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Environmental Factors Affecting Understory Diversity in Second-growth Deciduous Forests

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ABSTRACT.—The purpose of this study was to determine the most important nonanthropogenic factors affecting understory (herbs, shrubs and low-growing vines) diversity in forested landscapes of southern Indiana. Fourteen environmental variables were measured for 46 sites. Multiple regression analysis showed significant positive correlation between understory diversity and tree seedling diversity and soil subgroup. Slope aspect, soil rooting depth and number of standing dead trees were significantly negatively correlated with understory diversity. Mesic sites were more diverse in common understory species than xeric sites but had lower total cover and different species.

INTRODUCTION

The understory is typically the most diverse stratum within North American Eastern Deciduous Forests. High understory diversity has been attributed to intrastand heterogeneity due to differences in nutrient, light and water availability (Watt, 1947; Randall, 1952; Hutchinson, 1959; Grubb, 1977; Lubchenco, 1983; Beatty, 1984; Turner and Franz, 1986). Hutchinson's (1959) inquiry into why there are so many animal species can be restated: How can so many understory plant species coexist in deciduous forests, and why is this diversity not uniformly distributed in space or time?

There are at least three theoretical explanations for high understory diversity. First, based on the principles of competitive exclusion and niche partitioning, the potentially infinite number of available resource ratios may result in a large number of niches and coexisting species (Gause, 1934; Hutchinson, 1959; Tilman, 1988). Second, high species diversity may also be due to constant environmental change through time (*i.e.*, a disturbance regime), which does not allow a species the necessary time to outcompete another species (Huston, 1979; Sousa, 1979; Chesson and Warner, 1981; Clark, 1991). Third, species coexistence and high diversity could be a result of reciprocal selection for a balance of competitive abilities. A species cannot outcompete another species due to their differences in competitive abilities for different resources (Huston, 1979; Aarssen, 1983).

The general purpose of this study is to define the most important nonanthropogenic environmental variables affecting understory species diversity and distribution in second-growth deciduous forests between 80 and 120 years of age. Our study focuses on herbs, shrubs and low-growing vines as a single group of understory species and considers only intrastand heterogeneity on a spatial scale. Actual mechanisms behind high diversity (*i.e.*, niche partitioning, disturbance and reciprocal selection for balanced competitive abilities) were not tested in this study.

Three hypotheses are addressed: (1) effects of each chosen environmental variable on understory diversity will differ in importance, with water-related variables expected to be

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TABLE 1.—Site type definitions. Site types are designated either mesic or xeric on the basis of water availability. The authors realize that there is a gradient between the two extremes and that certain mesic areas may be better classified as wet. We chose to simplify the classification into two categories

Ridges (xeric)
1—Narrow (>10 m but <50 m wide, <8% slope gradient)
2—Broad sloping (>50 m wide, >8% but <15% slope gradient)
3—Broad flat (>50 m wide and <8% slope gradient)
Slopes
4—Gentle slope (<15% slope gradient) (both xeric and mesic)
5—Moderately steep north-facing slope (315°–135° slope aspect, 16–30% slope gradient) (mesic)
6—Moderately steep south-facing slope (136°–314° slope aspect, 16–30% slope gradient) (xeric)
7—Steep north-facing slope (315°–135° slope aspect, over 30% slope gradient) (mesic)
8—Steep south-facing slope (136°–314° slope aspect, over 30% slope gradient) (xeric)
Bottomland areas (mesic/wet)
9—Major (>67 m wide and about 0.6 km below the beginning of the water course)
10—Minor (<67 m wide, continuous upstream to the point that the bottom becomes V-shaped—a ravine)

the most important assuming that water is the most limiting resource of plants, (2) understory diversity as a single variable is expected to be significantly positively correlated with tree seedling diversity and not with sapling or tree diversity since herbs, shrubs and low-growing vines tend to share the lower forest stratum with tree seedlings and are expected to manifest a similar response to available resource ratios and (3) habitat heterogeneity resulting from topographic differences across a landscape will explain the nonuniform and nonrandom distribution of understory species.

