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Land-use legacies in a central Appalachian forest: differential response of trees and herbs to historic agricultural practices

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Abstract

Question: Are contemporary herb and tree patterns explained by historic land use practices? If so, are observed vegetation patterns associated with life-history characteristics, soil properties, or other environmental variables?

Location: Southeastern Ohio, USA.

Methods: Using archival records, currently forested sites were identified with distinct land use histories: cultivated, pasture (but not plowed), and reference sites which appear to have never been cleared. Trees were recorded by size and species on twenty 20 m×20 m plots; percent cover was estimated for each herb species in nested 10 m×10 m plots. Environmental characteristics were noted, and soil samples analysed for nutrient availability and organic matter. Nonmetric multidimensional scaling ordination was performed separately on both tree and herb datasets to graphically characterize community composition among plots. Life-history traits were investigated to explain observed compositional differences.

Results: Vegetation patterns were explained by current environmental gradients, especially by land-use history. Cultivated and pasture sites had similar tree composition, distinct from reference sites. Herb composition of pasture and reference sites was similar and distinct from cultivated sites, suggesting the 'tenacity' of some forest herbs on formerly cleared sites. Tilling removes rhizomatous species, and disfavors species with unassisted dispersal. These life-history traits were underrepresented on cultivated sites, although ant-dispersed species were not.

Conclusions: Historic land-use practices accounted for as much variation in species composition as environmental gradients. Furthermore, trees and herbs responded differently to past land-use practices. Life-history traits of individual species interact with the nature of disturbance to influence community composition.

Keywords: Agriculture; Dispersal; Disturbance; Historical ecology; Life-history traits; Reforestation; Soils; Succession.

Nomenclature: Cooperrider et al. (2001), except *Maianthemum racemosum* (L.) Link, *Packera aurea* (L.) A.& D. Löve, *Quercus montana* Willd.

Introduction

When Europeans initially colonized eastern North America, forests likely covered over 90% of the land area (Greeley 1925). Rapid, widespread clearing occurred in the nineteenth century, with forest cover reduced to <25%. The region is currently nearly 40% forested, yet present-day forests show the legacy of past land use (Dyer 2006). Widespread clearing promotes tree species that can readily disperse into open areas, and which tend to exhibit rapid growth, shade intolerance and are relatively short-lived (Matlack 1997; Foster et al. 1998; Dyer 2001; Vellend et al. 2007). A corresponding trend occurs with herbaceous communities, with disturbance-sensitive species being underrepresented in secondary forests. Factors that seem to consistently influence recolonization include seed production, germination requirements, seedling herbivory, and especially dispersal ability. These traits seem to emerge whether looking at individual species, or polythetic species groupings (Matlack 1994; Singleton et al. 2001; Bellemare et al. 2002; Dupouey et al. 2002; Eberhardt et al. 2003; Verheyen et al. 2003; Endels et al. 2007). In addition, conversion of temperate forest to agriculture alters soil physical, chemical and microbial properties, which may influence subsequent reforestation.

Despite a consensus on the importance of land-use legacy effects, contradictory findings have emerged. For example, compared with reference forests (i.e. sites that appear never to have been cleared), several studies have found higher levels of soil calcium (Ca), magnesium (Mg), and/or phosphorus (P) in formerly cultivated areas, while other studies have found no difference, or even reduced levels of one or more of these nutrients (Koerner

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et al. 1997; Richter & Markewitz 2001; Eberhardt et al. 2003; Falkengren-Grerup et al. 2006; Fraterrigo et al. 2006b; versus Glitzenstein et al. 1990; Bellemare et al. 2002; Fraterrigo et al. 2005). Similar ambiguities arise with respect to soil organic matter, carbon (C), nitrogen (N), and/or C:N ratios (Motzkin et al. 1996; Koerner et al. 1997; Falkengren-Grerup et al. 2006; versus Verheyen et al. 1999; Maloney et al. 2008). Whether changes in soil conditions exist, and the degree to which they persist, may result from pre-existing conditions (Dupouey et al. 2002; Flinn et al. 2005), and the nature and duration of agricultural activity (Motzkin et al. 1996; Wilson et al. 1997; Verheyen et al. 1999). With respect to dispersal, some studies indicate that differences in species composition are not related to dispersal mode, although the majority suggests that certain species face a dispersal limitation (cf. Singleton et al. 2001; Flinn & Marks 2004; versus Matlack 1994; Bellemare et al. 2002; Endels et al. 2007; Van der Veken et al. 2007). Species under-represented in secondary forests are often dispersed by gravity (barochory), ballistically (autochory) or by ants (myrmecochory), although Mitchell et al. (2002) conclude that historic land use does not necessarily limit ant dispersal.

Despite variation in research findings, appreciation of historical land-use legacies has informed our understanding of contemporary community structure. Given the geographic variation in environmental gradients, species composition and historic land-use practices, the role of history must be compared at a variety of places. In the deciduous forests of eastern North America, most historical ecological research has been focused on New England (Foster 1992; Motzkin et al. 1996; Foster et al. 1998; Bellemare et al. 2002; Eberhardt et al. 2003), central New York (Singleton et al. 2001; Flinn & Marks 2004; Flinn et al. 2005) and the southern Appalachians (Duffy & Meier 1992; Mitchell et al. 2002; Fraterrigo et al. 2006a). This study explores vegetation patterns related to historic land-use patterns in the central Appalachian region of Ohio. Owing to the area's isolation, relatively recent settlement history, and availability of archival records, it has been possible to identify currently forested sites that previously have been cultivated (plowed) or pasture (but not plowed), as well as older-growth reference sites. The goal is to elucidate any patterns that may emerge in both woody and herbaceous vegetation among sites with differing land-use histories, and to ascertain whether these patterns are related to life-history characteristics, soil properties, or other environmental variables.

