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Landscape patterns of understory composition and richness across a moisture and nitrogen mineralization gradient in Ohio (U.S.A.) *Quercus* forests

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Abstract

This study quantified relationships of understory vascular plant species composition and richness along environmental gradients over a broad spatial scale in second-growth oak forests in eastern North America. Species frequencies were recorded in 108 25 × 25 m plots in four study sites extending over 70 km in southern Ohio, U.S.A.. The plots were stratified into three long-term soil moisture classes with a GIS-derived integrated moisture index (IMI). In addition to the IMI, the environmental data matrix included eight soil and three overstory variables. Canonical correspondence analysis (CCA) indicated that variations in understory species composition were most strongly related to topographic variations in predicted moisture (IMI), N mineralization rate, nitrification rate, and soil pH. In addition, floristic variation at the regional scale was correlated with variations in soil texture, nitrification, pH, and PO_4^-, resulting from differences in the soil parent material complexes among sites. Species richness averaged 65 species/plot, and increased with moisture and fertility. Stepwise regression indicated that richness was positively correlated with N mineralization rate and nitrification rate, and inversely correlated with tree basal area. Greater richness on fertile plots was the largely the result of increasing forb richness. Forb richness per quadrat (2 m^2) was most strongly and positively related to N mineralization rate. Conversely, richness of understory individuals of tree species was greatest on xeric, less-fertile plots. Our results describe general, broad-scale species-environment relationships that occurred at both the topographic scale (long-term moisture status and fertility) and the regional scale (geomorphological differences among the sites). Strong species richness-N mineralization correlations indicate an important link between below-ground processes and above-ground biodiversity. Because *N* availability was a strong correlate to vegetation patterns at a broad-scale, our results suggest that the increasing rates of atmospheric N deposition in the region could have a major impact on understory vegetation dynamics.

Introduction

Since the classic studies of Whittaker (1956) and Bray & Curtis (1957), plant ecologists have sought to quantify the distribution of plant species along complex environmental gradients. In forested ecosystems, plant species composition and diversity are related to the availability of moisture, nutrients, and light, which are in turn related to topography, bedrock geology, soil characteristics, overstory structure, and land-use history.

In the northern hemisphere, solar radiation is greatest on southwest-facing slopes and least on northeast-facing slopes, thereby resulting in aspect-related gradients of humidity, soil moisture, and both air and soil temperatures (Wolfe et al. 1949; Hutchins et al. 1976; Xu et al. 1997). In forested landscapes with dissected topography, such aspect/moisture gradients are correlated with understory species composition (Allen & Peet 1990; Hix & Pearcy 1997) and diversity (Glenn-Lewin 1975; Huebner & Randolf 1995; Pausas & Carreras 1995). Indices of soil moisture based on combinations of site variables have also been correlated with variations in site productivity (McNab 1993; Fralish 1994) and overall plant species composition (Lieffers & Larkin-Lieffers 1987; Allen & Peet 1990; Lloyd et al. 1994).

In addition to their putative effect on species composition, such topographically-generated soil moisture and radiant energy gradients have been related to other ecosystem attributes and processes, including soil morphology and development (Finney et al. 1962; Pregitzer et al. 1983), nutrient cycling rates (Plymale et al. 1987; Morris & Boerner 1998), leaf litter decomposition rates (Boerner 1984a, Mudrick et al. 1994), mycorrhizal infection intensity (DeMars & Boerner 1995), soil enzyme activity (Decker et al., in press) and foliar nutrient dynamics (Boerner 1984b; Kost & Boerner 1985; Garten 1993). As N availability commonly limits plant growth in forested ecosystems (Aber et al. 1989), the effects of the topographic gradient on N availability may also affect species composition.

The availability of N is most easily (and often) measured as static pools of ammonium (NH_4^+) and nitrate (NO_3^-). However, N availability to plants is actually determined by the rate at which NH_4^+ and NO_3^- are produced through the processes of N mineralization and nitrification (Killham 1994). In upland forests, N mineralization rates have been related to tree species composition (Pastor et al. 1982; Zak et al. 1986; Garten et al. 1994) and productivity (Pastor et al. 1984; Liu & Muller 1993). However, studies relating understory vegetation to N mineralization and nitrification rates are only now beginning to emerge (Diekmann & Falkengren-Grerup 1998).

Long-term studies of deciduous forests in the eastern U.S. have demonstrated that the composition of oak-hickory (*Quercus-Carya)* forests has been shifting towards more mesophytic species, such as *Acer rubrum*, *A. saccharum* and *Liriodendron tulipifera* over the last 3–4 decades (Lorimer 1984; Abrams 1992). These changes are hypothesized to be the consequence of a suite of broad-scale environmental changes, including both chronic atmospheric deposition and changes in the prevailing disturbance regimes (e.g., increased suppression of fire, and decreased timber harvesting). The rapid pace of these changes makes it essential that we understand the relationships among topographically-generated gradients of moisture and nutrient availability, plant species composition and diversity, and the prevailing disturbance regime. Although numerous studies in the deciduous forests of eastern North America have documented species-environment relationships in single sites or over limited spatial scales, our objective was to examine these relationships for the rich understory layer at sufficiently broad geographic scale and with sufficient attention to environmental driving variables to produce a regional species-environment model.

Methods

Study Sites

In 1994, 27 sample plots were established in each of four study sites in the unglaciated Allegheny Plateau of southern Ohio. Arch Rock (39°12′ N, 82°23′ W) and Watch Rock (39°11′ N, 82°22′ W) are located in close proximity in the Raccoon Ecological Management Area (owned by Mead Paper Corp.) in Vinton County. Young's Branch (38°43′ N, 82°41′ W) and Bluegrass Ridge (38°36′ N, 82°31′ W) are located in the Wayne National Forest in Lawrence County, and are 50 and 70 km south of the Vinton sites, respectively. The study sites range from 75–110 ha and are characterized by relatively undisturbed, second-growth ($>$80 years since clear cutting) mixed-oak forest.

