

Using witness trees to assess forest change in southeastern Ohio

James M. Dyer

Abstract: In 1787, the U.S. Congress authorized the sale of the "Ohio Company Purchase", ca. 5000 km² in Appalachian Ohio. The land was surveyed using a township and range system shortly thereafter. Data on >5600 witness trees were transcribed from the survey records, and witness tree locations were plotted on a digital map. This information was used to evaluate presettlement forest composition and structure and to investigate vegetation–site relationships before widespread alteration of the forests had taken place. Presettlement conditions were compared with present conditions using forest inventory and analysis (FIA) data. Two hundred years ago, the forests of southeastern Ohio were dominated by large individuals of *Quercus alba* L., *Carya* Nutt. spp., *Quercus velutina* Lam., and *Fagus grandifolia* Ehrh. These four taxa accounted for 74% of all witness trees. Although almost 70% of the region is forested today, the second-growth forest has witnessed a decrease in *Quercus* and *Carya* and an increase in *Acer saccharum* Marsh., *Acer rubrum* L., and many early successional species in smaller size classes. Despite the significant shift in forest composition and structure, species in general seem to be occupying similar positions in the present-day landscape compared with the presettlement forest; topographic variables most strongly control species occurrence in this landscape.

Résumé : En 1787, le Congrès des États-Unis autorisait la vente de la « Ohio Company Purchase », soit environ 5000 km² dans les Appalaches en Ohio. Le terrain fut arpenté selon le système de canton et de district peu de temps après. Les données portant sur plus de 5600 arbres-témoins ont été transcrites à partir des relevés d'arpentage et la localisation des arbres-témoins a été intégrée à une carte digitalisée. Cette information a été utilisée pour déterminer la composition et la structure de la forêt avant la colonisation et pour étudier les relations entre la végétation et le site avant que la forêt ait été largement modifiée. La situation qui prévalait avant la colonisation a été comparée à la situation actuelle en utilisant les données d'Analyse et inventaire des forêts. Il y a 200 ans, les forêts du sud-est de l'Ohio étaient dominées par de grosses tiges de *Quercus alba* L., de *Carya* Nutt. spp., de *Quercus velutina* Lam. et de *Fagus grandifolia* Ehrh. Ces quatre taxons représentaient 74% de tous les arbres-témoins. Bien qu'aujourd'hui près de 70% de la région soit couverte de forêt, la forêt de seconde venue est caractérisée par une moins grande quantité de *Quercus* et de *Carya* et une plus grande quantité d'*Acer saccharum* Marsh., *Acer rubrum* L. et de plusieurs espèces de début de succession dans les plus petites classes de diamètre. Malgré les changements importants dans la composition et la structure de la forêt, les espèces semblent généralement occuper des positions analogues dans le paysage d'aujourd'hui comparativement à la forêt présente avant la colonisation; la présence des espèces dans ce paysage est avant tout déterminée par la topographie.

[Traduit par la Rédaction]

Introduction

Widespread clearing of eastern North American forests during the 19th and early 20th centuries profoundly altered landscape structure, leading to significant changes in the biotic make-up and environmental characteristics of remnant forest patches (Forman 1997). The intensity, frequency, and extent of this initial clearing in all likelihood represented a novel disturbance to the region's vegetation. This change, occurring within a life-span of most of the tree species, had a direct effect on the structure and composition of the second growth. During the 20th century, much of eastern North America, including Appalachia, experienced extensive natural reforestation; however, both the dominant species and the

overall age structure of the forest had changed markedly (Whitney 1994; Abrams and McCay 1996; Cowell 1998; Foster et al. 1998). Clearing and recovery have also resulted in dramatic indirect effects, including alteration of ecosystem properties, such as organic matter and cycling of nitrogen compounds (Foster et al. 1997), and permanent changes in sediment budgets and the hydrologic regime (Magilligan and Stamp 1997). Thus, the effects of intensive land conversion in the past are manifested in the present-day landscape. With the current emphasis on ecosystem management on both public and private lands, it is essential to acknowledge the bounds that historical land-use practices and alterations have placed on the future of environmental systems.

The goal of this paper is to use witness trees to reconstruct presettlement forest composition and structure for a ca. 5000 km² area in southeastern Ohio, one of the earliest areas to open to settlement following the colonial period. Vegetation–site relationships of the witness trees will also be assessed within a geographic information system (GIS) environment. This area is in many ways representative of the

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larger central Appalachia region, having a long history of Euro-American settlement and resource extraction, as compared with other parts of Appalachia such as eastern Kentucky and southern West Virginia. The degree to which forest characteristics have changed over the last 200 years will be assessed using contemporary forest inventory and analysis (FIA) data collected by the U.S. Forest Service.

Study area

Southeastern Ohio is a strongly dissected region located within the unglaciated Allegheny Plateau physiographic province. Most of the soils are underlain by shale, siltstone, sandstone, limestone, and coal (Lucht et al. 1985). Climatically, the region is at the poleward edge of Köppen's humid temperate (Cfa) climate type; Athens Ohio (39°N, 82°W, elevation 200 m) has an annual temperature of 11°C and annual precipitation of 99 cm (NOAA 1982). Predominant land cover is second-growth forest. Braun (1950) included the area in a Low Hills Belt of the Mixed Mesophytic Forest Region, with beech (*Fagus grandifolia* Ehrh.), white oak (*Quercus alba* L.), black oak (*Quercus velutina* Lam.), and hickory (*Carya* spp.) prevailing in uplands of the secondary forest. Gordon (1966) mapped the presettlement vegetation of the area as primarily mixed oak forests on the ridges, with beech forests in the valleys.

During the Fort Ancient period immediately preceding Euro-American contact, central Ohio Valley villages of Native Americans were confined to large streams and river valleys (Cowan 1987; Nass 1988); population density is believed to have been relatively low (Nass 1988). Maize agriculture became significant by this time (Cowan 1987; Watson 1989; Wagner 1996), and farming was limited principally to bottomlands (Loskiel 1794; Hammett 1997), supplemented with wild food resources (Ford 1977; Watson 1989; Wagner 1996). The Shawnee occupied the area in the late 1700s, although the area was in a state of flux. Hildreth (1848) describes conditions in Washington County in 1788, just prior to Euro-American settlement: "This spot had probably, at a remote period, been cultivated by the Indians, as many such places are found at various points on the Muskingum [River], covered with a growth of saplings, while the adjacent lands are coated with forest trees..." (p. 420). Although few would argue that the forests encountered by the first settlers were not influenced by Native American practices, it is uncertain if these were localized, or extensive impacts in this region.

It has been estimated that at the time of Euro-American settlement, Ohio was 95% forested (Griffith et al. 1993). According to Annual Reports of the Secretary of State, an eight-county region in southeastern Ohio (Fig. 1) was about 70% forested in 1850, and only about 50% forested by 1870. This figure declined steadily, dropping below 20% by 1910. Forest cover has been increasing throughout the 20th century for this area: 1942, 34%; 1952, 50%; 1968, 63%; 1979, 62%; and 1991, 68% (Diller 1944; Hutchinson and Morgan 1956; Kingsley and Mayer 1970; Dennis and Birch 1981; Griffith et al. 1993).

Ohio Company Purchase

In 1787, the U.S. Congress authorized the selling of lands in the newly opened Northwest Territory to "The Ohio Company of Associates"; the "Ohio Company Purchase" comprised nearly 5000 km² (Fig. 1). The city of Marietta, founded in 1788 at the confluence of the Muskingum and Ohio rivers in Washington County, became the first authorized Anglo-American settlement in the Northwest Territory. In accordance with the newly enacted land ordinance of 1785, the Ohio Company Purchase was surveyed using a rectilinear system. The exterior boundaries were surveyed 1788–1789, whereas many of the interior lines were surveyed

1796–1802. In contrast to later surveys conducted under the auspices of the federal government however, seven different sizes of tracts were surveyed to give each subscriber an equal division of land. Each subscriber was to receive a house lot (approximately 0.37 acres), as well as one 3-, 8-, 100-, 160-, 262-, and 640-acre lot (1 acre = 0.405 ha) (Sherman 1925). These latter "sections" were comprised of square parcels 1 mi (1.6 km) on a side; the smaller divisions and 262-acre "fractions" were less regular in their delineation (Fig. 1). All lot corners were marked with wood posts or corner trees, and "witnessed" by (usually) two trees, which were blazed and recorded by species and size. The Associates, comprised mostly of New Englanders, envisioned an internationally oriented economy (Cayton 1991); because of limited transportation access and continued westward expansion, however, small-scale woodland agriculture characterized the region until extractive industries (primarily coal) gained prominence around the turn of the 20th century (Buckley et al. 2000).