Materials and Methods

Study area

Hocking County is located in southeastern Ohio, USA, and is situated on the unglaciated Allegheny Plateau; climate is humid continental (Köppen's Dfa). The county lies within the Mesophytic forest region (Dyer 2006), characterized by high species diversity. A significant shift in composition has been noted since the presettlement period, with contemporary forests having a higher proportion of early-successional species (Dyer 2001). This change is attributable at least in part to land-use change over the last 200 yr. Southeastern Ohio witnessed extensive forest clearing for agriculture in the eighteenth and early nineteenth centuries, followed by widespread abandonment and reforestation – a pattern observed throughout the eastern US (Foster 1992; Matlack 1997; Flinn et al. 2005; Fraterrigo et al. 2006b). According to Annual Reports of the Ohio Secretary of State, forest cover in Hocking County decreased from about 70% in 1850, to about 35% in 1875, and 20% in 1900.

Hocking County was selected for study because of the availability of archival land use records for the late nineteenth and early twentieth century, with subsequent aerial photographic coverage throughout the twentieth century. Detailed analysis focused on sites within a 200 km^2 area (39.43°N 82.66°W), which at present is about 85% forested (US Geological Survey 2007). The area is highly dissected, with steep slopes and moderate relief (elevation range 195-355 m). Soils are underlain by sandstone, shale, and conglomerate (Lemaster & Gilmore 1989).

Historical land use

Although evidence indicates human occupation as far back as the Adena Culture (c. 800 BC to AD 1; Mills 1914), regional population densities were relatively low in pre-contact times, with intensive land-use activity limited principally to bottomlands (Loskiel 1794; Cowan 1987). This pattern continued into the post-contact period (Rypma 1961), until Native groups were forced out of the region in the early nineteenth century. Euro-American squatters were forcibly removed from what is now Hocking County in 1785, as the area became part of the 'Congress Lands,' authorized for sale in 1796 (Sherman 1925). The study area was surveyed 1798-1799 using a rectilinear system; records of witness trees for these surveys were consulted at the Auditor of State's office in Columbus, OH, USA.

Hocking County was established from existing counties in 1818. According to the 1820 US Federal Census, 739 people lived in the townships containing the study area; virtually all of the heads of households declared their occupation as 'farmer'. By 1850, 3629 people lived in the four townships (totaling 391 km^2) encompassing the study area. Farmers and laborers constituted the vast majority of listed occupations, and 40% of the land was listed as 'improved.' Individual farms were relatively small, and largely engaged in subsistence farming. Corn and wheat were primary crops, with livestock including sheep, hogs, cattle and horses. Throughout the nineteenth century, the application of lime, manure or commercial fertilizers was uncommon (Jones 1983). The population continued to increase throughout the nineteenth century, peaking in 1900. Following a steady decline through the mid-twentieth century, county population did not exceed the 1900 level until 1990.

In order to quantify land-use activity in a spatially explicit manner, tax assessment records covering the years 1890, 1900 and 1910 – years of peak population and agricultural activity – were obtained from the Ohio University Archives collection. For each property in the township, these records include a map showing parcel boundaries, and the number of acres in cultivation, pasture, and woodland. This spatial land-use information was georeferenced for the study area.

To assess twentieth century land-use patterns, black-and-white aerial photographs (nominal scale 1:20 000) were obtained for each study area. The photographs, covering the years 1938, 1957 and 1966, were scanned and then georeferenced in a GIS. Polygons were digitized representing three land-use classes: forested (closed canopy), cultivated (open sites with evidence of plowing) or pasture (herbaceous cover and no evidence of plowing, open canopy or absence of tree cover).

The tax assessment records combined with twentieth century aerial photograph coverage provide land-use data spanning over a century. These spatially explicit records (1) enable an overview of historic land-use intensity within the study area, and (2) allow the identification of individual study sites, with known land-use history, for vegetation sampling. Although the study area has a long history of human occupation, it was possible to identify sites that have been previously plowed, cleared for pasture but not plowed, or have been continuously forested throughout the twentieth century (and likely never cleared). The forests in each of these three groups – cultivated, pasture and reference – were sampled and evaluated for land-use legacy effects.

Contemporary vegetation and environmental variables

Coordinates of potential plot locations were first noted in a GIS, and located via GPS. The first corner of each 20 m×20 m (0.04 ha) plot was located randomly, with the plot boundary coinciding with the site's contour lines. Twenty plots were established at sites with continuous forest cover since at least 1966. Plots fell into three classes: formerly cultivated ($n = 7$), formerly pasture but not plowed ($n = 7$), and reference sites that have been continuously forested since 1890, and likely much longer ($n = 6$). Reference sites were selected from parcels heavily forested (averaging $>90\%$) 1890-1910. Cultivated sites were classified as cropland according to 1938 aerial photographs, and as pasture in 1951; each reverted to forest over the following two decades. Pastured sites were classified as pasture according to the 1938 photograph and all reverted to forest in the subsequent two decades.

