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Spatial and temporal variability of herbaceous vegetation in an eastern deciduous forest

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Abstract

We examined spatial and temporal variability of understory herbaceous vegetation on opposing north- and south-facing slopes in an eastern deciduous old-growth forest in southeastern Ohio, USA. Secondly, we explored the influence of sampling scale and analytical technique on our assessment of diversity patterns. The influence of aspect and seasonality were examined at varying sampling scales using observed richness, evenness, and H' diversity measures, non-parametric richness estimators, species-area curves, and SHE analysis. Herb layer composition, abundance, and diversity were strongly influenced by location (north slope vs. south slope), seasonal sampling period (April, June, August), and plot size (micro (2 m^2)- vs. meso (70 m^2)-scale samples). Although north and south plots were compositionally distinct, they followed similar courses of change through the growing season. Richness, evenness, and H' diversity were generally greater on the south plot whereas herbaceous abundance was greater on the north plot. Species composition and diversity showed marked phenological (temporal) changes, and comparison of diversity measures at micro- and meso-scales produced markedly different results. Minimum sample areas of 150–200 m^2 were needed to evaluate micro-scale richness in these species rich communities, suggesting that forest understories may be frequently undersampled in ecological studies. Comparison of observed and estimated meso-scale richness also suggested underestimation of richness in the north plot, particularly earlier in the growing season. Thus, sample size, area, and time of sampling appear critical to assessment of diversity in spatially and temporally variable communities such as herbaceous forest understories.

Introduction

Diversity patterns are fundamentally linked to the spatial and temporal variability of natural communities. Observed species richness, the number of species located in a sampling effort, is heavily dependent on the number and size of samples, with increasing numbers of species generally found with increased sampling intensity (Gleason 1922 MacArthur 1965). Even across large areas, the number of species observed in a sample may greatly underestimate true community richness, particularly in diverse systems or those containing many rare species (Lande 1996). Like richness, many measures of evenness are also dependent on sample size and area (Sheldon 1969 Wilson et al. 1999). Thus, diversity measures, comprised of these richness and evenness components, are similarly influenced by the spatial scale and intensity of sampling (e.g., Wilson et al. (1998) and Huston (1999)). In studies of temporally (seasonally) variable communities such as forest understories, phenological changes also influence species composition and importance, further affecting measures of community richness, evenness, and diversity. However, the influence of this spatial and temporal variability on natural patterns of herb layer diversity remains largely unexplored and poorly understood (Goebel et al. (1999) and Wilson et al. (1999), McCarthy et al. (2001) are exceptions).

In this study, we examined the spatial and temporal variability of understory herbaceous layer diversity in an eastern deciduous old-growth forest remnant. Diversity issues are of particular importance in old-growth systems, where such measures can provide important insights into forest diversity patterns and serve as benchmarks for comparison with the anthropogenically disturbed and actively managed forests that now dominate much of our landscape (Duffy and Meier 1992 McCarthy 1995 Roberts and Gilliam 1995). Herbaceous layer vegetation typically represents the largest component of deciduous forest diversity (Braun 1950) and may provide important indications of site quality, overstory regeneration patterns, ecosystem integrity, and conservation status (Bratton 1976 Duffy and Meier 1992 Hutchinson et al. 1999). However, despite the contribution of the herbaceous stratum to overall forest diversity, our understanding of herb layer diversity patterns remains limited, particularly relative to variations in site conditions and over time.

Our means of assessing community diversity patterns also has been frequently questioned. No single diversity index can fully capture the complex patterns of species richness and relative abundances (evenness) inherent in natural systems (Hurlbert 1971 Peet 1974 DeJong 1975). As a result, little consensus has been reached as to how diversity should be best measured and interpreted (Pielou 1966 Austin 1999), and a wide range of analytical techniques are commonly used (Peet 1975 Magurran 1988 Smith and Wilson 1996). Given the range of diversity measures available and the potentially strong influence of spatial and temporal scales (i.e., sampling frequency and intensity) on these measures, we must question how our choice of diversity estimation techniques and sampling procedures influence our characterization of herb layer diversity patterns. Therefore, the objectives of this study were: (1) to examine spatial and temporal patterns of understory diversity in an old-growth deciduous forest community and (2) to examine the extent to which our choice of analytical technique or scale of measurement influenced our assessment of community diversity.

Methods

Study site and field procedures

All field studies were conducted at Dysart Woods, a 23 ha mixed mesophytic old-growth forest remnant in southeastern Ohio, USA (39°59′5″ N, 80°59′50″ W; United States Geological Survey (1972)). Braun (1950) includes Dysart Woods in the Low Hills Belt section of the Mixed Mesophytic Forest Association, part of the Central Appalachian Unglaciated Allegheny Plateau Physiographic Province (Fenneman 1938). Mixed mesophytic forests occur on mesic slopes and bottomlands in the Central Appalachian Mountains and the Western Allegheny and Cumberland Plateaus of the eastern US. This vegetation is strongly influenced by topography, with canopy dominance of oaks (*Quercus* spp.) and hickories (*Carya* spp.) along upper slopes and ridgetops and mixed mesophytic tree species (e.g., *Fagus grandifolia*, *Liriodendron tulipifera*, *Aesculus flava*, *Acer saccharum*, *Quercus rubra*, *Q. alba*, *Fraxinus americana*, *Prunus serotina*) in coves and ravines. The climate of Dysart Woods is temperate continental (Rubel et al. 1981), with a mean yearly temperature of 10.7 °C and mean annual precipitation of 101.2 cm . Soils are primarily loams and silt loams, formed in limestone, siltstone, sandstone and shale residuum (Rubel et al. 1981). The topography is highly dissected, composed of steep hillsides and narrow sloping ridgetops. Elevations at the study site range from 325 to 425 m.