Methods

Vegetation data

Witness tree species and size-class data were transcribed from the original Ohio Company survey notes, located in the library of Marietta College (Ohio), and entered as a data layer using ArcView GIS. Trees were plotted at section (640-acre) and fraction (262-acre) corners, utilizing a Public Land Survey digital base map obtained from the Division of Geological Survey of the Ohio Department of Natural Resources (McDonald et al. 1997). Additional witness tree data were tallied for smaller land subdivisions in Athens County, but since these divisions were not included on the digital base map, locations were not entered into the GIS. These data were utilized, however, in a more detailed size-class comparison between presettlement and modern forest vegetation.

The question of surveyor bias is often raised regarding the selection of witness trees: whether species were selected based on their relative abundances or on some other subjective criterion. Bourdo (1956) concludes that, although the selection of trees was not random, individual preferences usually should not be important, since the choice of species adjacent to a corner was limited. He proposed a statistical test of bias that examines mean distances from survey corners to witness trees, with the assumption that surveyors would travel greater distances on average to preferred species. Although Grimm (1984) criticizes this approach on the grounds that the underlying assumption of a random distribution of trees will be violated, such an approach, if interpreted cautiously, may provide an indication of whether surveyor bias is problematical (Delcourt and Delcourt 1974). To test for surveyor bias toward a particular species or size class, distances to witness trees were analyzed using a one-way layout with means comparison ANOVA (SAS Institute Inc. 1989).

To assess changes in forest composition and structure over the last 200 years, USDA Forest Service FIA county-level data (Griffith et al. 1993) were summarized for the eight counties that encompass the original Ohio Company Purchase (Fig. 1). Although the instructions established by Congress did not comment on witness tree selection (Sherman 1925), it is intuitive that surveyors were unlikely to select very small individuals; this is born out by an examination of the size-class distributions of witness trees. To facilitate comparison with the witness trees, FIA data for this analysis included trees ≥ 9 in. (23 cm) in diameter, in stands of natural origin ($n = 364$ plots). Data on slope, aspect, physiographic class, and location also were obtained for each plot. Latitude and longitude coordinates for each plot are reported to the nearest 100", so that the exact location of the site may be within 3 km of what is reported.

Fig. 1. Location of Ohio Company Purchase showing physiographic regions within the unglaciated Allegheny Plateau; boundaries are transitional (after Brockman 1998). Inset map of Ohio shows Ohio Company Purchase and the eight counties used for FIA data. Enlargement of Athens County shows section and fraction lines. Two townships were set aside as “College Lands” and not initially subdivided.

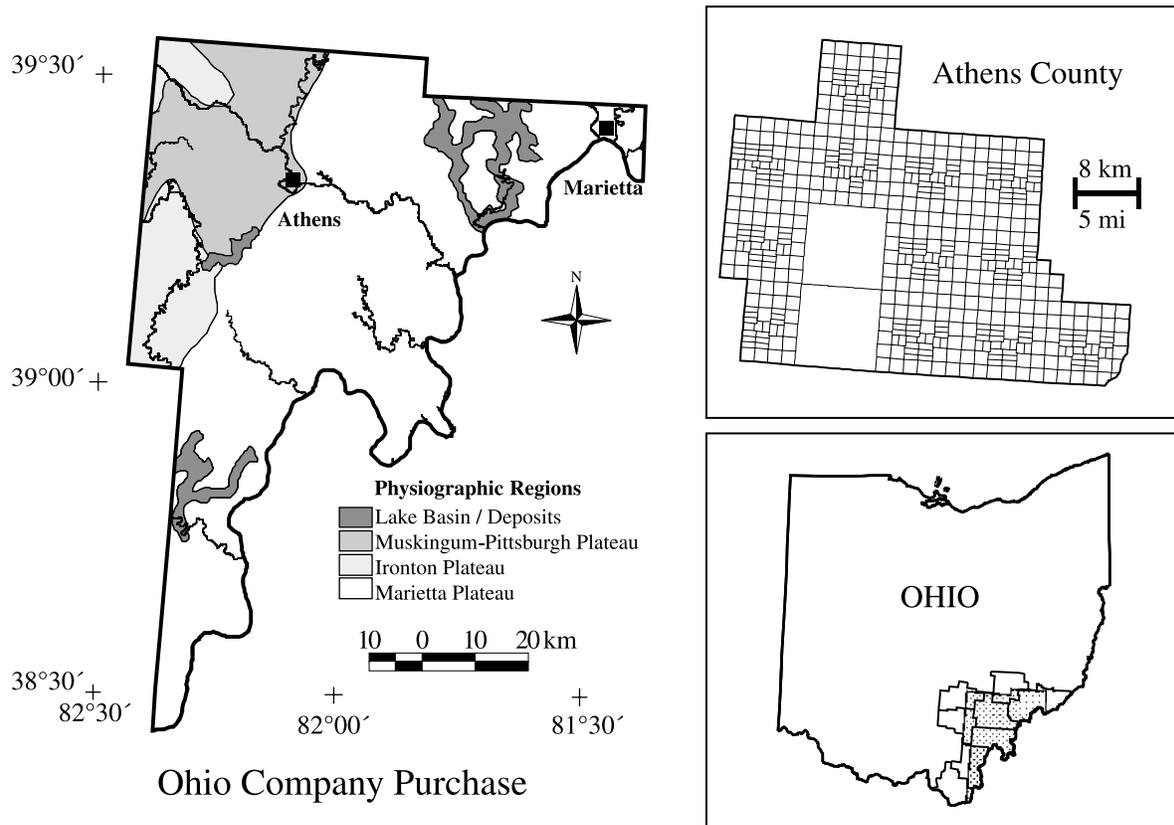


Table 1 lists witness trees recorded for the Ohio Company Purchase, and Table 2 presents 1991 FIA data for southeastern Ohio. In some instances surveyors recorded trees only to genus; these are indicated in Table 1. An attempt was made to create similar taxonomic groupings between the survey and FIA data. For example, according to Gordon (1966), “black oak” referred to by the surveyors probably included not only black oak, but also northern red oak (*Quercus rubra* L.) and scarlet oak (*Quercus coccinea* Muenchh.). These three species were combined from the FIA data, and the few instances of “red oak” used by the surveyors were collapsed into the single black oak group, since it was evident the surveyors were not consistently distinguishing among these species. The “yellow oak” used by the surveyors likely referred to chestnut oak (*Quercus prinus* L.), since chinquapin oak (*Quercus muehlenbergii* Engelm.) is far less abundant in this region. “Yellow oak” and “chestnut oak” were collapsed into a single yellow oak class, and these are compared with a combined grouping of chestnut oak and chinquapin oak in the FIA data. Other groupings are indicated in Tables 1 and 2.

Although a plot of witness trees enables one assessment of species composition at the time of Euro-American settlement, it does not allow a direct evaluation of community composition. For this reason, point data (witness tree locations) were used to derive a continuous forest association map, following the general methods of Batek et al. (1999). This involved assigning each section or fraction corner a value of “1” if a taxon was present, or “0” otherwise; this was performed separately for each taxon that accounted for $\geq 2\%$ of all witness trees. This new presence-absence field was used to create a grid theme in ArcView (30-m resolution), which was then used to create a Triangular Irregular Network (TIN; Burrough and McDonnell 1998) representing a probability surface for each taxon. The TIN was converted back to a grid with a spa-

tial resolution of 200 m (i.e., each cell is 4 ha). This new grid was then reclassified based on the probability that each target taxon was present in a particular cell: the cell was assigned a value of “1” if there was a ≥ 0.5 probability that it was present, “0” if otherwise. These individual-taxon grids were then combined, and a forest association image created.