Although these unglaciated sites are deeply dissected, the elevation for the vegetation plots ranges only from 208 to 307 m; all plots were established on slopes and ridgetops (not in valley floors). The sites are underlain by sandstones and siltstones of Mississipian and Pennsylvanian origin, with some areas of interbedded limestone at the Bluegrass Ridge study site. The soils are formed in residuum and colluvium and are, for the most part, moderately acidic silt loam alfisols with low water-holding capacity. The major soil association at Arch Rock, Watch Rock, and Young's Branch is Steinsburg-Gilpin Association (Typic Hapludalfs and Typic Dystrocrepts). Bluegrass Ridge is underlain by soils of the Upshur-Gilpin-Steinsburg Association (Typic Hapludalfs). The climate of the region is humid-continental; mean annual temperature, precipitation and frost-free days are 11.3 °C, 1024 mm, and 158 days.

The uplands were probably unaffected by logging until the mid-1800s. Each of the study sites was clear cut at least once between 1840 and 1900 to provide wood for charcoal used in the iron ore smelting industry that thrived during that period (Stout 1933). The large majority of the area of our four study sites shows no evidence of logging since 1910, although there are patches of 65–75 year old stands at Young's Branch and Bluegrass Ridge. In addition, a few small patches at Watch Rock, Arch Rock, and Bluegrass Ridge have decaying stumps, which provides evidence of limited selective logging, probably 30–40 years ago, which includes a few of our sample plots. Anecdotal evidence suggests that surface fires and livestock grazing may have occurred in some parts of the study sites through the 1930s (Hutchinson, unpublished manuscript).

Sutherland (1997) has documented that dormant season fires occurred frequently in the late 1800s and early 1900s in this region. During that period, fire return intervals of $>$20 yr were uncommon (Sutherland 1997). In contrast, over the last 50 years, the forests of the region have undergone strong fire suppression, increased browsing by white-tailed deer (*Odocoileus virginianus*), and increasing atmospheric N deposition; in 1997, atmospheric deposition in precipitation averaged 15–20 kg N ha^{-1} yr^{-1} in southern Ohio (NADP/NTN 1998).

Current overstory composition is similar to that described by presettlement witness tree surveys (ca. 1800). Oaks (*Quercus* spp.) constitute $>$70% of basal area in both witness tree assemblages and current forests (Yaussy and Sutherland, unpublished data). In contrast, the composition of the woody species in the subcanopy and understory has shifted over the last three decades to a dominance by more mesophytic species, such as *Acer saccharum, A. rubrum,* and *Nyssa sylvatica*.

Integrated moisture index

To best characterize the gradients of radiant energy and moisture generated by the range of aspect, elevation, and parent materials in this region, an Integrated Moisture Index (IMI) was developed within an Arc/Info GIS environment (Iverson et al. 1997). A suite of landscape features was used to create the IMI, and each was weighted by its relative ability to predict the distribution of several tree species and forest productivity (Iverson et al. 1997). Three topographic attributes were derived from U.S. Geological Survey (U.S.G.S.) 7.5-minute digital elevation model data (1:24,000 scale, 30-m resolution) in Arc/Info Grid (Environ. Sys. Res. Inst. 1994); a slope aspect shading index ('hillshade' – 40%), cumulative flow of water downslope ('flow accumulation' – 30%) and landscape shape ('curvature' – 10%). Hillshade captures the effects of differential solar radiation due to variation in slope angle, aspect, and position. Flow accumulation represents the accumulated flow of water downslope by counting cells in the GIS. Curvature indicates moisture accumulation in concave surfaces and excessive drainage on convex surfaces. Also, water holding capacity (20% weighting) was derived from digitized soil-series maps at a scale of 1:15 840 by the USDA Natural Resources Conservation Service. Details on the development and validation of the IMI for this region are given by Iverson et al. (1997).

The IMI was mapped for all four study sites, and the sites subsequently stratified into three relative IMI classes: xeric (IMI score $<$35), intermediate (35–50) and mesic ($>$50) conditions. Nine sample plots per IMI class per study site (total $N=108$) were then established using the IMI maps, and all plots were subsequently geo-referenced with a global positioning system. There were 33 xeric, 37 intermediate, and 38 mesic understory plots.

Field and laboratory methods

Vegetation. Each understory vegetation sample plot was 25 × 25 m, within which a stratified-random sampling design was used. Species frequency was determined using sixteen 1 × 2 m quadrats, consisting of 4 quadrats randomly located along each of 4 transects placed 5 m apart within the 25 × 25 m plot. Thus, a total of 1728 quadrats were sampled within the 108 sample plots.

To account for the differing phenologies of the understory species, sampling was conducted in the spring (April 26–June 14) and late-summer (August 22–September 14) of 1995. Herbaceous plants were recorded on a presence/absence basis in each quadrat. For understory individuals of tree species, we determined the presence of each species in each of 4 size classes: $<$30 cm height, 30 cm height to 2.99 cm diameter at breast height (dbh), 3–9.99 cm dbh, and $\geq$10 cm dbh. However, $>$85% of trees tallied were in the seedling class ($<$30 cm height). Nomenclature follows Gleason & Cronquist (1991).

Soils. In May 1995, two A-horizon samples (approx. 150 g) were taken at a depth of 15 cm at the opposite corners of each sample plot. Soil pH, organic C, extractable Ca, Mg, K., P, Al, NO_3^-, and NH_4^+, and soil texture were determined on all samples. Rates of N mineralization and nitrification were determined in aerobic incubations (data and methods given by Morris & Boerner 1998). Soil inorganic N pools, N mineralization rates, and nitrification rates reported here are consistent with those from other studies in the region (e.g., Boerner 1984a; Plymale et al. 1987).