Within each plot, all trees ($\geq$ 1 cm diameter at breast height (DBH) and >2 m in height) were tallied by species, and DBH recorded. These data were used to compute relative density and relative dominance for each species; importance values were also computed that equally weighted relative density and dominance. Herbaceous plants, as well as shrubs and vines unlikely to attain canopy status, were identified to species within a nested 10 m×10 m (0.01 ha) plot; in some instances, individuals could only be identified to genus. Percent cover of each taxon was estimated according to the following scale: 0-1%, 1-12%, 12-25%, 25-50%, 50-75%, and $>75\%$.

Slope and aspect were measured in each 0.04 ha plot using a Brunton compass, and per cent canopy cover and per cent exposed rock were estimated visually. A composite sample of the top 10 cm of mineral soil was collected from multiple sites in each plot (McCarthy 1997). Samples were analysed for pH (Ross combination electrode with 1:1 ratio of soil to water), plant available P, K, Mg and Ca (Mehlich III extraction), organic matter (loss on ignition), total C and N (combustion), C:N ratio and NH_4-N and NO_3-N (ion-selective electrode).

Life-history traits for each species occurring on the plots were compiled from numerous flora, published and online sources. Traits compiled for herbs included growth habit (forb, graminoid, fern, vine, subshrub), duration (annual, perennial), native status (native or introduced), dispersal mode (endozoochore, exozoochore, myrmecochore, anemochore, barochore, ballistic), type of fruit (berry, capsule, nutlet, etc.), seed size (length, in mm), shade tolerance (tolerant, intermediate, intolerant), presence of rhizome and vegetative reproduction (yes/no). Traits compiled for trees included dispersal mode, shade tolerance, native status (as with herbs), seed abundance, seedling vigor, drought tolerance, moisture use, fertility requirements, C:N requirements, palatability (low, medium, high), seed spread rate, relative growth rate, rate of vegetative spread (rapid, moderate, slow), seed bank persistence, resprouting ability and nitrogen fixing ability (yes/no).

Statistical analysis

Kruskal–Wallis tests were used to test whether environmental variables differed among land uses; Tukey's studentized range test was used to control for pair-wise comparisons (SAS 2003). To test for associations between individual species and land-use categories, presence/absence of individual tree and herb species occurring on >1 plot were analysed using G-tests (Sokal & Rohlf 1995). G-tests were also used to test for associations between land use categories and dispersal mode for herbs.

To graphically characterize community composition among the plots, non-metric multidimensional scaling (NMS) ordination was performed separately on both the tree and the herb data sets, retaining only those species that occurred on >1 plot. Community resemblance among the samples was expressed by Sørensen (Bray–Curtis) distances using Importance Values (trees) and cover class (herbs) in each plot. Analysis was performed using PC-ORD (McCune & Mefford 1999) using the 'slow-and-thorough' autopilot mode, assuming a random starting configuration. A Monte Carlo test of significance was performed using the best of 40 runs with the real data along with 50 runs with randomized data. Scree plots suggested that a three-dimensional solution was optimal for both tree and herb data sets. The NMS was then re-run specifying three dimensions and the best starting configuration. The amount of explained variance was expressed by the coefficient of determination between Sørensen distance in species space and Euclidean distance in ordination space. Environmental variables were superimposed on ordination diagrams using a joint plot, based on correlations between those variables and the ordination axes.

Results

Land-use history

According to the archival tax assessment records, over half of the study area was forested between 1890 and 1910, with about 13% under cultivation. Aerial photographs indicate that the percentages of cultivated and pasture land gradually declined throughout the twentieth century, with most trees establishing from the late 1930s to the early 1960s. Currently, the study area is 4% cultivated and 6% pasture (US Geological Survey 2007).

Environmental characteristics

Kruskal–Wallis tests indicated that reference sites had significantly ($P<0.05$) higher values of slope and soil organic matter, and lower soil Mg compared to cultivated sites. In addition, reference plots had higher rock cover and soil *P* than both cultivated and pasture sites (Table 1).

Tree stratum

A total of 37 tree species were identified on all plots; cultivated plots averaged 8.4 species per plot, reference sites averaged 7.2, and pasture sites 10.1 species. Ordination using the tree data was able to explain 92% of the variance in species composition. Figure 1a presents all sites plotted against two axes of the ordination; each axis accounted for 37% of the variation in species composition. (With NMS

Table 1. Median values of environmental variables by land use category.