Environmental data

In addition to an assessment of compositional and structural changes in the forests of southeastern Ohio since Euro-American settlement, an analysis of species-site relationships also was performed. A goal of this analysis was to see if taxa are demonstrating differences in site affinities now compared with 200 years ago. For instance, Abrams (1998) reports that red maple (*Acer rubrum* L.) is now widely distributed in the landscape, whereas previously it was more often restricted to poorly drained sites. To address this question, witness trees were evaluated with respect to several environmental variables, including slope, aspect, topographic position, and the integrated moisture index (IMI) (Iverson et al. 1997). This index is derived from a digital elevation model (DEM).

Fifty-two 7.5' DEMs were obtained for the study area and mosaicked together. This 30-m resolution DEM was resampled to 15 m, then to 7.5 m using bilinear interpolation. Three grids were derived from the DEM for input into the IMI: hillshade (capturing the effect of differential solar radiation due to variation in slope angle, aspect, and position and accounting for shading from adjacent hills), flow accumulation (representing the accumulated flow of water downslope), and curvature (describing landscape configuration, e.g., flat, convex, concave). These grids were combined to create the IMI, using the original relative weightings of Iverson et al. (1997) for their southeastern Ohio site: hillshade, 50%; flow ac-

Table 1. Witness trees for section and fraction divisions of the Ohio Company Purchase, with relative abundance for those taxa representing $\geq 2\%$ of the total.

Taxon	Surveyors' designations	Scientific name	Percentage of witness trees
White oak	White oak	<i>Quercus alba</i> L.	40.0
Hickory	Hickory, white hickory	<i>Carya</i> Nutt.	13.6
Black oak	Black oak, red oak		12.2
Beech	Beech	<i>Fagus grandifolia</i> Ehrh.	8.4
Sugar maple	Sugar, sugartree	<i>Acer saccharum</i> Marsh.	3.6
Red maple	Maple	<i>Acer rubrum</i> L.	3.2
Yellow oak	Yellow oak, chestnut oak		3.2
Yellow-poplar	Poplar	<i>Liriodendron tulipifera</i> L.	2.9
Ash	Ash, white ash, black ash, hoop ash, blue ash	<i>Fraxinus</i> L.	2.4
Other			10.6

Note: Other witness trees each representing $<2\%$ of the total, in decreasing order of frequency, were white maple, soft maple (*Acer saccharinum* L.), pine (*Pinus* L., pines native to southeastern Ohio are *Pinus virginiana* Mill., *Pinus echinata* Mill., or *Pinus rigida* Mill.), buckeye (probably *Aesculus octandra* Marsh.), American elm, elm, soft elm (*Ulmus americana* L., and *Ulmus rubra* Muhl.), gum (*Liquidambar styraciflua* L.), sycamore (*Platanus occidentalis* L.), pepperidge (*Nyssa sylvatica* Marsh.), chestnut (*Castanea dentata* (Marsh.) Borkh.), butternut, white walnut (*Juglans cinerea* L.), walnut, black walnut (*Juglans nigra* L.), basswood, lynn (*Tilia americana* L.), dogwood (*Cornus florida* L.), mulberry (*Morus rubra* L.), black cherry, cherry (*Prunus serotina* Ehrh.), boxelder (*Acer negundo* L.), birch (probably *Betula nigra* L.), oak (*Quercus* L.), locust (*Gleditsia triacanthos* L. or *Robinia pseudoacacia* L.), aspen (*Populus grandidentata* Michx. or *Populus tremuloides* Michx.), sassafras (*Sassafras albidum* (Nutt.) Nees), ironwood (*Carpinus caroliniana* Walt. or *Ostrya virginiana* (Mill.) K. Koch), and a thorn (*Crataegus* L.).

cumulation, 35%; and curvature, 15% (L.R. Iverson, personal communication).

Individual grid cells assume IMI values between 0 and 100. To facilitate comparison with FIA physiographic class descriptions, cells were assigned to one of four IMI classes (L.R. Iverson, personal communication): xeric, 0–35 (very dry soils where excessive drainage seriously limits growth and species occurrence); xeromesic, 36–50 (moderately dry soils where excessive drainage limits growth and species occurrence to some extent); mesic, 51–70 (deep, well-drained soils in which growth and species occurrence are only limited by climate); and hydromesic, 71–100 (moderately wet soils where insufficient drainage or infrequent flooding limits growth and species occurrence to some extent). The IMI may not be suitable for some hydromesic sites, since it expects water to run off via flow accumulation (L.R. Iverson, personal communication). Less than 3% of survey corners are classified as hydromesic.

Whereas most previous research of presettlement vegetation–site relationships involved deriving environmental data from topographic maps (e.g., Beatley 1959; Whitney 1982, 1986; Fralish et al. 1991; Cowell 1995; Abrams and McCay 1996), this study utilizes digital sources for environmental data. The IMI has been defined previously; the other site descriptors of slope and aspect were derived directly from the DEM. Aspect was transformed ($\cos(45 - \text{aspect}) + 1$), such that the new index aligns on a NE–SW axis and can be used as a surrogate for radiation load (Moore et al. 1990). In addition, four mutually exclusive topographic position categories were created using ArcView's grid surface-analysis tools (in order of creation): ridge, valley, cove, and sideslope. Ridge cells were defined by flow accumulation, having ≤ 3 "upslope" cells, and valleys were defined as having 0–5% slopes. Cove cells were defined by slope curvature, occurring on concave slopes (curvature less than -0.7 , representing 1 SD from mean slope; this was the smallest category, representing 10% of all section and fraction corners). Remaining cells were classified as sideslopes.

Whereas the environmental data were derived from grids with a 7.5 m resolution, survey corners of the public land survey base map are accurate to within 15 m (McDonald et al. 1997). To account for imprecision in locating witness trees, a 3×3 filter was run on each of the DEM-derived grids. Each cell in the new grids therefore represents a mean value of that cell and its eight immediate neighbors.

To determine if witness trees demonstrated an affinity for certain sites, a contingency table analysis was performed for each combination of species and environmental parameter. Presence of each of n taxa was compared with the C discrete categories of environmental variables derived from DEM data (slope, aspect, topographic position, and integrated moisture index) at each survey corner ($n = 2782$; $n = 2577$ for aspect since 205 sites are flat). Corners were also assigned to a physiographic region within the unglaciated Allegheny Plateau (Brockman 1998; see Fig. 1), and a contingency table analysis performed. Following the methods of Haberman (1973), the cell frequencies of each $n \times C$ contingency table possessing a significant G statistic were converted to standardized residuals. Standardized residuals represent the number of standard deviations by which the cell count departs from the expected count if the species showed no preference for any value of an environmental variable; in effect, it quantifies positive or negative association of a taxon for a particular environmental state (Strahler 1978). To minimize errors associated with small sample sizes (Sokal and Rohlf 1995), analysis was restricted to those taxa that accounted for $\geq 2\%$ of all witness trees.

Present-day species–site affinities also were assessed using a contingency analysis using FIA data for the eight-county area described above. For each witness tree taxon, presence on each FIA plot was determined and used to create a contingency table versus slope, aspect, and physiographic class. Since locational data given for each FIA plot are approximate, environmental data could not be computed using the DEM data, although each plot was assigned to a physiographic region (Brockman 1998). Whereas witness trees represent point samples, FIA plots are designed to cover a 1-acre (0.4-ha) sample area (Griffith et al. 1993), precluding direct comparison between the two procedures. Nevertheless, the FIA data may allow an indication of present-day species–site relationships.