Study sites were located on opposing north- and south-facing slopes in the largest stands of old-growth vegetation. The north slope site was a steep, linear NW-facing slope with a mean elevation of 400 m; the south slope site was a steep, slightly convex SSW-facing slope with a mean elevation of 410 m. Due to the limited extent of old-growth area, topographic variation, and the proximity of trails, the influence of slope aspect was unavoidably pseudoreplicated. On both slopes, one 50 × 70 m (0.35 ha) permanent study plot was established. This plot size was the largest possible to avoid the influence of hiking trails present on each slope. Each plot consisted of 35 circular quadrats (2 m^2) systematically arranged in a 50 × 70 m grid (10 m intervals between quadrats) on each slope. Thus, the 35–2 m^2 sample quadrats on the north and south slopes were nested within and comprised the single 70 m^2 sample plot on each slope. Within each 2 m^2 quadrat, percentage cover of each herbaceous vascular plant species over the 2 m^2 quadrat area was estimated visually, to the nearest percent, in April, June, and August of 1997, to capture phenological (temporal) variability in herbaceous composition and diversity (e.g., peak growth of spring ephemerals and late season graminoids and composites). Nomenclature follows Gleason and Cronquist (1991) and McCarthy et al. (2001) provide additional information on the study site, forest structure, and species composition at Dysart Woods.

Spatial and temporal diversity patterns

Compositional patterns were examined on the north and south plots across sampling dates (April, June, August) using non-metric multidimensional scaling (NMS) ordination. NMS differs markedly from other commonly used ordination techniques (e.g., Detrended Correspondence Analysis, Principal Components Analysis) in being a non-parametric, iterative technique that uses ranked distances to arrange sample plots along a number of axes determined by a minimal stress (departure from monotonicity) configuration. The placement of plots and number of axes in a NMS ordination are calculated as the solution minimizing the final stress between the dissimilarity in the original data matrix and that in the reduced ordination matrix. NMS has been shown to perform well with ecological data that tend to be non-normal and contain numerous zero entries (Clarke 1993). NMS ordination, using the global NMS procedure performed by PC-ORD (McCune and Mefford 1997), was conducted on the cover (%) data collected in the 35 north and 35 south slope understory quadrats during each of the three sampling periods.

Understory diversity patterns were assessed using observed richness (S; the number of species per sample), Shannon-Wiener diversity ($H' = -\Sigma \mathrm{p}_i \ln p_i$, where p_i is the proportion of individuals of the ith species; Shannon and Weaver (1963)), and evenness ($E = e^{H'}/S$; the proportional abundance of species in each sample; Buzas and Gibson (1969)) measures. Percentage cover estimates from north and south slope quadrats were used in the calculation of H' and E. Values of S, H', and E were calculated at two scales: mean per quadrat (35–2 m^2 quadrats on each slope; micro-scale) and total per plot (1–70 m^2 plot per slope; meso-scale), to examine the spatial variability of these measures. Microscale and mesoscale S, H', and E were calculated for each sampling date to evaluate the temporal variability (phenological changes) of understory diversity. Mean microscale diversity measures (S, H', E) were compared using two-way repeated measures analysis of variance (ANOVA) tests to examine the effects of plot location (north vs. south slope; fixed effect) and sampling date (the repeated measure, fixed effect). Variables were log transformed to meet normality and variance assumptions. Significance levels were adjusted for experiment-wise error using a Bonferroni correction. Significant differences were compared using *a posteriori* Bonferroni multiple comparisons (Sokal and Rohlf 1995).

These data were also examined using SHE analysis (SHE: S = richness, H = H' diversity, E = evenness; Buzas and Hayek (1996) and Hayek and Buzas (1997, 1998)). SHE analysis is a recently developed technique for diversity assessment that allows independent yet simultaneous evaluation of the relative contributions of richness and evenness to community diversity across sampling scales. In SHE analysis, the relative contributions of richness and evenness to H' diversity are partitioned using the decomposition formula: $H' = \ln(S) + \ln(E)$. This SHE analysis decomposition equation is derived from the following conditions: (1) maximum H' diversity occurs when all species are equally distributed ($H'_{\mathrm{Max}} = \ln(S)$), and (2) E is related to H' by the equation $E = \mathrm{e}^{H'}/S$. Thus, the SHE decomposition formula, $H' = \ln(S) + \ln(E)$, indicates that H' diversity equals its maximum value, $\ln(S)$, less the amount of unevenness, $\ln(E)$ (subtracted because evenness $\leqslant 1$ and $\ln(E)$ will be $\leqslant 0$), in the sample. In this way, SHE analysis partitions H' diversity into richness and evenness components and allows independent evaluation of their contributions to H'.