	Cultivated	Pastured	Reference
Slope (%)*	15^{a}	25^{ab}	55^{b}
Rock cover (%)*	0^{a}	0^{a}	15^{b}
Organic matter (%)*	1.8^{a}	2.2^{ab}	3.35^{b}
P (ppm)*	8^{a}	6^{a}	15.5^{b}
Mg (ppm)*	142^{a}	126^{ab}	50.5^{b}
Herb cover (%)	70	35	45
pH	5.2	5.2	5.2
Ca (ppm)	394	529	558
K (ppm)	91	88	92.5
NH_4-N (ppm)	6.5	6	7
NO_3-N (ppm)	5	4	6
Total N (%)	0.27	0.26	0.38
Total organic C (%)	1.45	1.57	2.65
C:N Ratio	6.0	7.5	9.9

Variables that Kruskal–Wallis tests indicated were significantly different ($P<0.05$) between land-use categories are indicated by an asterisk; superscripts indicate values which are significantly different ($P<0.05$) according to Tukey's studentized range tests.

ordination, axes are not necessarily numbered in order of 'importance'; Axis 1, not shown, accounted for 19% of the variation.) A clear pattern emerges along Axis 2, in which reference sites are compositionally distinct from cultivated and pasture sites. The overlap of the cultivated and pasture sites suggests that they are compositionally similar. The ordination stabilized at a final stress of 8.61, suggesting a good ordination allowing for reliable inferences (McCune & Grace 2002). Joint plots, an overlay of radiating lines from the center of the ordination, were used to indicate correlations between ordination axes and environmental variables. (The angle and length of the line indicate the direction and strength of the relationship.) An association is revealed between Axis 2 and tree ages of the plots, and percent rock cover. Axis 3 segregates sites along a gradient related to aspect, and soil pH and Ca. Plots situated along the top half of Axis 3 have an easterly aspect, pH range of 5.2-6.0, and average soil Ca of 856 ppm, whereas those plots along the bottom half of Axis 3 have a westerly aspect, a pH range of 4.4-5.2, and average soil Ca of 358 ppm.

The G-tests indicated that only two tree species showed a significant ($P<0.05$) association with a particular land-use category. *Quercus montana* only occurred on reference sites and *Pinus virginiana* only occurred on cultivated sites. Aerial photographic analysis indicated that although some cleared areas in the study area were planted with pine, all sampled plots seem to have reforested naturally.

Despite the lack of association between most tree species and land-use history of the plots, a number of life-history traits appear to be associated with previously cleared sites compared with reference sites. In Fig. 1b, the 24 individual tree species occurring on > 1 plot are shown in ordination space. Although no single life-history trait seemed to correlate highly with species' position in ordination space, a suite of 'early successional' traits emerge. Figure 1b distinguishes those tree species possessing two or more traits favorable for colonizing open sites: wind-dispersed seed, shade intolerance, rapid/moderate growth rates and drought tolerance. Species with multiple early-successional traits tend to occur to the left of Axis 2 (formerly cultivated and pasture plots).

Acer rubrum serves as an ideal example of an early-successional species associated with agricultural clearing. It comprised 24.9% of trees found on cultivated and pasture sites, whereas on the reference sites, *A. rubrum* only accounted for 1.9% of all trees. The most abundant tree on the reference sites was *Acer saccharum*, accounting for almost half (48.1%) of stems. In terms of basal area, *A. saccharum* comprised 19.6% of reference plots, placing it third behind *Liriodendron tulipifera* (30.8%) and *Q. montana* (21.8%). The abundance of both *A.*

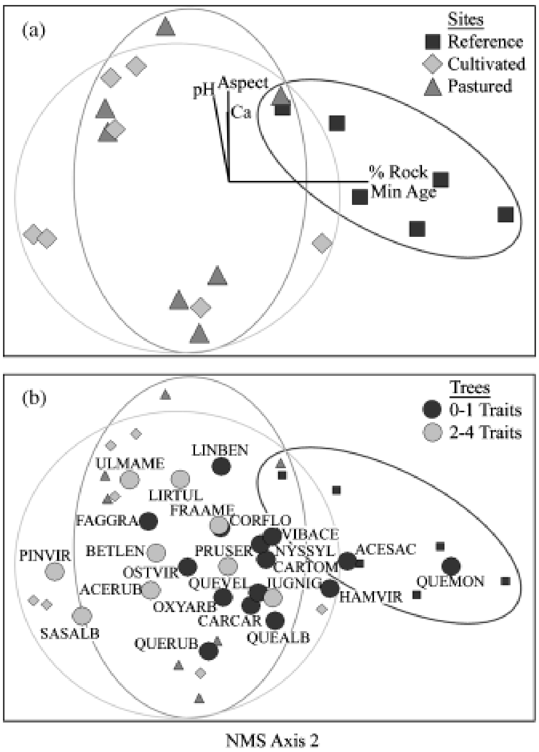

Fig. 1. (a) Non-metric multidimensional scaling (NMS) ordination of sites based upon tree data. Ellipses circumscribe sites of common land-use history, indicated by symbols. Reference sites are compositionally distinct from cultivated and pasture sites. Radiating lines indicate relative strength and direction of correlation of environmental variables with axes of community ordination; the overlapping 'Per cent Rock' and 'Minimum Age' vectors are the same length. (b) Same ordination as in (a), with tree species occurring on more than one site plotted in ordination space. Trees are coded with respect to the number of early successional traits they possess: wind-dispersed seed, shade intolerance, rapid/moderate growth rates, drought tolerance; *Acer. rubrum* (ACERUB), *Acer saccharum* (ACESAC), *Betula lenta* (BETLEN), *Carpinus caroliniana* (CARCAR), *Carya tomentosa* (CARTOM), *Cornus florida* (CORFLO), *Fagus grandifolia* (FAGGRA), *Fraxinus americana* (FRAAME), *Hamamelis virginiana* (HAMVIR), *Juglans nigra* (JUGNIG), *Lindera benzoin* (LINBEN), *L. tulipifera* (LIRTUL), *Nyssa sylvatica* (NYSSYL), *Ostrya virginiana* (OSTVIR), *Oxydendrum arboreum* (OXYARB), *Pinus. virginiana* (PINVIR), *Prunus serotina* (PRUSER), *Quercus alba* (QUEALB), *Quercus montana* (QUEMON), *Quercus rubra* (QUERUB), *Quercus velutina* (QUEVEL), *Sassafras albidum* (SASALB), *Ulmus americana* (ULMAME), *Viburnum acerifolium* (VIBACE).

