

Scale dependence of vegetation-environment correlations: A case study of a North Carolina piedmont woodland

Reed, R. A.^{1,2}, Peet, R. K.^{1*}, Palmer, M. W.³ & White, P. S.¹

¹Department of Biology CB#3280, University of North Carolina, Chapel Hill, NC 27599-3280, USA;

*Tel. +1 919 9626942; Fax +1 919 9621625; E-mail Robert_Peet@UNC.EDU;

²Present address: Department of Botany, University of Wyoming, P.O. Box 3165, Aven Nelson Building, Laramie, WY 82071-3165, USA;

³Present address: Department of Botany, Oklahoma State University, Stillwater, OK 74078, USA

Abstract. Vegetation and its correlation with environment has been traditionally studied at a single scale of observation. If different ecological processes are dominant at different spatial and temporal scales, the results obtained from such observations will be specific to the single scale of observation employed and will lack generality. Consequently, it is important to assess whether the processes that determine community structure and function are similar at different scales, or whether, how rapidly, and under what circumstances the dominant processes change with scale of observation. Indeed, early work by Greig-Smith and associates (Greig-Smith 1952; Austin & Greig-Smith 1968; see Greig-Smith 1979; Kershaw & Looney 1985; Austin & Nicholls 1988) suggested that plant-plant interactions are typically important at small scales, but that the physical environment dominates at large scales.

Using a gridded and mapped 6.6 ha portion of the Duke Forest on the North Carolina piedmont for a case study, we examined the importance of scale in vegetation studies by testing four hypotheses. First, we hypothesized that the correlation between vegetation composition and environment should increase with increasing grain (quadrat) size. Our results support this hypothesis. Second, we hypothesized that the environmental factors most highly correlated with species composition should be similar at all grain sizes within the 6.6-ha study area, and should be among the environmental factors strongly correlated with species composition over the much larger extent of the ca. 3500 ha Duke Forest. Our data are not consistent with either portion of this hypothesis. Third, we hypothesized that at the smaller grain sizes employed in this study ($\leq 256 \text{ m}^2$), the composition of the tree canopy should contribute significantly to the vegetation pattern in the understory. Our results do not support this hypothesis. Finally, we predicted that with increased extent of sampling, the correlation between environment and vegetation should increase. Our data suggest the opposite may be true.

This study confirms that results of vegetation analyses can depend greatly on the grain and extent of the samples employed. Whenever possible, sampling should include a variety of grain sizes and a carefully selected sample extent so as to ensure that the results obtained are robust. Application of the methods used here to a variety of vegetation types could lead to a better understanding of whether different ecological processes typically dominate at different spatial scales.

Keywords: Canonical Correspondence Analysis; Canopy influence; Detrended Correspondence Analysis; Forest; Grain; Sample extent; Scale; Soil.

Nomenclature: Kartesz (in press).

Introduction

Studies of vegetation structure and of correlations between vegetation and environment traditionally have been conducted at a single scale of observation; that is, employing one quadrat size and sampling one extent of area. However, if different ecological processes are dominant at different spatial and temporal scales, the interpretation that the ecological observer places on the vegetation pattern will be highly dependent on the scale of observation employed (Allen & Starr 1982; Allen, O'Neill & Hoekstra 1984; Wiens 1986; Palmer 1990a). For this reason it is important to know whether the processes that determine community structure at different scales are similar, and if not, how and under what circumstances the dominant processes change with scale of observation.

The critical importance of scale of observation for ecological studies has been illustrated by numerous investigations representing many aspects of ecology. These include patterns of species abundance (Hairston 1959), interspecific associations (Fekete & Szöcs 1974), population density and community composition (Greig-Smith 1952, Wiens 1986), and species richness (Shmida & Wilson 1985; Auerbach & Shmida 1987; Palmer 1990b). This wide recognition of the importance of scale has led to a search for an appropriate theoretical framework for studies of spatial scale (e.g. Allen, O'Neill & Hoekstra 1984; Levin 1988; O'Neill 1989; Allen & Hoekstra 1990; O'Neill et al. 1991), and specifically to the introduction of the concepts of grain and extent as

crucial but separate aspects of spatial scale (see Allen, O'Neill & Hoekstra 1984; Wiens 1989, 1990; Norton & Lord 1990). *Grain* refers to the lower limit of resolution, be it a crystal on a photographic plate, a pixel in a remotely-sensed image, or a quadrat in a vegetation study. In most vegetation studies, the grain employed is substantially larger than, and proportional to, the size of the life-form of the targeted suite of species. For example, 1 m² is a common quadrat size for grassland studies and 1000 m² is commonly used for forest investigations. *Extent* refers to the size of the area over which the individual samples are distributed. Extent can be important because of the spatial autocorrelation inevitably present in vegetation, which in turn results from either spatial autocorrelation in the physical environment, or dispersal processes. A third variable, unrelated to scale, is often considered in the same context as grain and extent; this is *intensity*, or total area sampled. We will not discuss intensity in this paper.

Few ecologists have systematically examined the implications of varying either grain or extent. Perhaps the best known of the related studies are the mean square / block size investigations conducted by Greig-Smith and his associates (e.g. Greig-Smith 1952; Kershaw & Rouse 1971; see reviews by Greig-Smith 1979; Kershaw & Looney 1985; Ver Hoef, Cressie & Glenn-Lewin in press). However, their studies were devised, not to look specifically at the importance of grain size in vegetation research, but to determine at which scales changes in the vegetation or its correlations with the environment are most pronounced. That work led to the proposition that in herbaceous communities morphological factors dictate species composition at small scales (5 - 20 cm), plant-plant competitive interactions dominate at medium scales (0.25 - 1.5 m), and environmental factors are most important at larger scales (> 1.5 m) (see Austin & Nicholls 1988). Variation in vegetation pattern across multiple scales has also been explored by combining block-variance analysis with principal components analysis (Noy-Meir & Anderson 1971; Walker et al. 1972).

Few (e.g. Austin & Nicholls 1988; Weir & Wilson 1988; Thórhallsdóttir 1990) have sampled vegetation using more than one quadrat size and have compared the results. The only consistent observation from these studies is that the larger quadrats generally show stronger correlations with the measured environmental variation.

Forests of the piedmont of southeastern North America in general, and the Duke Forest in particular, have been studied extensively, and the relationship between their compositional variation and the physical environment is well documented (e.g. Oosting 1942; Nemeth 1968; Peet & Christensen 1980, 1988; Palmer 1990a; Farrell & Ware 1991). Specifically, soil pH, available calcium and available magnesium are well

known to correlate strongly with both compositional variation and species diversity when vegetation is sampled at grain sizes of 1000 m² over extents of several hundreds of hectares or more. Here we report on the compositional variation of a portion of the forest at smaller scales (≤ 6.6 ha), and the relationship between that compositional variation and measured environmental variables in that limited area.

In this study we examined the understory vegetation of a portion of the Duke Forest located on the North Carolina piedmont to test four specific hypotheses. First, we hypothesized that the correlation between vegetational composition and environment increases with increasing grain (quadrat) size. We expected this to be true because plant-plant interactions are most likely to moderate plant-environment correlations at those small grain sizes where the plants are in intimate contact, and also because the smaller numbers of plants in small quadrats should lead to increased variance due to sampling error. Although the herbaceous understory species do not exhibit the conspicuous clonal growth found in woodlands of the midwestern states (e.g. Whitford 1949), the spatial autocorrelation produced by localized seed rain could still result in reduced predictability of vegetation from environment at small scales (Shmida & Wilson 1985).