Using SHE analysis, $\ln(S)$, $\ln(E)$, and H' values were calculated cumulatively, with the addition of each sample. Results were examined graphically to evaluate relationships among diversity measures from a single 2 m^2 quadrat (micro-scale) to the cumulative measure of 70 m^2 (meso-scale) across all 35 quadrats. SHE analysis was also used to infer the species abundance distribution best representing each sample community, based on Hayek and Buzas (1997, 1998). Species abundance distributions are statistical distributions that model the relative abundances of species in a community. These distributions are often used to describe patterns of community organization or resource partitioning. Hayek and Buzas (1997, 1998) found that the broken stick distribution (MacArthur 1957) was distinguished by constant $\ln(E)$ across sample sizes, the log series (Fisher et al. 1943) by constant H' across sample sizes, and the log normal distribution (Preston 1948) by a constant ratio of $\ln(E)/\ln(S)$. See Hayek and Buzas (1997, 1998) for a complete discussion of SHE analysis.

Bootstrap-derived species-area curves were used to further evaluate the influence of spatial scale on understory diversity. Species-area curves were created for the north and south plots during each sampling period. These curves were generated using the PC-ORD software (McCune and Mefford 1997), which subsampled the north and south plot data sets at all possible sample sizes (all possible subsamples) to determine mean richness at each subsample size.

Observed meso-scale species richness values (70 m^2; the total number of species on the north or south plot) were compared to estimations of total meso-scale richness generated by non-parametric richness estimators. Richness estimators are resampling techniques developed to reduce the bias of sample data. Because the number of species observed in a sampling effort is likely to underestimate the actual, total number of species present in that community (Lande 1996), richness estimators more heavily weight rare or infrequent species such as uniques (species occurring in only one quadrat) and duplicates (species occurring in exactly two quadrats) for a given sample size (e.g., Palmer (1990, 1991) and Chazdon et al. (1998)). Literature studies have suggested the use of multiple non-parametric richness estimators to reduce sampling bias and obtain more robust, reliable estimations of community richness (Chazdon et al. 1998 Gimaret-Carpentier et al. 1998). We used the following non-parametric, incidence-based richness-estimators in the examination of our data: (1) the Chao 2 estimator, incorporating the number of uniques and duplicates into richness estimation (Chao 1987); (2) the first-order Jackknife estimator, incorporating the number of uniques and the number of quadrats sampled (Burnham and Overton 1979 Heltshe and Forrester 1983); (3) the second-order Jackknife estimator, employing the number of uniques, duplicates, and sample quadrats (Smith and van Belle 1984); (4) the bootstrap estimator, based on the proportion of quadrats containing each species (Smith and van Belle 1984); and (5) the Incidence based Coverage Estimator (ICE), weighting species found in $\leqslant 10$ sampling units (Lee and Chao (1994); adapted by Chazdon et al. (1998)). Formulas for each estimator are provided in Table 1.

A comparison of richness estimators showed Chao 2 and ICE to provide relatively consistent and reliable richness estimations with low sensitivity to sample size, patchy species distributions, and sample order (Chazdon et al. 1998). Jackknife 1 and 2 produced higher richness values than other estimators examined but Jackknife 1 generally showed higher precision and Jackknife 2 lower bias at small sample sizes. Although some studies have discouraged use of the bootstrap estimator for estimation of terrestrial plant species richness, indicating low reliability and high bias (Colwell and Coddington 1994 Chazdon et al. 1998), this estimator was also used in the present study for comparative purposes. Detailed reviews of these and other richness-estimators can be found in Colwell and Coddington (1994) and Chazdon et al. (1998), and Walther and Morand (1998).

The adequacy of our 35 2-m^2 quadrats for assessing micro-scale (2 m^2) richness was evaluated using minimum sample size calculations. The minimum sample size necessary to obtain a 95% confidence interval within 5% of actual or true mean richness for north and south slope herb communities was calculated for each sample period (i.e., the number of samples necessary to be 95% confident that our sample mean lies within 5% of the true mean). The required sample size was calculated as: $N = (s^2 t^2_{\alpha(2),(n-1)})/(d \cdot x)^2$, where s^2 is the sample variance, t is the two-tailed critical value of Student's t with $n-1$ degrees of freedom, d is the permitted width of error around the mean, and x is the sample mean (Stoecker 1995 Zar 1996).

Results

Species composition

Non-metric multidimensional scaling (NMS) ordination of herb-layer data showed composition to vary with time of sampling (April, June, August) and quadrat location (north vs. south plot; Figure 1). The NMS ordination was best fit by a two-axis solution, as determined by a Monte Carlo randomization test ($P < 0.05$) and visual examination of the NMS scree plot. The first two NMS axes accounted for 57.1% of the variability in the data (axis 1 = 33.0%, axis 2 = 24.1%; final stress = 29.25; final instability = 0.0109). Axis 1 showed strong separation (marked difference in species composition and abundance) of north and south slope quadrats. Axis 2 showed compositional separation of quadrats based on sampling date. North and south slope quadrats, although compositionally

Table 1. Formulas for species richness estimators used in this study.