Results

Forest composition

The presettlement forests of southeastern Ohio were dominated by white oak, which accounted for 40.0% of all witness trees (Table 1). White oak is still the most abundant species today, but it accounts for only 14.5% of trees (≥ 23 cm DBH) on the 364 FIA plots (Table 2). Although

Table 2. Current FIA data for the eight-county region of southeastern Ohio, showing species combined to create similar taxonomic groupings as the witness trees.

Taxon	Scientific name	Percentage of FIA trees	
		Individual species	Combined grouping
White oak	<i>Quercus alba</i> L.		14.5
Black oak	<i>Quercus velutina</i> Lam.	6.2	13.6
	<i>Quercus rubra</i> L.	5.4	
	<i>Quercus coccinea</i> Muenchh.	2.0	
Yellow-poplar	<i>Liriodendron tulipifera</i> L.		10.8
Hickory	<i>Carya</i> spp.	7.4	8.0
	<i>Carya cordiformis</i> (Wangenh.) K. Koch	<0.1	
	<i>Carya laciniosa</i> (Michx. f.) Loud.	0.1	
	<i>Carya ovata</i> (Mill.) K. Koch	0.4	
Sugar maple	<i>Acer saccharum</i> Marsh.	7.4	7.6
	<i>Acer nigrum</i> Michx. f.	0.2	
Yellow oak	<i>Quercus prinus</i> L.	7.1	7.2
	<i>Quercus muehlenbergii</i> Engelm.	0.1	
Red maple	<i>Acer rubrum</i> L.		5.4
Ash	<i>Fraxinus nigra</i> Marsh.	0.1	4.8
	<i>Fraxinus pennsylvanica</i> Marsh.	<0.1	
	<i>Fraxinus americana</i> L.	4.7	
Pine	<i>Pinus strobus</i> L.	0.1	4.3
	<i>Pinus rigida</i> Mill.	1.1	
	<i>Pinus echinata</i> Mill.	0.3	
	<i>Pinus virginiana</i> Mill.	2.9	
American beech	<i>Fagus grandifolia</i> Ehrh.		3.6
Elm	<i>Ulmus</i> L. spp.	0.6	2.6
	<i>Ulmus americana</i> L.	1.3	
	<i>Ulmus rubra</i> Muehl.	0.7	
Sycamore	<i>Platanus occidentalis</i> L.		2.6
Aspen	<i>Populus grandidentata</i> Michx.	2.3	2.5
	<i>Populus tremuloides</i> Michx.	0.2	
Black cherry	<i>Prunus serotina</i>		2.5
Buckeye	<i>Aesculus</i> L. spp.	1.0	2.2
	<i>Aesculus octandra</i> Marsh.	0.4	
	<i>Aesculus glabra</i> Willd.	0.8	
Other			7.8

Note: Percent frequencies are shown for combined taxa that account for $\geq 2\%$ of all trees (≥ 23 cm DBH); individual species contributions are also included. Data are summaries for Athens, Gallia, Hocking, Lawrence, Meigs, Morgan, Vinton, and Washington counties. Frequencies for individual species may not sum to the value for the combined taxonomic grouping due to rounding error. The "other" category includes 28 taxa, each accounting for $< 2\%$ of the total.

yellow oak has increased relative to the presettlement forest, all oaks combined have decreased from 55.4 to only 35.3% today. Hickory has declined from 13.6 to 8.0%, and American beech is much less common on FIA plots (3.6%) compared with the presettlement forest (8.4%). It has been suggested that surveyors may have been biased toward beech in their selection of witness trees, since they are readily discernible in a forest stand and are easy to blaze with their thin smooth bark (e.g., Gordon 1969). If surveyors were biased toward beech (or any other species), it can be hypothesized that they would travel greater distances to select it over other species. However, ANOVA tests revealed no statistical difference among any species in terms of mean distance from survey corner to witness tree, suggesting that the greater abundance of beech in the presettlement forest was not an artifact of the sampling procedure.

Two shade-tolerant species have increased in abundance over the last 200 years: sugar maple (*Acer saccharum* Marsh.) and red maple. Other species that have increased significantly are shade intolerant: yellow-poplar (*Liriodendron tulipifera* L.), pine (*Pinus* spp.), aspen (*Populus tremuloides* Michx. and *Populus grandidentata* Michx.), black cherry (*Prunus serotina* Ehrh.), and ash (*Fraxinus* spp.). In 1790, four taxa accounted for 74% of all witness trees: white oak, hickory, black oak, and beech. Two hundred years later, a greater degree of evenness is displayed, with nine taxa accounting for 76% of all FIA trees; the first four taxa account for 47% of present-day trees in southeastern Ohio. The Shannon–Wiener diversity index is 2.19 for the presettlement data and 3.07 for the FIA data.

Figure 2 presents maps of witness tree occurrence for individual taxa. Most taxa are distributed widely across the study area, although some species are more abundant in particular physiographic regions (Fig. 1). The *G* test results indicate that hickory and beech occur more frequently than expected by chance in the Muskingum-Pittsburgh Plateau, sugar maple and red maple demonstrate a slight positive association with the Marietta Plateau, and white oak occurs more frequently in lake basins or deposits than would be expected with a random distribution. In this highly dissected area, however, topography exerts a stronger influence on the vegetation than any regional gradient (Braun 1950). This fine-scale variation can be discerned in measures of spatial autocorrelation within DEM-derived maps of the study area. Computing Moran's *I* on aspect at various lagged distances indicates that, at distances of about 150–200 m, grid cells no longer display significant autocorrelation. A semivariogram created by kriging 5000 randomly generated points within a 1-km² area on the IMI map reveals that semivariance increases to about 200 m. Thus, the dominant scale of variation (the “grain”) of this landscape, to which the vegetation may be expected to respond, is ca. 200 m, representing local topographic variation.

If vegetation associations occur at this topographically defined scale, it may be invalid to map fine-scale vegetation patterns using the witness tree data (Manies and Mladenoff 2000). In essence, survey corners represent vegetation samples collected at a coarser scale than the dominant pattern. The forest association map created using interpolation of witness trees reveals a complex spatial pattern lacking clear geographic interpretation at this coarse scale, suggesting a

lack of correspondence with the dominant vegetation pattern. The resultant map also differs sharply from Gordon's (1966) map of *Natural vegetation of Ohio at the time of the earliest land surveys*. A statewide vegetation map is necessarily generalized, and his shows that this region was dominated by mixed oak forest (primarily white oak – black oak – hickory or white oak, with white oak – black oak and chestnut oak – chestnut (*Castanea dentata* (Marsh.) Borkh.) on the ridge tops), with beech forests (beech, red maple, sugar maple, and yellow-poplar) in the valleys. Compositionally, this characterization of the region is accurate, and the species – topographic position relationships are supported by the *G*-test results (see below). However, the witness tree data suggest that these relationships occur at a fine scale and not on a broad scale as indicated on the map. An examination of the preliminary notes used to construct Gordon's map, located in the Museum of Biological Diversity at Ohio State University, indicates that much of the data for this region of Ohio derived from fieldwork conducted ca. 1930s, after extensive clearing of the forests had taken place. No information was found for Hocking County in the preliminary notes.

Forest structure

Figure 3 presents size-class comparisons between witness trees and FIA data ($n = 55$ plots) for Athens County. This analysis includes witness trees for the smaller, irregular land subdivisions ($n = 2505$ trees), instead of just section and fraction trees ($n = 1076$ for Athens County) used in the analysis of the entire Ohio Company Purchase.