rubrum and *A. saccharum* on the study sites contrasts sharply with witness trees surveyed 1798-1799. *A. rubrum* and *A. saccharum* each comprised 3.1% of the 130 witness trees noted in a 29-section area (one section $\approx 2.6\,\mathrm{km}^2$) encompassing the study area. (Given the sample size, potential surveyor bias in witness tree selection was not statistically tested. However, Dyer (2001) found no evidence of bias in the adjacent land subdivision, conducted by the same surveyors.) The percentage of *L. tulipifera*, however, was largely unchanged since the presettlement period (10.8% presettlement versus 11.0% on all study sites). The increase in *Acer* throughout the landscape since settlement has largely been at the expense of *Quercus*, *Carya*, and *Castanea dentata*. These taxa constituted 20.8%, 14.6% and 9.2% of witness trees, respectively, whereas on the study sites *Quercus* comprised 5.7% and *Carya* 3.8% of trees; *C. dentata* was extirpated by chestnut blight (*Cryphonectria parasitica*) in the mid-twentieth century.

Herb stratum

A total of 71 herbaceous species were identified on all plots; cultivated plots averaged 19.4 species per plot, reference sites averaged 19.8 and pasture sites 15.0 species. Ordination using the herb data was able to explain 73% of the variance in species composition. Figure 2 indicates all sites plotted against two axes of the ordination using only these herb data. Axis 2 accounted for 37% of the variation in species composition and Axis 3, 30%. (Axis 1 only accounted for 6% of the variation.) In contrast to the tree data, ordination of the herb data reveals that it is the cultivated sites that are compositionally distinct from pasture and reference sites. The overlap of pasture and reference sites indicates a similar herb composition among these sites with different land use histories. The ordination stabilized at a final stress of 13.8, again indicating a satisfactory ordination. As with the tree ordination, soil Ca correlated with the ordination axes, although the relationship was not as closely linked with one particular axis. Plots with the lowest Ca are located at the top right of Fig. 2, and highest values are found in the lower left.

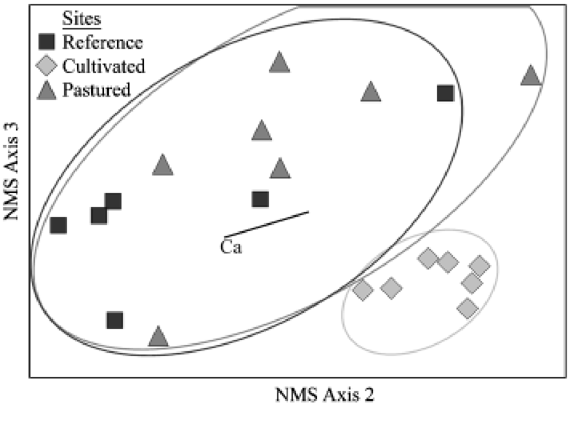

Fig. 2. Non-metric multidimensional scaling (NMS) ordination of sites based upon herb data. Ellipses circumscribe sites of common land-use history, indicated by symbols. Cultivated sites are compositionally distinct from reference and pasture sites. The radiating line indicates the relative strength and direction of the correlation between soil Ca and the community ordination axes.

Compared with tree species, a greater number of herb species were restricted to certain land-use histories. As ordination results suggested that reference sites were compositionally similar to pasture sites, and that these sites were distinct from cultivated sites, individual species were plotted based on frequency of occurrence in these two land-use groupings. Figure 3 presents the results for those 49 species occurring on more than one plot. Site affinities between individual species and land use histories are evident, and G-tests confirmed that several species were associated with particular land-use histories; these species are indicated in Fig. 3. Of the various life-history traits that were investigated, two in particular showed an association with land-use patterns: mode of dispersal and whether the species was rhizomatous. These traits are included with the species listed in Fig. 3. Of the 14 species listed in Fig. 3 that occurred only on reference and/or pasture sites, 13 (93%) have rhizomes; seven (50%) had unassisted dispersal (barochores or autochores) and were also rhizomatous. By contrast, of the nine species that occurred only on cultivated sites, or whose G-statistic indicated a significant association with cultivated sites, only three (33%) had rhizomes, including two violets; the two were also the only species with gravity or ballistic dispersal. The G-tests revealed a statistical association ($P<0.05$) with rhizomatous species, as well as rhizomatous species with unassisted dispersal, but not mode of dispersal only. Ant dispersal (myrmecochory) did not appear associated with land-use history (see Fig. 3); 21% (3/14) of reference/pasture-only species were myrmecochores, as were 22% (2/9) of cultivated species. The only non-native species listed in Fig. 3 are *Lonicera japonica*, *Rosa multiflora* and *Polygonum cespitosum*. All were associated with cultivated sites.

