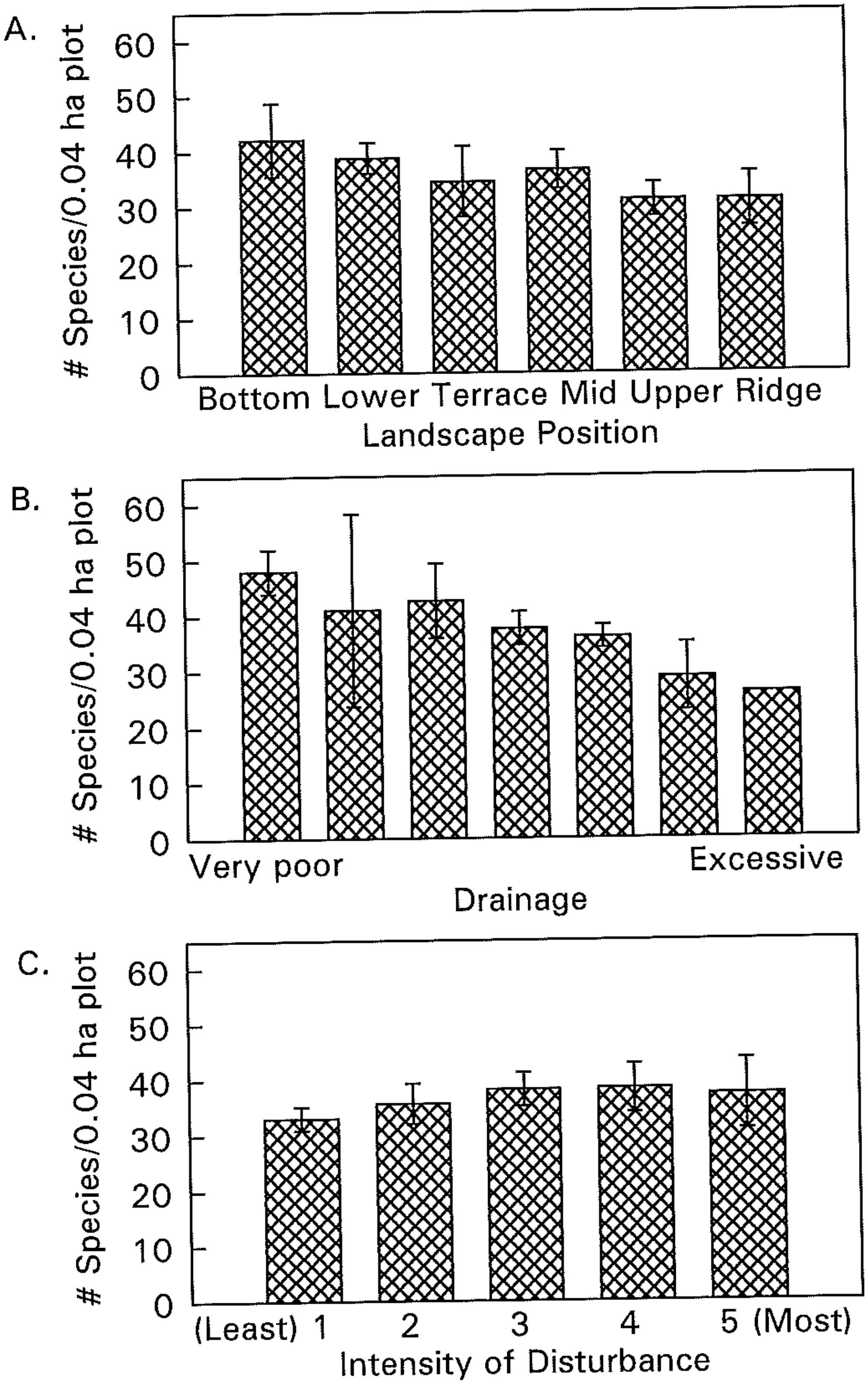

Figure 7. Species richness (# species/0.04 ha) in relation to A) landscape position, B) drainage, and C) intensity of disturbance in study of forest vegetation in Petersham, Massachusetts, U.S.A. Error bars indicate one standard error.

significantly with increasing drainage: species richness is highest on poorly-drained sites and lowest on excessively-drained sites (Figure 7).

Species richness shows no significant relationships to solar irradiation, natural disturbance, forest management, or land-use history (Table 7). Mean species richness is higher, but not significantly so, in plots with evidence of forest fire (43.2 species/0.04 ha) than those without (35.6 species/0.04 ha). Species richness tends to decrease with increasing damage caused by the 1938 hurricane: undamaged sites averaged 37.0 species/0.04 ha, but destroyed sites averaged 27.4 species/0.04 ha. Mean species richness is slightly lower on continually forested sites (33.8 species/0.04 ha) than on former pastures (37.8 species/0.04 ha) or cropland (37.2 species/0.04 ha). Species richness is also higher in post-1870 secondary woodlands (40.9 species/0.04 ha) than in pre-1870 secondary woodlands (34.0 species/0.04 ha).

Species diversity is significantly associated with canopy dominance (ANOVA, df=2, F=5.227, p=0.008) (Table 8). High species richness is associated with canopy dominance by *Acer rubrum* and *Pinus strobus*; and low species richness, with *Tsuga canadensis*. High species richness is also found in two plots dominated by *Acer saccharum* and *Betula alleghaniensis*; and low species richness, in three plots dominated by *Fagus grandifolia*.

Canopy Dominance

The dominant canopy species defined by importance values include eight species and are less diverse than when defined by either total basal area (9 species) or density (11 species) (Table 9). By all measures of dominance, the most important dominant species are *Acer rubrum*, *Pinus strobus*, and *Tsuga canadensis*; and statistical analyses were limited to these three species. *Fagus grandifolia* is an important dominant species by density only, and *Quercus rubra* is important by importance value and total basal area. Canopy dominance shows

Table 9. Number and percentage (in parentheses) of all 70 plots dominated by each individual canopy dominant species based on density (#/0.04 ha), total basal area (m^2/0.04 ha), and importance value (relative density + relative basal area) in Petersham, Massachusetts, U.S.A.

Dominant species	Density	Basal Area	Importance
Acer rubrum	22 (31)	15 (21)	18 (26)
Acer saccharum	2 (3)		1 (1)
Betula alleghaniensis	1 (1)	1 (1)	1 (1)
Betula lenta	3 (4)	2 (3)	2 (3)
Castanea dentata	1 (1)		
Fagus grandifolia	4 (6)	2 (3)	3 (4)
Fraxinus americana		1 (1)	
Hamamelis virginiana	2 (3)		
Ostrya virginiana	1 (1)		
Pinus strobus	6 (9)	15 (21)	12 (17)
Quercus rubra	1 (1)	12 (17)	6 (9)
Quercus velutina		1 (1)	
Tsuga canadensis	27 (39)	21 (30)	27 (39)

significant relationships with landscape position, past land use, and intensity of disturbance, but not with other physiographic or historical variables (Table 7).

Canopy dominance is significantly associated with landscape position: *Acer rubrum* dominates upper slopes and ridges, *Pinus strobus* dominates few bottoms and terraces, and *Tsuga canadensis* dominates lower slopes and few upper slopes and ridges (Table 10). Canopy dominance differs significantly according to both past land use and intensity of disturbance. *Acer rubrum* and *Pinus strobus* dominate moderately and more disturbed sites formerly cleared as pasture. *Tsuga canadensis*, on the other hand, dominates the less disturbed primary woodland sites.

Species Distributions

Frequency of occurrence varies considerably among species. Of the 174 species identified, only 13 percent of the species (n=23 species) are found in ≥50 percent of all plots, but 40 percent (n=70 species) occur in <5 percent of the plots. Common species (occurring in ≥10 plots) include 18 trees, 15 shrubs and woody vines, 14 ferns and fern allies, and 25 forbs (Table 11). Only one graminoid occurs in ≥10 plots. The most significant variables related to the distributions of the 73 common species were species richness, canopy dominance, geomorphology, landscape position, drainage, and past land use.

Distributions of 32 species are significantly related to species richness (Table 12). Not surprisingly, the majority (n=28 species) are associated with high species richness (>42 species/0.04 ha). These rich-site species include six shrubs, eight ferns, one graminoid, 12 forbs, but only one tree (*Crataegus*); and generally represent species found in pooly-drained depositional basins and stream valleys. Only four species are found more frequently on moderately-diverse sites (32-40 species/0.04 ha), and no species are associated with low species richness (<32 species/0.04 ha).

Table 10. Number and percentage (in parentheses) of plots dominated by individual canopy species in relation to landscape position, past land use, and intensity of disturbance in Petersham, Massachusetts, U.S.A. Dominant species are based on importance values (relative density + relative basal area).

	Canopy Dominant		
	Acer	Pinus	Tsuga
Number of plots	18 (26)	12 (17)	27 (39)
<u>Landscape Position</u>			
Bottoms and terraces	3 (4)	1 (1)	6 (9)
Lower slopes	3 (4)	3 (4)	15 (21)
Mid slopes	3 (4)	4 (6)	4 (6)
Upper slopes and ridges	9 (13)	4 (6)	2 (3)
<u>Past Land Use</u>			
Woodland	2 (3)	3 (4)	14 (20)
Former pasture	10 (14)	7 (10)	9 (13)
<u>Intensity of Disturbance</u>			
(Least) 1	1 (1)		14 (20)
2	4 (6)	7 (10)	2 (3)
3	9 (13)	5 (7)	9 (13)
4	2 (3)		1 (1)
(Most) 5	2 (3)		1 (1)

Table 11. Number and proportion of 70 plots in which the 73 common species (n≥10 plots) occur in study of forest vegetation in Petersham, Massachusetts, U.S.A.