METHODS AND MATERIALS

Study area.—Data were collected from 46 sites in the Pleasant Run Unit of Hoosier National Forest, southeast of Bloomington, Indiana. This area is considered a part of the Beech Maple Forest region as defined by Braun (1950). However, this area borders Braun's Western Mesophytic Forest region, which may change the expected species composition to a mixture including oak and hickory as well as beech and maple (Braun, 1950; Vankat, 1979). Study sites were located within an area approximating 35 ha of noncontiguous U.S. Forest Service land. The actual area sampled was 9.2 ha. The criteria used for selecting sites required that each site: (1) be dominated by trees 80 years of age or older, (2) have no evidence of recent cutting (for at least 40 years), or other obvious human disturbances, and (3) be 0.4 ha or more. Age, disturbance history and size of each site were determined from records of the Wayne-Hoosier National Forest (USDA Forest Service) and by direct observation.

Stratified random sampling from a list of USDA Forest Service stands 80 years or older was used to select sites representing ten different site types based on topographic differences such as slope aspect and gradient and whether the site was a bottomland or ridge (Table 1). There were five or six sites per site type except for site types 2 and 9, each having one site. All data were collected between 10 May and 2 August 1990.

Environmental variables.—Our choice of environmental variables was based on four factors influencing plant growth: light, water, nutrients and plant interactions (*i.e.*, potential competition). Direct measurement of these variables was not feasible, but rather, "surro-

gate" variables were chosen. The surrogate environmental variables measured at each site included (1) site type (*i.e.,* topographically defined land forms such as a south-facing slope or a ridge), (2) slope aspect, (3) slope gradient, (4) soil subgroup, (5) depth of the O horizon (litter zone), (6) depth of A horizon (humified zone), (7) soil rooting depth (determined by excavating a pit and measuring the distance to the deepest visible root), (8) number of standing dead trees, (9) number of fallen dead trees, (10) canopy opening, (11) understory diversity, (12) tree seedling diversity, (13) sapling diversity and (14) canopy tree diversity.

Canopy opening, number of standing and fallen dead trees, slope aspect, and gradient and site type were chosen as surrogate measures for both light intensity and soil moisture. Soil subgroup and rooting depth were chosen as additional surrogate measures of soil moisture. All of these surrogate measures potentially influence the amount of light reaching the understory layer and/or the amount of available water or rate of evapotranspiration due to changes in (1) Sun's orientation to Earth, (2) angle of incident light, (3) temperature, (4) soil water holding capacity and (5) soil water availability (Pianka, 1978; Canham *et al.,* 1990; Lipscomb and Nilsen, 1990; Chazdon and Pearcy, 1991).

Soil subgroup, site type, depth of O horizon, depth of A horizon and number of fallen dead trees were chosen as surrogate variables for nutrient availability. Fallen dead trees contribute to the O horizon, and the depth of the litter layer might be correlated with nutrient flow into the A and lower horizons (Buol *et al.,* 1989; Klinka *et al.,* 1990). A thick A horizon should correspond to a productive and possibly diverse understory. Certain soil types, *i.e.,* those with moderate clay content, may provide more available nutrients (Buol *et al.,* 1989). Certain site types, such as bottomlands, receive runoff, which might be high in nutrient content, from higher topographic positions.

Soil moisture, nutrients and light are shared by understory species as well as tree seedings, saplings and trees. These plants are likely to be competing for the same resources; species that share the same forest stratum should be the most interactive (Grubb, 1977). However, canopy trees and saplings are likely to be affecting the understory species via throughfall and light interception (Turner and Franz, 1986).