Overstory and light. Tree basal area was calculated from diameter at breast height (dbh) measurements taken for each tree ≥10.0 cm dbh per plot in 1995. Stand age was estimated from cores taken from two large trees per plot. Understory light conditions were estimated by hemispherical photography in July 1995. The global light index is a combined percentage of the diffuse and direct beam radiation throughout the growing season. Calculations for the global light index are described in detail by Canham (1988).

Data analysis. Canonical correspondence analysis (CCA) was used to examine vegetation-environment relationships using PC-ORD Vers. 3.05 (McCune & Mefford 1997). Although we included twelve environmental variables in our initial, exploratory data analysis, we reduced the suite of variables used in the final analysis by removing variables that were weakly correlated to the CCA axes or which were autocorrelated with other variables that demonstrated stronger correlations with the CCA axes. The six variables in the final analysis were IMI, nitrogen mineralization rate, soil pH, net nitrification rate, extractable PO_4^-, percent sand, and percent clay. Stepwise multiple regression was also used to analyze the relationships between environmental conditions and species richness. Soil nutrient concentrations were logarithmically transformed for CCA and regression analysis, to account for the assumption that a one-unit difference in nutrient concentration is more important for plant survival and growth when concentrations are low than at high concentrations (Palmer 1993).

Results

Vegetation. In all, 315 vascular plant species were identified in the four study sites, of which 199 (63%) were forbs, 47 (15%) were graminoids, 35 (11%) were tree species, and 34 (11%) were shrubs or woody vines. Of the total, 86 (27%) occurred at ≥10% mean frequency per plot in at least one of the IMI classes and were thereby considered common (Table 1). Annuals and biennials were <5% of the taxa identified and native taxa comprised 97.8% of the species. The most frequent non-native species (*Rosa multiflora*) occurred in <1% of the quadrats.

Environmental conditions. The IMI was positively correlated with N mineralization rate, NH_4^+, and NO_3^- ($p < 0.001$), nitrification rate ($p < 0.01$) and pH ($p < 0.05$) (Table 2). The mean concentration of NH_4^+ and N mineralization rate were approximately 2× as great in soils from mesic plots than in soils from the xeric plots. In contrast, NO_3^- and nitrification rates were approximately 10× and 3× greater, respectively, in soils from mesic plots than in soils from xeric plots (Table 3). pH was also significantly greater in mesic plots (4.51) than xeric plots (3.85).

Many of the soil fertility variables were positively correlated. Particularly strong correlations were present between NH_4^+ and N mineralization rate ($r = 0.65$), and between pH and nitrification rate ($r = 0.66$) and NO_3^- ($r = 0.79$) (Table 2). Available P was positively correlated with pH, NO_3^-, and nitrification rate, but not with IMI, NH_4^+, or nitrogen mineralization rates (Table 2). In contrast, soil texture and overstory conditions (tree basal area, global light index, and stand age) were not significantly correlated with IMI or variables associated with soil fertility (Table 2).

Soil texture and nutrient status also varied among the four study sites. Soils from the northern sites (Arch Rock and Watch Rock) had greater silt content than soils from the southernmost site, Bluegrass Ridge, which had a greater percentage of sand and clay (Table 3). The soils of the two southern sites also had higher pH and more available PO_4^-, and higher nitrifcation rates (Table 3).

Species-environment relationships. The frequency of most of the common species increased or decreased consistently along the topographic moisture gradient, as represented by IMI (Table 1). As composition changed with moisture, the relative proportion of life forms also shifted. All of the species that occurred at >25% frequency on xeric plots were woody (*Acer rubrum*, *Cornus florida*, *Quercus alba*, *Q. prinus*, *Q. velutina*, *Sassafras albidum*, *Smilax glauca*, *Smilax rotundifolia*, and *Vaccinium pallidum*), with the exception of *Carex wildenovii* (Table 1). Conversely, most of the species that increased in frequency with increasing IMI were forbs (e.g., *Anemonella thalictroides*, *Arisaema triphyllum*, *Asarum canadense*, *Cimicifuga racemosa*, *Gallium triflorum*, *Geranium*

Table 1. Mean frequency for each common species per IMI class (XER = Xeric; INT = Intermediate; MES = Mesic). Common species are defined as occurring at >10% mean frequency in one or more IMI classes. Life forms (LF) are abbreviated as F = forb, G = graminoid, SV = shrub/vine, and T = tree. N = 33 xeric, 37 intermediate, and 38 mesic plots. Nomenclature is from Gleason and Cronquist (1991).