Species	Number	Proportion
Trees (n=18 species)		
Acer pensylvanicum	11	0.16
Acer rubrum	70	1.00
Acer saccharum	15	0.21
Amelanchier	24	0.34
Betula alleghaniensis	34	0.49
Betula lenta	46	0.66
Betula populifolia	18	0.26
Carya ovata	13	0.19
Castanea dentata	32	0.46
Crataegus	16	0.23
Fagus grandifolia	32	0.46
Fraxinus americana	26	0.37
Pinus strobus	62	0.89
Prunus serotina	41	0.59
Quercus alba	42	0.60
Quercus rubra	60	0.86
Quercus velutina	29	0.41
Tsuga canadensis	55	0.79
Shrubs and Woody Vines (n=15)		
Cornus alternifolia	12	0.17
Corylus cornuta	28	0.40
Hamamelis virginiana	27	0.39
Ilex verticillata	26	0.37
Kalmia angustifolia	11	0.16
Kalmia latifolia	21	0.30
Lonicera canadensis	11	0.16
Nemopanthus mucronatus	13	0.19
Vaccinium angustifolium	55	0.79
Vaccinium corymbosum	41	0.59
Vaccinium pallidum	14	0.20
Viburnum acerifolium	34	0.49
Viburnum alnifolium	15	0.21
Viburnum nudum	45	0.64
Viburnum dentatum	17	0.24
Ferns and Fern Allies (n=14 species)		
Athyrium filix-femina	15	0.21
Dennstaedtia punctilobula	49	0.70
Dryopteris cristata	12	0.17
Dryopteris marginalis	11	0.16
Dryopteris spinulosa	33	0.47
Lycopodium clavatum	23	0.33
Lycopodium complanatum	16	0.23
Lycopodium lucidulum	16	0.23
Lycopodium obscurum	53	0.76
Onoclea sensibilis	13	0.19
Osmunda cinnamomea	39	0.56
Polystichum acrostichoides	16	0.23
Pteridium aquilinum	33	0.47
Thelypteris noveboracensis	38	0.54
Graminoids and Forbs (n=26 species)		
Anemone quinquefolia	10	0.14
Aralia nudicaulis	59	0.84
Arisaema triphyllum	16	0.23
Aster acuminatus	20	0.29
Aster divaricatus	24	0.34
Brachyelytrum erectum	24	0.34
Clintonia borealis	28	0.40
Coptis trifolia	28	0.40
Cornus canadensis	19	0.27
Cyprepidium acaule	10	0.14
Epigaea repens	11	0.16
Gaultheria procumbens	47	0.67
Goodyera pubescens	10	0.14
Maianthemum canadense	61	0.87
Medeola virginiana	53	0.76
Mitchella repens	66	0.94
Monotropa uniflora	56	0.80
Panax trifolium	10	0.14
Parthenocissus quinquefolia	13	0.19
Rubus hispidus	35	0.50
Rubus pubescens	11	0.16
Smilacina racemosa	17	0.24
Toxicodendron radicans	14	0.20
Trientalis borealis	66	0.94
Trillium undulatum	14	0.20
Uvularia sessilifolia	47	0.67

Table 12. Species distributions significantly associated ($P<0.05$) with species richness (# species/0.04 ha) in Petersham, Massachusetts, U.S.A. Values are the proportion of plots in each species richness class in which each species occurs, and the associated significance values were determined by the likelihood ratio G-statistic.

	Species Richness (#/0.04 ha)				
Species (no. of plots)	0-30	30-42	42-75	G	P
<u>Low Species Richness (0-30 species/0.04 ha plot, n=23)</u>					
<u>Intermediate Species Richness (30-42 species/0.04 ha plot, n=26)</u>					
Amelanchier (24)	0.08	0.53	0.38	12.62	0.002
Dennstaedtia punctiloba (49)	0.52	0.92	0.61	11.67	0.003
Gaultheria procumbens (47)	0.43	0.88	0.66	11.82	0.003
Monotropa uniflora (56)	0.73	0.96	0.66	8.44	0.015
<u>High Species Richness (42-75 species/0.04 ha plot, n=21)</u>					
Anemone quinquefolia (10)	0.00	0.11	0.33	12.09	0.002
Arisaema triphyllum (16)	0.08	0.03	0.61	25.28	0.000
Aster acuminatus (20)	0.08	0.38	0.38	7.61	0.022
Aster divaricatus (24)	0.08	0.46	0.47	11.46	0.003
Athyrium filix-femina (15)	0.04	0.11	0.52	16.85	0.000
Brachyeletrum erectum (24)	0.13	0.26	0.66	15.17	0.001
Coptis trifolia (28)	0.17	0.34	0.71	14.30	0.001
Cornus alternifolia (12)	0.00	0.11	0.42	16.86	0.000
Crataegus (16)	0.00	0.15	0.57	24.25	0.000
Dryopteris cristata (12)	0.04	0.03	0.47	18.37	0.000
Dryopteris marginalis (11)	0.04	0.07	0.38	10.65	0.005
Dryopteris spinulosa (33)	0.34	0.26	0.85	19.58	0.000
Ilex verticillata (26)	0.08	0.30	0.76	23.62	0.000
Kalmia angustifolia (11)	0.00	0.15	0.33	11.83	0.003
Maianthemum canadense (61)	0.73	0.88	1.00	8.71	0.013
Onoclea sensibilis (13)	0.04	0.03	0.52	21.42	0.000
Osmunda cinnamomea (39)	0.30	0.53	0.85	14.74	0.001
Parthenocissus quinquefolia (13)	0.04	0.00	0.57	30.28	0.000
Polystichum acrostichoides (16)	0.08	0.15	0.47	10.28	0.006
Rubus hispidus (35)	0.13	0.57	0.80	23.35	0.000
Rubus pubescens (11)	0.00	0.03	0.47	23.34	0.000
Smilacina racemosa (17)	0.04	0.26	0.42	10.41	0.005
Thelypteris noveboracensis (38)	0.13	0.61	0.90	30.86	0.000
Toxicodendron radicans (14)	0.04	0.03	0.57	24.67	0.000
Uvularia sessifolia (47)	0.30	0.80	0.90	21.71	0.000
Viburnum acerifolium (34)	0.21	0.61	0.61	10.34	0.006
Viburnum dentatum (17)	0.04	0.15	0.57	18.38	0.000
Viburnum nudum (45)	0.30	0.76	0.85	17.66	0.000

Distributions of 15 species are significantly related to overstory type defined by the canopy dominant species (Table 13). Dominance by *Pinus strobus* was associated with the greatest number of significant species (n=8); dominance by *Acer rubrum* is associated with only two species (*Lycopodium complanatum* and *Lycopodium lucidulum*). Six species of trees are significantly associated with canopy dominance. *Betula lenta*, *Castanea dentata*, *Prunus serotina*, and *Quercus rubra* occur more frequently on sites dominated by *Pinus strobus*; and *Tsuga canadensis* and *Betula alleghaniensis* occur more frequently in plots dominated by *Tsuga canadensis*.

Geomorphology is significantly related to the distribution of 29 species (Table 14). The largest number of significant associations are with depositional basins (n=15 species) and unstratified marginal moraines (n=6 species). Only two species are found more frequently on stratified glacial deposits and stream valleys. Shrubs (n=4 species) are the prevalent life form associated with unstratified marginal moraines. Two species of *Lycopodium* are significantly associated with unstratified till on bedrock ridges; and six ferns (including three species of *Dryopteris*) occur more frequently in depositional basins.

Landscape position is significantly related to the distribution of 19 species (Table 15). Twelve species are associated with bottoms and terraces; fewer species occur more frequently on intermediate or upper slope positions. Three ferns but no shrubs are found more frequently on bottoms and terraces.

Drainage is significantly associated with the distributions of 25 species (Table 16). Poorly-drained sites (which include very poorly-drained, poorly-drained and imperfectly-drained sites) are associated with 15 species. Eight of the remaining species are associated with well-drained sites. The nine ferns represented 36 percent of the significant species but only 20 percent of the species analyzed. Six species associated with poor drainage are not found on excessively-

Table 13. Species distributions significantly associated ($P<0.05$) with canopy dominant species in Petersham, Massachusetts, U.S.A. Canopy dominance was based on importance values (relative density + relative basal area). The values are the proportion of plots dominated by each canopy dominant in which each species occurs, and the associated significance values were determined by the likelihood ratio G-statistic.

	Dominant Canopy Species				
Species (no. of plots)	Acer	Pinus	Tsuga	G	P
<u>Acer rubrum (n=18)</u>					
Lycopodium complanatum (13)	0.44	0.25	0.07	8.72	0.013
Lycopodium lucidulum (13)	0.33	0.00	0.25	7.39	0.025
<u>Pinus strobus (n=12)</u>					
Betula lenta (37)	0.83	0.91	0.40	14.27	0.001
Castanea dentata (23)	0.55	0.66	0.18	11.00	0.004
Corylus cornuta (24)	0.44	0.83	0.22	13.44	0.001
Lycopodium clavatum (18)	0.44	0.50	0.14	7.08	0.029
Parthenocissus quinquefolia (11)	0.27	0.41	0.03	9.79	0.007
Prunus serotina (31)	0.72	0.83	0.29	13.68	0.001
Quercus rubra (50)	0.94	1.00	0.77	6.14	0.047
Viburnum acerifolium (24)	0.44	0.75	0.25	8.46	0.015
<u>Tsuga canadensis (n=27)</u>					
Betula alleghaniensis (27)	0.27	0.25	0.70	11.28	0.004
Osmunda cinnamomea (33)	0.44	0.33	0.77	8.98	0.011
Trillium undulatum (11)	0.05	0.08	0.33	6.94	0.031
Tsuga canadensis (47)	0.61	0.75	1.00	15.39	0.000
<u>Multiple Associations</u>					
Maianthemum canadense (50)	1.00	1.00	0.74	11.56	0.003

Table 14. Species distributions significantly associated ($P<0.05$) with geomorphology in Petersham, Massachusetts, U.S.A. Values are the proportion of plots in each geomorphological type i which each species occurs, and the associated significance values were determined by the likelihood ratio G-statistic.

	Geomorphology						
Species (no. of plots)	Bedrock	Basin	Stream	Moraine	Outwash	G	P
<u>Unstratified Till on Bedrock Ridges (n=21)</u>							
Betula lenta (45)	0.95	0.40	0.50	0.66	0.53	15.65	0.00
Lycopodium clavatum (22)	0.57	0.00	0.10	0.41	0.26	16.73	0.00
Lycopodium complanatum (15)	0.42	0.10	0.00	0.08	0.26	12.30	0.01
<u>Stratified and Unstratified Depositional Basins (n=10)</u>							
Arisaema triphyllum (15)	0.00	0.90	0.20	0.16	0.13	32.66	0.00
Athyrium filix-femina (14)	0.04	0.70	0.30	0.16	0.06	19.16	0.00
Coptis trifolia (28)	0.19	0.90	0.40	0.33	0.46	15.72	0.00
Crataegus (15)	0.19	0.60	0.20	0.16	0.06	9.68	0.04
Dryopteris cristata (11)	0.04	0.80	0.00	0.00	0.13	30.36	0.00
Dryopteris marginalis (10)	0.09	0.40	0.30	0.08	0.00	11.02	0.02
Dryopteris spinulosa (32)	0.42	0.90	0.60	0.25	0.33	12.80	0.01
Fraxinus americana (24)	0.33	0.70	0.40	0.41	0.06	12.24	0.01
Ilex verticillata (25)	0.28	0.90	0.40	0.25	0.20	15.85	0.00
Onoclea sensibilis (13)	0.00	0.80	0.20	0.08	0.13	27.68	0.00
Osmunda cinnamomea (39)	0.28	1.00	0.80	0.50	0.60	20.83	0.00
Parthenocissus quinquefolia (12)	0.04	0.50	0.20	0.25	0.06	10.62	0.03
Rubus hispidus (35)	0.57	0.90	0.30	0.66	0.20	16.52	0.00
Rubus pubescens (10)	0.04	0.80	0.00	0.08	0.00	31.86	0.00
Toxicodendron radicans (14)	0.04	0.70	0.30	0.25	0.00	23.18	0.00
<u>Stream Valleys in Unstratified Till (n=10)</u>							
Aster divaricatus (22)	0.28	0.30	0.60	0.50	0.06	10.82	0.02
<u>Unstratified Marginal Moraine (n=12)</u>							
Castanea dentata (31)	0.61	0.40	0.10	0.83	0.20	20.04	0.00
Corylus cornuta (27)	0.47	0.40	0.30	0.66	0.13	9.57	0.04
Hamamelis virginiana (26)	0.19	0.20	0.40	0.66	0.53	10.54	0.03
Quercus alba (40)	0.76	0.30	0.40	0.83	0.46	11.87	0.01
Vaccinium pallidum (14)	0.33	0.00	0.00	0.41	0.13	14.34	0.00
Viburnum acerifolium (33)	0.57	0.30	0.40	0.83	0.26	11.64	0.02
<u>Stratified Outwash and Ice-Contact Drift (n=15)</u>							
Clintonia borealis (28)	0.14	0.60	0.50	0.33	0.66	13.22	0.01
<u>Multiple Associations</u>							
Aster acuminatus (20)	0.09	0.50	0.50	0.50	0.13	13.04	0.01
Betula alleghaniensis (34)	0.33	0.80	0.80	0.41	0.40	11.03	0.02
Trientalis borealis (64)	1.00	1.00	0.70	1.00	0.93	10.86	0.02

Table 15. Species distributions significantly associated ($P<0.05$) with landscape position in Petersham, Massachusetts, U.S.A. Values are the proportion of plots in each landscape position in which each species occurs, and the associated significance values were determined by the likelihood ratio G-statistic.