Second, we hypothesized that the environmental factors most highly correlated with species composition and richness should be similar at all grain sizes within the 6.6 ha study area, and should be among the environmental factors strongly correlated with species composition over the much larger extent of the ca. 3500 ha Duke Forest. This hypothesis derived, in part, from the observation of Palmer (1990a) that within the Duke Forest the variables most strongly correlated with large-scale (≥ 1000 m²) vegetation variation (i.e. pH, Ca, Mg) show marked small-scale (≤ 1 m²) variation, although Palmer did observe a marked shift in the correlation structure between scales. Similarity is not as readily testable as difference and might better be viewed as a null hypothesis. However, our goal was not a rigorous statistical test, but only to examine the consistency of vegetation-environment correlations across grain sizes so as to assess whether conspicuous differences in correlations could be found that are inconsistent with this hypothesis.

Our third hypothesis was that at the grain sizes employed in this study (≤ 256 m²), especially the smaller ones, the intensity of tree competition and the species composition of the tree canopy should significantly influence understory species composition. We expected that variation in tree competition and species composition would lead to small-scale differences in resource availability for the forest understory community.

Finally, we hypothesized that with increased extent of sampling the correlation between environment and vegetation should increase. The basis for this hypothesis was simply that because of the spatial autocorrelation in vegetation and in environment, samples spread over a larger area are more likely to capture a larger portion of the range of environmental and vegetational variation.

Our primary motivation for testing these four hypotheses was to determine how the dominant ecological processes in this forest system change with scale of observation, and what implications such scale-dependence has for devising sampling schemes. Further, we view this study as illustrating an approach that, if applied to multiple study areas, might lead to development of a more general understanding of the scales at which specific ecological processes are most important.

Methods

Study site

The study site was located in the Oosting Natural Area of the Duke Forest, Orange County, North Carolina. This second-growth piedmont hardwood forest is dominated by *Liriodendron tulipifera* (tulip poplar), several *Quercus* species (primarily *Q. rubra* and *Q. alba*; red oak, white oak), *Liquidambar styraciflua* (sweetgum), several *Carya* species, (primarily *C. tomentosa*; mockernut hickory), and *Pinus taeda* (loblolly pine) and *P. echinata* (short-leaf pine) (for details see App. 1; also Bornkamm 1975).

Bornkamm (1975) mapped the vegetation of the Oosting Natural Area and identified the vicinity of the study site as supporting a *Caryo-Quercetum liquidambaretosum*, a community characteristic of poorly-drained upland soils. This community is roughly equivalent to the Dry-Mesic Eutrophic Forest of Peet & Christensen (1980) and the Basic Oak-Hickory Forest of Schafale & Weakley (1990). The soils that support such vegetation are usually of the Iredell or Orange series, derive from intrusive mafic rock, have higher pH and available calcium than is typical for the region, and have subsoils dominated by shrink-swell, montmorillonitic clays. The mean pH of 6.0 and mean available Ca of 1395 ppm obtained from the 289 soils samples (see App. 2) greatly exceed the median values of around 4.4 and 160 respectively obtained by Peet & Christensen in their survey of Duke Forest vegetation (1980, pers. comm.). However, the range of values found in this study does fall within the range found in their study.

The study area has been owned and protected by Duke University since the mid-1940s. The relatively even size distribution of the dominant trees, together with the

abundance of such typically successional species as *Liriodendron* and *Liquidambar*, suggests that the site was largely cutover, probably in the late 1800s. With the exception that a considerable population of small (≈ 3 -10 cm stump diameter) *Juniperus virginiana* was cut, probably between 1930 and 1950, there is no evidence of disturbance this century.

Study-plot design

The study plot was designed specifically to address questions related to scale and spatial pattern. The plot was a 256 m \times 256 m square containing a grid of 256 16 m \times 16 m cells. Within each cell, eight nested quadrats (grain sizes) extend from the south-west corner in an exponential series of quadrupling area, from 0.0156 m² to 256 m² (0.125 m to 16 m on a side).

Presence was recorded for all vascular plant species at grain sizes ≤ 16 m² in all 256 grid cells, and at all grain sizes (≤ 256 m²) in the central 100 grid cells. All trees ≥ 2 cm diameter at breast height (DBH) were mapped to the nearest 0.1 m and recorded by species and DBH to the nearest 1 mm. The relative elevation (lowest value set to equal 0.0) of each corner of each 16 m \times 16 m grid cell was determined to the nearest cm using a surveyor's transit.

Soil samples were collected as close to each grid cell corner as possible (usually within 5 - 10 cm) at a point diagonal to the nested quadrats, for a total of 289 samples. Soil samples were extracted with a stainless steel soil core, 10 cm deep by 4 cm across. Soil samples were analyzed for cation exchange capacity (CEC), pH, percent organic matter content (ORG), bulk density (DNS), and available (Mehlich 3 extractant; Mehlich 1984) sulfur, phosphorus, calcium, magnesium, potassium, sodium, boron, iron, manganese, copper, zinc, and aluminum (see App. 2). Soil analyses were performed by Brookside Farms Laboratory Association, Inc., New Knoxville, OH. These variables include most of the environmental variables variously known or suspected to influence Southeastern piedmont forest vegetation, excepting only nitrogen mineralization rates and the ratio of 1:1 to 2:1 clays (see Peet & Christensen 1980).

Data summarization and analysis

Outliers in any data set create statistical difficulties due to the disproportionate influence they exert on the outcome of any statistical analysis. To rectify this problem, data are often normalized by various transformations, which reduce the effects of outliers on the analysis. The Shapiro-Wilk statistic (Shapiro & Wilk 1965) was calculated and a frequency distribution was plotted for each soil variable to assess normality of the data. The

variables CEC, ORG, S, P, Ca, Mg, Na, B, Fe, Cu, and Zn were subsequently log-transformed, and DNS was exponentially transformed to increase normality and thereby reduce the influence of outliers.

For each grain size, characteristic soil attributes were calculated using block kriging (Journel & Huijbregts 1978; Robertson 1987; Hohn 1988). Block kriging is a spatial interpolation technique that derives the value of a given variable at a given unsampled point within a matrix of sampled points by interpolating from the surrounding sample points. It takes into account all nearby points, but the closer a point is to the targeted point, the more it is weighted. This is approximately equivalent to taking the weighted mean value for the midpoint of the quadrat. Therefore, the values for the small quadrats were primarily estimated by one sample, and those for the large quadrats primarily by four samples (although more than four were used).