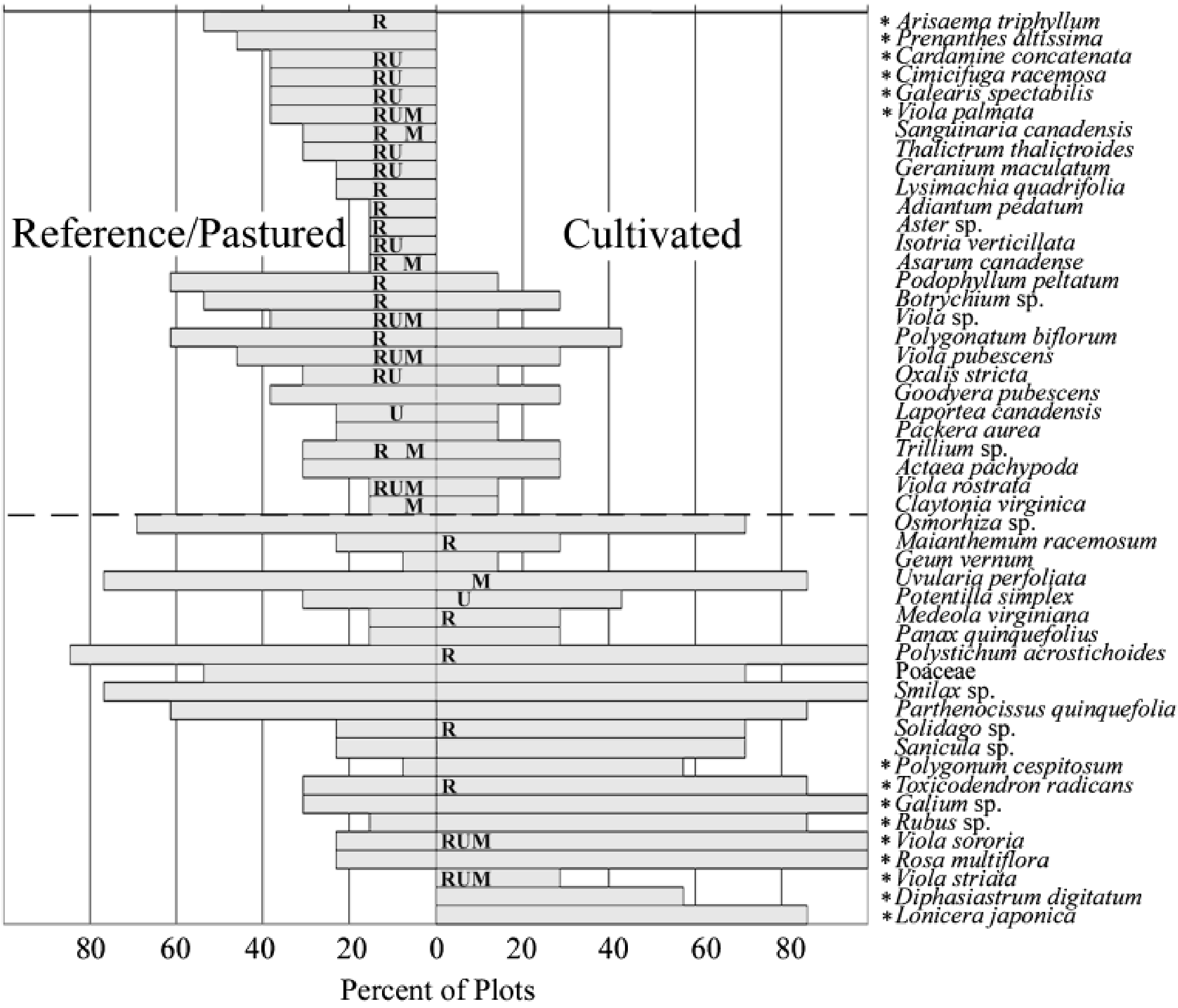

Fig. 3. Distribution on cultivated versus reference and pasture sites, for herbs occurring on more than one plot. Horizontal dashed line separates species more common on reference and pasture sites (top) from those more common on cultivated sites (bottom). Asterisks indicate species statistically associated with a particular land-use history (G-tests, $P < 0.05$). Letters indicate life-history traits: rhizomatous (R), unassisted dispersal (U), myrmecochore (M). *A. triphyllum* is included with rhizomatous species because its large corm would also be susceptible to plowing.

Discussion

Although historic records do not provide continuous documentation of past land-use practices, field data support the land-use classification of the study sites: the composition and structure of trees, combined with site inaccessibility, strongly indicate long-standing forest cover of the reference sites. In addition, the fact that graminoids comprised $<1\%$ on all pasture plots suggests that they were unlikely to have been formerly cultivated sites (cultivated sites converted to pasture likely would have been seeded; R. L. McCulley, grassland ecologist, pers. comm., 2007.) Evidence of cultivation on the remaining sites was clearly observed on aerial photographs. It is reasonable to assume that all three classes of sites experienced grazing in the past, and the nature of historic grazing could influence successional patterns (Copenheaver 2008). Although it is not possible to accurately assess the intensity or duration of past grazing activity, distinctive patterns were observed on the sites based on whether or not they were cleared or tilled.