Species	LF	XER	INT	MES	Species	LF	XER	INT	MES
Acer rubrum	T	76.3	66.4	57.8	*Lindera benzoin*	SV	1.7	15.6	28.3
Acer saccharum	T	4.8	22.5	30.7	*Liriodendron tulipifera*	T	14.3	30.9	33.3
Adiantum pedatum	F	0.0	1.6	10.6	*Monarda fistulosa*	F	0.7	2.0	10.1
Amelanchier arborea	T	23.3	6.6	7.3	*Nyssa sylvatica*	T	21.5	13.8	20.0
Amphicarpaea bracteata	F	18.8	21.4	17.2	*Osmorhiza spp.*	F	1.5	7.1	17.9
Anemonella thalictroides	F	2.9	15.0	55.4	*Ostrya virginiana*	T	11.6	8.2	3.0
Arisaema triphyllum	F	1.5	16.8	32.8	*Panicum boscii*	G	20.2	15.5	3.1
Aristolochia serpentaria	F	7.0	11.8	11.1	*Panicum dichotomum*	G	11.9	3.5	0.9
Asarum canadense	F	0.0	5.4	32.1	*Parthenocissus quinquifolius*	SV	23.9	49.8	43.2
Aster divaricatus	F	1.7	10.0	24.0	*Pilea pumila*	F	0.2	6.1	12.8
Botrychium virginianum	F	1.7	13.7	11.3	*Polystichum acrosticoides*	F	1.5	20.2	37.0
Brachyelytrum erectum	G	6.4	20.6	22.2	*Polygonatum biflorum*	F	23.2	15.6	6.1
Carex digitalis	G	5.3	9.9	9.5	*Potentilla canadensis*	F	16.4	18.4	9.7
Carex gracilescens	G	4.0	11.8	15.5	*Poa cuspidata*	G	13.4	15.3	17.0
Carex wildenovii	G	26.3	11.0	1.9	*Podophyllum peltatum*	F	2.9	10.9	14.4
Carpinus caroliniana	T	0.4	4.9	12.3	*Prunus serotina*	T	11.4	12.2	7.1
Carya cordiformis	T	3.1	7.2	10.8	*Quercus alba*	T	36.8	22.9	15.8
Carya glabra	T	19.3	14.8	11.6	*Quercus coccinea*	T	11.2	3.9	0.7
Cercis canadensis	T	14.9	24.3	9.0	*Quercus prinus*	T	28.7	8.4	3.3
Chimaphila maculata	F	9.9	3.8	1.2	*Quercus rubra*	T	11.2	11.2	10.4
Cimicifuga racemosa	F	0.2	12.2	30.7	*Quercus velutina*	T	25.4	11.7	4.7
Circaea lutetiana	F	1.5	7.1	17.9	*Rosa carolina*	SV	23.5	11.7	5.7
Claytonia virginiana	F	0.7	4.6	10.8	*Rubus spp.*	SV	20.2	26.5	15.1
Cornus florida	T	44.1	37.3	29.3	*Sassafras albidum*	T	66.7	30.3	13.2
Crataegus spp.	T	13.4	10.2	9.4	*Sanguinaria canadensis*	F	0.0	2.3	13.4
Cunila oreganoides	F	12.1	1.2	0.0	*Sanicula spp.*	F	8.5	17.6	14.2
Danthonia spicata	G	10.8	1.0	0.0	*Scutellaria spp.*	F	2.6	8.7	23.1
Dentaria laciniata	F	2.6	19.7	20.0	*Smilacinia racemosa*	F	19.5	40.1	34.5
Desmodium glutinosum	F	4.4	15.1	14.1	*Smilax glauca*	SV	40.6	31.7	16.8
Desmodium nudiflorum	F	41.0	53.3	37.5	*Smilax rotundifolia*	SV	59.4	36.5	27.3
Dioscorea quaternata	F	2.8	12.0	21.9	*Solidago caesia*	F	9.6	15.1	10.6
Eupatorium rugosum	F	3.9	14.3	20.8	*Thelypteris hexagonoptera*	F	0.2	2.5	11.8
Fagus grandifolia	T	10.1	10.2	17.4	*Tiarella cordifolia*	F	0.0	2.3	34.7
Fraxinus americana	T	22.6	45.7	34.9	*Toxicodendron radicans*	SV	10.3	16.9	15.1
Galium aparine	F	3.1	11.8	16.3	*Trillium grandiflorum*	F	0.0	7.9	45.1
Galium circazans	F	17.5	27.1	29.5	*Ulmus rubra*	T	5.7	27.6	25.9
Galium concinnum	F	0.0	5.8	11.3	*Uvularia perfoliata*	F	11.2	50.3	52.1
Galium triflorum	F	8.5	35.4	36.3	*Vaccinium palidum*	SV	51.7	10.2	1.2
Geranium maculatum	F	4.4	36.3	62.3	*Vaccinium stamineum*	SV	13.4	5.3	0.7
Hamamelis virginiana	SV	2.0	6.1	11.5	*Viburnum acerifolium*	SV	10.1	29.8	34.4
Helianthus divaricatus	F	10.8	4.6	0.7	*Viola spp.*	F	15.8	34.4	37.7
Hieraceum venosum	F	12.1	0.3	0.0	*Viola triloba*	F	15.1	26.3	25.3
Hydrangea arborescens	SV	0.7	4.8	20.3	*Vitis spp.*	SV	20.4	24.5	16.1

Table 2. Pearson product moment correlation matrix for the 12 environmental variables. Bonferroni-adjusted probabilities are denoted by $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. N = 108 plots. Abbreviations are listed in Table 1.

	IMI	NMIN	NH_4^+	NITRIF	NO_3^-	PH	PO_4^-	SAND	CLAY	BA	LIGHT	AGE
IMI	1.000											
#NMIN	***0.572	1.000										
#NH_4^+	***0.507	***0.654	1.000									
#NITRIF	**0.375	***0.506	**0.400	1.000								
#NO_3^-	***0.465	***0.455	***0.450	***0.608	1.000							
PH	*0.352	***0.434	***0.443	***0.658	***0.785	1.000						
#$PO4^-$	0.166	0.240	0.257	**0.394	***0.422	***0.530	1.000					
SAND	−0.228	0.109	0.013	0.158	−0.118	0.149	**0.391	1.000				
CLAY	−0.214	0.043	−0.078	0.010	−0.250	−0.048	0.288	***0.841	1.000			
BA	−0.103	−0.086	−0.077	−0.105	−0.103	−0.061	0.260	0.118	0.136	1.000		
LIGHT	−0.042	−0.142	−0.069	−0.225	−0.196	−0.310	−0.070	−0.192	−0.117	0.046	1.000	
AGE	−0.009	−0.154	−0.209	−0.163	−0.080	−0.147	0.009	−0.057	0.015	0.160	−0.037	1.000

Log-transformed.

Table 3. Environmental variables used in statistical analyses. The mean and + the standard error of the mean (in parentheses) are reported for each variable for the three IMI classes and the four study sites.