	Landscape Position					
Species (no. of plots)	Bottom	Lower	Midslope	Ridge	G	P
Bottoms and Terraces (n=13)						
Betula alleghaniensis (34)	0.69	0.66	0.28	0.26	11.73	0.008
Coptis trifolia (28)	0.76	0.54	0.28	0.05	22.48	0.000
Dryopteris cristata (12)	0.38	0.12	0.28	0.00	11.98	0.007
Epigaea repens (11)	0.30	0.16	0.21	0.00	8.66	0.034
Osmunda cinnamomea (39)	0.84	0.83	0.28	0.21	27.03	0.000
Thelypteris noveboracensis (38)	0.69	0.66	0.64	0.21	12.12	0.007
Trillium undulatum (14)	0.38	0.37	0.00	0.00	20.98	0.000
Tsuga canadensis (55)	0.92	0.91	0.78	0.52	11.09	0.011
Lower Slopes (n=24)						
Aster acuminatus (20)	0.38	0.45	0.21	0.05	10.95	0.012
Clintonia borealis (28)	0.61	0.66	0.07	0.15	22.57	0.000
Cornus canadensis (19)	0.46	0.50	0.00	0.05	22.80	0.000
Viburnum alnifolium (15)	0.30	0.37	0.00	0.10	12.15	0.007
Mid Slopes (n=14)						
Castanea dentata (32)	0.15	0.33	0.71	0.63	13.05	0.005
Monotropa uniflora (56)	0.53	0.83	1.00	0.78	10.93	0.012
Panax trifolium (10)	0.00	0.12	0.35	0.10	8.30	0.040
Ridges and Upper Slopes (n=19)						
Betula lenta (46)	0.46	0.45	0.85	0.89	14.69	0.002
Lycopodium complanatum (16)	0.15	0.08	0.21	0.47	9.49	0.023
Lycopodium clavatum (23)	0.00	0.22	0.54	0.18	16.46	0.001
Lycopodium obscurum (53)	0.30	0.72	0.93	0.72	16.40	0.001
Quercus rubra (60)	0.50	0.88	0.93	0.90	9.46	0.024
Viburnum nudum (45)	0.70	0.61	0.80	0.18	14.08	0.003
Excessively drained (n=11)						
Betula lenta (46)	0.20	0.72	0.70	0.81	10.95	0.012

Table 16. Species distributions significantly associated ($P<0.05$) with drainage in Petersham, Massachusetts, U.S.A. Values are the proportion of plots in each drainage class in which each species occurs, and the associated significance values were determined by the likelihood ratio G-statistic.

	Drainage					
Species (no. of plots)	Poor	Moderate	Well	Excessive	G	P
Poorly drained (n=10)						
Arisaema triphyllum (16)	0.70	0.27	0.09	0.09	15.36	0.002
Betula alleghaniensis (34)	0.90	0.50	0.45	0.18	12.41	0.006
Brachyeletrum erectum (24)	0.70	0.44	0.22	0.18	9.51	0.023
Cornus canadensis (19)	0.60	0.33	0.22	0.00	12.36	0.006
Coptis trifolia (28)	0.90	0.50	0.29	0.09	18.71	0.000
Dryopteris cristata (12)	0.70	0.11	0.06	0.09	17.83	0.000
Dryopteris spinulosa (33)	0.80	0.66	0.35	0.18	13.13	0.004
Ilex verticillata (26)	0.60	0.50	0.35	0.00	13.62	0.003
Lycopodium lucidulum (16)	0.50	0.16	0.25	0.00	9.77	0.021
Onoclea sensibilis (13)	0.60	0.27	0.06	0.00	17.63	0.001
Osmunda cinnamomea (39)	1.00	0.72	0.48	0.09	25.21	0.000
Rubus hispidus (35)	0.70	0.66	0.45	0.18	8.79	0.032
Rubus pubescens (11)	0.50	0.11	0.09	0.09	8.05	0.045
Trillium undulatum (14)	0.50	0.11	0.22	0.00	10.52	0.015
Viburnum dentatum (17)	0.40	0.33	0.22	0.00	8.12	0.044
Moderately well drained (n=18)						
Thelypteris noveboracensis (38)	0.70	0.77	0.41	0.36	8.65	0.034
Well drained (n=31)						
Castanea dentata (32)	0.20	0.27	0.64	0.45	9.76	0.021
Dennstaedtia punctiloba (49)	0.40	0.66	0.87	0.54	10.15	0.017
Gaultheria procumbens (47)	0.40	0.50	0.87	0.63	11.97	0.007
Lonicera canadensis (11)	0.10	0.00	0.25	0.18	8.55	0.036
Vaccinium pallidum (14)	0.07	0.12	0.07	0.47	11.43	0.010
Multiple Associations						
Trientalis borealis (66)	1.00	0.83	1.00	1.00	9.04	0.029

drained sites.

Significant interactions among geomorphology, landscape position, and drainage are illustrated by the 20-25 percent of the species significantly associated with at least two of these variables (Table 17). Species significantly associated with at least two variables are found mostly on poor drainage, on bottoms and terraces, and in depositional basins. Fewer species occur more frequently on combinations of well- or excessively-drained upper slopes and ridges of marginal moraine or bedrock ridges.

Past land use is significantly associated with the distributions of 19 species (Table 18). More species are associated with former pasture (n=12) than woodland (n=7). Significant species on former pastures include a high proportion of trees (n=6 species); no ferns are found significantly more frequently in woodland. No species are restricted solely to either woodland or former pasture: all species occur in at least low frequencies on both land uses.

Distributions of few species are significantly associated with the remaining factors. *Quercus rubra* and *Aster divaricatus* occur more frequently on sites with high annual solar irradiation. *Prunus serotina* is found more frequently on sites undamaged in the 1938 hurricane; and *Aster acuminatus*, *Hamamelis virginiana*, *Smilacina racemosa*, and *Uvularia sessifolia* are associated with evidence of fire. *Amelanchier* occurs more frequently on sites with >3 cut stumps; *Aralia nudicaulis*, *Lycopodium lucidulum*, and *Panax trifolium* occur more frequently where there is no evidence of cutting. *Thelypteris noveboracensis* and *Uvularia sessilifolia* are found preferentially in pre-1870 secondary woodlands, and *Betula populifolia* and *Monotropa uniflora* occur more frequently in post-1870 secondary woodlands.

Life forms vary considerably in the number of significant associations with different variables (Table 19). Trees are primarily associated with past land use and secondarily with physiographic

Table 17. Number and percentage (in parentheses) of 73 common species ($n \geq 10$ plots) shared among geomorphology, landscape position, and drainage in study of forest vegetation in Petersham, Massachusetts, U.S.A. Shared species are those which are significantly associated with at least two physiographic variables; these species are listed in the combination of the two variables in which they occur most frequently. Combinations without numbers do not occur in sample plots.

	Landscape Position (n=19 species)			
	Bottom	Lower	Mid	Upper
<u>Geomorphology (n=29 species)</u>				
Depositional basin	3 (4)	0 (0)	0 (0)	0 (0)
Stream valley		0 (0)		
Stratified outwash	0 (0)	1 (1)	0 (0)	0 (0)
Marginal moraine		0 (0)	1 (1)	1 (1)
Bedrock ridge		0 (0)	0 (0)	2 (3)

	Drainage (n=25 species)			
	Poor	Moderate	Well	Excessive
<u>Geomorphology (n=29 species)</u>				
Depositional basin	9(13)	0 (0)	0 (0)	
Stream valley		0 (0)	0 (0)	
Stratified outwash	0 (0)	0 (0)	0 (0)	0 (0)
Marginal moraine			1 (1)	0 (0)
Bedrock ridge		0 (0)	1 (1)	1 (1)
<u>Landscape Position (n=19 species)</u>				
Bottom and terrace	5 (7)	1 (1)		0 (0)
Lower slope	1 (1)	0 (0)	0 (0)	0 (0)
Mid slope	0 (0)	0 (0)	1 (1)	0 (0)
Upper slope and ridge		0 (0)	0 (0)	1 (1)

Table 18. Species distributions significantly associated ($P<0.05$) with past land use in Petersham, Massachusetts, U.S.A. Values are the proportion of former cropland and woodland in which each species occurs, and the associated significance values were determined by the likelihood ratio G-statistic.

Species (no. of plots)	Woodland	Pasture	G	P
<u>Woodland (n=24)</u>				
Clintonia borealis (25)	0.75	0.21	16.38	0.000
Coptis trifolia (26)	0.62	0.34	4.41	0.036
Gaultheria procumbens (35)	0.79	0.50	5.17	0.023
Kalmia latifolia (16)	0.45	0.15	6.16	0.013
Medeola virginiana (42)	0.91	0.62	6.87	0.009
Trillium undulatum (14)	0.45	0.09	9.96	0.002
Tsuga canadensis (44)	1.00	0.62	15.85	0.000
<u>Former Pasture (n=32)</u>				
Acer saccharum (13)	0.04	0.37	10.03	0.002
Aster divaricatus (20)	0.20	0.46	4.20	0.040
Corylus cornuta (20)	0.20	0.46	4.20	0.040
Crataegus (12)	0.08	0.31	4.68	0.031
Fraxinus americana (23)	0.25	0.53	4.61	0.032
Ilex verticillata (21)	0.20	0.50	5.17	0.023
Lycopodium complanatum (10)	0.04	0.28	6.22	0.013
Maianthemum canadense (48)	0.75	0.93	3.98	0.046
Polystichum acrostichoides (15)	0.12	0.37	4.66	0.031
Prunus serotina (33)	0.41	0.71	5.21	0.022
Quercus alba (30)	0.37	0.65	4.41	0.036
Toxicodendron radicans (12)	0.08	0.31	4.68	0.031

Table 19. Number of species of each life form with significant logistic regression models or significantly associated (tested by likelihood ratio G-statistic) with important physiographic and historical variables in forest plots in Petersham, Massachusetts, U.S.A. Values are the number of significant species in each life form.