Environmental characteristics

Previous studies have noted the link between past land-use decisions and site conditions, including drainage and accessibility, as well as slope and rockiness observed in this study (Foster 1992; Smith et al. 1993; Bellemare et al. 2002). Given the small-parcel ownership characteristic of these sites, farmers were making land-use decisions based on conditions within their farms, and not broader-scale environmental gradients (Flinn et al. 2005). Thus, many differences observed on disjunct sites with similar land-use histories may be ascribed to those land-use practices rather than pre-existing conditions.

In the present study, the historical footprint regarding soil fertility and past land-use activity appears minimal; significant changes either did not occur in the past or they were not persistent. Organic matter was lower on cultivated sites compared with reference sites, which may be attributable to reduced inputs of plant debris on cultivated sites, enhanced decomposition under higher soil temperatures and physical mixing of the soil through plowing (Richter & Markewitz 2001). Similarly, reduced soil P observed on cultivated and pasture sites may represent agricultural depletions caused by removal of plant biomass, erosion accompanying tillage or crop uptake (McLauchlan 2006). Wilson et al. (1997) reported progressively increasing soil P with time under woodland, although the explanation was unclear the increase may have be caused by indirect factors associated with reforestation (e.g. immigration of faunal populations, guano inputs). Elevated soil Ca concentrations were not observed in cultivated sites, suggesting that these sites were not limed. The higher soil Mg concentrations in cultivated sites may therefore reflect natural environmental variability. Although soil differences were relatively minor, striking differences are evident in vegetation composition and related to past land-use activity.

Compositional differences: tree stratum

When examining the tree stratum, formerly cultivated and pasture sites were similar in composition, with both being distinct from reference sites. Ordination revealed an axis unrelated to land-use history, which indicates that species are responding to well-established contemporary environmental gradients (Dyer 2001; McCarthy et al. 2001). An equally important 'land-use gradient' was also apparent, with reference sites forming a distinct cluster separate from cultivated and pasture sites (Fig. 1a). This axis correlates both with 'per cent rockiness' (rocky sites would less likely be cleared for agriculture; Bellemare et al. 2002) and with stand age; in this latter sense, it can be interpreted as a successional axis. Many of the life-history traits observed on the former cultivated and pasture sites are characteristic of species able to colonize open sites. This pattern has been observed frequently on former agricultural sites (Foster et al. 2003; Maloney et al. 2008). Given the relatively young age of the cultivated and pasture sites compared with the reference sites, it is too soon to predict whether the observed compositional differences will be maintained. Considering the dominance of *A. rubrum* on these formerly cleared sites, as well as its average life-span and shade tolerance, it is plausible that the observed compositional differences will be maintained indefinitely (Glitzenstein et al. 1990).

Only two species showed a statistically significant association with a particular land-use category. *Quercus montana*, which is characteristically associated with more xeric topographic ridge settings, occurred more often on reference sites than would be expected by chance. These topographic settings would be less conducive for agriculture, and would explain the species abundance; a similar association with *Q. montana* was noted by Glitzenstein et al. (1990) in eastern New York. The other species associated with sites of a particular land-use history was *P. virginiana*. The bare mineral soil of cultivated sites facilitates the germination requirements of *Pinus*, and the association between *Pinus* and former cultivated land has been noted throughout the eastern US. (Glitzenstein et al. 1990; Orwig & Abrams 1993; Motzkin et al. 1996).

Compositional differences: herb stratum

In contrast to the tree stratum, pasture sites were similar to reference sites, and it was the cultivated sites that were distinct in terms of their herb composition. As with trees, ordination suggested that herbs are responding to gradients in fertility (Fig. 2), as has been noted in other forests of Appalachian Ohio (Hutchinson et al. 1999; Small & McCarthy 2002). Although there is a relationship to present-day environmental gradients, it is historical land-use that seems to impose a stronger imprint on the herb layer. In accord with previous studies, 'disturbance sensitive' species seem to be under-represented on formerly cultivated sites (Bratton & Meier 1998; Dupouey et al. 2002).

Compared with dominant tree species, herb composition is more highly variable throughout the eastern US, which makes it difficult to identify individual species that appear to be sensitive to land-use history across different regions. Despite this limitation, several species in the present study (occurring on more than one plot) have also been noted in other studies, and in concert with other information may serve as indicators of past land-use activity. Singleton et al. (2001), working in central New York state, noted several species that were more abundant on reference sites that had not been cleared for agriculture, compared to formerly plowed sites: *Asarum canadense*, *Prenanthes* sp., *Geranium maculatum*, *Podophyllum peltatum* and *Arisaema triphyllum*. Each of these taxa was also more abundant on reference and pasture sites in the present study, with *A. canadense* showing a statistically significant relationship (Fig. 3). Glitzenstein et al. (1990), working in eastern New York, also found *A. triphyllum* to be more abundant on former pasture sites and reference sites that had never been cleared for agriculture. On formerly cultivated sites, Singleton et al. (2001) observed a higher abundance of *Diphasiastrum digitatum* (syn. *Lycopodium digitatum*) and Glitzenstein et al. (1990) noted that *Rubus* was rare in primary woodlands; both taxa are significantly associated with formerly cultivated sites in the present study. In southeastern Ohio, *D. digitatum* is often seen as an indicator of past agricultural activity (pers. obs.).