Variable (abbreviation)	Units	IMI class			Site N→S			
		Xeric (N=33)	Inter. (N=37)	Mesic (N=38)	WR (N=27)	AR (N=27)	YB (N=27)	BR (N=27)
Moisture Index	0 to 100	30.5	42.2	59.0	45.6	46.8	44.9	40.9
(IMI)		(0.68)	(0.86)	(1.24)	(2.64)	(3.23)	(2.27)	(1.68)
Sand	percent	28.5	29.2	26.1	25.6	25.4	27.0	33.6
(SAND)		(1.04)	(0.98)	(0.88)	(0.73)	(0.97)	(1.01)	(1.04)
Clay	percent	14.0	14.4	12.6	12.6	12.7	13.3	15.9
(CLAY)		(0.49)	(0.51)	(0.33)	(0.42)	(0.33)	(0.55)	(0.55)
pH	pH	3.85	4.19	4.51	4.13	3.92	4.33	4.43
(pH)		(0.09)	(0.10)	(0.11)	(0.15)	(0.08)	(0.14)	(0.12)
Ammonium $NH4^+$	mg/kg soil	7.19	12.29	14.85	14.88	11.59	8.2	11.85
(NH4)		(0.69)	(0.85)	(1.42)	(1.97)	(1.24)	(0.76)	(0.86)
Nitrate NO_3^-	mg/kg soil	0.85	2.63	8.98	7.93	1.42	5.37	2.57
(NO3)		(0.28)	(0.86)	(2.07)	(2.75)	(0.47)	(1.52)	(0.95)
N mineralization rate	mgNH_4^+/	59.80	81.35	117.07	99.94	86.49	73.44	89.46
(NMIN)	g soil/30d	(4.78)	(4.73)	(6.31)	(8.33)	(7.06)	(7.00)	(7.75)
Nitrification rate	mgNO_3^-/	8.99	17.77	24.54	13.27	5.79	20.88	29.94
(NITRIF)	g soil/30d	(4.17)	(4.01)	(4.34)	(4.39)	(1.26)	(5.60)	(6.00)
Phosphorus PO_4^-	mg/kg soil	0.14	0.19	0.19	0.10	0.13	0.25	0.22
(PO4)		(0.02)	(0.02)	(0.01)	(0.01)	(0.01)	(0.03)	(0.01)
Tree basal area	m^2/ha	26.6	26.6	25.4	24.5	26.0	27.9	26.2
(BA)		(0.77)	(1.12)	(0.96)	(0.73)	(0.86)	(1.34)	(1.38)
Global light index	0 to 100	6.70	6.65	6.66	7.02	6.52	6.51	6.63
(LIGHT)		(0.50)	(0.53)	(0.71)	(0.95)	(0.68)	(0.53)	(0.52)
Stand Age	years	116.4	109.5	108.3	112.8	108.7	121.9	101.3
(AGE)		(3.55)	(3.99)	(3.60)	(4.62)	(2.14)	(5.26)	(3.87)

Table 4. Canonical correspondence analysis statistics: eigenvalues and correlations of environmental variables to CCA Axis 1 and 2.

	Axis 1	Axis 2
Eigenvalue	0.332	0.153
	Correlation	
Environmental variable	Axis 1	Axis 2
IMI	−0.836	0.403
Nitrogen mineralization rate	−0.780	−0.036
pH	−0.688	−0.449
Nitrification rate	−0.662	−0.550
PO_4^-	−0.325	−0.526
Percent clay	0.245	−0.580
Percent sand	0.155	−0.766

maculatum, *Tiarella cordifolia*, *Trillium grandiflorum*, and *Uvularia perfoliata*). Approximately 25% of the common species were most frequent on the intermediate plots, including some of the most frequent species observed (e.g., *Desmodium nudiflorum*, *Fraxinus americana*, *Parthenocissus quinquifolius*, and *Smilacina racemosa*).

Canonical correspondence analysis (CCA) indicated that the primary separation of plots in ordination space was accounted for by Axis 1 (eigenvalue = 0.332; Table 4). Axis 1 depicted variation in species composition constrained by the six environmental variables. Axis 1 represented the topographic moisture-fertility gradient and was strongly correlated with IMI, N mineralization rate, pH, and nitrification rate (Figure 1; Table 4).

CCA Axis 2 accounted for additional variation in species composition (eigenvalue = 0.153) and was most strongly correlated with soil texture variables (Figure 1; Table 4). Along Axis 2, the northern sites (Arch Rock and Watch Rock) had higher scores than the most southerly site (Bluegrass Ridge) (Figure 1) and the plots at Young's Branch, located 20 km north of Bluegrass Ridge, were generally intermediate. In addition to soil texture, Axis 2 was inversely correlated with nitrification rate, PO_4^-, pH, and positively correlated with IMI.

The plots classified as xeric in the sampling design exhibited relatively distinct species composition along Axis 1, and varied less along Axis 2 (Figure 1). The intermediate and mesic plots were less distinct along Axis 1 and exhibited greater compositional variation along Axis 2.

Species richness. Species richness per 25 × 25 m plot ranged from 23–106 and averaged 65 (SE 1.7), and mean species richness per quadrat (2 m^2) ranged from 6 to 30 and averaged 17 (SE 0.5). Stepwise regression analysis indicated that total richness per plot was positively related to N mineralization rate and nitrification rate, and inversely related to tree basal area (Table 5). The richness of forbs/2m^2 exhibited the strongest relationship to the set of environmental variables (Table 5). Most of the variation in the model was accounted for by N mineralization rate and soil NO_3^-. A series of linear regressions confirmed that forb richness/2 m^2 was also positively correlated with nitrification rate ($r^2 = 0.366$; $p < 0.0001$), IMI ($r^2 = 0.354$; $p < 0.0001$), pH ($r^2 = 0.321$; $p < 0.0001$), and NH_4^+ ($r^2 = 0.318$; $p < 0.0001$), and inversely but weakly related to tree basal area ($r^2 = 0.072$; $p < 0.005$) (Figure 2). In contrast, tree species richness/2 m^2 was inversely related to IMI and soil $NO_3{}^-$, and positively related to percent sand (Table 5). Graminoid richness and shrub/vine richness were weakly correlated with the environmental variables we measured (Table 5).