Variable	Trees	Shrubs	Ferns	Grass	Forbs	Total
Total Species Analyzed	18	15	14	1	25	73
UNIVARIATE SPECIES ANALYSES						
<u>Physiography</u>						
Geomorphology	6	5	8		10	29
Landscape Position	4	2	4		9	19
Drainage	4	4	9	1	7	25
Solar irradiation	1				1	2
<u>Natural Disturbances</u>						
Evidence of fire		1			3	4
Hurricane damage	1					1
<u>Forest Management</u>						
Number of stumps	1		1		2	4
<u>Land-use History</u>						
Past land use	6	3	2		8	19
Age of secondary woodlands	1		1		2	4
LOGISTIC REGRESSION MODELS						
No Significant Model	6	7	4		6	26
<u>Physiography</u>						
Geomorphology		1				1
Landscape position	5	2	4		5	16
Drainage	1	2	6	1	3	13
Solar irradiation						0
<u>Natural Disturbances</u>						
Hurricane damage	1					1
Evidence of fire					1	1
<u>Forest Management</u>						
Number of stumps	1				2	3
<u>Land-use History</u>						
Intensity of disturbance	4	1			1	6
Age of secondary woodlands	1	1			4	6

variables. Both shrubs and ferns are rarely associated with land-use history and are more likely to be associated with drainage or geomorphology. Distributions of forbs are associated equally among most physiographic and historical variables.

Models of Species Distributions

Stepwise logistic regression successfully modelled distributions of 46 species in relation to physiographic and historical variables (Table 20). Selected variables correctly predict 55 to 86 percent (mean: 69 percent) of species' presence and absence. The most important variables include landscape position (n=16 species), drainage (n=13 species), intensity of disturbance, and age of secondary woodlands (both n=6 species). Solar irradiation is never the most significant variable (but is a secondary variable for four species); and number of stumps, geomorphology, hurricane damage, and evidence of fire are the most significant variables for ≤ 3 species each.

The relative importance of individual variables differs among life forms (Table 19). More trees are successfully modelled by intensity of disturbance (n=4 species); and fewer, by drainage or age of secondary woodlands (both n=1). More ferns, on the other hand, are modelled by drainage (n=6 species), but few are modelled by variables describing natural disturbance, forest management, or land-use history. Shrubs are also modelled less by natural disturbance or forest management. Forbs are successfully modelled by a variety of physiographic and historical variables.

DISCUSSION

Community Patterns

The modern forests of Petersham are dominated by species characteristic of the transition hardwoods-white pine-hemlock region. These species include both northern (*Acer saccharum* and *Betula*

Table 20. Models of species distributions selected by logistic regression to best predict the occurrence of 73 common species (n≥10 plots) in Petersham, Massachusetts, U.S.A. Success measures the proportion of species presence and absence correctly predicted by the selected variable(s).

Species (no. of plots)	Model [Constant * Variable(s)]	Success
<u>Geomorphology</u>		
Hamamelis virginiana (27)	Geomorphology	0.584
<u>Landscape Position</u>		
Aster acuminatus (20)	Position	0.670
Betula alleghanienis (34)	Position	0.618
Betula lenta (46)	Position	0.640
Castanea dentata (32)	Position	0.555
Clintonia borealis (28)	Position * Disturbance	0.696
Coptis trifolia (28)	Position * Drainage * Age	0.733
Cornus canadensis (19)	Position	0.696
Lycopodium clavatum (23)	Position	0.598
Lycopodium complanatum (16)	Position * Damage	0.760
Osmunda cinnamomea (39)	Position * Drainage	0.743
Quercus alba (42)	Position * Stumps * Disturbance * Fire	0.669
Thelypteris noveboracensis (38)	Position	0.567
Trillium undulatum (14)	Position * Disturbance * Fire	0.860
Tsuga canadensis (55)	Position * Age	0.764
Vaccinium pallidum (14)	Position * Fire	0.737
Viburnum alnifolium (15)	Position	0.717
<u>Drainage</u>		
Arisaema triphyllum (16)	Drainage	0.735
Athyrium filix-femina (15)	Drainage * Age	0.733
Brachyeletrum erectum (24)	Drainage	0.601
Dryopteris cristata (12)	Drainage	0.801
Dryopteris spinulosa (33)	Drainage * Solar * Age	0.650
Ilex verticillata (26)	Drainage * Disturbance	0.638
Lycopodium lucidulum (16)	Drainage * Stumps	0.711
Lycopodium obscurum (53)	Drainage	0.693
Onoclea sensibilis (13)	Drainage	0.776
Quercus rubra (60)	Drainage * Solar	0.819
Rubus hispidus (35)	Drainage	0.552
Rubus pubescens (11)	Drainage	0.777
Viburnum dentatum (17)	Drainage * Disturbance	0.698
<u>Solar Irradiation</u>		
<u>Hurricane Damage</u>		
Betula populifolia (18)	Damage	0.645
<u>Evidence of Fire</u>		
Smilacina racemosa (17)	Fire	0.666
<u>Number of Stumps</u>		
Aralia nudicaulis (59)	Stumps * Drainage	0.771
Kalmia latifolia (21)	Stumps	0.607
Pinus strobus (62)	Stumps * Solar	0.832
<u>Intensity of Disturbance</u>		
Acer saccharum (15)	Disturbance	0.700
Corylus cornuta (28)	Disturbance	0.556
Crataegus (16)	Disturbance	0.677
Maianthemum canadense (61)	Disturbance	0.802
Prunus serotina (41)	Disturbance * Geomorphology	0.623
Quercus velutina (29)	Disturbance * Age	0.615
<u>Age of Secondary Woodland</u>		
Fagus grandifolia (32)	Age	0.547
Gaultheria procumbens (47)	Age * Moist	0.620
Medeola virginiana (53)	Age	0.664
Parthenocissus quinquefolia (13)	Age * Damage	0.742
Toxicodendron radicans (14)	Age * Drainage	0.748
Vaccinium angustifolium (55)	Age * Disturbance	0.726

alleghaniensis) and southern components (*Carya ovata*, *Fraxinus americana*, *Prunus serotina*, *Quercus alba*, *Quercus rubra*, and *Quercus velutina*). Distributions of the two important conifers, *Pinus strobus* and *Tsuga canadensis*, are centered on the New England region (Nichols 1935; Westveld 1956). *Acer rubrum* is a ubiquitous species and occurs on all sites regardless of physiography or history.

The modern forests differ from those found in New England historically. Prior to European settlement, even and uneven-aged stands were maintained by recurring disturbances, and vegetation cycled between shade-intolerant species (*Acer rubrum* and *Betula*) and the more shade-tolerant, slow-growing hardwoods and *Tsuga canadensis* (Whitney and Foster 1988). The presettlement forests included many of the same species but in different abundances: *Acer saccharum*, *Castanea dentata*, *Fagus grandifolia*, *Pinus strobus*, and *Tsuga canadensis* were more common; but *Betula* was less common (Westveld 1956; Foster 1992; Foster et al. 1992). The central hardwoods (*Castanea dentata*, *Pinus strobus*, and *Quercus*) occurred on xeric ridges; and northern hardwoods (*Acer*, *Betula*, *Fagus grandifolia*, and *Fraxinus americana*) and *Tsuga canadensis* were found in cool, moist coves (Raup and Carlson 1941; Foster et al. 1992). Species associated with swamps included *Acer rubrum* and *Picea rubens*.

Overall species diversity (174 species) and mean species richness (36.2 species/0.04 ha) are intermediate in comparison to other temperate forests (*cf*. Peet 1978). Spatial distribution of species richness reflects the concentration of both rare and common species in specific habitats. Species diversity in small woodlands often corresponds to heterogeneity in the physical habitat structure and frequent disturbances (Brown 1988; Dzwonko and Loster 1988). In Petersham, intermediate species diversity reflects the lack of habitat heterogeneity or frequent disturbance; Petersham is largely vegetated by mature, upland forest.

Species diversity often increases in more disturbed and fragmented woodlands, but the component species include fewer woodland species and more open-site species. For example, active floodplains are more diverse because of frequent flooding (Hack and Goodlett 1960). High diversity often is associated with intermediate stages of succession which include both early and late successional species (Horn 1974). In less disturbed woodlands, species richness may decrease as stands develop successionally and exclude shade-intolerant and non-woodland species (Levenson 1981; Peet et al. 1983; Dzwonko and Loster 1988). However, species diversity may increase in later stages of succession, as early successional species are supplemented by late successional species (Drury and Nisbet 1973; Peet et al. 1983).

Overstory type, defined by the dominant canopy species, is largely restricted to four species: *Acer rubrum*, *Pinus strobus*, *Quercus rubra*, and *Tsuga canadensis*. *Pinus strobus* is significantly associated with the distributions of the most species. *Acer rubrum* and *Pinus strobus* dominate more disturbed sites (especially secondary woodlands formerly cleared as pasture); shade-tolerant *Tsuga canadensis*, on the other hand, dominates mature forests in less disturbed primary woodlands. During secondary succession in central New England, *Acer rubrum* and *Pinus strobus* remain important but are supplanted by the more shade-tolerant *Tsuga canadensis*. On well and excessively-drained sites, *Pinus strobus* and *Betula populifolia* are replaced by *Tsuga canadensis* and *Quercus rubra* (Spurr 1956).

The influence of overstory type on species composition may also reflect the impact of overstory trees on light environment, microclimate, and litter and soil properties (Whitney and Foster 1988; Collins 1990). *Tsuga canadensis* and *Fagus grandifolia* are associated with low diversity, and *Acer rubrum* and *Pinus strobus* are associated with high diversity. *Tsuga canadensis* and *Pinus strobus* stands are characterized by high C/N ratios, Al and Fe concentrations, soil organic matter, available nitrogen, cation exchange capacity, and litter depth;

and low calcium, moisture, temperature, pH, and A horizon depth (Beatty 1982; Whitney and Foster 1988). However, understory light levels differ, and the paucity of species associated with *Tsuga canadensis* probably reflects greatly reduced light levels. In *Tsuga* stands, vernal species are rare and are replaced by species reaching maximum growth in late summer and fall (Beatty 1982; Whitney and Foster 1988).

Physiography and Soils

Distributions of forest species reflect physiographic and soil gradients, especially those relating to moisture and soil fertility. Many species specialize in a limited range of conditions in which they are competitively superior (Drury and Nisbett 1973). To a large degree, species distributions are controlled by spatial heterogeneity in physiography and soils. In Petersham, forest composition largely reflects the control exerted by several interrelated physiographic factors (geomorphology, landscape position, and drainage). Both geomorphology and landscape position play an important role in controlling drainage patterns; geomorphology also controls physical, chemical, and minerological characteristics of the substrate (Buol et al. 1980).