Understory species distributions may be explained by the different site types, a surrogate measure of intrastand heterogeneity. For instance, disturbance-prone site types, such as bottomlands, narrow ridges and steep slopes, have relatively high numbers of canopy openings due to windfall, erosion, or flooding (Pickett and White, 1985; Adamowicz, 1987). Intermediate levels of disturbance may promote high diversity (Connell, 1978; Lubchenco, 1978, 1983). Moreover, certain site types, such as bottomlands and north slopes, are expected to have higher levels of soil water availability compared to site types such as ridges and south-facing slopes (Pianka, 1978; Lipscomb and Nilsen, 1990). Each site type was designated mesic or xeric on the basis of topography (Table 1).

Vegetation sampling.—Plant species were sampled in four equidistant subplots along a 150-m transect on each site. A subplot contained one 16-m^2 (4 × 4 m) quadrat for understory species cover estimates and tree seedling counts, one 100-m^2 circular plot for sapling measurements, and one 500-m^2 circular plot for canopy tree measurements. Percent cover for herbaceous species, shrubs and low-growing vines was estimated to the 1% level (species designated <1% in cover were arbitrarily given a numerical value of 0.5%) and density of tree seedlings was counted in each of the 16-m^2 quadrats. Tree seedlings were defined as individuals of tree species under 1 m tall. Saplings (individuals of tree species less than 10 cm dbh and taller than 1 m) were counted in the 100-m^2 circular plot in each subplot. This circular plot was centered on one of four corners (randomly determined) of each quadrat. Live, down and standing dead trees over 10 cm dbh were counted and measured in the

500-m^2 circular plot in each subplot using the same central point as the 100-m^2 circular plots. The understory, as defined here, includes herbs, shrubs and low-growing vines that will never attain canopy height and thus face similar microenvironmental conditions.

Diversity indices for understory, tree seedlings, saplings and trees were calculated using the Simpson diversity index (Ghent, 1991). Ghent argues that the Simpson index is preferable to other indices because the variance of a given species count equals the rank orderings of the species defined by the Simpson index.

Soil analysis and topographic measures.—A soil pit was excavated at each site to characterize the soil horizons and parent material. The soil pit was located on a random bearing between 4 and 12 m distant from a randomly chosen corner of one quadrat within the site (usually the first quadrat vegetatively sampled). Augers, which were located at one randomly chosen corner of each of the four quadrats per site, were used to determine the soil horizons and rooting depth at each subplot. Soils were classified to the subgroup level using information about texture, pH, horizons present, depth to bedrock, color and pedon structure, shape and size.

Topographic measurements included slope gradient and slope aspect at each subplot. Slope aspect was measured using a Silva compass, and slope gradient was measured as a percent using a Suunto clinometer.

The degree of southness (S) of a given slope was determined by $S = SIN(X\text{-}90°)$, where X is the actual azimuth. It was necessary to convert the radial aspect values to linear values for linear regression analysis. Thus, south, southeast, and southwest-facing slopes are positive; north, northeast, and northwest-facing slopes are negative; and east and west slopes are zero. We assume that the most important aspect differential is between north and south-facing slopes. However, it is true that west-facing slopes tend to be drier than east-facing slopes due to predominant wind directions and higher ambient temperatures (Lipscomb and Nilsen, 1990).

Canopy opening estimates.—A wide-angle lens set at infinity was used to photograph the canopy above each subplot. The camera was mounted on a tripod 1 m above the ground and aimed directly upwards before exposures. At a typical canopy height, the area in each photograph was estimated to be about 70 m^2. Color prints (7 × 10 cm) were made from the developed film, and a transparent grid of 4-mm^2 squares was placed over each photograph. If a given square was filled 50% or more with open sky (absence of leaves, branches or tree trunks), it was counted as open canopy.

The use of a wide-angle lens and grid to measure canopy opening is a simplified form of more sophisticated techniques, such as hemispherical photography using a fish-eye lens (Horn, 1971; Canham *et al.*, 1990). Our canopy values are estimates of potential light intensity, not actual light intensity. This estimate of potential light intensity does not differentiate a sapling-dominated site from a tree-dominated site.