We assume the competitive influence of a canopy tree on understory vegetation varies directly with the size of the tree and inversely with distance from the tree, an approach widely applied in the forestry literature. Lorimer (1983) evaluated many potential indices of tree canopy influence (CI) and found that indices based on stem diameter as a measure of size worked best for predicting the competitive influence of one tree upon another. Tree influence does not extend indefinitely, so for practical reasons we limited tree influence to within a fixed multiple of 8-m canopy radii. The family of indices we used take the form

$$CI_s = \sum_i \left[\left(\frac{DBH_i^a}{DIST_i^b + 0.1} \right) - \left(\frac{DBH_i^a}{r * 16 + 0.1} \right) \right]$$

where CI_s = canopy influence of species s , DBH_i = diameter at breast height of stem i , $DIST_i$ = distance in m from midpoint of a quadrat to stem i , r = width of influence in number of 8 m canopy crown radii, and a and b = fitted constants. Note that we added 0.1 m to all distances to avoid problems with division by zero.

12 variations of CI were tested, including all permutations of a DBH exponent (a) of 1 or 2, a distance exponent (b) of 1, 2, or 3, and a search radius of 16 m or 32 m ($r = 1$ or 2). The resulting indices were used as the sole environmental variable in 12 separate Detrended Canonical Correspondence Analyses (DCCA; see below, ter Braak 1991) of the species composition data. The formula which resulted in the highest first-axis correspondence between vegetation and environment was selected. This index had a DBH exponent of 2, a distance exponent of 1, and a search radius of 16 m ($r = 1$). To avoid edge effects in the calculation of canopy influence, only the inner 196 grid cells were included in

analyses involving the CI variables.

Canopy influence for the four smallest grain sizes ($0.0156 \text{ m}^2 - 1 \text{ m}^2$) was assumed to be identical. In order to accommodate variation in canopy influence within the four larger grain sizes ($4 - 256 \text{ m}^2$), CI was calculated for the center of each square meter within a given size plot, and the separate values were averaged. In addition to total canopy influence, the canopy influences of the five dominant genera of trees in the plot (see App. 1; *Carya*, *Liquidambar*, *Liriodendron*, *Pinus*, *Quercus*) were calculated separately in order to compare the influences of the principal early (*Liquidambar*, *Liriodendron*, *Pinus*) and late (*Carya*, *Quercus*) successional species.

Because, for the two largest grain sizes (64 m^2 and 256 m^2), species composition data were available only for the central 100 grid cells, all analyses were performed with two different sample sizes. The inner 196 cells (hereafter, the '196-cell data set') were used at grain sizes $0.0156 \text{ m}^2 - 16 \text{ m}^2$ so as to provide the maximum possible sample size and extent, and the inner 100 cells (hereafter, the '100-cell data set') were used at all eight grain sizes ($0.0156 \text{ m}^2 - 256 \text{ m}^2$) in order to use the full range of grain sizes available.

Extent was varied by distributing 64 grid cells of the 16 m^2 grain size over two different expanses of the plot. Four replicates of each were tested. For the smaller extent, the 64 cells were contiguous in each of the four quadrants of the plot respectively (CN1 - CN4). For the larger extent, the 64 cells were distributed in four regular grids (GRA-GRD) over the entire $256 \text{ m} \times 256 \text{ m}$ area (actually $240 \text{ m} \times 240 \text{ m}$) by selecting every other grid square, each of the four small grids originating in one of the four corners of the large grid. The 16-m^2 grain size was chosen for the study of extent because it was the largest grain size sampled over the entire plot area, and thus provided the greatest amount of data.

In order to avoid the potential circularity of canopy species predicting themselves, analyses of vegetation response included only 'obligate' understory species, where 'obligate' understory species are defined as those species present in the data set but which do not occur in the tree map data set and, therefore, are known to be confined to the understory.

Direct and indirect gradient analysis methods were used to identify correspondence between the environmental variables and species composition. Detrended Correspondence Analysis (DCA), an indirect gradient method, maximizes the separation between stands along ordination axes based on species composition, and has been shown to be a powerful tool for detecting pattern in communities (Hill & Gauch 1980; Peet et al. 1988). Canonical Correspondence Analysis (CCA) and Detrended Canonical Correspondence Analysis (DCCA), direct gradient methods, constrain the vegetation pattern

extracted to be a linear combination of the measured environmental variables, and are thus valuable complements to DCA for identification of significant environmental variables (ter Braak 1986, 1987a). Only axes 1, 2, and 3 are presented in the Results and Discussion sections because the fourth axes had consistently small eigenvalues.

Monte Carlo permutation tests were used to assess the significance of the DCA and DCCA ordination axes. These tests randomly assign environmental data to the vegetation data and calculate the magnitude of the eigenvalue for each replication. If 95 % of the eigenvalues are less than the observed eigenvalue, then the axis can be viewed as significant. With this method, ordination axes are entered as covariables successively, one at a time until the result is no longer significant. For example, if on the first run axis 1 were found to be significant, then in the next run variation attributable to axis 1 would be partialled out as a covariable in order to test the significance of axis 2. If axis 2 were found to be significant, in the next run axes 1 and 2 would be designated covariables in order to assess the significance of axis 3, and so on.

Ordinations and Monte Carlo tests were performed using the program CANOCO (version 3.12; ter Braak 1987b, 1991), which has been demonstrated to be a robust method for these purposes (Palmer 1990c). Soil, topographic, and canopy influence variables were individually regressed on the first three ordination axes to assess significance of the multiple correlation of each variable with the ordination axes. Statistical analyses were conducted using SAS version 6.06 (Anon. 1990).

Results

Vegetation-environment correlations

Multiple correlations between the first three DCA axes and the individual environmental variables were generally higher at the larger grain sizes, both for the 100- and 196-cell data sets (Table 1). In addition, the number of significant environmental variables (or gradients) extracted by CCA, which is indicated by the number of significant ordination axes, also increased with grain size (Table 2). Both of these results support our first hypothesis that the correlation between vegetation and environment increases with increasing grain size.

Nearly all environmental variables were significantly correlated with species composition for at least one grain size. However, the particular variables that showed significant correlation differed between grain sizes, and no overall pattern was evident (Table 1). This result

contradicts hypothesis 2, that environmental variables strongly correlated with vegetation should be consistent across grain sizes.

The environmental variables that most consistently showed significant correlations with species composition generally differed, even at large grain sizes, from those previously shown to be strongly correlated with species composition in nearby piedmont forests (i.e. pH and available calcium; see Peet & Christensen 1980; Palmer 1990a). Elevation, iron, manganese, and aluminum showed the most consistent correlations with the DCA axes; these were significant at all six grain sizes in the 196-cell data set, and at three to four of the largest grain sizes in the 100-cell data set (Table 1).

Canopy influence

Correlations of canopy influence (CI) with understory species composition were weak and inconsistent with respect to grain size (Table 1). While particular CI variables were significant at various grain sizes in each data set, there was no indication at any grain size that the species composition of the canopy near a sample was a major determinant of understory species composition.

As with the vegetation-environment correlations, the CI vegetation correlations were higher at larger grain sizes (Table 1). Some correlation between CI and understory vegetation was anticipated for all scales because both depend, to some extent, on the same soil variables. However, the higher CI-vegetation correlations at larger grain sizes were unexpected because canopy tree influence was anticipated to be important only at a scale smaller than or equal to that of the individual tree.

Correlations of total canopy influence (CI summed across all species) with understory composition were consistently weak and insignificant (Table 1). We found no indication in our data that the density or size of nearby trees influenced understory composition.