Estimator	Formula
Chao 2	$S_{Chao2} = S_{Obs} + \frac{Q_1^2}{2Q_2}$
Jackknife 1	$S_{Jack1} = S_{Obs} + \frac{Q_1(m-1)}{m}$
Jackknife 2	$S_{Jack2} = S_{Obs} + \left[\frac{Q_1(2m-3)}{m} - \frac{Q_2(m-2)^2}{m(m-1)}\right]$
Bootstrap	$S_{Boot} = S_{Obs} + \sum_{k=1}^{S_{obs}} (1-p_k)^m$
Incidence-based Coverage Estimator	$S_{ICE} = S_{Freq} + \frac{S_{Infr}}{C_{ICE}} + \frac{Q_1}{C_{ICE}}\gamma_{ICE}^2$ $C_{ICE} = 1 - \frac{Q_1}{N_{Infr}}$ $N_{Infr} = \sum_{j=1}^{10} jQ_j$ $\gamma_{ICE}^2 = \max\left\{\frac{S_{Infr} \quad m_{Infr} \quad \sum_{j=1}^{10} j(j-1)Q_j}{C_{ICE}(m_{Infr}-1) \quad (N_{inf})^2} - 1, 0\right\}$

Key to variables:
S_{Obs} Total number of species observed in all quadrats
S_{Freq} Number of species occurring in > 10 quadrats
S_{Infr} Number of species occurring in $\leqslant 10$ quadrats
Q_j Number of species occurring in j number of quadrats
m Total number of quadrats
m_{Infr} Number of quadrats having at least one S_{Infr}
p_k Proportion of quadrats containing species k

distinct, followed a similar temporal (phenological) trajectory over the growing season.

Early spring (April) north slope quadrats generally grouped together on the NMS ordination (Figure 1), dominated by ephemeral spring herbs such as *Claytonia virginica* and *Cardamine concatenata*. In June, importance of spring ephemerals in the north quadrats decreased and importance of *Impatiens pallida*, *Osmorhiza claytonii*, *Podophyllum peltatum*, and *Galium aparine* increased. By August, most herb layer species had declined in abundance but *O. claytonii*, *Cimicifuga racemosa*, and *Viola pubescens* remained important. South slope quadrats showed similar phenological trends to those of the north slope, as evidenced by parallel clouds of points on the NMS ordination (Figure 1), but had greater importance of graminoids (Poaceae, Cyperaceae, and Juncaceae) and composites (Asteraceae) than north quadrats. In April, south quadrats were dominated by *Claytonia virginica*, with secondary importance of *Floerkea proserpinacoides*, *Aster divaricatus*, and *Galium aparine*. In June, dominance shifted to *O. claytonii*, *G. aparine*, *A. divaricatus*. June and August south slope samples showed considerable overlap on the NMS ordination (Figure 1), due to high importance of *Aster divaricatus* and *O. claytonii* in both sample periods.

Spatial and temporal diversity patterns

Observed Micro- and Meso-Scale Richness, Evenness, and Diversity. At the micro-scale (quadrat; 2 m^2), observed richness of north slope quadrats decreased significantly over the growing season (Table 2). Micro-scale richness of south slope quadrats did not change significantly from April to June but decreased in August. Comparison of north vs. south quadrats showed no difference in micro-scale richness

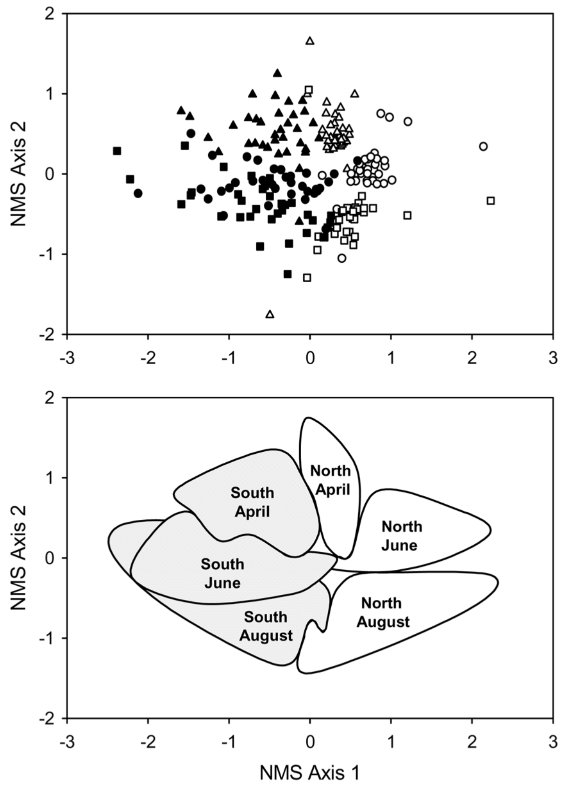

Figure 1. Non-metric multidimensional scaling (NMS) ordination of 210 2-m^2 understory sampling quadrats (35 north and 35 south slope quadrats sampled during April, June, and August sampling periods) at Dysart Woods, Ohio, USA. The first two NMS ordination axes account for 33.0% and 24.1% of the variability in the data, respectively. The upper panel shows the location of individual sample quadrats along axes 1 and 2 in NMS ordination space. The lower panel groups clouds of sampling points based on slope aspect and sampling period.