Species distribution description.—Herb, shrub and vine species were categorized by site type. A common species was arbitrarily defined as any species that occurred in five or more subplots (two or more sites) in a particular site type. Site types 2 and 9, which only had one site each, therefore, had no common species. Mean number of total species, mean number of common species, and mean percent cover of common species per site type were calculated. Species were also designated mesic or xeric according to site types in which they occurred and their cover value.

Data analysis.—All calculations (diversity, degree of southness) and counts were conducted on the subplot level and then averaged for each site. Multiple regression analyses (SAS Users Guide, 1985) using understory as the dependent variable were conducted. Two general types of models were run: the first included slope aspect and slope gradient (but

TABLE 2.—Model 1 with understory diversity (Simpson index) as the dependent variable and slope aspect and gradient included as independent variables. F Value = 2.1, P > F = 0.039, R-square = 0.58, n = 46

Variable	Parameter estimate	Standard error	P > |T|
Intercept	12	6.9	0.088
Seedling diversity	0.87	0.42	0.049*
Tree diversity	0.52	0.73	0.48
Sapling diversity	−1.2	0.73	0.11
Slope aspect	−2.4	1.2	0.054*
Canopy opening	0.029	0.016	0.078
Typic hapludalf soil	0.56	3.1	0.86
Typic dystrochrept soil	3.0	0.83	0.42
Fluventic dystrochrept soil	8.0	3.3	0.021*
Typic fragiudalf soil	2.4	3.0	0.44
Typic udifluvent soil	5.5	5.8	0.35
Lithic dystrochrept soil	2.4	4.0	0.55
Ultic hapludalf soil	1.8	3.1	0.57
Slope gradient	−1.0	0.045	0.43
A horizon	−0.073	0.22	0.74
O horizon	0.92	0.78	0.25
Soil rooting depth	−0.082	0.038	0.037*
Standing dead trees	−1.2	0.54	0.029*
Fallen dead trees	0.14	0.24	0.58

* = P ≤ 0.05 level of significance

not site type) among the independent variables; the second included site type but not slope aspect and slope gradient among the independent variables. Site type and slope aspect/gradient could not be included in the same regression models because site type is partly defined by slope aspect and gradient. Dummy variables were used to categorize the site and soil type variables; site types 2 and 9 and the aquic hapludalf soil type (the least frequent soil type) were used as the reference variables. Paired sample t-tests showed that the aquic hapludalf soil type was not significantly more or less diverse than any other soil type. These t-tests also showed that site types 2 and 9 were not significantly more or less diverse than any other site type. Significance was defined at the P ≤ 0.05 level.

RESULTS

Understory diversity.—In multiple regression Model 1, understory diversity is significantly positively correlated with tree seedling diversity and the soil subgroup fluventic dystrochrept (a bottomland soil) and significantly negatively correlated with south-facing slopes (slope aspect), soil rooting depth and number of standing dead trees (Table 2). Model 2 (Table 3) shows a significant positive correlation between understory diversity and tree seedling diversity as well as a significant negative correlation with number of standing dead trees. There is no significant relationship between site type and understory diversity. Instead, it appears that including these site types masked the importance of the fluventic dystrochrept soil type, which is not significantly correlated with herb diversity in Model 2. A simple regression analysis with herb diversity as the dependent variable and date as the independent variable showed no correlation between herb diversity and sampling date.