Canopy dominance is significantly associated with landscape position: *Acer rubrum* dominates upper slopes and ridges, and *Tsuga canadensis* dominates lower slopes and few upper slopes and ridges; and *Pinus strobus* dominates few bottoms and terraces. Dominance of the more xeric ridges and upper slopes by *Acer rubrum* contradicts other studies in which this species dominated poorly-drained sites (Spurr 1956; Walker 1975). This discrepancy may reflect successional changes: poorly-drained sites were less disturbed or were abandoned prior to 1870 and now support a more mature, shade-tolerant flora.

Distributions of the most species are associated with geomorphology and drainage (40 and 36 percent of the 73 common species, respectively). Species richness is highest on poorly-drained depositional basins and stream valleys, which are also associated with the largest number of species distributions. Unstratified tills on bedrock ridges and stratified outwash and contact drift support a less diverse flora; however, well- and excessively-drained ridges and upper slopes are significantly associated with the distributions of several species.

Species distributions have been related to depositional history, geomorphology, substrate, and topographic position; however, the unifying resources are interpreted as water and nutrient availability (Hack and Goodlett 1960; Collins 1990; Whitney 1991; Host and Pregitzer 1992). In central New England, xerophytic trees occur on sites underlain by permeable tills; the distributions of other trees depend on depth to water tables perched on compact tills (Stout 1952; Spurr 1956; Lyford et al. 1963; Walker 1975). Southern species (*Carya ovata*, *Castanea dentata*, and *Quercus rubra*) occur on xeric, south-facing slopes and ridges, and the northern hardwoods (*Betula alleghaniensis* and *Fagus grandifolia*) and *Tsuga canadensis* occur on cool, moist bottomlands and coves.

The species associated with unstratified marginal moraines resemble a xeric *Quercus*-shrub community. Drainage is generally well or excessive; and important species include *Quercus alba*, *Castanea dentata*, *Corylus cornuta*, *Hamamelis virginiana*, *Vaccinium pallidum*, and *Viburnum acerifolium*. Host and Pregitzer (1992) identified similar oak-dominated communities in southern Michigan, where important shrubs include *Hamamelis virginiana*, *Vaccinium angustifolium*, and *Gaylussacia baccata*.

Potential solar irradiation measures light availability as influenced by latitude, slope aspect, and slope gradient. Most species, including trees which directly absorb incoming irradiation, are distributed independent of potential solar irradiation. Potential annual solar irradiation measures potential light levels above the canopy, not in the forest understory. Distributions of understory species instead reflect the structure and composition of the overstory, which filters incoming solar irradiation (Collins and Wein 1993).

Natural Disturbance

Natural disturbances can dramatically alter overstory composition and structure; yet in this study neither evidence of fire nor hurricane damage is significantly associated with forest composition. Windthrow and fire represent two of the most important natural disturbances in central New England (other significant disturbances include pathogens and insect defoliation). Infrequent and isolated windthrow and fire events may be insufficient to alter vegetation composition, although single large-scale events can drastically change vegetation communities (Foster 1988; Sprugel 1991). Both fire and windthrow have significant impacts on age structure, size, density, and crown height of forest patches; and available resources and competition for these resources can change dramatically following removal or modification of the overstory structure (Tande 1979; Foster and King 1986; Foster 1988; Foster and Boose 1992).

In central New England, fires occurred infrequently in the presettlement forests (Patterson and Backman 1988; Foster and Zebryk 1993). Following European settlement, fire frequency increased, and evidence of fire may reflect burning either during or after agricultural land uses. Human-set fires were used to rejuvenate grasslands and to burn slash following logging (Foster 1992). In southwestern New Hampshire, fire-return intervals were 6-43 years during the historical period; but many of these fires occurred within 20 years of major windthrow events, which provided significant fuel accumulations (Foster 1988).

Fire periodicity, intensity, and extent are largely determined by local meteorological and physiographic conditions and have significant impacts on forest heterogeneity and structure. Mesic forests are characterized by less frequent but more intensive fires (Tande 1979; Foster 1983; Foster and King 1986). Frequent, low-intensity fires, which burn mostly understory vegetation and surface litter, often have minimal impact on forest composition. Established hardwoods and understory species sprout or sucker vigorously after all but the most severe fires (Foster 1985; Raup and Carlson 1941).

Damage inflicted by the 1938 hurricane explains little variation in forest composition. The 1938 hurricane had a major impact on forest structure in central New England, and the lack of significant effects on species composition is surprising given the catastrophic damage caused by hurricane winds (Foster 1988; Foster and Boose 1992). Only *Prunus serotina* was significantly associated with hurricane damage. Apparently the impacts of the 1938 hurricane were largely confined to overstory structure or were short-lived in terms of forest composition.

Hurricane damage is heterogenous in both intensity (damage ranged from none to >75 percent of stems broken or uprooted) and distribution across the landscape (most patches were <2 ha in size). During the past 400 years in central New England, severe windstorms occurred at least 12 times, and four major hurricanes were responsible for catastrophic forest damage (Foster and Boose 1992). The heterogeneity in forest damage suggests that forest vegetation should differ across the landscape. However, New England forests have developed with a history of recurrent windthrow, so that most species may be adapted to survive windthrow disturbance.

Forest Management

Forest management, measured by the number of stumps, shows few signficant relationships to forest composition. Like natural disturbances, forest harvesting drastically alters forest microenvironments and resource availability. The lack of significant relationships with species composition may reflect the fact that sites suffering recent logging were excluded from the sampling. During 1890-1910, much of the old-field *Pinus strobus* was logged and replaced by hardwoods. Subsequent cutting of the hardwoods resulted in coppice growths of hardwood sprouts. Despite selective cutting of hardwoods, logging has favored sprout hardwoods (*Acer rubrum*, *Castanea dentata*, *Quercus rubra*) and the shade-tolerant *Tsuga canadensis* (Raup and Carlson 1941; Foster et al. 1992).

The lack of response to logging may indicate the ability of species composition to recover quickly following canopy closure. Logging removes large quantities of forest biomass and alters overstory composition and structure, and removal of the overstory increases light and resource availability and decreases competition. These additional resources are exploited by understory species, especially spring ephemerals; and dramatic increases in abundance and distribution follow overstory removal (Hughes 1992). After several years, the spatial distribution of woodland species resembles that found prior to overstory removal. Although relative importance differs, understory composition is nearly identical in undisturbed and logged secondary stands (Hughes and Fahey 1991; Muller 1982). Logging is similar to hurricane damage in the loss of overstory structure and soil scarification. Since New England forests developed with a history of windthrow, many species may be pre-adapted to survive logging disturbances.

Land-Use History

Besides physiography, land-use history represents the other important group of variables explaining forest composition. All land-use history variables are significantly interrelated: woodland history, intensity of disturbance, and age of secondary woodlands.Historical land-use patterns, to some degree, were controlled by physiography and soil (*cf.* Iverson 1988). Among the physiographic variables, land-use history is only associated with landscape position (more intensive land uses occur at higher slope positions). Land-use boundaries marked by stone walls often change abruptly at slight changes in geomorphology and/or drainage.

Canopy dominance is associated with past land use and intensity of disturbance, but not age of secondary woodlands. *Acer rubrum* and *Pinus strobus* dominate former pastures with intermediate levels of disturbance; and *Tsuga canadensis* dominates the less disturbed primary woodlands. These patterns reflect the patterns of secondary succession discussed previously. *Pinus strobus* was the dominant old-field species on many sites, but *Acer rubrum* dominated poorly or moderately-drained sites. In contrast, the shade-tolerant *Tsuga canadensis* dominates mature, late-successional forests on less disturbed sites (Nichols 1935; Spurr 1956).

Species associated with primary woodlands are generally considered to be northern species adapted to cool, moist climates; and secondary woodland species represent southern species adapted to more xeric conditions (Whitney and Foster 1988). In this study, species associated with primary woodlands generally have distributions centered in the hemlock-white pine-northern hardwoods region of eastern North America (Nichols 1935). Species associated with former pasture occur throughout this region but also occur frequently in more southern deciduous forests (especially *Prunus serotina* and *Toxicodendron radicans*).

Primary woodland species also represent shade-tolerant species (e.g. *Tsuga canadensis*). Most trees associated with former pasture are shade-intolerant species (*Fraxinus americana*, *Prunus serotina*, and *Quercus alba*). Only *Acer saccharum* is shade-tolerant; however, its association with former pasture no doubt reflects planting as sugarbush. This association of shade tolerance and land-use history again reflects the successional trends discussed previously.

Few species are significantly associated with the age of secondary woodlands, probably because most stands are too old to resemble early successional stands. Most sites were abandoned prior to 1900, and many were abandoned prior to 1870. In this study, only *Thelypteris noveboracensis* and *Uvularia sessilifolia* are found more frequently in pre-1870 secondary woodlands, and *Betula populifolia* and *Monotropa uniflora* occur more frequently in post-1870 secondary woodlands.

In young successional or largely fragmented forests, land-use history remains the prevailing influence on both overstory and understory composition. In central New England, *Betula lenta*, *Quercus alba*, and *Tsuga canadensis* were associated with stands >50 years old; and *Betula populifolia*, *Pinus strobus*, *Pinus rigida*, *Populus grandidentata*, *Prunus serotina*, *Juniperus communis*, and *Comptonia* were associated with stands <50 years old (Foster 1992; Whitney, Unpublished). In Europe, primary woodlands support a distinct and more diverse woodland flora than found in secondary woodlands, even those located adjacent to primary woodlands or those 700-900 years of age (Hermy and Stieperaere 1981; Peterken and Game 1984; Dzwonko and Loster 1990).

The inability of woodland species to colonize secondary woodlands, whether isolated or adjacent to existing primary woodlands, reflects poor spatial mobility exacerbated by barriers to migration (Peterken and Game 1984). In this study, primary woodland species are mostly spring-flowering perennial herbs that propagate vegetatively or by berries (*Clintonia borealis*, *Medeola virginiana*, and *Trillium undulatum*. In contrast, most species found more frequently on former pasture are summer-flowering trees, shrubs, or ferns. These species reproduce both vegetatively and sexually by either wind-dispersed samaras or spores (*Acer saccharum*, *Fraxinus americana*, *Lycopodium complanatum*, and *Polystichum acrostichoides*) or edible nuts, drupes, pomes, or berries (*Corylus cornuta*, *Crataegus*, *Ilex verticillata*, *Maianthemum canadense*, *Prunus serotina*, *Quercus rubra*, and *Toxicodendron radicans*).

Secondary woodland species often reproduce by wind-dispersed propagules (hovering and flying anemochores), conspicuous fleshy fruits or nuts dispersed by frugivorous birds or mammals (endozoochores), and high rates of vegetative reproduction (e.g. *Lycopodium complanatum* and *Maianthemum canadense*). In contrast, primary woodland species often are characterized by poorly-dispersed propagules (heavy anemochores, ant-dispersed myrmechores, and barochores), low rates of vegetative expansion (e.g. *Medeola virginiana*), and infrequent sexual reproduction (Raup and Carlson 1941; Whitney and Foster 1988; Dzwonko and Loster 1990, 1992).