Sample extent

The particular environmental variables showing strong correlations with species composition were not consistent between the four quadrants of the plot. The south-west quadrant (CN1), wherein a small stream occurred, deviated most dramatically from the other three (Table 3). The chance occurrence of extreme values of one environmental gradient, here topographic position, can mask the importance of other variables. The above example illustrates the importance of choice of sample area and matching the extent of the sampling with the objective of the study.

Table 1. Coefficients of multiple determination of environmental variables as predicted by DCA axes 1, 2 and 3 at each grain size. Variable name abbreviations are defined in App. 1. * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Variable	Grain size (m ²)					
	0.0156	0.0625	0.25	1.0	4.0	16.0
CEC	0.006	0.021	0.071 **	0.018	0.083 ***	0.027
pH	0.104 *	0.046	0.106 ***	0.088 ***	0.118 ***	0.073 **
ORG	0.009	0.003	0.042	0.031	0.000	0.052 *
S	0.042	0.075 *	0.021	0.039	0.132 ***	0.133 ***
P	0.003	0.001	0.042	0.024	0.077 **	0.086 ***
Ca	0.039	0.035	0.103 ***	0.038	0.095 ***	0.039
Mg	0.032	0.049	0.087 **	0.043 *	0.133 ***	0.035
K	0.152 **	0.060 *	0.043	0.113 ***	0.122 ***	0.100 ***
Na	0.057	0.040	0.005	0.015	0.021	0.055 *
B	0.069	0.040	0.070 **	0.076 **	0.121 ***	0.067 **
Fe	0.204 ***	0.124 ***	0.151 ***	0.193 ***	0.156 ***	0.261 ***
Mn	0.258 ***	0.152 ***	0.093 ***	0.089 ***	0.143 ***	0.138 ***
Cu	0.061	0.013	0.022	0.021	0.062 **	0.023
Zn	0.050	0.015	0.034	0.005	0.028	0.030
Al	0.130 *	0.096 **	0.063 **	0.055 *	0.138 ***	0.264 ***
DNS	0.020	0.003	0.035	0.067 **	0.049 *	0.154 ***
ELE	0.391 ***	0.173 ***	0.163 ***	0.197 ***	0.290 ***	0.306 ***
CI- <i>Carya</i>	0.028	0.001	0.004	0.053 *	0.068 **	0.062 **
CI- <i>Liquidambar</i>	0.116 *	0.054	0.015	0.039	0.064 **	0.097 ***
CI- <i>Liriodendron</i>	0.021	0.006	0.008	0.033	0.025	0.020
CI- <i>Pinus</i>	0.062	0.007	0.046 *	0.004	0.015	0.037
CI- <i>Quercus</i>	0.103 *	0.089 **	0.001	0.033	0.114 ***	0.089 ***
CI-Total	0.020	0.033	0.003	0.026	0.017	0.016

Variable	Grain size (m ²)							
	0.0156	0.0625	0.25	1.0	4.0	16.0	64.0	256.0
CEC	0.030	0.031	0.082 *	0.029	0.025	0.086 *	0.085 *	0.243 ***
pH	0.030	0.068	0.127 **	0.070	0.049	0.068	0.068	0.317 ***
ORG	0.087	0.012	0.030	0.024	0.015	0.025	0.038	0.370 ***
S	0.125	0.108 *	0.070	0.020	0.012	0.035	0.017	0.109 *
P	0.008	0.016	0.038	0.002	0.014	0.014	0.035	0.322 ***
Ca	0.022	0.041	0.132 **	0.050	0.038	0.093 *	0.097 *	0.369 ***
Mg	0.031	0.038	0.065	0.037	0.005	0.051	0.055	0.056
K	0.007	0.005	0.050	0.067	0.009	0.006	0.128 **	0.352 ***
Na	0.021	0.015	0.030	0.042	0.049	0.050	0.028	0.032
B	0.073	0.057	0.089 *	0.048	0.043	0.062	0.035	0.244 ***
Fe	0.097	0.064	0.039	0.055	0.083 *	0.046	0.088 *	0.304 ***
Mn	0.051	0.010	0.039	0.009	0.084 *	0.123 **	0.105 *	0.304 ***
Cu	0.094	0.065	0.070	0.015	0.013	0.039	0.010	0.146 **
Zn	0.008	0.079	0.021	0.039	0.067	0.117 **	0.114 **	0.173 ***
Al	0.054	0.040	0.069	0.051	0.047	0.133 **	0.207 ***	0.396 ***
DNS	0.096	0.012	0.033	0.033	0.004	0.099 *	0.148 **	0.375 ***
ELE	0.133	0.071	0.034	0.071	0.021	0.105 *	0.218 ***	0.500 ***
CI- <i>Carya</i>	0.012	0.033	0.001	0.012	0.013	0.025	0.022	0.013
CI- <i>Liquidambar</i>	0.071	0.003	0.007	0.004	0.029	0.027	0.030	0.027
CI- <i>Liriodendron</i>	0.053	0.108 *	0.037	0.040	0.023	0.030	0.047	0.074
CI- <i>Pinus</i>	0.015	0.081	0.056	0.026	0.030	0.044	0.154 **	0.063
CI- <i>Quercus</i>	0.159	0.129 *	0.020	0.016	0.011	0.054	0.029	0.165 ***
CI-Total	0.110	0.025	0.018	0.023	0.017	0.022	0.023	0.008

The vegetation by environment correlation matrices for the four replicates at the large (240 m × 240 m) extent were less consistent than expected (Table 3), but the variables with the strongest correlations were generally the same as those with the strongest correlations when using the full 196- and 100-cell data sets (Fe, Mn, Al,

ELE; see Table 1).

The observed correlations between the first three DCA axes and the environmental variables were weaker for the data sets with the larger extent (Table 3), a result in direct conflict with our fourth hypothesis. These results may reflect a greater complexity of gradient

structure at large scales with more interactions between the environmental variables. This could have the effect that specific relationships between vegetation and environment might be less readily detected using simple measures of correlation. Alternatively, we may have failed to measure one or more variables that are particularly important for explanation of composition at large extents.

Discussion

Vegetation-environment correlations

Our first hypothesis, that the correlation between vegetation and environment should increase with increasing grain size, was supported by our results. This was found both with respect to the number of significant correlations of environmental variables with the DCA axes and the number of significant orthogonal axes extracted using CCA (i.e. independent environmental gradients). Further, the specific factors strongly correlated with vegetation changed with grain size.

The decline in correlation between vegetation and environment at small scales might be attributable to plant-plant interactions. Such interactions are most likely to moderate plant-environment correlations at those small grain sizes where the plants are in physical contact or are competing for the same resource supplies. We might expect the decline in vegetation-environment correlations with grain size to be most pronounced for herbs and woody seedlings because

Table 2. Significance of CCA ordination axes as determined by Monte Carlo permutation tests at each grain size for both data sets (* = $p < 0.05$).