Understory species distribution patterns.—One hundred and ninety-eight understory species

TABLE 3.—Model 2 with understory diversity (Simpson index) as the dependent variable and site type included as an independent variable. F Value = 1.9, P > F = 0.069, R-square = 0.69, n = 46

Variable	Parameter estimate	Standard error	P > |T|
Intercept	21	9.8	0.045
Seedling diversity	0.94	0.45	0.050*
Tree diversity	−1.2	0.87	0.17
Sapling diversity	−0.69	0.70	0.33
Canopy opening	−0.034	0.020	0.11
Typic hapludalf soil	−1.0	3.4	0.77
Typic dystrochrept soil	2.1	3.9	0.59
Fluventic dystrochrept soil	−0.49	5.2	0.93
Typic fragiudalf soil	0.41	3.1	0.90
Typic udifluvent soil	−4.3	6.7	0.53
Lithic dystrochrept soil	−0.27	4.9	0.96
Ultic hapludalf	−1.6	3.8	0.67
A horizon	−0.089	0.23	0.70
O horizon	0.95	0.85	0.28
Soil rooting depth	−0.087	0.045	0.066
Standing dead trees	−1.2	0.55	0.040*
Fallen dead trees	−0.21	0.26	0.43
Narrow ridge	−6.4	3.9	0.12
Broad flat ridge	−4.5	3.4	0.20
Gentle slope	−3.3	3.6	0.37
Moderate north slope	−1.8	3.5	0.60
Moderate south slope	−8.2	4.8	0.10
Steep north slope	−3.8	3.6	0.31
Steep south slope	−9.0	5.1	0.090
Narrow bottomland	2.5	3.0	0.41

* = $P \leq 0.05$ level of significance.

were observed, and 55 of these species were common. The bottomland site type contained about twice as many common species (Table 4) than the next richest site type (steep north-facing slope). Unlike the average number of common species, the average number of total species for each site type were similar (Table 4). Mean percent cover of the understory flora differed considerably among site types (Table 4). For instance, site types 6 and 8 (south-facing slopes) had the highest average percent cover per subplot (41% and 36%, respectively), whereas site types 3 (broad ridge) and 5 (moderate north-facing slope) had the lowest average percent cover per subplot (16% and 17%, respectively). However, aside from site type 3, the mesic site types typically had lower average percent cover per subplot than the xeric site types. Thus, xeric site types, which are not species poor, tend to be dominated by a few species resulting in more species that can be categorized as rare.

There were 32 species found only in mesic site types (5, 7, 10) and four species found only in xeric site types (1, 3, 6, 8). Seven and eight species were designated as mainly mesic and mainly xeric, respectively (Table 5). Four species could not be classified.

DISCUSSION

Our first hypothesis predicting that the effects of each surrogate environmental variable on understory diversity would differ in importance and that the water-related variables

TABLE 4.—Mean number of understory species, mean number of common understory species, and mean percent cover of common understory species per subplot in each site type. Common is defined as occurring in five or more subplots (after multiplying by 0.83 the site types in which 24 instead of 20 subplots were sampled). Numbers in parentheses are the site type numbers

Site type	Mean # of species	Mean # of common species	Mean % cover of common species
Narrow ridge (1)	2.6	0.7	32
Broad ridge (3)	2.4	0.6	16
Broad, gentle slope (4)	3.7	0.8	21
Moderate north slope (5)	3.8	1.0	17
Moderate south slope (6)	2.9	0.6	41
Steep north slope (7)	2.4	1.2	23
Steep south slope (8)	2.6	0.7	36
Bottomland (10)	4.4	2.1	26

would be the most important was confirmed; namely, slope aspect, soil subgroup, rooting depth, and number of standing dead trees were significantly correlated with understory diversity.

South-facing slopes were significantly negatively correlated with understory diversity. Slope aspect is inherently related to available soil moisture and atmospheric moisture. Lipscomb and Nilsen (1990) measured soil water availability on northeast and southwest slopes in the Appalachian Mountains of Virginia using predawn leaf water potentials. Northeast and southwest slopes had similar predawn water availabilities. However, southwest slopes had significantly lower leaf water availability during midday. Lipscomb and Nilsen concluded that the difference in midday leaf water potential was due to higher atmospheric moisture demand (rather than soil water availability) caused by higher ambient temperatures.