in April but significantly greater richness of south quadrats in June and August. At the meso-scale (plot; 70 m^2), observed north plot richness was slightly greater in April and August than in June (Table 2). In the south plot, conversely, meso-scale richness was greatest in June and lower in April and August. For each sampling date, meso-scale richness on the south plot exceeded that of the north plot.

Observed micro- and meso-scale H' diversity patterns were similar to those of species richness (Table 2). In north slope quadrats, micro-scale H' decreased significantly from April and June to August. South slope quadrats also showed a decline in micro-scale H' from June to August. Like richness, micro-scale H' did not differ significantly between north and south quadrats in April but was greater in south quadrats in June and August. Meso-scale H' was greatest on the north plot in April and on the south plot in June. South plot meso-scale H' exceeded that of the north plot during each sampling period.

In both sets of quadrats, micro-scale evenness increased significantly from April to August (Table 2). No significant differences between north and south quadrats were found during any sampling period. At the meso-scale, evenness was greatest on the north plot in June, on the south plot in August. Again, meso-scale evenness in the south plot consistently exceeded that of the north plot.

The SHE analysis graphs also showed greater observed richness (ln(S)) and H' diversity on the south plot relative to the north plot during each sample period (Figure 2). This trend was maintained at all sampled spatial scales, from micro- (2 m^2; low x-axis values) to meso- (70 m^2; high x-axis values) scale. SHE analysis graphs showed that the greater H' diversity on the south plot in April and June resulted from greater richness (higher ln(S) curve), rather than evenness. In August, greater south plot H' resulted from both greater richness and evenness. Growing season trends were also evident, with greatest north plot evenness and H' diversity in April and greatest south plot richness and H' and lowest evenness in June (Figure 2). Greater abundance of herbaceous vegetation on the north plot relative to the south plot was evident in April and June (total percentage cover along x-axis; Figure 2). In August, abundance of north plot herbs greatly declined but south plot abundance remained relatively constant.

The SHE analysis ln(S) curves showed differences in species-area relationships between plots. Throughout the growing season, the south plot showed rapid accumulation of species in initial samples, with few additional species in later samples (leveling of ln (S) curve; (Figure 2)). On the north plot, April and June plots showed more gradual accumulations of species. All north plot sampling dates showed continued increase in ln(S) curves with additional samples.

Finally, based on Hayek and Buzas (1997, 1998), SHE analysis was used to indicate the species abundance distributions represented in our data (Figure 2). Cumulative ln(E)/ln(S) remained relatively constant in each plot, indicating that each sample community was best fit by a log normal species abundance distribution.

Richness and Sample Size Estimations. Non-parametric estimations of species richness were considerably higher than total observed richness (meso-scale; 70 m^2) for the north plot, particularly in April (Ta-

Table 2. Summary richness (*S*), Shannon-Wiener diversity (*H*′) and evenness (*E*) statistics for 35 understory sampling quadrats located in north and south plots at Dysart Woods, Belmont County, Ohio. Micro-scale indicates mean value (± SE) per 2 m^2 quadrat; meso-scale indicates total value across all 35 quadrats in each plot (70 m^2). Different letters indicate significant differences between quadrat column means (i.e., between north and south quadrats and sampling periods; ANOVA, $P < 0.0001$; multiple comparisons with Bonferroni correction, $P < 0.05$).

	S		*H*′		*E*	
	Micro-scale	**Meso-scale**	**Micro-scale**	**Meso-scale**	**Micro-scale**	**Meso-scale**
North						
April	7.09 (0.25)^{a}	19	1.58 (0.05)^{ac}	1.98	0.717 (0.020)^{ab}	0.381
June	5.06 (0.23)^{b}	16	1.35 (0.05)^{a}	1.87	0.799 (0.018)^{bd}	0.403
August	3.46 (0.24)^{c}	18	0.96 (0.07)^{b}	1.88	0.827 (0.022)^{cd}	0.362
Total		33		2.15		0.486
South						
April	7.03 (0.38)^{a}	27	1.54 (0.06)^{ac}	2.35	0.710 (0.020)^{a}	0.388
June	7.51 (0.55)^{a}	38	1.61 (0.09)^{c}	2.82	0.740 (0.019)^{ab}	0.442
August	5.46 (0.42)^{b}	27	1.31 (0.10)^{a}	2.56	0.794 (0.021)^{bc}	0.479
Total		47		2.82		0.554

ble 3). Estimated richness values for the south plot were only slightly greater than observed richness values. Like observed richness, south plot estimations consistently exceeded north plot estimations (with the exception of some April estimations; Table 3).