Given the regional variability in herb composition, it may be more informative to examine life-history traits (rather than particular species) that may be influenced by land-use history. Numerous studies have observed that species with limited dispersal ability (autochores, barochores) are often underrepresented in younger secondary forest (Matlack 1994; Bellemare et al. 2002; Verheyen et al. 2003; Van der Veken et al. 2007). Unassisted dispersal can be seen as an adaptive response to stable environments with high recruitment probability (Endels et al. 2007). In the present study, unassisted dispersal is a trait underrepresented in formerly cultivated sites. However, ant dispersal (myrmecochory), a trait also associated with dispersal limitation into secondary forests, was not associated with land-use history.

Although some myrmecochores were restricted to reference sites (*A. canadense*) or reference and pasture sites (*Sanguinaria canadensis*, *Viola palmata*), a number seemed insensitive to the land-use history of the site (e.g. *Claytonia virginica*, *Uvularia perfoliata*, *Viola pubescens*). Glitzenstein et al. (1990) found *U. perfoliata* to be present on sites regardless of land-use history and *V. palmata* to be absent from formerly cultivated sites. Two species of ant-dispersed violets were significantly associated with formerly cultivated sites in this study: *Viola sororia* and *Viola striata*.

The assumption that myrmecochores should be underrepresented in secondary forests is based on typically short dispersal distances (Culver & Beattie 1978; Hughes & Westoby 1990), and a reduction in ant populations in cleared areas. However, Culver & Beattie (1978) point out a difference between North America and Europe regarding the large, very active and intensive-foraging wood ants. Whereas in Europe these ants often occur in forests, in the US they are found along forest edges and rarely occur in deep woods. Although ant-dispersed seeds may be more common in deep woods, plant species that co-occur with wood ants, such as *V. striata*, may experience long-distance dispersal and colonize cleared sites. Mitchell et al. (2002) concluded that in their North Carolina site, myrmecochores could colonize disturbed sites if mature plants were present. Myrmecochory may not be a consistent trait underrepresented in secondary forests as myrmecochores differ in attractiveness to ants, ant species differ in their capacity to disperse seeds and there is both landscape and regional variation in ant species composition (Culver & Beattie 1978).

The life-history trait that seemed most strongly linked to historic land-use was the presence of a rhizome. Plowing would remove these species (Elmore et al. 2006), explaining their underrepresentation in formerly cultivated sites. Rhizomatous species having unassisted dispersal would be especially underrepresented. Forest clearing without plowing, however, would not necessarily remove rhizomatous species, which contributes to the similarity between herb composition on former pasture sites and reference sites. Although rhizome presence is not frequently considered, in the present study this trait is more strongly linked to historic land-use patterns than mode of dispersal.

Conclusions

In many areas of the deciduous forest, anthropogenic disturbance may exceed natural disturbance in terms of intensity and magnitude (Foster et al. 1998). Human disturbances differ in duration, intensity and spatial extent, however, and these differences strongly influence ecological response (Donohue et al. 2000; Copenheaver 2008). In eastern North America, agricultural clearing represents the most extensive anthropogenic disturbance; many of these formerly cleared areas are now reforesting. To understand compositional changes on reforested sites, it is insufficient to merely distinguish between old growth and secondary forests. Specific land-use practices leave distinctive 'signatures' on reforested sites.

Current findings confirm the individualistic response of species to disturbance; life-history traits interact with the nature of the disturbance to influence species response. Trees with a suite of early successional characteristics – wind dispersal, shade intolerance, rapid growth and drought tolerance – were favored by agricultural clearing. Whether the site was plowed or not did not appear to be a critical distinction; cultivated and pasture sites had similar composition. In contrast, herb species composition was similar on former pasture and reference sites, suggesting a 'tenacity' of many herbs species on cleared land. Formerly cultivated sites had a distinctive herb species composition, in which rhizomatous species were underrepresented. Herb species with limited dispersal (autochores, barochores) were also underrepresented on the former plowed sites, although myrmecochores were not. Although other factors may be important in herb recruitment, including germination requirements (Beatty 1984) or disruption of the rhizosphere (Fraterrigo et al. 2006a; Kulmatiski et al. 2006), dispersal mode is clearly linked to recruitment on cleared sites, is important in determining community structure (Jacquemyn et al. 2001) and is one of the more readily definable traits for a number of woodland herbs.

Historic land-use practices accounted for as much variation in species composition as environmental gradients of aspect or soil fertility. Knowledge of historic land use, despite difficulties in its documentation, can be critical to our understanding of present-day ecological systems. Our understanding of species response to historic disturbance is hindered, however, by an incomplete knowledge of woodland herb ecology (Whigham 2004), yet it is the herb layer that accounts for the most diversity in deciduous forests and plays a critical role in numerous ecosystem functions (Roberts 2004).

In a compelling review, Sprugel (1991) identified historical legacies preserved in several exemplary ecological systems, prompting the question 'what is natural?' Given the extensive clearing of deciduous forests and our growing appreciation of historic land-use effects, it is evident that very few 'natural' areas likely remain in eastern North America and elsewhere. Although it may be possible to 'shift' overstory vegetation to a pre-agricultural state, this is a much more tenable prospect with herbaceous communities. In order to target areas with high conservation value, the identification of areas with minimal land use impacts – a lack of cultivation – may serve as an initial screening in efforts to identify areas of biological significance.

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