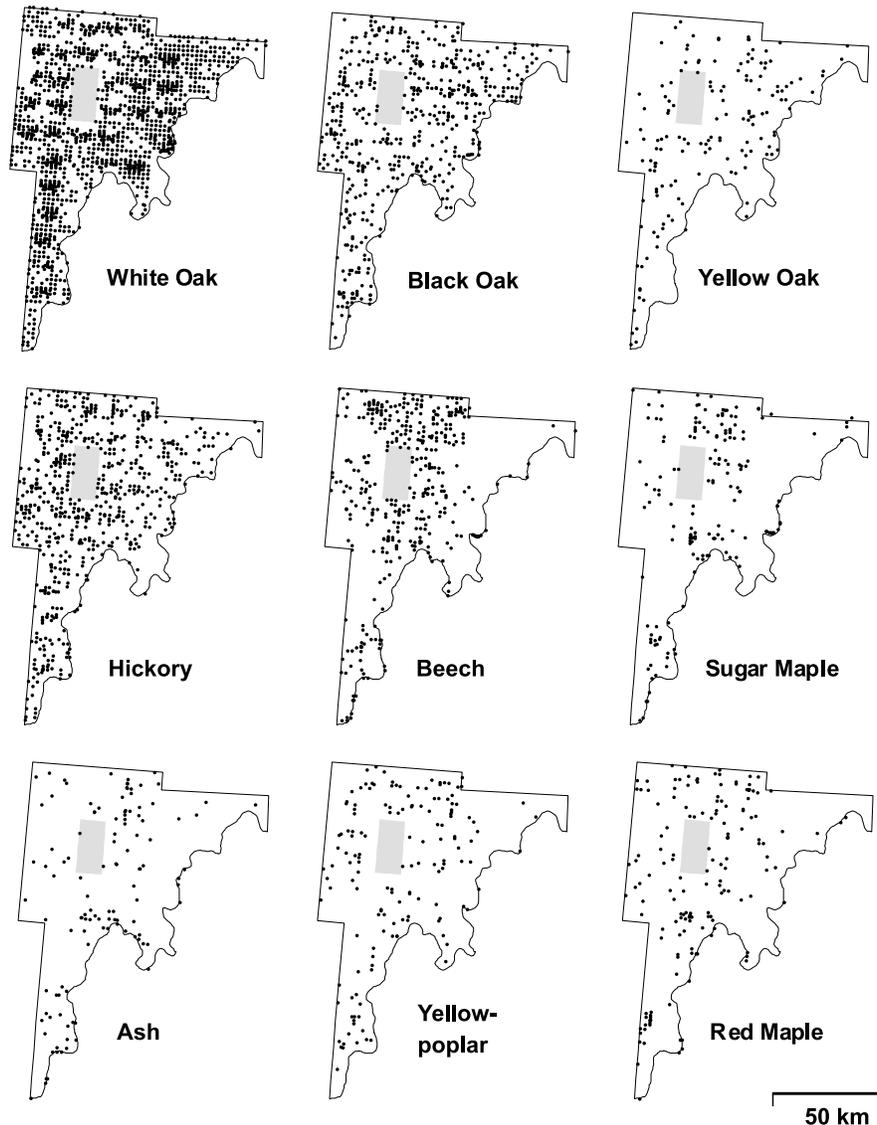
An examination of the size-class distribution of all witness trees clearly indicates that surveyors were estimating diameters, favoring even numbers (e.g., 10, 12, 14 in.). ANOVA tests did reveal a statistically significant ($p < 0.001$) difference in mean distances traveled by size class, traveling greater distances to select trees ≥ 9 in. (23 cm). This bias makes sense given the difficulties in blazing smaller trees. Although there was a general trend of traveling greater distances to larger trees, this may reflect lower densities in areas with larger sized trees.

When the analysis is limited to trees ≥ 9 in. (23 cm) DBH, the relative increase in smaller size-classes is evident in today's forests. In particular, the oaks, yellow-poplar, and ash had a greater percentage of individuals in the larger size-classes 200 years ago. For Athens County and the entire study area as a whole, the most abundant witness trees < 9 in. (23 cm) DBH (white oak, hickory, beech, black oak) were also the most abundant in the larger size classes.

Vegetation–site relationships

Figure 4 illustrates the corrected standardized residuals for those taxa possessing a significant ($p < 0.05$) *G* statistic. These values express the degree of association between the taxon and specific site factors. Topographic position, aspect, and slope all play a role in segregating species within this highly dissected landscape. Red maple, sugar maple, beech, and yellow-poplar are negatively associated with ridge positions and further segregate between slope and valley positions. White oak, yellow oak, and black oak preferentially occur on ridge positions. Similar patterns were observed in northeastern Ohio (Whitney 1982) and in the Allegheny

Fig. 2. Point distributions of witness trees accounting for $\geq 2\%$ of total. Stippled area was not divided into sections and fractions (see Fig. 1).



Mountains and Ridge and Valley regions of West Virginia (Abrams and McCay 1996), although in West Virginia, beech was associated with mountain-top positions. For the presettlement vegetation, black oak is positively associated with “high heat load” aspects (135° – 315°), while red maple and yellow-poplar are positively associated with “low heat load” aspects. Although the FIA data were collected as areal samples and not as point samples as with the witness trees, a similar result emerges, with sugar maple and yellow-poplar more frequently occurring on low heat load aspects and white oak, yellow oak, and black oak occurring more frequently on high heat load aspects. In terms of slope, sugar maple demonstrates a positive association with more gentle slopes, whereas white oak and black oak occur more frequently on steeper slopes in the presettlement forest. Sugar maple, beech, and yellow oak occur more frequently on FIA plots with steep slopes.

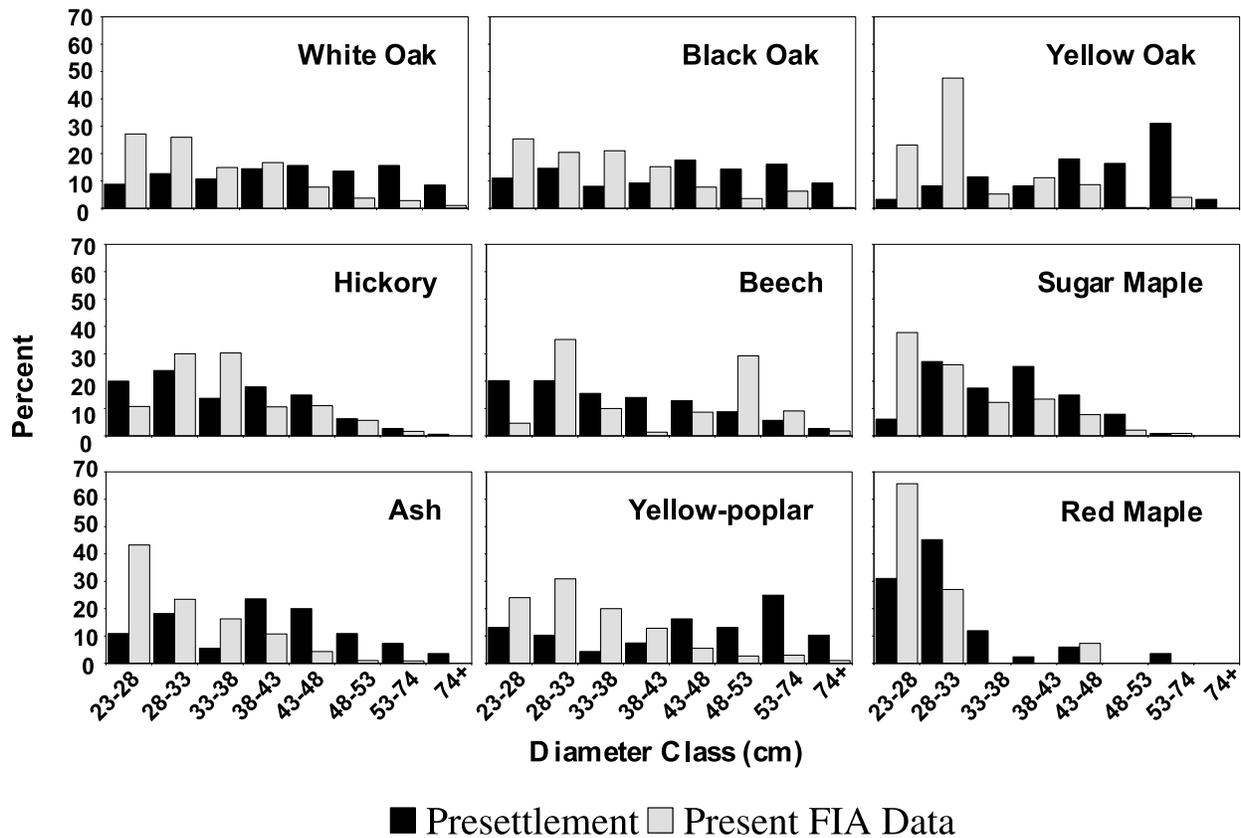
The IMI, which incorporates the influences of topography, slope, and aspect, is able to discriminate among the greatest number of witness tree taxa compared with individual site

factors. Red maple, sugar maple, beech, ash, and yellow-poplar all occur more frequently on mesic sites, whereas white oak, yellow oak, and black oak occur more frequently on more xeric sites. No taxon demonstrates an affinity for a specific physiographic class using the FIA data. This can largely be attributed to the fact that there is very little variability between plots, with 89% of all plots being classified as mesic.