Bootstrap-derived species-area curves, generated for the north and south plots during each sampling period, generally corresponded with the results of the SHE analysis and richness estimators (Figure 3). The curves showed greater south plot richness at all sampling scales and more rapid initial accumulation of south plot species. Greater south plot richness was particularly evident in the comparison of June species-area curves.

Estimation of the sample size needed for a 95% confidence interval within 5% of true mean micro-scale richness in all cases suggested inadequate sampling. Required sample sizes were calculated to be considerably larger than our 35 quadrats. For the north plot in April, June, and August, approximately 71, 110, and 260 quadrats, respectively, were necessary to estimate richness with a 95% confidence interval no wider than 5% of the mean. For the south plot, estimated sample sizes were 159, 291, and 325 quadrats, respectively. Reducing our desired precision to a 95% confidence interval no wider than 10% of the mean (perhaps a more reasonable level for community studies) reduced the number of samples required, although these were still generally larger than our sample size of 35 quadrats. For the north plot, 19, 29, and 69 quadrats, and for the south plot, 41, 74, and 83 quadrats, respectively, would be necessary in April, June, and August.

Discussion

Our herb layer data showed strong patterns of spatial variability, with dramatic changes in understory composition and diversity relative to plot location. We generally found greater micro- and meso-scale herbaceous diversity on the south-facing plot and greater herbaceous abundance on the north-facing plot. Overall species composition also differed between plots. Such differences may result from variations in site conditions associated with topographic aspect. The importance of aspect on ecosystem properties such as microclimate (Wolfe et al. 1949 Cantlon 1953), soil formation (Franzmeier et al. 1969), and vegetation abundance and diversity (McCarthy et al. 1987) has been recognized in the central Appalachians and other north-temperate areas of moderate to high relief. In these systems, south-facing slopes generally experience higher temperatures, greater light intensity, and lower moisture availability than north-facing slopes, producing marked differences in plant community composition and structure (Wolfe et al. 1949 Cantlon 1953). McCarthy et al. (2001) found similar microclimatic differences between the north and south plots at Dysart Woods. These north and south slope microclimatic differences are typically greatest just above ground level, thus exerting a particularly strong influence on herbaceous communities (Cantlon 1953). Al-

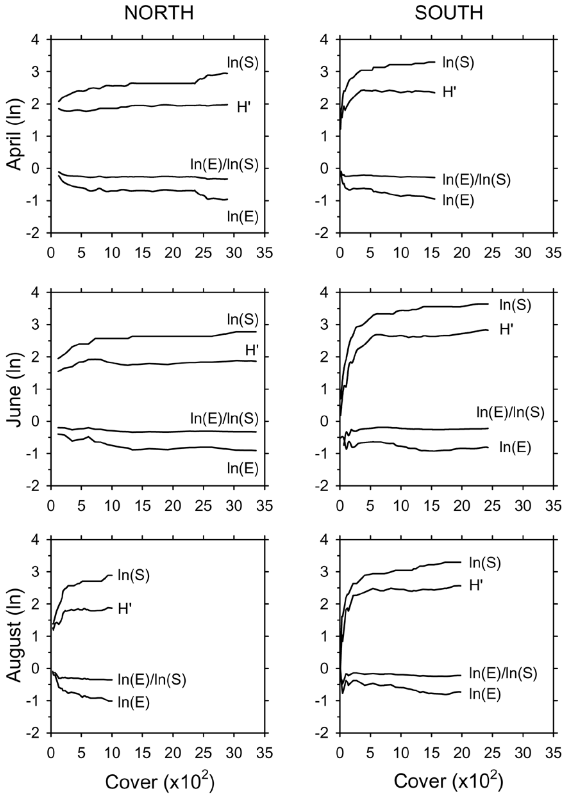

Figure 2. The results of SHE analyses on data collected in 35-2 m^2 understory sampling quadrats on the north and south slope plots in April, June, and August at Dysart Woods, Ohio, USA. The *x*-axis on each graph represents the accumulation of understory vascular plant species (expressed as percentage cover) across the 35 sampling quadrats, from a single 2 m^2 quadrat to 70 m^2 across all 35 quadrats. The *y*-axis represents the natural log of richness (ln(*S*)), evenness (ln(*E*)), the ratio of evenness to richness (ln(*E*)/ ln(*S*)), and Shannon-Wiener *H'* diversity.

though we found consistently greater diversity on the south plot at our study site, other studies in our region have reported opposing results. For example, Hutchinson et al. (1999) found the greatest herb richness on mesic, north-facing slopes in deciduous forests of southern Ohio. Like our study, however, Hutchinson et al. (1999) found increased graminoid richness on south-facing slopes and greater forb abundance on north-facing slopes. Olivero and Hix (1998), in a study of herbaceous layer vegetation on north- and south-facing forested slopes of southeastern Ohio, found no difference in herbaceous richness or diversity with aspect position in their old-growth forest stands. Unfortunately, our inability to replicate north and south slopes in this study inhibits direct inferences about the influence of aspect on herbaceous layer vegetation at this site.