Species, which are able to disperse onto new sites, may not tolerate the altered soil and nutrient conditions found on former agricultural lands. Cultivation removes large quantities of biomass, changes structure, increases pH and bulk density, and depletes soil organic matter and nitrogen pools (Daniels et al. 1983; Goldin and Lavkulich 1988). In Petersham, most of the cleared land was utilized as pasture and grassland. Conversion of forest to pasture results in distinct changes in soil chemistry and morphology: B horizon depth increases, clay content increases, and structure weakens (Daniels et al. 1983). Liming also results in the increased downward movement of calcium and magnesium; however, nineteenth-century agriculture in New England relied on few soil amendments (Hamburg 1984).

Altered soil conditions on former agricultural lands persist long after abandonment. Soil organic matter and nitrogen pools continue to increase 70-80 years after abandonment but remain below predisturbance levels (Jenkinson 1977; Daniels et al. 1983; Hamburg 1984). Competition among species may limit the ability of some species to colonize reforested sites or to tolerate the soil conditions found there. In this study, more intensive land uses are associated with enriched-site species (*Acer saccharum*, *Fraxinus americana*, and *Polystichum acrostichoides*); and primary woodlands are associated with species found on impoverished sites (e.g. *Tsuga canadensis*).

Physiography, History, and Forest Composition

Species composition reflects the distribution of individual species across the landscape. The occurrence of species in a particular space and time indicates their ability to become established and to persist. In the landscape defined by physiography and history, species distributions reflect spatial mobility, resource availability, and competitive ability. In Petersham few species are solely limited to woodlands with specific land-use histories. In contrast, individual species are restricted to specific physiographic conditions. For example, many species found on poorly-drained depositional basins are not found on well-drained bedrock ridges.

Interactions among physiographic and historical variables complicate interpretation of vegetation patterns and the processes controlling these patterns. However, clear relationships exist among forest composition, physiography (geomorphology, landscape position, and drainage), and land-use history (past land use and intensity of disturbance). Solar irradiation, natural disturbances, and forest management are less important determinants of forest composition.

When considered collectively, distribution and abundance of all vegetative life forms are related to physiography and land-use history. However, distributions of most ferns and shrubs are significantly associated with geomorphology and drainage, but not natural disturbances, forest management, or land-use history. In contrast, distributions of trees and forbs are significantly related to both physiography and land-use history. The relative importance of land-use history is greater for trees than for understory vegetation. This fact probably reflects the longer generation time characteristic of many trees and the continued impact of natural and human disturbances on overstory composition. Additional physiographic and historical factors may explain tree distribution and abundance: e.g. stand age or more quantitative measures of forest management.

Two groups of variables directly explain forest composition: physiography (geomorphology, landscape position, and drainage) and land-use history (past land use and intensity of disturbance). Based on this study, physiographic and historical factors can be ranked in terms of their long-term relative importance to forest composition: PHYSIOGRAPHY > LAND-USE HISTORY > NATURAL DISTURBANCE = FOREST MANAGEMENT. Despite >200 years of intensive land-use history, forest composition in Petersham is largely controlled by physiography. However, the continued influence of land-use history indicates that intensive human disturbances have long-lasting impacts.

The impacts of natural and human disturbances persist on different temporal scales which are dependent on the intensity and frequency of disturbances. In Petersham, the impacts of land-use history persist longer than those of windthrow, fire, or forest management. Intensive agricultural land uses completely remove forest cover from the landscape, and woodland species persist at the few forest sites remaining in the deforested landscape. In contrast, fire, windthrow, and logging do not entirely eliminate forest cover; instead, these disturbances primarily alter forest structure and temporarily affect understory composition and abundance (Tande 1979; Foster 1985; Hughes 1991; Hughes and Fahey 1992).

Except for the severe disturbances caused by agricultural land uses, secondary succession following disturbances approximates Egler's (1954) notion of "initial floristics". On disturbed sites with residual propagules or individuals, secondary succession proceeds rapidly following disturbance (Drury and Nisbet 1973). In New England, many woodland species are clonal and/or perennial and are adapted to survive repeated windthrow and fire disturbances. These species persist in low numbers or quickly reinvade following all but the most severe disturbances (Whitney 1991). Composition remains constant but abundance varies over time: certain species are suppressed by temporarily dominant species (Egler 1954; Drury and Nisbett 1973).

Following more intensive land uses, secondary succession approximates the notion of "relay floristics" (Egler 1954). Composition passes through stages in which larger and more complex species replace earlier arrivals (Drury and Nisbett 1973). Many forest species, especially understory species, do not occur in the early stages of old-field succession, but slowly colonize reforested sites following canopy development. Slow colonizers include many of those identified as primary or ancient woodland species; and some of these species do not colonize secondary woodlands after hundreds of years (*cf.* Peterken and Game 1984; Dzwonko and Loster 1990, 1992).

Disturbances obscure and complicate vegetation-site relationships, but species-site relations increase in importance during succession (Lyford et al. 1963; Whitney 1991). As Whitney (1991) states, "time has also favored the reestablishment of predisturbance overstory vegetation-site relationships". Habitat tolerances are greatest in early succession and diminish in late succession, as increased competition results in decreasing niche breadth and increasing site fidelity. Ultimately competition limits species to preferred sites in which they are competitively superior (Drury and Nisbet 1973; Christensen and Peet 1984). Early successional species disperse widely and abundantly and then grow and mature quickly on exposed sites; but they are replaced by stress-intolerant but competitively superior species, characterized by longevity and size (Horn 1974; Drury and Nisbet 1973).

In a continually changing landscape, the relative importance of physiographic and historical factors changes relative to the timing of disturbance events. In the past, natural disturbances such as fires and windthrow were important influences on forest composition (Spurr 1956; Foster 1988). Both natural disturbances and forest management do not exert a long-lasting influence on forest composition, but recent disturbances can have dramatic effects on short-term vegetation composition and structure. In contrast, land-use history continues to be a dominant influence on forest composition in landscapes fragmented by intensive human land uses or recently reforested by young successional woodlands (Peterken and Game 1984; Whitney and Foster 1988; Foster 1992). In a reforested landscape, the legacy of land-use history persists but is overshadowed by physiographic controls on forest composition.

REFERENCES CITED

Austin, M. P. and O. B. Williams. 1988. Influence of climate and community composition on the population demography of pasture species in semi-arid Australia. Vegetatio 77: 43-49.

Beatty, S. W. 1982. Influence of microtopography and canopy species on spatial patterns of forest understory plants. Ecology 65: 1406-1419.

Beers, T. W., P. E. Dress, and L. C. Wensel. 1964. Aspect transformation in site productivity research. Journal of Forestry 64: 691-692.

Brown, J. H. 1988. Species diversity. Pp. 57-89 in Myers, A. A. and P. S. Giller (eds.). Analytical Biogeography: an Integrated Approach to the Study of Animal and Plant Distributions. Chapman and Hall, London.

Buol, S. W., F. D. Hole, and R. J. McCracken. 1980. Soil Genesis and Classification. Second Edition. The Iowa State University Press, Ames.

Christensen, N. L. and R. K. Peet. 1984. Convergence during secondary forest succession. Journal of Ecology 72: 25-36.

Collins, B. S. and G. R. Wein. 1993. Understory vines: distribution and relation to environment on a southern mixed hardwood site. Bulletin of the Torrey Botanical Club 120: 38-44.

Collins, S. L. 1990. Habitat relationships and survivorship of tree seedlings in hemlock-hardwood forest. Canadian Journal of Botany 68: 790-797.

Daniels, W. L., D. F. Amos, and J. C. Baker. 1983. The influence of forest and pasture on the genesis of a humid temperate-region Ultisol. Journal of the Soil Science Society of America 47: 560-566.

Davis, M. B. 1958. Three pollen diagrams from central Massachusetts. American Journal of Science 256: 540-570.

Davis, M. B. 1983. Quaternary history of deciduous forests of eastern North America and Europe. Annals of the Missouri Botanical Garden 70: 550-563.

Davis, R. A. 1983. Depositional Systems: a Genetic Approach to Sedimentary Geology. Prentice-Hall, Englewood Cliffs.

Drury, W. H. and I. C. T. Nisbet. 1973. Succession. Journal of the Arnold Arboretum 54: 331-368.

Duffy, D. C. and A. J. Meier. 1992. Do Appalachian herbaceous understories ever recover from clearcutting? Conservation Biology 6: 196-201.

Dzwonko, Z. and S. Loster. 1988. Species richness of small woodlands on the western Carpathian foothills. Vegetatio 76: 15-27.

Dzwonko, Z. and S. Loster. 1990. Vegetation differentiation and secondary succession on a limestone hill in southern Poland. Journal of Vegetation Science 1: 615-622.

Dzwonko, Z. and S. Loster. 1992. Species richness and seed dispersal to secondary woods in southern Poland. Journal of Biogeography 19: 195-204.

Egler, F. E. 1954. Vegetation science concepts I. initial floristic composition, a factor in old-field vegetation development. Vegetatio 4: 412-417.

Eschman, D. F. 1966. Surficial Geology of Athol Quadrangle Worcester and Franklin Counties, Massachusetts. Geological Survey Bulletin 1163-C.

Farrell, J. D. and S. Ware. 1991. Edaphic factors and forest vegetation in the Piedmont of Virginia. Bulletin of the Torrey Botanical Club 118: 161-169.

Foster, D. R. 1983. The history and pattern of fire in the boreal forest of southeastern Labrador. Canadian Journal of Botany 61: 2459-2471.

Foster, D. R. 1985. Vegetation development following fire in *Picea mariana* (black spruce)-*Pleurozium* forests of south-eastern Labrador, Canada. Journal of Ecology 73: 517-534.

Foster, D. R. 1988. Species and stand response to catastrophic wind in central New England, U.S.A. Journal of Ecology 76: 135-151.

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

Foster, D. R. and E. R. Boose. 1992. Patterns of forest damage resulting from catastrophic wind in central New England, U.S.A. Journal of Ecology 80: 79-98.

Foster, D. R. and G. A. King. 1986. Vegetation patterns and diversity in S.E. Labrador, Canada: *Betula papyrifera* (birch) forest development in relation to fire history and physiography. Journal of Ecology 74: 465-483.

Foster, D. R. and T. Zebryk. 1993. Long-term vegetation dynamics and disturbance history of a *Tsuga*-dominated forest in central New England. Ecology, in press.

Foster, D. R., T. Zebryk, P. Schoonmaker, and A. Lezberg. 1992. Post-settlement history of human land-use and vegetation dynamics of a *Tsuga canadensis* (hemlock) woodlot in central New England. Journal of Ecology 80: 773-786.

Frank, E. C. and R. Lee. 1966. Potential Solar Beam Irradiation on Slopes: Tables for 30° to 50° Latitude. U. S. Forest Research Paper RM-18.

Fuentes, E. R., R. Aviles, and A. Segura. 1989. Landscape change under indirect effects of human use: the Savanna of central Chile. Landscape Ecology 2: 73-80.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club 53: 7-26.