Discussion

Because variation in soil moisture and evapotranspiration (AET) over topographic gradients have proven to be important factors controlling vegetation and the functioning of ecosystems, the IMI was designed to be an easily-generated index that could be mapped across the landscape (Iverson et al. 1997). In addition to portraying the complex topographic gradients of moisture and radiant energy in a manner that facilitated spatially-explicit mapping, the IMI also proved to be positively correlated with N availability and pH. Thus, this single, integrated index was capable of representing a complex moisture-fertility gradient from xeric, acidic soils with low N availability on upper south-facing slopes to mesic, less-acidic soils with more available nitrogen on lower north-facing slopes. This complex topographic gradient of moisture and fertility was the primary gradient to which variations in composition and richness of understory plants were correlated: moisture, N availability, and pH were positively correlated with species richness and the proportion of forbs.

The transition to a more herbaceous understory along the moisture gradient is likely related to a suite of physiological traits (Grime 1979). Some woody

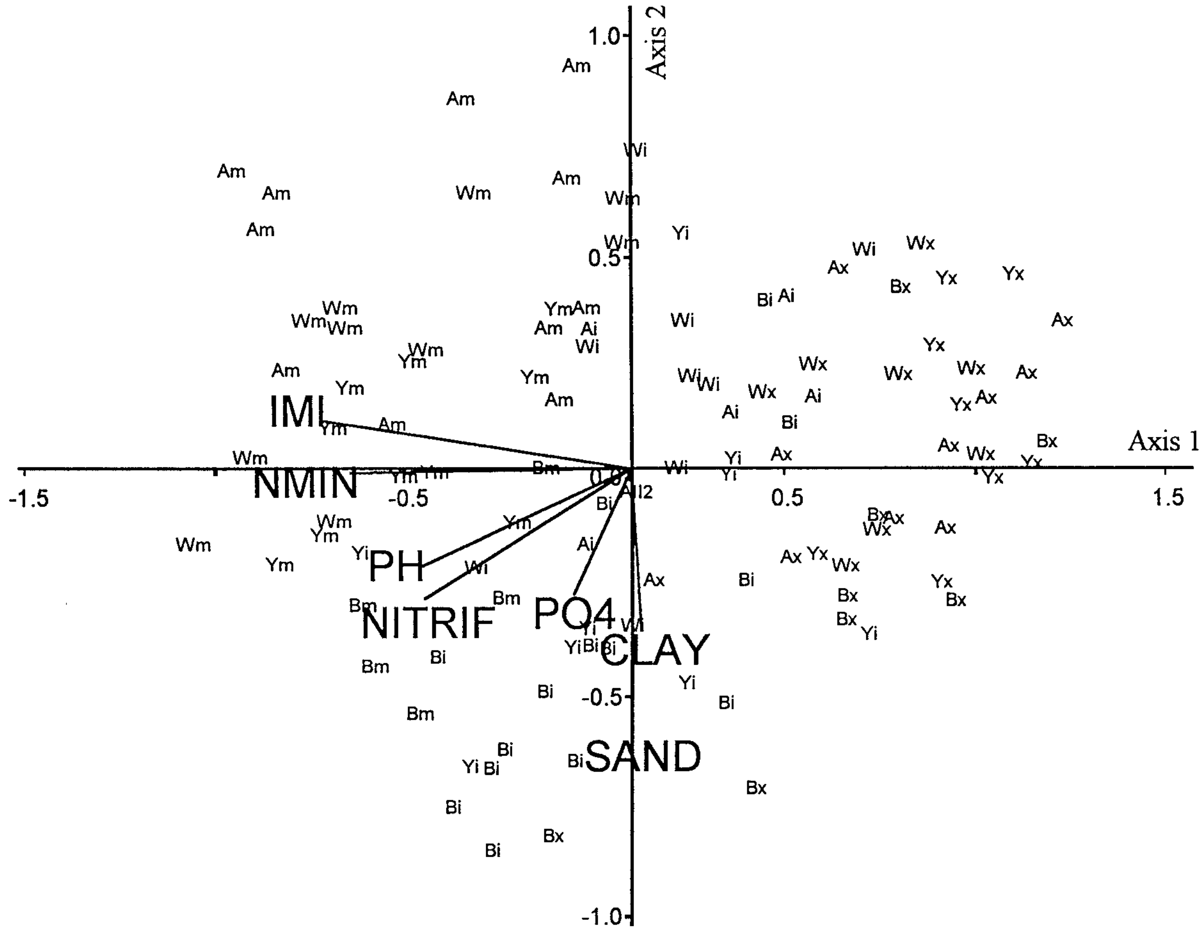

Figure 1. Canonical correspondence analysis of the 108 plots and 6 environmental variables. Each plot is designated by study site (A = Arch Rock, W = Watch Rock, Y = Young's Branch, and B = Bluegrass Ridge) and moisture class (x = xeric, i = intermediate, m = mesic). See Table 1 for environmental variable abbreviations. Vectors represent the strength and direction of the relationship between environmental variables and variation in species composition.

plants (e.g. *Quercus* spp., *Vaccinium* spp.) can tolerate xeric conditions at the surface by developing deep roots (Abrams 1990; Kozlowski et al. 1991; Matlack et al. 1993), while mesic forb species in our region are commonly shallowly rooted (Hutchinson, personal observation) and thus more susceptible to dry surface soils. In addition to moisture acquisition and storage, species vary in their ability to modify conductance rates by closing stomata when evaporative demand is high (Lipscomb & Nilson 1990). Air temperature in oak forests has been shown to be inversely related to herbaceous diversity (Xu et al. 1997), suggesting that evaporative demand also limits the persistence of forbs on xeric slopes. Although there are many forb and graminoid species in the region that are adapted to xeric, open conditions (e.g., species-rich barrens or prairie openings; see Braun 1928; Annala & Kapustka 1983), they are uncommon in the forested matrix encompassing our study sites and thus do not truly represent exceptions to this generalization.