In addition to understory diversity trends associated with plot location or aspect, seasonal patterns were also evident in our data. Both the north and south plots showed considerable phenological change during the growing season, with greatest north slope observed richness and *H'* diversity early in the growing season, due to the importance of spring ephemerals, and greatest south slope richness and *H'* diversity in early summer, due to the importance of graminoids and composites (McCarthy et al. 2001). Evenness generally increased on both slopes during the growing season. Goebel et al. (1999), in a study of old-growth forest understories in southeastern Ohio, found similar patterns of increased richness and *H'* diversity on south-facing slopes in early summer but no seasonal trends of evenness. Interestingly, north and south slope quadrats in our study were compositionally distinct but samples followed similar phenological trajectories over the course of our study, suggesting similar courses of compositional change during the growing season.

SHE analysis showed herb layer evenness to decrease generally with increasing sample size. Wilson et al. (1999) found similar decreases in evenness with increasing spatial grain in herbaceous communities of New Zealand. In their analysis, Wilson et al. (1999) note that species richness can only increase or remain constant with increasing spatial scale or sample size, whereas evenness may increase or decrease. Thus, changes in evenness with increasing spatial scales may better reflect true changes in species diversity and abundance patterns. The relationship between evenness and spatial scale may provide insights into diversity patterns beyond those of species richness or composite diversity measures (e.g., *H'*) alone and, therefore, should be included as a fundamental component of diversity assessment (Wilson et al. 1999).

In our study, simultaneous graphing of evenness and richness data showed that decreases in evenness were accompanied by increases in species richness on both slopes during all sample periods. On the north slope, decreases in evenness paralleled increases in species richness, resulting in little to no changes in *H'* diversity with increasing sample size. This decreasing evenness of north slope quadrats suggests that added species tend to be relatively uncommon or rare. On the south slope, increases in richness greatly outweighed decreases in evenness during each sample period, resulting in increased *H'* diversity with sam-

Table 3. Total observed and estimated meso-scale (70 m^2) herb layer richness values for the north and south plots at Dysart Woods for each of the three 1997 sampling periods. Observed richness represents the number of species found across all 35 sample quadrats in each 70 m^2 plot during each sample period. Jack 1 = Jackknife 1, Jack 2 = Jackknife 2, Boot = Bootstrap, ICE = Incidence-based coverage estimator. Mean represents the arithmetic mean of the five calculated richness estimators. See Table 1 for formulae and text for descriptions of each richness estimator.

	Observed Richness	**Richness Estimator**					
		Chao 2	**Jack 1**	**Jack 2**	**Boot**	**ICE**	**Mean**
North							
April	19	>44.0*	26.8	34.3	21.9	47.9	35.0
June	16	28.5	20.9	24.7	18.0	24.7	23.4
August	18	21.1	22.9	23.9	21.4	23.5	22.6
South							
April	27	28.5	29.9	30.0	28.7	28.4	29.1
June	38	40.6	43.8	43.1	41.3	41.4	42.0
August	27	29.7	30.9	31.9	29.0	28.6	30.0

* The value of the Chao 2 estimator was undefined because no duplicates (species occurring in only two 2.0 m^2 quadrats; Q_2 divisor) were present in the data set ($Q_2 = 0$). To estimate Chao 2, the number of unique species (species occurring in one quadrat; Q_1) was reduced by one and the number of duplicate species (Q_2) increased by one. The resulting Chao 2 approximation of 44 species is, thus, lower than the true Chao 2 estimate.

ple size. (This is also evident in the north slope August sample.) This suggests that the species added with increased sampling tend to be relatively common or have abundances similar to existing species. Our richness estimators supported these conclusions, responding to more numerous rare species on the north slope by producing higher estimates of total (meso-scale) community richness.

Discrimination of species-abundance distributions using SHE analysis indicated that each sample, throughout the growing season, was best fit by a log normal species-abundance distribution. Such a distribution indicates that communities are mature and relatively diverse, with a high proportion of rare species, as found in the old-growth understory herb community at Dysart Woods. In our use of SHE analysis, we were concerned about the ability of SHE analysis to discriminate only three species-abundance distributions, though many others have been fit to plant community data (Wilson 1991). In addition, the April north plot data show both cumulative $\ln(E)/\ln(S)$ and H' to be relatively constant with increasing numbers of samples. While constant $\ln(E)/\ln(S)$ suggests the data to be best fit by a log normal distribution, constant H' indicates a log series distribution. This suggests that the north plot spring community may exhibit characteristics intermediate between log normal and log series distributions, as might be expected of a community with a small number of abundant species and a relatively large proportion of rare species (Magurran 1988). Such a large number of unique species on the north slope was found in April, producing our high estimated richness values.