Gleason, H. A. and A. Cronquist. 1991. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. Second Edition. The New York Botanical Garden, Bronx.

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

Goldin, A. and L. M. Lavkulich. 1988. Historical land clearing in the Fraser Lowland of British Columbia and Washington State: I. effects on soil genesis. Soil Science Society of America Journal 52: 467-473.

Greig-Smith, P. 1983. Quantitative Plant Ecology. Third Edition. Butterworths, London.

Hack, J. T. and J. C. Goodlett. 1960. Geomorphology and forest ecology of a mountain region in the central Appalachians. U. S. Geological Survey Professional Paper 347.

Hamburg, S. P. 1984. Effects of forest growth on soil nitrogen and organic matter pools following release from subsistence agriculture. Pp. 145-158 in E. L. Stone (ed.). Forest Soils and Treatment Impacts. Proceedings of the Sixth North American Forest Soils Conference, June 1983. University of Tennessee, Knoxville.

Hermy, M. and H. Stieperaere. 1981. An indirect gradient analysis of the ecological relationships between ancient and recent riverine woodlands to the south of Bruges (Flanders, Belgium). Vegetatio 44: 43-49.

Horn, H. S. 1974. The ecology of secondary succession. Annual Review of Ecology and Systematics 5: 25-37.

Host, G. E. and K. S. Pregitzer. 1992. Geomorphic influences on ground-flora and overstory composition in upland forests of northwestern lower Michigan. Canadian Journal of Forest Research 22: 1547-1555.

Hughes, J. W. 1992. Effect of removal of co-occurring species on distribution and abundance of *Erythronium americanum* (Liliaceae), a spring ephemeral. American Journal of Botany 79: 1329-1336.

Hughes, J. W. and T. J. Fahey. 1991. Colonization dynamics of herbs and shrubs in a disturbed northern hardwood forest. Journal of Ecology 79: 605-616.

Iverson, L. R. 1988. Land-use changes in Illinois, USA: the influence of landscape attributes on current and historic land use. Landscape Ecology 2: 45-61.

Jacobsen, G. L., T. Webb III, and E. C. Grimm. 1987. Patterns and rates of vegetation change during the deglaciation of eastern North America. Pp. 277-288 in Ruddiman, W. F. and H. E. Wright, Jr. (eds.). North America and Adjacent Oceans during the Last Deglaciation. The Geology of North America, Volume K-3. Geological Society of America, Boulder.

Jenkinson, D. S. 1977. The nitrogen economy of the Broadbalk Experiments: I. nitrogen balance in the experiments. Pp. 103-109 in Rothamstead Experimental Station Report for 1976, Part 2.

Lee, S. and D. Lee. 1830. Plan of Petersham, Worcester County, Mass. Massachusetts Archives, Boston.

Levenson, J. B. 1981. Woodlots as biogeographic islands in southeastern Wisconsin. Pp. 13-39 in Burgess, R. L. and D. M. Sharpe (eds.). Forest Island Dynamics in Man-Dominated Landscape. Springer, Berlin.

Lyford, W. H., J. C. Goodlett, and W. H. Coates. 1963. Landforms, soils with fragipans, and forest on a slope in the Harvard Forest. Harvard Forest Bulletin No. 30.

Mabry, C. M. and T. Korsgren. 1993. Fifty years of vegetation change following catastrophic wind in central New England, U.S.A. Journal of Vegetation Science, in review.

MacConnell, W. P. 1975. Remote Sensing 20 Years of Change in Massachusetts: 1951/52-1971/72. Massachusetts Agricultural Experiment Station Bulletin No. 630.

Massachusetts State Planning Board. 1938. Land Utilization Town of Petersham. WPA Project No. 17788.

Middleton, J. and G. Merriam. 1983. Distribution of woodland species in farmland woods. Journal of Applied Ecology 20: 625-644.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. Wiley, New York.

Muller, R. N. 1982. Vegetation patterns in the mixed mesophytic forest of eastern Kentucky. Ecology 63: 1901-1917.

Nichols, G. E. 1935. The hemlock-white pine-northern hardwood region of eastern North America. Ecology 16: 403-422.

Patterson, W. A. and A. E. Backman. 1988. Fire and disease history of forests. Pp. 603-622 in Huntley, B. and T. Webb III (eds.). Vegetation History. Kluwer, Den Hague.

Peet, R. K. 1978. Forest vegetation of the Colorado Front Range: patterns of species diversity. Vegetatio 37: 65-78.

Peet, R. K., D. C. Glenn-Lewin, and J. W. Wolf. 1983. Prediction of man's impact on plant species diversity: a challenge for vegetation science. Pp. 41-54 in Holzner, W., M. J. A. Werger, and I. Ikusima (eds.). Man's Impact on Vegetation. Dr. W. Junk Publishers, Den Haag.

Peterken, G. F. 1981. Woodland Conservation and Management. Chapman and Hall, London.

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

Raup, H. M. and R. E. Carlson. 1941. The history of land use in the Harvard Forest. Harvard Forest Bulletin No. 20.

Smith, D. M. 1962. The Practice of Silviculture. Seventh Edition. John Wiley & Sons, Inc., New York.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry: the Principles and Practice of Statistics in Biological Research. Second Edition. W. H. Freeman and Company, New York.

Sprugel, D. G. 1991. Disturbance, equilibrium, and environmental variability: what is 'natural' vegetation in a changing environment. Biological Conservation 58: 1-18.

Spurr, S. H. 1956. Forest associations in the Harvard Forest. Ecological Monographs 26: 245-262.

Spurr, S. H. 1957. Local climate in the Harvard Forest. Ecology 38: 37-46.

Steinberg, D. and P. Colla. 1991. LOGIT: A Supplementary Module for SYSTAT. SYSTAT, Evanston.

Stout, B. B. 1952. Species distribution and soils in the Harvard Forest. Harvard Forest Bulletin No. 24.

Tande, G. F. 1979. Fire history and vegetation pattern of coniferous forests in Jasper National Park, Alberta. Canadian Journal of Botany 57: 1912-1931.

Taylor, W. H. and C. F. Hotz. 1985. Soil Survey of Worcester County, Massachusetts, Northeastern Part. U. S. Department of Agriculture, Soil Conservation Service.

Ter Braak, C. J. F. 1986. Canonical correspondance analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167-1179.

Ter Braak, C. J. F. 1990. CANOCO - A FORTRAN Program for Canonical Community Ordination by Partial Detrended Canonical Correspondance Analysis, Principle Components Analysis and Redundancy Analysis. TNO Institute of Applied Computer Science, Wageningen.

United States Department of Agriculture. Unpublished. Soil Survey of Worcester County, Massachusetts, Northwestern Part (Interim Maps). U. S. Department of Agriculture, Soil Conservation Service.

United States Department of Agriculture. 1981. Soil Survey Manual. U. S. Department of Agriculture, Soil Conservation Service.

Walker, B. H. 1975. Vegetation-site relationships in the Harvard Forest. Vegetatio 29: 169-178.

Wentworth, C. K. 1922. A scale of grade and class terms for clastic sediments. Journal of Geology 30: 507-521.

Westveld, M. 1956. Natural forest vegetation zones of New England. Journal of Forestry 54: 332-338.

White, D. W., W. Worthen, and E. W. Stiles. 1990. Woodlands in a post-agricultural landscape in New Jersey. Bulletin of the Torrey Botanical Club 117: 256-265.

Whitney, G. G. 1991. Relation of plant species to substrate, landscape position, and aspect in north central Massachusetts. Canadian Journal of Forest Research 21: 1245-1252.

Whitney, G. G. and D. R. Foster. 1988. Overstorey composition and age as determinants of the understorey flora of woods of central New England. Journal of Ecology 76: 867-876.

Whitney, P. 1793. Worcester County: America's First Frontier. Isaiah Thomas, Worcester.

Woodford, E. M. 1855. Map of the Town of Petersham, Worcester County, Massachusetts. R. Clark, Philadelphia.

Zebryk, T. M. 1991. Holocene Paleoecology of a Forested Peatland in Central New England, U.S.A. M.F.S. Thesis, Harvard University.

Appendix 1. Extrapolation of 1870 and 1900 land uses based on stand categories on 1937-1939 vegetation maps of Petersham, Massachusetts, U.S.A. (Harvard Forest Archives Map P3.2). The 1937-1939 vegetation maps were prepared during white pine blister rust surveys by the United States Department of Agriculture. Land uses in 1870 and 1900 were classified as either forested or non-forested. Extrapolation was based on vegetation studies of forest succession following agricultural abandonment [especially Spurr (1956) and Foster (1992)].

Stand types indicating land abandoned prior to 1870 (forested in both 1870 and 1900):

Hardwood
Hardwood-Gray Birch
Hardwood-Hemlock
Hardwood-Hemlock-Gray Birch
Hardwood-Hemlock-Scattered White Pine (DBH >6")
Hardwood-Hemlock-Spruce
Hardwood-Hemlock Swamp
Hardwood-White Pine (DBH <6")
Hardwood-White Pine (DBH >6")-Scattered White Pine (DBH <6")
Hardwood-White Pine (DBH 10")
Hardwood-30% White Pine (DBH >6")
Hardwood-40% White Pine (DBH 6")
Hardwood-50% White Pine (DBH 4")
Hardwood-50% White Pine (DBH <6")
Hardwood-Scattered White Pine (DBH <3")
Hardwood-Scattered White Pine (DBH <6")
Hardwood-Scattered White Pine (DBH <6") Swamp
Hardwood-Scattered White Pine (DBH >6")-Gray Birch
Hardwood-Spruce-White Pine (DBH <6")
Hardwood Swale
Hardwood Swamp

Stand types indicating land abandoned between 1870 and 1900 (non-forested in 1870 but forested in 1900):

White Pine (DBH >6")
White Pine (DBH >6") Blowdown
White Pine (DBH >6")-Scattered Hardwood-White Pine (DBH 4")
White Pine (DBH >6")-White Pine (DBH 4")
White Pine (DBH >6")-White Pine (DBH 5")
White Pine (DBH >6")-White Pine (DBH <6")
White Pine (DBH >6")-White Pine (DBH 6")
White Pine (DBH 14")-White Pine (DBH 3")

Stand types indicating land abandoned between 1900 and 1937 (non-forested in both 1870 and 1900):

Gray Birch-Hardwood
Gray Birch-Hardwood-Scattered White Pine (DBH <6")
Gray Birch-Scattered White Pine (DBH >6")-White Pine (DBH <6")
Gray Birch-White Pine (DBH <6")
Gray Birch-40% White Pine (DBH <6")
Old Field White Pine (DBH <6")
Pastured White Pine (DBH <6")
Scattered White Pine (DBH 3")
White Pine (DBH <6")

Stand types indicating open land in 1937 (non-forested in both 1870 and 1900):

Field
Grass Swale
Open
Open Pasture

No extrapolation made because exact vegetation type unknown:

Brush
Cut in 1930
Cut in 1935 Light White Pine (DBH <1")
Cut in 1937-Scattered White Pine (DBH <6")
Cut 5 Years-Hardwood-Scattered White Pine (DBH <6")
Mature-Hardwood-50% White Pine (DBH 4")
Partly Cut 5 Years-Hardwood-Hemlock
Swale

Appendix 2. Field key to land-use history based on examination of soil profiles in Petersham, Massachusetts, U.S.A. The land uses identified by this key represent the most intensive land use that occurred on a given site. At each step, a site must meet <u>all</u> requirements of the selected choice; indicators provide supporting evidence 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 degrees to minimize erosion, and 5) no apparent charcoal layer.