It is possible that the apparent relationship between understory diversity and slope aspect in our study is due to a higher atmospheric moisture demand (*i.e.*, a higher evaporation rate) rather than limited soil water availability. A higher atmospheric moisture demand is a potential stress. Environmental stress, like disturbance, may augment competitive exclusion resulting in lower diversity (Paine, 1966; Lubchenco, 1978; Pianka, 1978; Basanta *et al.*, 1989). Plant species on south-facing slopes may thus be under environmental stress due to the potentially higher atmospheric moisture demand.

The only soil subgroup positively correlated with understory diversity was fluventic dystrochrept, which was found only in bottomlands. The most common soil subgroups found in our study area were typic hapludalf and typic dystrochrept; the six other soil subgroups occurred infrequently. Dystrochrepts belong to the embryonic Inceptisol soils which have little organic matter content and low base saturation levels, making the soil potentially low in essential plant nutrients (Buol *et al.*, 1989). However, the higher soil moistures often associated with alluvial soils, such as fluventic dystrochrept, may explain the corresponding higher understory diversity.

Soil rooting depth was significantly negatively correlated with understory diversity. Deep root growth may indicate less soil water availability in the upper soil layers. Understory species of older stands, unlike pioneer understory species, tend to produce shallow root systems. Most herbs, shrubs and vines in our study area have relatively shallow root systems and may be dependent on soil moisture in the upper soil horizons (Randall, 1952). Consequently, understory species in certain site types may not only be experiencing a low at-

TABLE 5.—Percent cover for common understory species in each site type and mesic/xeric classification. A species is common for a particular site type if it occurred in 5 or more subplots (2 or more sites) per site type; site types 2 and 9 are not included because those categories contained only 1 site each. The more xeric site types are 1, 3, 6, and 8; the more mesic site types are 5, 7, and 10. Site type 4, the broad gentle slope, includes both mesic and xeric sites. Classification key is: M = only mesic, X = only xeric, +M = in all site types but highest cover in mesic site types, +X = in all site types but highest cover in xeric site types, −M = in some xeric site types but highest cover in mesic site types, −X = in some mesic site types but highest cover in xeric site types, ? = in site type 4 (both mesic and xeric)

Species	1	3	6	8	4	5	7	10	Classification
Actea alba							12		M
Adiantum pedatum							9	5	M
Amphicarpa bracteata								56	M
Arisaema triphyllum				7		18	43	15	−M
Aster shortii				4					X
Bromus purgans								7	M
Carex albursina						6	13	6	M
C. jamesii								9	M
C. lexiculmis		3			10	1		7	−M
C. picta	38	31	578	320	140	49		24	+X
C. platyphylla								3	M
Circaea quadrisulcata							10	14	M
Cryptotaenia canadensis								5	M
Cunila origanoides	14		7	8					X
Cystopteris fragilis								16	M
Danthonia spicata	4								X
Dentaria lanciniata						5	26	16	M
Desmodium nudiflorum	12	4	30	47		6		20	−X
Dioscorea quaternata	3				6	4	3	4	−M
Galium aparine						2	6	10	M
G. circaezans		3	4	3	3	3	8	9	+M
G. concinnum						45	73	27	M
G. triflorum							18		M
Geum sp.								1	M
Hamamelis virginiana	5		16				4		−X
Hybanthus concolor								4	M
Impatiens capensis								8	M
Linera benzoin							42	10	M
Osmorhiza claytoni							10	18	M
Oxalis grandis								4	M
Panicum boscii								19	M
Parthenocissus quinquefolia	8	8	6	8	14	26	30	15	+M
Pilia pumila						7	6	45	M
Poa sylvestris								5	M
Podophyllum peltatum					6				?
Polygonatum biflorum		5	11	6	5	7	3	2	+X
Polystichum acrostichoides						21	64	13	M
Potentilla simplex					7			5	−M
Prenanthes alba					4				?
Rubus sp.	4							8	−M
Sanguinaria canadensis								5	M