Abundance data derived from visual cover estimations rather than biomass measurements were used to evaluate understory diversity patterns and species-abundance distributions at Dysart Woods. This practice has been cautioned by Chiarucci et al. (1999), who suggest that some subtle aspects of community structure may be less apparent when using cover- rather than biomass-derived data. However, they indicate that their results may not be consistent between community types, as relatively few have been examined. Pielou (1975) reported no effect of abundance measure on species-abundance distributions. Like our research, many studies providing important contributions to our understanding of forest diversity patterns are limited to the use of cover estimates and other biomass surrogates because they focus on threatened, rare, or protected ecosystems, where destructive sampling cannot be performed.

Species richness estimators were used to approximate the actual number of species present in our forest understory communities. Results suggest that the 35 2-m^2 sample quadrats on the south plot provided a reasonably good representation of meso-scale richness. However, the large discrepancy between observed and estimated richness values on the north plot, particularly in April, suggests that our sample size of 35 quadrats may have been insufficient to ad-

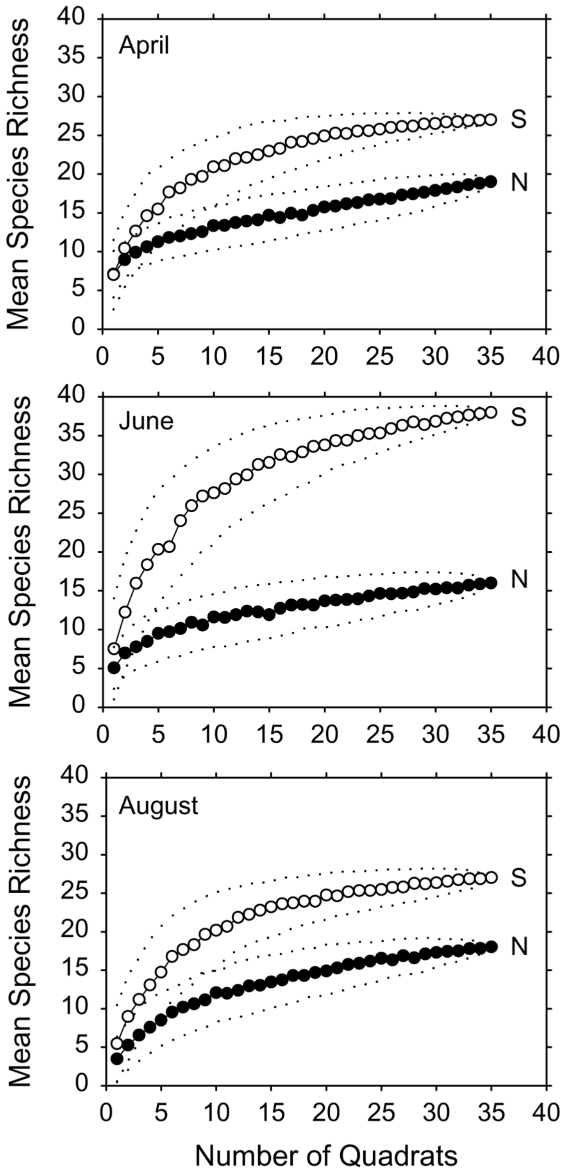

Figure 3. Bootstrap-derived species–area curves (± 2 SD) for the 35-2 m^2 understory sampling quadrats on the north and south slopes at Dysart Woods, Ohio, USA, during the three sampling periods (S = South plot; N = North plot).

equately capture the actual total number of species that exist in the north plot community. The high estimated richness for the north slope in April, and to a lesser extent in June, relative to observed richness, may have resulted from several uncommon or patchily distributed species, as evidenced by lower north plot evenness and increasing species-area curves.

Clearly, the location and time of sampling and the size of the sampling area are critical considerations in the assessment of richness, evenness, and diversity patterns in spatially and temporally variable communities such as herbaceous forest understories. In our study, comparisons of herbaceous diversity at micro- and meso-scales resulted in markedly different evaluations of community diversity. Thus, based on the results of this and other studies, evaluation of both alpha- (within-habitat) and beta- (between-habitat) diversity at varying spatial scales seems essential for a comprehensive assessment of community diversity patterns. Likewise, in studies of phenologically variable species such as forest understory herbs, seasonal measurements are needed to capture temporal patterns of diversity. The abundance and species composition of understory herbs in our sample quadrats changed considerably during the growing season. Many studies of forest understory communities fail to account for these early-, mid-, and late-growing season changes, considering only single sampling periods such as early spring (e.g., Rogers (1982)), midsummer (e.g., Olivero and Hix (1998)), or undefined single samples (e.g., Roberts and Gilliam (1995) and De Grandpré et al. (2000)), or combine spring and summer samples for analyses (e.g., Hutchinson et al. (1999) and Ruben et al. (1999)). Our results further suggest that forest understory communities may be frequently undersampled in ecological studies, potentially biasing our understanding of forest diversity patterns. In species rich communities, minimum sample sizes of 75–100 quadrats (2-m^2 quadrats used in the present study) or minimum sample areas of 150–200 m^2 may be necessary to adequately evaluate micro-scale richness. Communities containing relatively large proportions of rare species may require even larger sample areas and sizes. Thus, careful assessment of species distribution patterns in space and time, represented by adequate sampling to capture natural patterns of variation, is essential to characterizing and understanding natural patterns of forest understory diversity.

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