Discussion

Prior to Euro-American settlement in the late 18th century, total forest cover in southeastern Ohio probably approached 100%. Following a period of intensive resource extraction, forest cover reached its minimum in the early 20th century; subsequently, the trend has been one of steady reforestation, and now this central Appalachian site is almost 70% forested. This trend toward reforestation parallels similar trends seen elsewhere in the eastern United States (e.g., Cowell 1993; Smith et al. 1993; Foster 1995; Matlack 1997).

Fig. 3. Size-class diagrams for taxa accounting for $\geq 2\%$ of witness trees. The ordinate represents the percent frequency of a particular size class relative to all individuals of that taxon. Solid bars are witness trees for Athens County, including those for irregular land divisions. Shaded bars are 1991 data (trees ≥ 23 cm DBH) for 55 FIA plots in Athens County.



As is the case with these other sites, the composition and structure of the regional forests have changed dramatically.

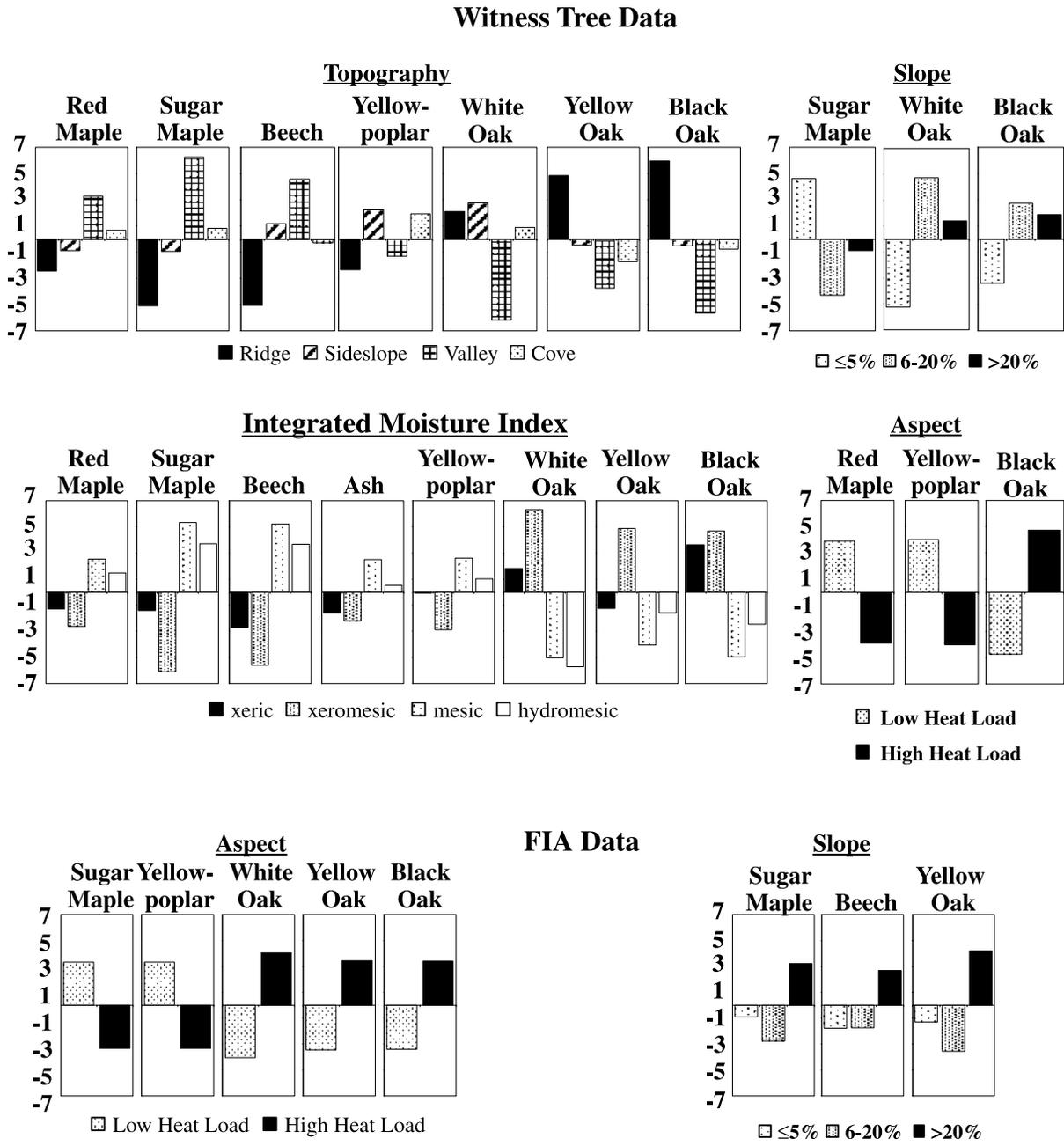
The fact that most of the region's forest originated this century is highlighted by size-class analysis; the modern forest is generally characterized by smaller stems compared with presettlement. In addition, there has been a shift in the dominant species. White oak dominated the presettlement forest but is now far less abundant. Sugar maple and red maple, on the other hand, have increased in abundance.

Loeb (1987) suggested that large numbers of white oak in colonial surveys in eastern New Jersey and southeastern New York might have been the result of surveyors accentuating its importance to attract settlers. However, Whitney (1982) also found high numbers of white oaks in his northeastern Ohio study site. This site, like the southeastern Ohio site, is located within the unglaciated Allegheny Plateau and was surveyed as part of the U.S. Military District in the early 19th century. Whitney reports the same five taxa as being most common witness trees as in the Ohio Company Purchase, with white oak accounting for 40.9% of all witness trees there. This is nearly identical to the 40.0% value with this study and suggests that white oak was formerly much more abundant regionally. It is highly unlikely that different groups of surveyors would exhibit identical biases across the different surveys.