Grain size (m ²)	Axis number				
	1	2	3	4	5
a) 196 cells					
0.0156	0.01 *	0.40			
0.0625	0.02 *	0.41			
0.25	0.01 *	0.55			
1.0	0.01 *	0.18			
4.0	0.01 *	0.02 *	0.03 *	0.06	
16.0	0.01 *	0.01 *	0.01 *	0.01 *	0.09
b) 100 cells					
0.0156	0.95				
0.0625	0.33				
0.25	0.73				
1.0	0.45				
4.0	0.63				
16.0	0.01 *	0.14			
64.0	0.01 *	0.01 *	0.14		
256.0	0.01 *	0.01 *	0.01 *	0.05 *	0.39

their small root systems constrain physical interactions to small areas. At large grain sizes, direct plant-plant interaction effects are averaged out and the overall compositional patterns reflect primarily the broader, coarser-grained variations of the physical environment. However, while block variance studies (see Greig-Smith 1979; Kershaw & Looney 1985) have shown small-scale plant-plant interactions to be important in some herb-dominated vegetation, to date there is little evidence of plant-plant interactions influencing composi-

Table 3. Coefficients of multiple determination of environmental variables as predicted by DCA axes 1, 2 and 3 for four replicates at two different extents. CN1 - CN4 are the four replicates at a 128 m × 128 m extent; GRA-GRD are the four replicates at a 240 m × 240 m extent; 0 - 15 represents the use of all 256 grid cells in the DCA ordination, and is included for comparison purposes. * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

	CN1	CN2	CN3	CN4	GRA	GRB	GRC	GRD	0 - 15
CEC	0.002	0.084	0.260 ***	0.157 *	0.019	0.128 *	0.097	0.125 *	0.038 *
pH	0.237 ***	0.240 ***	0.409 ***	0.223 **	0.047	0.195 **	0.225 **	0.099	0.083 ***
ORG	0.050	0.116	0.047	0.011	0.102	0.103	0.138 *	0.038	0.046 **
S	0.045	0.224 **	0.326 ***	0.252 ***	0.158 *	0.054	0.218 **	0.144 *	0.169 ***
P	0.033	0.317 ***	0.206 **	0.226 **	0.226 **	0.163 *	0.158 *	0.066	0.134 ***
Ca	0.066	0.141 *	0.327 ***	0.173 **	0.018	0.163 *	0.113	0.129 *	0.036 *
Mg	0.042	0.206 **	0.348 ***	0.225 **	0.052	0.194 **	0.249 ***	0.030	0.081 ***
K	0.413 ***	0.158 *	0.266 ***	0.177 **	0.169 *	0.127 *	0.212 **	0.091	0.092 ***
Na	0.134 *	0.058	0.002	0.054	0.097	0.040	0.144 *	0.043	0.050 **
B	0.185 **	0.160 *	0.321 ***	0.244 ***	0.039	0.123 *	0.228 **	0.112	0.080 ***
Fe	0.518 ***	0.107	0.082	0.124 *	0.228 **	0.387 ***	0.066	0.284 ***	0.204 ***
Mn	0.528 ***	0.109	0.081	0.363 ***	0.110	0.335 ***	0.174 **	0.226 **	0.110 ***
Cu	0.012	0.006	0.147 *	0.169 *	0.061	0.033	0.145 *	0.081	0.021
Zn	0.030	0.112	0.118	0.152 *	0.037	0.027	0.006	0.123 *	0.021
Al	0.382 ***	0.339 ***	0.324 ***	0.258 ***	0.225 **	0.135 *	0.166 *	0.206 **	0.256 ***
DNS	0.072	0.218 **	0.160 *	0.239 ***	0.141 *	0.233 **	0.162 *	0.037	0.141 ***
ELE	0.640 ***	0.146 *	0.020	0.220 **	0.170 *	0.327 ***	0.349 ***	0.342 ***	0.243 ***

tion of woodland herb communities. For example, Rogers (1983) sought evidence of competitive interaction in small woodland plots (10 cm × 20 cm, 50 cm × 100 cm), but without success.

The increase in the number of significant environmental variables (or 'gradients') with increased grain size could also be a consequence of sampling error. With small grain sizes, only a few plants fit in a sample, and in that case chance alone will greatly influence which ones are included. The inclusion of many species, which is possible only with the larger samples obtained at large grain sizes, is probably necessary to detect subtle patterns.

The small grain size of the soil samples (ca. 10 cm diameter) makes them susceptible to influence by small-scale soil variation. The high variance and small number of soil samples, coupled with their relatively wide spacing (16 m), could result in errors in the estimation of mean quadrat values. Because one small grain sample cannot adequately represent the entire grid cell, it is inevitable that at larger quadrat sizes much of the small-scale variation in soil variables will be averaged or missed altogether (Palmer 1990a; Lechowicz & Bell 1991). However, the soil values for the large-grain samples were based less on a single sample and more on an average of several samples than were the small-grain samples, which could partially explain the higher plant-soil correlations at larger grain sizes.

Most previous studies have implicitly assumed that the emergent patterns of association between vegetation and environment are consistent across a wide range of spatial scales, an assumption called into question by our results. Palmer has similarly found different vegetation - environment patterns at different scales of observation. By observing understory vegetation both within and among 0.1-ha plots, he found that the small-scale (within plot) patterns were not miniature versions of the large-scale (among plot) patterns. Our findings and Palmer's imply that extrapolation between spatial scales of factors strongly correlated with vegetation composition is dangerous and likely to lead to errors in interpretation.

Dominant environmental factors

Earlier studies of piedmont forests in general (e.g. Nemeth 1968; Farrell & Ware 1991), and the Duke Forest in particular (e.g. Peet & Christensen 1980; Palmer 1990a), have found compositional variation to be strongly correlated with soil pH, calcium, and magnesium. The results of the present study are not consistent with these earlier findings. Instead, the soil variables that are most strongly correlated with the vegetation are aluminum, iron and manganese. While our analyses show pH and cation availability to be significantly correlated with

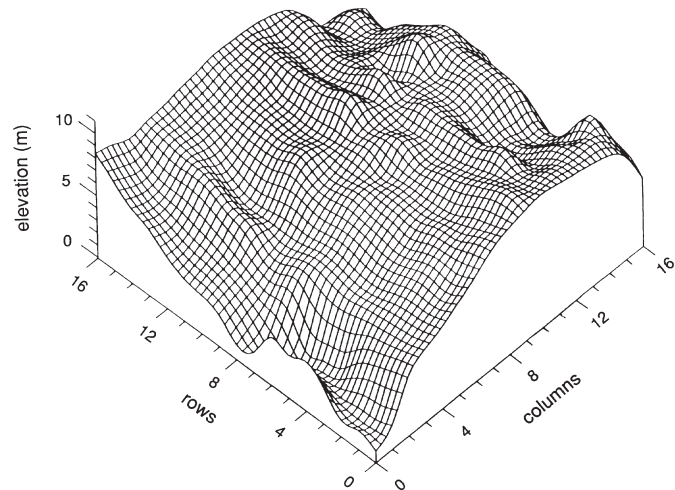
vegetation patterns, these correlations are inconsistent across grain sizes and not as strong as those with Al, Fe, and Mn (Table 1).