The species richness of understory individuals of tree species was inversely related to moisture and fertility. This may be the consequence of greater competition from forbs for light and space in mesic areas (Grime 1979).

Although synthetic topographic moisture indices have correlated well with vegetation patterns in other studies (e.g., Allen & Peet 1990), Stephenson (1998) found that AET and water deficit were better predictors of forest types than soil water balance in the Sierra Nevada Mountains of California, and concluded that vegetation responded differently to the dryness caused

Table 5. Indepedent variables entered in the stepwise regression models for mean species richness/plot, mean forb richness/quadrat (2 m^2), and mean tree richness/2 m^2. + or − denotes the direction of the relationship, and r^2 values are cumulative at each step. N = 108 plots.

Dependent variable	Step	Independent variable	*F*	r^2-cum.	*p*-value
Richness/plot (32 m^2)	1	+N mineralization rate	27.40	0.342	0.0001
	2	−Tree basal area	12.81	0.417	0.001
	3	+Nitrification rate	9.07	0.464	0.003
Forb richness/2 m^2	1	+N mineralization rate	13.36	0.416	0.0001
	2	$+NO_3^-$	11.19	0.561	0.001
	3	−Tree basal area	8.51	0.596	0.004
	4	+IMI	8.42	0.624	0.005
	5	+Nitrification rate	6.65	0.647	0.011
Tree richness/2 m^2	1	−IMI	8.95	0.203	0.003
	2	+Percent sand	7.79	0.256	0.006
	3	$-NO_3^-$	7.16	0.304	0.009
Graminoid richness/2 m^2	1	−Tree basal area	8.02	0.056	0.006
	2	−IMI	6.43	0.111	0.013
Shrub/vine richness/2 m^2	1	−IMI	5.17	0.046	0.025

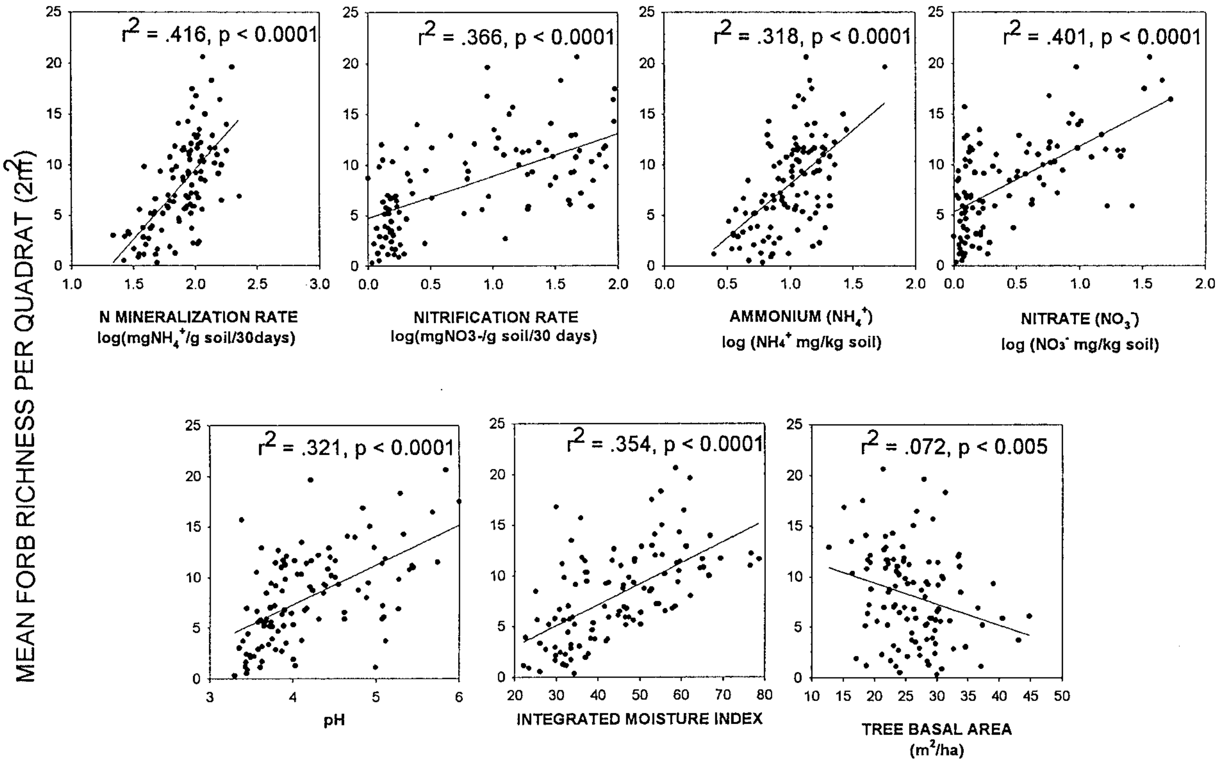

Figure 2. Simple linear regression analyses of forb richness/2 m^2 (dependent variable) and several environmental factors (independent variables). N=108 plots.

by evaporative demand than to the dryness caused by low soil water holding capacity. In our study sites, where changes in elevation and macroclimate were small, and soil formations similar, the IMI correlated well with plant species composition.