A survey of Dysart Woods, an old-growth remnant in Belmont County, Ohio, about 70 km northeast of Marietta, found white oak to be dominant in the largest size classes

but virtually absent in the smaller size classes (Lafer and Wistendahl 1970; McCarthy et al. 2001). The change in composition noted since presettlement, with a dramatic decrease in oaks and hickories, and an increase in more mesophytic species, such as sugar maple, supports the observations in the old-growth stand and, indeed, throughout the eastern forests (e.g., McCarthy et al. 1987; Abrams and Downs 1990; Foster 1995). It is widely speculated that recurring surface burns of the forests by Native Americans favored more fire-tolerant species such as oaks and chestnut, and retarded later successional species; a subsequent decrease in fire frequency since settlement has contributed to the oak decline (e.g., Abrams 1992, 1998; Delcourt and Delcourt 1997; Lorimer et al. 1994; Foster 1995). Fire was no doubt used as a management tool in southeastern Ohio, as Hildreth (1848) describes for Washington County in 1788: "Yearly autumnal fires of the Indians, during a long period of time, had destroyed all the shrubs and undergrowth of woody plants, affording the finest hunting grounds..." (p. 485). Similar accounts of yearly burnings near Marietta can be found in other accounts from the early settlement period (e.g., Barker 1958). It is uncertain, however, how extensively these methods were practiced. Dendroecological records in southeastern Ohio indicate increased fire frequency after settlement, with fire suppression beginning ca. the 1930s (Sutherland 1997; McCarthy et al. 2001). In a dendroecological analysis of Dysart Woods, McCarthy et al. (2001) found evidence of only six presettlement fires and

Fig. 4. Corrected standardized residuals for taxa accounting for $\geq 2\%$ of witness trees, that demonstrated a significant ($p < 0.05$) *G* statistic. Residuals express the degree of association between the taxon and specific site factors; positive and negative values indicate positive or negative association, respectively.



concluded that Native American fires may not have been as dramatic in the dissected uplands of southeastern Ohio as others have suggested. Instead, the authors hypothesize that recent climatic change may be responsible for the decrease in oak reproduction, with climate of the recent past being warmer and drier than present, thereby favoring oak regeneration. A palynological study of two sites in the glaciated Allegheny Plateau region of Ohio, one north of the study area and the other about 40 km west, offers support for this “drier past” hypothesis. Snyder et al. (1991) concluded that since European settlement, regional precipitation has increased 2–4 cm, and January temperatures increased by about 1°C, al-

though July temperatures have remained relatively unchanged.

In addition to a decrease in the dominant oaks and hickories with an increase in more shade-tolerant species such as sugar maple and red maple, a second evident trend is a dramatic increase in early successional species, such as yellow-poplar, ash, pine, aspen, and black cherry, following widespread clearing earlier this century. The dramatic decline in beech since 1790 can also be attributed to poor dispersal ability following land clearing (cf. Smith et al. 1993; Simard and Bouchard 1996). Past land-use history has clearly favored those trees with greater dispersal ability. In addition,

habitat fragmentation has also led to an increase in the deer population, but there are no data to suggest that over-browsing has limited oak regeneration in southeastern Ohio.

Although the nature of the witness tree data (point samples) and FIA data (area samples) precludes direct comparison, the limited conclusion can be drawn that the dominant forest taxa are occupying similar environmental sites today as they did in the presettlement forest, although relative abundances have changed significantly. The combining of some species into composite groups may have masked some vegetation–site relationships, but it would appear that many of the dominant taxa have wide ecological amplitudes within the study area. Using 7.5' DEMs to assess vegetation–site relationships, the IMI was able to discriminate the greatest number of species compared with other site factors. The IMI incorporates the influence of slope, aspect, and topographic position on evaporative demand and water availability. Topography exerts a stronger influence on vegetation pattern than broad-scale regional gradients in this ca. 5000 km² area.

Conclusions

The forests of southeastern Ohio differ markedly from the regional forest of only 200 years ago. Significant shifts in species composition and structure likely have been accompanied with concomitant changes in understory vegetation, nutrient cycling, and sedimentation and erosion rates. Oak and hickory have decreased in abundance, while sugar maple and red maple have increased. Similar changes have been reported throughout the eastern forests and often attributed to a decrease in fire frequency following Euro-American settlement. Fire no doubt was a management tool utilized by Native Americans, but it is yet unclear whether these practices were widespread or localized. A climatic change, with wetter conditions today, may contribute to the decrease in oaks at this central Appalachian site. Presettlement forest records provide baseline data critical for evaluating present-day environmental conditions.

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References

- Abrams, M.D. 1992. Fire and the development of oak forests. *BioScience*, **42**: 346–353.
- Abrams, M.D. 1998. The red maple paradox. *BioScience*, **48**: 355–364.
- Abrams, M.D., and Downs, J.A. 1990. Successional replacement of old-growth white oak by mixed mesophytic hardwoods in southwestern Pennsylvania. *Can. J. For. Res.* **20**: 1864–1870.
- Abrams, M.D., and McCay, D.M. 1996. Vegetation–site relationships of witness trees (1780–1856) in the presettlement forests of eastern West Virginia. *Can. J. For. Res.* **26**: 217–224.
- Barker, J. 1958. *Recollections of the first settlement of Ohio*. Marietta College, Marietta, Ohio.
- Batek, M.J., Rebertus, A.J., Schroeder, W.A., Haithcoat, T.L., Compas, E., and Guyette, R.P. 1999. Reconstruction of early nineteenth-century vegetation and fire regimes in the Missouri Ozarks. *J. Biogeogr.* **26**: 397–412.
- Beatley, J.C. 1959. The primeval forests of a Periglacial area in the Allegheny Plateau (Vinton and Jackson Counties, Ohio). Ohio State University, Columbus, Ohio. *Bull. Ohio Biol. Surv. New Ser.* **1**(1).
- Bourdo, E.A. 1956. A review of the General Land Office survey and of its use in quantitative studies of former forests. *Ecology*, **37**: 754–768.
- Braun, E.L. 1950. *Deciduous forests of eastern North America*. Hafner Publishing Co., New York.
- Brockman, C.S. 1998. Physiographic regions of Ohio. 1:2,110,000 scale (approx.) map. Ohio Department of Natural Resources, Division of Geological Sciences. Columbus.
- Buckley, G.L., Anderson, T.G., and Bain, N.R. 2000. Living on the fringe: a geographic profile of Appalachian Ohio. *In A geographic perspective of Pittsburgh and the Alleghenies: from Precambrian to post-industrial*. Association of American Geographers, Washington, D.C. pp. 140–147.
- Burrough, P.A., and McDonnell, R.A. 1998. *Principles of geographical information systems*. Oxford University Press, Oxford, U.K.
- Cayton, A.R.L. 1991. Marietta and the Ohio Company. *In Appalachian frontiers: settlement, society, & development in the preindustrial era*. University Press of Kentucky, Lexington. pp. 187–200.
- Cowan, W.C. 1987. *First farmers of the Middle Ohio Valley: Fort Ancient societies, A.D. 1000–1670*. Cincinnati Museum of Natural History, Cincinnati.
- Cowell, C.M. 1993. Environmental gradients in secondary forests of the Georgia Piedmont, U.S.A. *J. Biogeogr.* **20**: 199–207.
- Cowell, C.M. 1995. Presettlement Piedmont forests: patterns of composition and disturbance in central Georgia. *Ann. Assoc. Am. Geogr.* **85**: 65–83.
- Cowell, C.M. 1998. Historical change in vegetation and disturbance on the Georgia Piedmont. *Am. Midl. Nat.* **140**: 78–89.
- Delcourt, H.R., and Delcourt, P.A. 1974. Primeval magnolia–holly–beech climax in Louisiana. *Ecology*, **55**: 638–644.
- Delcourt, H.R., and Delcourt, P.A. 1997. Pre-Columbian Native American use of fire on southern Appalachian landscapes. *Conserv. Biol.* **11**: 1010–1014.
- Dennis, D.D., and Birch, T.W. 1981. Forest statistics for Ohio—1979. USDA For. Serv. Resour. Bull. NE-68.
- Diller, O.D. 1944. Ohio's forest resources. Ohio Agricultural Experiment Station, For. Publ. 76.
- Ford, R.I. 1977. Evolutionary ecology and the evolution of human ecosystems: a case study from the Midwestern U.S.A. *In Explanation of prehistoric change*. University of New Mexico Press, Albuquerque. pp. 153–184.
- Forman, R.T.T. 1997. *Land mosaics: the ecology of landscapes and regions*. Cambridge University Press, Cambridge, U.K.
- Foster, D.R. 1995. Land-use history and four hundred years of vegetation change in New England. *In Principles, patterns, and processes of land use change: some legacies of the Columbian encounter*. SCOPE Publication. John Wiley & Sons, New York. pp. 253–319.
- Foster, D.R., Aber, J.D., Melillo, J.M., Bowden, R.D., and Bazzaz, F.A. 1997. Forest response to disturbance and anthropogenic stress. *BioScience*, **47**: 437–445.
- Foster, D.R., Motzkin, G., and Slater, B. 1998. Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. *Ecosystems*, **1**: 96–119.