The differences between the environmental correlations found in this study and those described in earlier investigations of piedmont forests could be the result of at least two factors. First, this site might simply be edaphically unusual. Ultramafic and diabase intrusions, although uncommon, do occur in the Duke Forest, and the discontinuous occurrence of these rock types in the plot could be responsible for the unusual correlations (Mann et al. 1965; Allen & Wilson 1968; Butler & Secor 1991; Ragland 1991). While the presence of an ultramafic intrusion within the plot cannot easily be confirmed, the high average pH, high Mg/Ca ratio and relatively high values of Cu, Fe, Mn and Zn all suggest the possibility (App. 2). The Mg/Ca ratio tends to be greater along the ridge on the eastern edge of the plot than elsewhere, and this ratio is also significantly correlated with high concentrations of Cu, Fe, Mn and Zn. In addition, the occurrence of certain species in the plot suggests unusual parent material. For example, *Asimina triloba* (Pawpaw), typically a calcicole found in floodplains, occurs on the ridge.

A second and related possibility is that the difference is a consequence of the difference in spatial extents of the various studies. Earlier investigations looked at forest community variation over thousands of hectares scattered over several disjunct areas. The present study examines variation over an extent of 6.6 contiguous ha. At a small extent the occurrence of some unusual environmental condition, like an ultramafic intrusion, would have a large effect. In a study of much greater spatial extent, or with a larger range of environmental conditions, uncommon local variations would be less important.

In the present study elevation was strongly correlated with vegetation. However, in previous studies of piedmont forests elevation has generally been found to have little or no correlation with vegetation. The difference is explainable in terms of extent of sample. As Whittaker (1956, 1960) and Austin, Cunningham & Fleming (1984) have explained, topography is not strictly an environmental variable, but instead acts as a surrogate for a complex array of intercorrelated environmental variables which together can greatly influence plant distribution. In this case, elevation probably relates strongly to soil moisture and nutrient availability. Elevation increases by 10 m from the lowest point, a stream in the south-west corner, to the highest point on top of a small ridge along the eastern edge (Fig. 1). In effect, elevation at the extent of the present study is a surrogate for topographic position along a gradient from hill top to stream bottom. However, over the greater extents sampled in previous studies, topographic posi-

Fig. 1. Topography of the sample plot. X- and Y-axes represent the physical boundaries of the plot grid; the Z-axis represents relative elevation. The gridding interpolation method is kriging, and the actual grid was smoothed using cubic spline interpolation in order to eliminate its original angular appearance. The X-axis points almost due north. A stream is present at the southwestern corner of the grid, and a ridge runs just inside the eastern edge.



tion was not strongly correlated with elevation because the average background elevation shifted across the extent of the study area.

Canopy influence

Our results did not support the expectation that the intensity of tree competition and the species composition of the overstory would contribute to the distributional patterns of the understory. The failure of both the species-specific canopy influence and the total canopy influence variables to correlate strongly or consistently with ordination axes suggests that the canopy trees have little effect on the distribution of the understory vegetation. One possible explanation is that the canopy trees and the understory plants are both correlated with the same soil and topographic variables, with the result that correlations with the canopy trees contribute little new information on the understory composition. Further, canopy trees, being long-lived individuals, are more likely to reflect past chance disturbance events than the present environmental conditions, with which the shorter-lived herbs are more likely to be in equilibrium. Thus, the understory can be expected to show stronger correlations with the environment than would the canopy.

Another possibility is that the distribution of canopy influence across the plot may be relatively constant owing to greater growth of trees where resources are in greater supply. Perhaps trees grow until the background resource supplies are drawn down to a consistent, growth-limiting level (e.g. Tilman 1982). In this event, local effects of individual canopy trees on the understory directly below would not be detected due to the low level of variation in the CI variables. This explanation requires that the overall canopy closure is relatively constant and that large gaps are uncommon. If large

gaps were present, the understory would almost certainly reflect the localized relaxation in competition.

Sample extent

All vegetation exhibits local variation, and the larger the extent of vegetation sampled, the more such local variation is likely to be included. We observed patterns in data sets derived from four contiguous 64-cell samples, four overlapping 64-cell samples, the central 100-cell sample and the central 196-cell sample. Even though the data all came from the same 256 m × 256 m plot, and grain size was kept consistent, there were major differences in the results obtained using these different data sets. Many of the differences were probably due to differences in extent. The 100-cell sample was different from the 196-cell sample for the same reason that the south-west corner 64-cell sample differed from the other 64-cell samples: the small stream present in one corner of the overall plot. When a data set included the area around this stream, the different environmental conditions that the stream introduced distorted and partially obscured the other gradients extracted in the analysis. The impact of the chance inclusion of a small but unusual portion of our relatively small 6.6-ha area illustrates how a modest change in extent of sampling can have a large effect on the results obtained.

We hypothesized that sampling over a larger area, or extent, would yield higher correlations between vegetation and environment because the samples would be likely to capture a larger portion of the range of variation in vegetation and environment. When we tested this, we found that the vegetation-environment correlations did not increase with increased extent. This may simply reflect the greater complexity of the data and the larger number of interacting factors encountered when sam-

ples are collected over a larger area.

Vegetation samples can be concentrated in one area or spread over a larger area, and there are potential advantages to both strategies. Our results suggest that concentration of samples in one area may lead to lower generality with respect to regional patterns, but it may serve to keep the data simple enough to be readily interpretable, and may thus allow some locally important processes to be detected that otherwise would be masked by more widely varying factors.

Conclusions

Ecologists wishing to study relationships between vegetation and environment must inevitably make decisions about the grain size and extent of the samples they use. Our results show that these decisions, while often made in a casual manner, can greatly influence the strength and nature of the vegetation-environment relationships observed. Substantial variation in vegetation structure can be overlooked by examining vegetation at only one grain size or one extent. Investigators must be aware of the scale-related limitations of any study. The inclusion of multiple scales of observation in ecological investigations through involvement of several grain sizes, several extents, or both, can be critical for understanding vegetation patterns and processes.

Acknowledgements. We appreciate the assistance of Katia Wolf and Sue McAlister with collection of species-composition data, and Julia Larke, Michael Casey, Mary Cassie Shaw, and David Yehle with tree mapping and soil-sample collection. We thank J. B. Wilson and two anonymous reviewers for helpful comments on the manuscript. This study was supported by an NSF REU supplemental grant to RKP (BSR-8905926) and a UNC-CH Parent's Council Award to RAR. MWP, Julia Larke, and Katia Wolf were supported by the North Carolina Botanical Garden.