1a. Profile meets ≥ 2 requirements .... WOODLAND (5)
- Requirements: Oa depth ≥ 2.0 cm
  - A depth < 3.0 cm
  - E depth ≥ 1.0 cm
- Indicators: A color dark brown or black
  - Bs and/or Bhs horizons

1b. Profile does not meet ≥ 2 requirements 2
- Requirements: Not met by 1a.

2a. Profile meets ≥ 1 requirements .... PASTURE OR WOODLAND (4)
- Requirements: A depth < 5.0 cm
  - E depth ≥ 1.0 cm
- Indicators: Oa depth ≥ 2.0 cm

2b. Profile does not meet either requirement 3
- Requirements: Not met by 2a.

3a. Ap horizon 4
- Requirements: Homogenous A horizon
  - Abrupt A/B boundary
  - Surface lithics or boulders ≤ 2 percent
  - A gravels < 10 percent
- Indicators: Wide stone walls or rock piles
  - Small stones in walls and piles
  - Level or slight microrelief

3b. No Ap horizon .... PASTURE (3)
- Requirements: Not met by 3a.
- Indicators: Narrow or no stone walls
  - No small stones in stone walls

4a. Thick Ap horizon .... DEEP TILLAGE (1)
- Requirements: A depth ≥ 12.0 cm
- Indicators: A gravels ≤ 2 percent

4b. Shallow Ap horizon .... SHALLOW TILLAGE OR PASTURE (2)
- Requirements: A depth < 12.0 cm

Appendix 3. Complete list of the vascular flora identified in 70 vegetation plots in study of forest vegetation in Petersham, Massachusetts, U.S.A. Nomenclature follows Gleason and Cronquist (1991).

LYCOPODIALES

Lycopodiaceae

Lycopodium annotinum	
Lycopodium clavatum	Running pine
Lycopodium complanatum	Northern ground cedar
Lycopodium lucidulum	
Lycopodium obscurum	Ground pine

EQUISETALES

Equisetaceae

Equisetum arvense	Common horsetail
Equisetum sylvaticum	Woodland horsetail

POLYPODIALES

Osmundaceae

Osmunda cinnamomea	Cinnamon fern
Osmunda claytoniana	Interrupted fern
Osmunda regalis	Royal fern

Polypodiaceae

Polypodium virginiana	Common polypody

Dennstaedtiaceae

Dennstaedtia punctilobula	Hay-scented fern
Pteridium aquilinum	Bracken fern

Adiantaceae

Adiantum pedatum	Maidenhair fern

Aspleniaceae

Athyrium filix-femina	Lady fern
Athyrium thelypteroides	Silvery glade fern
Dryopteris cristata	Crested wood fern
Dryopteris marginalis	Marginal wood fern
Dryopteris (spinulosa)	Spinulose wood fern
Polystichum acrostichoides	Christmas fern
Thelypteris noveboracensis	New York fern
Thelypteris palustris	Marsh fern
Thelypteris phegopteris	Northern beech fern
Thelypteris simulata	Massachusetts fern

Onocleaceae

Matteuccia struthiopteris	Ostrich fern
Onoclea sensibilis	Sensitive fern

TAXALES

Taxaceae

Taxus canadensis	American yew

PINALES

Pinaceae

Picea glauca	White spruce
Picea rubens	Red spruce
Pinus strobus	White pine
Tsuga canadensis	Eastern hemlock

Cupressaceae

Juniperus communis	Common juniper

DICOTYLEDONEAE

Lauraceae

Lindera benzoin	Spicebush

Ranunculaceae

Actaea alba	Doll's eyes
Anemone quinquefolia	Wood anemone
Caltha palustris	Marsh marigold
Coptis trifolia	Goldthread
Ranunculus recurvatus	Hooked crowfoot
Thalictrum pubescens	Tall meadow rue

Berberidaceae

Berberis thunbergii	Japanese barberry

Hamamelidaceae

Hamamelis virginiana	Witch hazel

Ulmaceae

Ulmus americana	American elm

Urticaceae

Boehmeria cylindrica	False nettle
Pilea pumila	Clearweed

Fagaceae

Castanea dentata	Chestnut
Fagus grandifolia	American beech
Quercus alba	White oak
Quercus rubra	Northern red oak
Quercus velutina	Black oak

Juglandaceae	
Carya glabra	Pignut hickory
Carya ovata	Shagbark hickory
Betulaceae	
Betula alleghaniensis	Yellow birch
Betula lenta	Sweet birch
Betula papyrifera	White birch
Betula populifolia	Gray birch
Carpinus caroliniana	Hornbeam
Corylus cornuta	Beaked hazel
Ostrya virginiana	Hop hornbeam
Tiliaceae	
Tilia americana	Basswood
Sarraceniaceae	
Sarracenia purpurea	Pitcher plant
Violaceae	
Viola conspersa	American dog violet
Viola cucullata	Blue marsh violet
Salicaceae	
Populus grandidentata	Big-toothed aspen
Populus tremuloides	Quaking aspen
Brassicaceae	
Cardamine pensylvanica	Pennsylvania bitter cress
Ericaceae	
Epigaea repens	Trailing arbutus
Gaultheria procumbens	Wintergreen
Gaylussacia baccata	Black huckleberry
Kalmia angustifolia	Sheep laurel
Kalmia latifolia	Mountain laurel
Lyonia ligustrina	Maleberry
Vaccinium angustifolium	Common lowbush blueberry
Vaccinium corymbosum	Highbush blueberry
Vaccinium pallidum	Hillside blueberry
Pyrolaceae	
Chimaphila maculata	Spotted wintergreen
Chimaphila umbellata	Pipsissewa
Moneses uniflora	One-flowered shinleaf
Pyrola chlorantha	
Pyrola elliptica	Elliptic shinleaf
Pyrola rotundifolia	Rounded shinleaf
Pyrola secunda	One-sided shinleaf

Monotropaceae

Monotropa hypopithys	Pinesap
Monotropa uniflora	Indian pipe

Primulaceae

Lysimachia quadrifolia	Whorled loosestrife
Lysimachia terrestris	Swamp candles
Trientalis borealis	Starflower

Grossulariaceae

Ribes lacustre	Spiny swamp currant

Saxifragaceae

Chrysosplenium americanum	
Saxifraga pensylvanica	Swamp saxifrage
Tiarella cordifolia	Foamflower

Rosaceae

Amelanchier species	Serviceberry
Crataegus species	Hawthorn
Dalibarda repens	Dewdrop
Fragaria virginiana	Wild strawberry
Potentilla simplex	Old-field five fingers
Prunus serotina	Wild black cherry
Prunus virginiana	Chokecherry
Rubus allegheniensis	Common blackberry
Rubus canadensis	Smooth blackberry
Rubus hispidus	Swamp dewberry
Rubus idaeus	Red raspberry
Rubus pubescens	Dwarf raspberry
Sorbus americana	American mountain ash
Spiraea alba	Meadowsweet

Fabaceae

Amphicarpaea bracteata	Hog peanut
Apios americana	Common groundnut
Desmodium nudiflorum	Naked tick trefoil

Onagraceae

Circaea lutetiana	Enchanter's nightshade
Epilobium coloratum	Eastern willow herb

Cornaceae

Cornus alternifolia	Alternate-leaved dogwood
Cornus canadensis	Bunchberry
Cornus florida	Flowering dogwood
Cornus racemosa	Northern swamp dogwood
Nyssa sylvatica	Black gum

Celastraceae

Euonymus alatus	Winged burning bush

Aquifoliaceae	
Ilex verticillata	Winterberry
Nemopanthus mucronatus	Common mountain holly
Vitaceae	
Parthenocissus quinquefolia	Virginia creeper
Vitis labrusca	Fox grape
Polygalaceae	
Polygala paucifolia	Flowering wintergreen
Aceraceae	
Acer pensylvanicum	Striped maple
Acer rubrum	Red maple
Acer saccharum	Sugar maple
Anacardiaceae	
Toxicodendron radicans	Common poison ivy
Oxalidaceae	
Oxalis acetosella	Northern wood sorrel
Oxalis stricta	Common yellow wood sorrel
Geraniaceae	
Geranium maculatum	Wild geranium
Balsaminaceae	
Impatiens capensis	Jewelweed
Araliaceae	
Aralia nudicaulis	Wild sarsparilla
Panax trifolium	Dwarf ginseng
Apiaceae	
Hydrocotyle americana	Marsh pennywort
Apocynaceae	
Apocynum androsaemifolium	Spreading dogbane
Asclepiadaceae	
Asclepias exaltata	Tall milkweed
Solanaceae	
Solanum dulcamara	Bittersweet nightshade
Lamiaceae	
Lycopus uniflorus	Northern water horehound
Scutellaria lateriflora	Mad-dog skullcap

Oleaceae	
Fraxinus americana	White ash
Scrophulariaceae	
Chelone glabra	White turtlehead
Melampyrum lineare	Cowwheat
Rubiaceae	
Galium lanceolatum	Wild licorice
Mitchella repens	Partridgeberry
Orobanchaceae	
Epifagus virginiana	Beechdrops
Caprifoliaceae	
Diervilla lonicera	Bush honeysuckle
Lonicera canadensis	Fly honeysuckle
Sambucus canadensis	Common elder
Sambucus racemosa	Red-berried elder
Viburnum acerifolium	Maple-leaved viburnum
Viburnum alnifolium	Hobblebush
Viburnum dentatum	Arrowwood
Viburnum nudum	Witherod
Asteraceae	
Achillea millefolium	Common yarrow
Aster acuminatus	Whorled aster
Aster divaricatus	White heart-leaved aster
MONOCOTYLEDONAEAE	
Araceae	
Arisaema triphyllum	Jack-in-the-pulpit
Juncaceae	
Luzula campestris	Wood rush
Cyperaceae	
Carex debilis	Stalked sedge
Carex disperma	
Carex intumescens	Bladder sedge
Poaceae	
Agrostis capillaris	Rhode Island bent
Brachyelytrum erectum	
Festuca rubra	Red fescue
Panicum lanuginosum	Panic-grass

Liliaceae

Clintonia borealis	Bead lily
Maianthemum canadense	Canada mayflower
Medeola virginiana	Indian cucumber root
Polygonatum pubescens	Solomon's seal
Smilacina racemosa	False Solomon's seal
Streptopus roseus	Twisted stalk
Trillium erectum	Purple trillium
Trillium undulatum	Painted trillium
Uvularia sessilifolia	Bellwort

Smilacaceae

Smilax herbacea	

Orchidaceae

Cypripedium acaule	Pink lady's slipper
Goodyera pubescens	Rattlesnake plantain