- Fralish, J.S., Crooks, F.B., Chambers, J.L., and Harty, F.M. 1991. Comparison of presettlement, second-growth and old-growth forest on six site types in the Illinois Shawnee Hills. *Am. Midl. Nat.* **125**: 294–309.
- Gordon, R.B. 1966. Natural vegetation of Ohio at the time of the earliest land surveys. 1:500,000-scale map. Ohio Biological Survey, Columbus.
- Gordon, R.B. 1969. The natural vegetation of Ohio in pioneer days. Ohio State University, Columbus. *Bull. Ohio Biol. Surv. New Ser.* **3**(2).
- Griffith, D.M., DiGiovanni, D.M., Witzel, T.L., and Wharton, E.H. 1993. Forest statistics for Ohio 1991. USDA For. Serv. Resour. Bull. NE-128. FIA data available online: <http://www.srsfia.usfs.msstate.edu/tables.htm>
- Grimm, E.C. 1984. Fire and other factors controlling the Big Woods vegetation of Minnesota in the mid-nineteenth century. *Ecol. Monogr.* **54**: 291–311.
- Haberman, S.J. 1973. The analysis of residuals in cross-classified tables. *Biometrics*, **29**: 205–220.
- Hammett, J.E. 1997. Interregional patterns of land use and plant management in Native North America. *In* People, plants, and landscapes: studies in paleoethnobotany. University of Alabama Press, Tuscaloosa. pp. 195–216.
- Hildreth, S.P. 1848. Pioneer history: being an account of the first examinations of the Ohio Valley, and the early settlements of the Northwest Territory. H.W. Derby & Co., Cincinnati, Ohio.
- Hutchison, O.K., and Morgan, J.T. 1956. Ohio's forests and wood-using industries. USDA For. Serv. Central States For. Exp. Stn. For. Surv. Release 19.
- Iverson, L.R., Dale, M.E., Scott, C.T., and Prasad, A. 1997. A GIS-derived integrated moisture index to predict forest composition and productivity of Ohio forests (USA). *Landsc. Ecol.* **12**: 331–348.
- Kingsley, N.P., and Mayer, C.E. 1970. Timber resources of Ohio. USDA For. Serv. Resour. Bull. NE-19.
- Lafer, N.G., and Wistendahl, W.A. 1970. Tree composition of Dysart Woods, Belmont County, Ohio. *Castanea*, **35**: 302–308.
- Loeb, R.E. 1987. Pre-European settlement forest composition in east New Jersey and southeastern New York. *Am. Midl. Nat.* **118**: 414–423.
- Lorimer, C.G., Chapman, J.W., and Lambert, W.D. 1994. Tall understorey vegetation as a factor in the poor development of oak seedlings beneath mature stands. *J. Ecol.* **82**: 227–237.
- Loskiel, G.H. 1794. History of the mission of the United Brethren among the Indians in North America. Brethren's Society for the Furtherance of the Gospel, London, U.K.
- Lucht, T.E., Brown, D.L., and Martin, N.H. 1985. Soil survey of Athens County, Ohio. USDA Soil Conservation Service, Washington, D.C.
- Magilligan, F.J., and Stamp, M.L. 1997. Historical land-cover changes and hydrogeomorphic adjustment in a small Georgia watershed. *Ann. Assoc. Am. Geogr.* **87**: 614–635.
- Manies, K.L., and Mladenoff, D.J. 2000. Testing methods to produce landscape-scale presettlement vegetation maps from the U.S. public land survey records. *Landsc. Ecol.* **15**: 741–754.
- Matlack, G.R. 1997. Four centuries of forest clearance and regeneration in the hinterland of a large city. *J. Biogeogr.* **24**: 281–295.
- McCarthy, B.C., Hammer, C.A., Kauffman, G.L., and Cantino, P.D. 1987. Vegetation patterns and structure of an old-growth forest in southeastern Ohio. *Bull. Torrey Bot. Club*, **114**: 33–45.
- McCarthy, B.C., Small, C.J., and Rubino, D.L. 2001. Composition, structure, and dynamics of Dysart Woods, an old-growth mixed mesophytic forest of southeastern Ohio. *For. Ecol. Manage.* **140**: 193–213.
- McDonald, J., Wickstrom, L.H., and Steck, C.D. 1997. History of Ohio's oil- and gas-well location maps and their conversion to digital form. *In* Ohio Geological Society Fifth Annual Technical Symposium, 12 Nov. 1997, Akron, Ohio. Ohio Geological Society, Columbus. pp. 52–64. Digital data available online: http://www.dnr.state.oh.us/odnr/geo_survey/
- Moore, I.D., Gryson, R.B., and Ladson, A.R. 1990. Digital terrain modelling: a review of hydrological, geomorphological, and biological applications. *Hydrol. Process.* **5**: 3–30.
- Nass, J. 1988. Fort Ancient agricultural systems and settlement: a view from southwestern Ohio. *N. Am. Archaeol.* **9**: 319–348.
- National Oceanic and Atmospheric Administration (NOAA). 1982. Monthly normals of temperature, precipitation, and heating and cooling degree-days 1951–1980. National Oceanic and Atmospheric Administration, Asheville, N.C. *Climatogr. U.S.* **81** (Ohio).
- SAS Institute Inc. 1989. SAS/STAT user's guide, version 6. 4th ed. SAS Institute Inc., Cary, N.C.
- Sherman, C.E. 1925. Ohio cooperative topographic survey. Vol. 3. Original Ohio land subdivisions. Ohio State Reformatory, Columbus.
- Simard, H., and Bouchard, A. 1996. The precolonial 19th century forest of the Upper St. Lawrence region of Quebec: a record of its exploitation and transformation through notary deeds of wood sales. *Can. J. For. Res.* **26**: 1670–1676.
- Smith, B.E., Marks, P.L., and Gardescu, S. 1993. Two hundred years of forest cover changes in Tompkins County, New York. *Bull. Torrey Bot. Club*, **120**: 229–247.
- Snyder, G.G., Shane, L.C.K., and Kapp, R.O. 1991. Palynological studies associated with the Mound City Group National Monument, Chillicothe, Ohio. Final Report to the National Park Service. Hopewell Culture National Historical Park, 16062 State Route 104, Chillicothe, OH 45601-8694, U.S.A.
- Sokal, R.R., and Rohlf, F.J. 1995. Biometry: the principles and practice of statistics in biological research. 3rd ed. W.H. Freeman, New York.
- Stephenson, N.L. 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *J. Biogeogr.* **25**: 855–870.
- Strahler, A.H. 1978. Binary discriminant analysis: a new method for investigating species–environment relationships. *Ecology*, **59**: 108–116.
- Sutherland, E.K. 1997. History of fire in a southern Ohio second-growth mixed-oak forest. *In* Proceedings of the 11th Central Hardwood Forest Conference, 23–26 Mar. 1997, Columbia, Mo. Edited by S.G. Pallardy, R.A. Cecich, H.E. Garrett, and P.S. Johnson. USDA For. Serv. Gen. Tech. Rep. NC-188. pp. 172–183.
- Wagner, G. 1996. Feast or famine? Seasonal diet at a Fort Ancient community. *In* Case studies in environmental archaeology. Plenum Press, New York. pp. 255–272.
- Watson, P.J. 1989. Early plant cultivation in the eastern woodlands of North America. *In* Foraging and farming: the evolution of plant exploitation. Unwin Hyman, London. pp. 555–571.
- Whitney, G.G. 1982. Vegetation–site relationships in the presettlement forests of northeastern Ohio. *Bot. Gaz.* **143**: 225–237.
- Whitney, G.G. 1986. Relation of Michigan's presettlement pine forests to substrate and disturbance history. *Ecology*, **67**: 1548–1559.
- Whitney, G.G. 1994. From coastal wilderness to fruited plain: a history of environmental change in temperate North America 1500 to the present. Cambridge University Press, Cambridge, U.K.