The IMI has proven to be a powerful tool for quantifying and understanding variations in both ecological pattern and process at the watershed and landscape scales (Iverson et al. 1997; Morris & Boerner 1998; Decker et al., in press). However, for studies of vegetation at a finer scale, the IMI is probably of limited use because of the limitations imposed by the quality and resolution of the digital elevation and soil data (Iverson et al. 1997). For example, examination of the species composition on a plot-by-plot basis revealed a small percentage of plots in which the species composition suggested that actual soil moisture was quite different from that predicted by IMI. This was likely the consequence of smaller-scale soil and/or drainage patterns not predictable based on the data resolution.

N is most often the primary factor limiting tree growth in temperate deciduous forests (Aber et al. 1989). Several studies have related forest types to N mineralization and nitrification gradients (e.g., Pastor et al. 1982; Liu & Muller 1993); here we extend these relationships to the understory vegetation layer. In addition to moisture, N availability was correlated with floristic variation and richness over the forested landscape. Nitrogen mineralization rate was the variable most strongly related to total richness and forb richness, and was also more strongly correlated with compositional variation than the more static measure of NH_4^+ concentration. However, because nitrogen mineralization rate was correlated with moisture and other measures of fertility, other variables that do not appear in the models are nonetheless significant (e.g., pH, NH_4^+). In deciduous forests in Sweden, Diekmann & Falkengren-Grerup (1998) also reported that a species index derived from mineralization and nitrification rates was strongly related to floristic variation.

Fertilization experiments have shown that species richness is often greatest at intermediate levels of fertility and reduced at very high levels (Tilman 1987; Theodose & Bowman 1997). However, in our upland sites, understory richness was greatest at the highest levels of fertility (and associated soil properties). These results suggest that soils with low N availability select for species with low relative growth rates (Grime 1979), which in our region are typically woody, and exclude many forbs, which represent the majority of the species pool. There remains a strong N gradient across our forested landscape despite atmospheric deposition rates of 15–20 kg ha^{-1} yr^{-1}. Even if sites with low N availability are becoming more fertile as a consequence of N-deposition, successful establishment by the more N demanding species may be limited by other soil factors (e.g., moisture, pH, availability of other nutrients) and slow plant migration rates (Matlack 1994).

Forests in southern Ohio and surrounding regions are experiencing a rapid shift in tree species composition from *Quercus spp.* dominating the overstory to shade-tolerant (e.g., *Acer rubrum*, *Nyssa sylvatica*) and shade-tolerant/nutrient demanding (e.g., *Acer saccharum*, *Ulmus rubra*, *Fagus grandifolia*) species in the sapling and seedling layers (Norland & Hix 1996). It is unknown if similar increases in the abundance of shade-tolerant, nitrophilous herbaceous species are occurring in regional oak forests; however, this trend has been reported from European forests and woodlands (Falkengren-Grerup 1986; Bråkenhielm & Qinghong 1995).

Generally, overstory characteristics were not related to patterns of understory vegetation in this study. However, tree basal area was inversely but weakly correlated with total understory species richness and forb richness, and because basal area was not correlated with the moisture-fertility gradient, it did appear as a significant factor in the stepwise regression model for richness. Other studies have also shown negative correlations of understory richness and/or cover with tree basal area (Gilliam & Turrill 1993; Stone & Wolfe 1996; Brunet et al. 1997; Goldblum 1997) presumably because of differential light availability. However, tree basal area was not significantly correlated with understory light intensity in this study. It is possible that the basal area-richness relationship could be a residual effect of higher light levels in the past in lower basal area plots which may have allowed establishment of shade intolerant species that persist despite current low light levels.

A secondary compositional gradient was present among our study sites and was most strongly correlated with higher percent sand in the southern sites, and also higher percent clay, nitrification rate, PO_4^-, and pH (Figure 1). This secondary vegetation trend is probably not a gradual gradient, but the consequence of three somewhat different parent material complexes affecting soil chemistry and texture, resulting in floristic variation. Watch Rock and Arch Rock are on sandstone, siltstone, and shale parent material complexes, and Young's Branch is similar but with slightly more sand and clay content. Bluegrass Ridge, to the south, is a sandstone and shale complex with some interbedded limestone that has relatively higher proportions of sand and clay. Whereas species compositional variation along CCA Axis 1 may be interpreted as response to long-term moisture status and evaporative demand, the secondary moisture gradient along CCA Axis 2 may be related to variations in the short-term moisture patterns (wetting-drying kinetics) caused by variations in soil texture. Also, parent material and pH have been shown to control patterns of vegetation when variation is more abrupt, as in comparisons of neighboring calcareous and non-calcareous soils (Howell & Vankat 1981; Wentworth 1981). However, the relatively small-scale, heterogeneous nature of the interbedded limestone at Bluegrass Ridge probably reduced the overall importance of bedrock to composition. As parent material variation produced soils with higher pH in the southern sites, rates of nitrification (carried out primarily by a specific guild of bacteria not tolerant of low pH) were higher (see also, Zak et al. 1986; Plymale et al. 1987). Thus, floristic variation related to pH and nitrification occurred at both the topographic scale (across the primary moisture-fertility gradient) and, to a lesser extent, at the regional scale, related to geomorphogical variation among the four study sites.

Much of the unexplained variation in vegetation may result from fine-scale environmental heterogeneity (Palmer & Dixon 1990). Small-scale variation in microtopography and canopy structure causes resources and, thus, vegetation, to be patchily distributed in deciduous forests (Beatty 1984; Chazdon 1988; Boerner & Koslowsky 1989; Griffith 1996).

This study has added significantly to our understanding of the distribution of understory plant species across topographically complex landscapes. Our broad-scale approach to sampling with spatially-explicit estimates of moisture has yielded insights to factors controlling vegetation at the topographic and regional scales. Also, an important linkage between ecosystem functioning (i.e., nitrogen mineralization rates and nitrification rates) and diversity, suggested by others (e.g., Grime 1979), has been described. The knowledge gained from this study can provide practical guidance for predicting vegetation response to environmental change and conservation and restoration efforts in the future.

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