References

- Anon. 1990. SAS Inst. Inc. 1990. *SAS system. Version 6.06*. SPSS Inc., Chicago, IL.
- Allen, T. F. H. & Hoekstra, T. W. 1990. The confusion between scale-defined levels and conventional levels of organization in ecology. *J. Veg. Sci.* 1: 5-12.
- Allen, T. F. H. & Starr, T. B. 1982. *Hierarchy: perspectives for ecological complexity*. University of Chicago Press, Chicago, IL.
- Allen, E. P. & Wilson, W. F. 1968. *Geology and mineral resources of Orange County, North Carolina*. North Carolina Department of Conservation and Development, Division of Natural Resources, Bull. 81.
- Allen, T. F. H., O'Neill, R. V. & Hoekstra, T. W. 1984. *Interlevel relations in ecological research and management: some working principles from hierarchy theory*. USDA For. Serv., Rocky Mtn. For Range Exp. Stn., GTR RM-110: 1-11.
- Auerbach, M. & Shmida, A. 1987. Spatial scale and the determinants of plant species richness. *Trends Ecol. Evol.* 2: 238-242.
- Austin, M. P. & Greig-Smith, P. 1968. The application of quantitative methods to vegetation survey. II. Some methodological problems of data from rain forest. *J. Ecol.* 56: 827-844.
- Austin, M. P. & Nicholls, A. O. 1988. Species associates within herbaceous vegetation in an Australian *Eucalyptus* forest. In: During, H. J., Werger, M. J. A. & Williams, J. H. (eds.) *Diversity and pattern in plant communities*, pp. 95-114. SPB Academic Publishing, The Hague.
- Austin, M. P., Cunningham, R. B., & Fleming, P. M. 1984. New approaches to direct gradient analysis using environmental scalars and statistical curve-fitting procedures. *Vegetatio* 55: 11-27.
- Bornkamm, R. 1975. *A vegetation map of the Oosting natural area, Orange Co., North Carolina with a discussion of the Beech-Maple climax type in the piedmont*. Techn. Paper 3, School of Forestry and Environmental Studies, Duke University, Durham, NC.
- Burrough, P. A. 1983. Multiscale sources of spatial variation in soil. I. Applications of fractal concepts to nested levels of soil variation. *J. Soil Sci.* 34: 577-597.
- Butler, J. R. & Secor, D. T. 1991. The central piedmont. In: Horton, J. W. & Zullo, V. A. (eds.) *The geology of the Carolinas*, pp. 59-78. University of Tennessee Press, Knoxville, TN.
- Farrell, J. D. & Ware, S. 1991. Edaphic factors and forest vegetation in the piedmont of Virginia. *Bull. Torrey Bot. Club* 118: 161-169.
- Fekete, G. & Szöcs, Z. 1974. Studies on interspecific association processes in space. *Acta Bot. Acad. Sci. Hung.* 20: 227-241.
- Gauch, H. G. 1982. *Multivariate analysis in community ecology*. Cambridge University Press, Cambridge.
- Graves, J. H. & Monk, C. D. 1985. A comparison of soils and vegetation over marble and schist along tributaries to Panther Creek, Stephens County, Georgia. *Castanea* 50: 146-163.
- Greig-Smith, P. 1952. The use of random and contiguous quadrats in the study of the structure of plant communities. *Ann. Bot. (Lond.) N. S.* 16: 293-316.
- Greig-Smith, P. 1979. Pattern in vegetation. *J. Ecol.* 67: 755-779.
- Hairston, N. G. 1959. Species abundance and community organization. *Ecology* 40: 404-416.
- Hill, M. O. & Gauch, H. G. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42: 47-58.
- Hohn, M. E. 1988. *Geostatistics and petroleum geology*. Van Nostrand Reinhold, New York.
- Journel, A. G. & Huijbregts, C. 1978. *Mining geostatistics*. Academic Press, London.
- Kartesz, J. T. In press. *A synonymized checklist of the vascular flora of the United States, Canada, and Greenland*. 2nd.

- ed. Timber Press, Portland, OR.
- Kershaw, K. A. & Looney, J. H. H. 1985. *Quantitative and dynamic plant ecology*. 3rd. ed. Arnold, Baltimore, MD.
- Kershaw, K. A. & Rouse, W. R. 1971. Studies on lichen-dominated systems. II. The growth pattern of *Cladonia alpestris* and *Cladonia rangiferina*. *Can. J. Bot.* 49: 1401-1410.
- Lechowicz, M. J. & Bell, G. 1991. The ecology and genetics of fitness in forest plants. II. microspatial heterogeneity of the edaphic environment. *J. Ecol.* 79: 687-696.
- Levin, S. A. 1988. Pattern, scale, and variability: an ecological perspective. In: Hastings, A. (ed.) *Community Ecology. Lecture notes in biomathematics 77*: 1-22. Springer-Verlag, New York.
- Lieth, H. 1980. Untersuchungen über den Mineralstoffspiegel im De la Howe Forest, McCormick County, South Carolina. *Veröff. Geobot. Inst. Eidg. Tech. Hochsch. Stift. Rübel Zürich* 69: 162-170.
- Lorimer, C. G. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. *For. Ecol. Manage.* 6: 343-360.
- Mann, V. I., Clarke, T. G., Hayes, L. D., & Kirstein, D. S. 1965. *Geology of the Chapel Hill quadrangle, North Carolina*. North Carolina Department of Conservation and Development, Division of Mineral Resources, Special Publ. 1.
- Mehlich, A. 1984. Mehlich 3 soil test extraction modification of Mehlich 2 extractant. *Comm. Soil Sci. Plant Anal.* 15: 1409-1416.
- Nemeth, J. C. 1968. The hardwood vegetation and soils of Hill Demonstration Forest, Durham County, North Carolina. *J. Elisha Mitchell Sci. Soc.* 84: 482-491.
- Norton, D. A. & Lord, J. M. 1990. On the use of 'grain size' in ecology. *Funct. Ecol.* 4: 719.
- Noy-Meir, I. & Anderson, D. J. 1971. Multiple pattern analysis, or multiscale ordination: towards a vegetation hologram? In: Patil, G. P., Pielou, E. C. & Waters, W. E. (eds.) *Statistical Ecology. Vol. 3*, pp. 204-231. Penn. State University Press, University Park, PA.
- Økland, R. H., Eilertsen, O. & Økland, T. 1990. On the relationship between sample plot size and beta diversity in boreal coniferous forests. *Vegetatio* 87: 187-192.
- O'Neill, R. V. 1989. Perspectives in hierarchy and scale. In: Roughgarden, J., May, R. M. & Levin, S. A. (eds.) *Perspectives in Ecological Theory*, pp. 140-156. Princeton University Press, Princeton, NJ.
- O'Neill, R. V., Gardner, R. H., Milne, B. T., Turner, M. G. & Jackson, B. 1991. Heterogeneity and spatial hierarchies. In: Kolasa, J. & Pickett, S. T. A. (eds.) *Ecological Heterogeneity*, pp. 85-96. Springer-Verlag, New York.
- Oosting, H. J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. *Am. Midl. Nat.* 28: 1-126.
- Palmer, M. W. 1988. *Spatial scale and pattern in hardwood forests of the North Carolina piedmont*. Ph. D. Diss. Duke University, Durham, NC.
- Palmer, M. W. 1990a. Spatial scale and patterns of species-environment relationships in hardwood forests of the North Carolina piedmont. *Coenoses* 5: 79-87.
- Palmer, M. W. 1990b. Spatial scale and patterns of vegetation, flora, and species richness in hardwood forests of the North Carolina piedmont. *Coenoses* 5: 89-96.
- Palmer, M. W. 1990c. Putting things in even better order: the advantages of canonical correspondence analysis. *Bull. Ecol. Soc. Am.* 71: 277.
- Palmer, M. W. & Dixon, P. M. 1990. Small-scale environmental heterogeneity and the analysis of species distributions along gradients. *J. Veg. Sci.* 1: 57-65.
- Peet, R. K. & Christensen, N. L. 1980. Hardwood forest vegetation of the North Carolina piedmont. *Veröff. Geobot. Inst. Eidg. Tech. Hochsch. Stift. Rübel Zürich* 69: 14-39.
- Peet, R. K. & Christensen, N. L. 1988. Changes in species diversity during secondary forest succession on the North Carolina piedmont. In: Doring, H. J., Werger, M. J. A. & Williams, J. H. (eds.) *Diversity and pattern in plant communities*, pp. 233-245. SPB Academic Publishing, The Hague.
- Peet, R. K., Knox, R. G., Case, J. S. & Allen, R. B. 1988. Putting things in order: the advantages of detrended correspondence analysis. *Am. Nat.* 131: 924-934.
- Ragland, P. C. 1991. Mesozoic igneous rocks. In: Horton, J. W. & Zullo, V. A. (eds.) *The geology of the Carolinas*, pp. 171-190. University of Tennessee Press, Knoxville, TN.
- Robertson, G. P. 1987. Geostatistics in ecology: interpolating with known variance. *Ecology* 68: 744-748.
- Rogers, R. S. 1983. Small-area coexistence of vernal forest herbs: Does functional similarity of plants matter? *Am. Nat.* 121: 834-850.
- Schafale, M. P. & Weakley, A. S. 1990. *Classification of the natural communities of North Carolina: Third approximation*. North Carolina Natural Heritage Program, N. C. Dept. Envir., Health, and Nat. Res., Raleigh, NC.
- Shapiro, S. S. & Wilk, M. B. 1965. An analysis of variance test for normality (complete samples). *Biometrika* 52: 591-611.
- Shmida, A. & Wilson, M. V. 1985. Biological determinants of species diversity. *J. Biogeogr.* 12: 1-20.
- ter Braak, C. J. F. 1986. Canonical Correspondence Analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167-1179.
- ter Braak, C. J. F. 1987a. The analysis of vegetation-environment relationships by Canonical Correspondence Analysis. *Vegetatio* 69: 69-77.
- ter Braak, C. J. F. 1987b. *CANOCO—a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis (version 2.1)*. TNO Institute of Applied Computer Science, Wageningen, The Netherlands.
- ter Braak, C. J. F. 1991. *CANOCO version 3. 12*. Agricultural Mathematics Group, Wageningen, The Netherlands.
- Thórhallsdóttir, T. E. 1990. The dynamics of a grassland community: a simultaneous investigation of spatial and temporal heterogeneity at various scales. *J. Ecol.* 78: 884-908.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, NJ.
- Ver Hoef, J., Cressie, N. A. C. & Glenn-Lewin, D. C. In press. Spatial models for spatial statistics. *J. Veg. Sci.*
- Walker, J., Noy-Meir, I., Anderson, D. J. & Moore, R. M. 1972. Multiple pattern analysis of a woodland in south