TABLE 5.—Continued

Species	1	3	6	8	4	5	7	10	Classification
Sanicula canadensis							3	7	M
Smilacina racemosa						6			M
Smilax rotundifolia	423	242	107	185	199	63	14	24	+X
Solidago caesia				5					X
Stellaria pubera						12		5	M
Syndesmon thalictroides							10		M
Tovara virginiana								11	M
Toxicodendron radicans		4			3			15	−M
Vaccinium vacillans	28	12	53	76	12	8			−X
Verbesina helianthoides								11	M
Viburnum acerfolium	91	9	10	50	13	49	56	24	+X
Viola pubescens								6	M
V. triloba	5				3	5		7	−M
Vitis sp.	10	3	4	6	2			4	−X

mospheric moisture stress but also a low soil moisture stress, both of which could lead to lower diversity values.

Sites with more standing dead trees had significantly lower understory diversity. The number of standing dead trees may indicate older stands (Oliver and Larson, 1990). However, the second-growth forests in our study area are not representative of mature temperate forests of Indiana. The sites in this study have a history of anthropogenic disturbance; most timber harvesting occurred under private ownership before the establishment of the Hoosier National Forest and forests were clearcut or cleared for subsistence farming. Without more information about each site's history, we can only assume that number of standing dead trees is an appropriate surrogate measure of light intensity and soil moisture and that the resulting increase in light intensity or decrease in soil moisture had a negative effect on understory diversity.

The second hypothesis stated that tree seedling diversity would be significantly correlated with understory diversity, whereas sapling and tree diversity would not be correlated. This hypothesis was also supported by the results of our regression models. Maguire and Forman (1983) found that total percent cover of herbs and tree seedlings were negatively correlated in a hemlock-hardwood forest; they attributed this to competition for the shared resources. Facelli and Pickett (1991) also showed a negative effect of herbs on tree seedlings due to competitive effects. In their study, removal of a dominant herb resulted in an increase in tree seedling size. If tree seedlings and understory species are indeed competing, as these two studies suggest, it is reasonable to conclude that diversity of understory species and tree seedlings would be negatively correlated. Our results show a positive correlation between tree seedling and understory diversity, which may indicate that understory species and tree seedlings in our study area are not competing. However, a positive correlation between the diversity values is more indicative of similar responses to given resources. Equivalent competitive abilities might be the mechanism behind similar diversity values of understory and tree seedling species (Paine, 1966; Lubchenco, 1978; Tilman, 1988).

Our third hypothesis (stating that habitat heterogeneity as defined by site types would explain the nonuniform distribution of herbs, shrubs and low-growing vines) was also supported by our data. Although none of the site types was significantly related to understory

diversity in the regression models, the models were not created to test for nonuniform distribution of understory species; equivalent species diversity values could, therefore, represent areas of very different species composition. Species groupings within each site type indicate that not only are there more common species in the mesic sites on average, species composition also differs considerably from the xeric sites (Tables 4 and 5). This relationship between apparent water availability and species distribution also supports the apparent relationship between water-related surrogate variables and understory diversity. Van Kley's (1993) classification key of the Brown County Hills (includes Pleasant Run Unit) and the Crawford Upland (south of our study area) also follows a moisture gradient adding support to the hypothesis water-related environmental variables are the most important in explaining understory diversity values and the nonuniform distribution of species.

We have partly answered the question: Why are there so many understory species and why are they not distributed uniformly? The use of multiple regression analysis and diversity indices may not be the most informative method of defining important variables; studies involving experimental methods that address both temporal and spatial scales should follow. However, our study did suggest the variables on which these experiments should focus. In addition, we suggest that subsequent studies include site history (anthropogenic and natural disturbance) as an independent variable. The composition and consequent diversity values of any second-growth forest are obviously influenced by previous perturbations as well as environmental factors.

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