- central Queensland. I. The original trees and shrubs. *Aust. J. Bot.* 20: 105-118.
- Weir, D. A. & Wilson, J. B. 1988. Micro-pattern in an area of New Zealand alpine vegetation. *Vegetatio* 73: 81-88.
- Whitford, P. W. 1949. Distribution of woodland plants in relation to succession and clonal growth. *Ecology* 30: 199-208.
- Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. *Ecol. Monogr.* 26: 1-80.

- Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* 30: 279-338.
- Wiens, J. A. 1986. Spatial scale and temporal variation in studies of shrub steppe birds. In: Diamond, J. & Case, T. J. (eds.) *Community Ecology*, pp. 154-172. Harper and Row, New York.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Funct. Ecol.* 3: 385-397.
- Wiens, J. A. 1990. On the use of 'grain' and 'grain size' in ecology. *Funct. Ecol.* 4: 720.

Received 16 September 1991;

Revision received 7 August 1992;

Final revision received 24 November 1992;

Accepted 1 December 1992.

App. 1. Importance values of canopy tree species. Density = stems \geq 2 cm dbh/ha; Basal area = m²/ha; Frequency = number of 256-m² grid cells in which the species occurred; IV = (relative density + relative basal area + relative frequency)/3.

Species	Density	Basal area	Frequency	IV
<i>Liriodendron tulipifera</i>	144.0	12.740	240	18.49
<i>Cornus florida</i>	361.2	0.664	250	12.38
<i>Liquidambar styraciflua</i>	82.6	3.043	180	7.03
<i>Acer rubrum</i>	146.7	.649	207	6.63
<i>Quercus alba</i>	52.2	3.011	166	6.10
<i>Quercus rubra</i>	29.6	3.867	133	5.97
<i>Cercis canadensis</i>	92.1	0.085	148	4.07
<i>Oxydendrum arboretum</i>	52.2	0.042	162	3.80
<i>Carpinus caroliniana</i>	88.9	0.112	116	3.64
<i>Juniperus virginiana</i>	57.0	0.125	176	3.58
<i>Carya tomentosa</i>	33.7	1.326	123	3.53
<i>Quercus velutina</i>	10.1	2.064	90	3.49
<i>Fagus grandifolia</i>	41.1	0.585	133	3.12
<i>Pinus taeda</i>	13.0	1.751	56	2.65
<i>Nyssa sylvatica</i>	34.7	0.159	129	2.51
<i>Carya ovata</i>	23.2	0.881	90	2.46
<i>Pinus echinata</i>	11.0	1.409	54	2.25
<i>Morus rubra</i>	24.6	0.021	107	1.88
<i>Carya glabra</i>	17.7	0.435	76	1.74
<i>Fraxinus</i> spp.	10.4	0.143	46	0.93
<i>Quercus falcata</i>	4.3	0.512	23	0.86
18 additional species	27.4	0.678	111	2.90
Totals	1366.1	44.088	2839	100.00

App. 2. Summary of physical, soil-chemical and canopy-influence attributes. CEC = cation exchange capacity; Density = soil bulk density; CI = canopy influence.

a. Study site.

Variable	Mean	Minimum	Maximum
pH	6.0	4.4	7.2
S (ppm)	22.8	14.0	48.0
P (ppm)	13.1	8.0	36.0
C (ppm)	1395.1	149.0	5706.0
Mg (ppm)	219.5	61.0	461.0
K (ppm)	133.7	30.0	269.0
Na (ppm)	10.2	6.0	28.0
B (ppm)	0.6	0.2	0.5
Fe (ppm)	109.6	43.0	348.0
Mn (ppm)	293.8	71.0	569.0
Cu (ppm)	1.8	0.6	3.8
Zn (ppm)	4.0	1.1	28.6
Al (ppm)	859.4	212.0	1234.0
CEC (meq)	11.6	3.8	32.7
Density (g/cm ³)	0.8	0.3	1.0
Organic matter (%)	8.4	3.0	51.6
Elevation (m)	6.0	0.0	10.1
CI-Carya	14.9	0.0	173.0
CI-Liquidambar	17.6	0.0	194.0
CI-Liriodendron	83.0	1.4	445.6
CI-Pinus	23.1	0.0	239.3
CI-Quercus	64.0	0.1	522.7

b. Statistics (means) for comparable forest types in Duke Forest (R. K. Peet & N. L. Christensen unpubl.).

Variable	Dry Eutrophic	Mesic Eutrophic	Mesic Mesotrophic
pH	5.6	5.2	4.6
Ca (ppm)	999.75	737.29	204.36
Mg (ppm)	220.10	166.59	58.37
K (ppm)	74.28	109.59	58.64
P (ppm)	3.39	6.24	2.80
Mn (ppm)	815.0	459.4	490.0
Al (ppm)	1.8	11.4	105.0
Organic (%)	9.8	6.9	6.0