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SPATIAL SCALE AND PATTERNS OF VEGETATION, FLORA AND SPECIES RICHNESS IN HARDWOOD FORESTS OF THE NORTH CAROLINA PIEDMONT

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Abstract. Hardwood forests in the Duke Forest, Durham and Orange Counties, North Carolina, USA, were studied in order to determine whether plant community patterns on the landscape scale were also present on a scale less than 0.1 hectare. I randomly located forty $2m^2$ subplots in each of thirty 0.1 hectare hardwood forest plots, and estimated the percent cover of species under 1 m tall in each subplot. I evaluated the similarity of small-scale (within-plot) patterns to large-scale (among-plot) patterns with a Monte Carlo test for correspondence analysis eigenvalues. Similarities were much stronger for floristic (presence-absence) data than for abundance data. Although the similarities are statistically significant, within-plot patterns are not miniature versions of among-plot patterns. Species richness of 0.1 ha plots is strongly related to soil cations. Within-plot variation in species richness is only weakly related to cations, implying that large scale determinants of richness are detectable but unimportant on the small scale.

Introduction

Interpretable patterns in the composition of plant communities occur at all spatial scales. All plant species have distributions which can be described with respect to microsites, stands, habitat types, landscapes, biogeographical provinces, and continents. However, species distributions do not necessarily have the same determinants at each spatial scale (Shmida and Wilson 1985, Levin 1987). Thus, when we examine the results of an ecological study based on a single scale of observation, we cannot know the applicability of these results to other scales. The generality of a study will depend on the degree to which plant communities are self-similar, that is, the degree to which patterns are observed across spatial scales.

Clearly, there is no single "correct" scale at which to study plant communities. The size of plots in forest communities have generally ranged from points (Bratton 1976) to several square decimeters (Rogers 1983) to square meters (Beals and Cope 1964) to hundredths of hectares (Davison and Forman 1982) to tenth hectares (Peet and Christensen 1980) to hectares (Hubbell and Foster 1986). The aims of ecological studies differ, and ecologists can be expected to construct sampling designs which correspond to *a priori* notions of scales at which the processes under investigation are important. It is of interest, however, to determine whether these processes operate across a range of spatial scales.

Species diversity, as well as species composition, can have scale-dependent patterns. Whittaker (1965) introduced the concepts of alpha, beta, and gamma diversity in order to distinguish patterns of diversity operating on different spatial scales. Alpha diversity refers to the species diversity within a given habitat (or quadrat). Beta diversity refers to the change in species composition as one moves from one location in the landscape (or position along an environmental gradient) to another. Gamma diversity refers to the species diversity of the entire landscape. The most straightforward measure for alpha and gamma diversity is species richness, or the number of species in a defined area. Beta diversity is measured in terms of rates of change, half changes, ordination axis lengths, or gleasons (Bratton 1975, Wilson and Mohler 1983, Christensen and Peet 1984).

This distinction of three levels of diversity is at first glance intuitively pleasing. Upon further consideration, however, the distinction between alpha and gamma diversity breaks down. This is because there is no universally applicable concept of what constitutes a "habitat" and a "landscape". For example, alpha diversity can be defined as the average number of species in a square meter quadrat and gamma diversity as the total number of species in a one-hectare forest stand. An equally legitimate definition is for alpha diversity to refer to the species in one hectare plots and for gamma diversity to refer to all the species in the bioregion. At all scales, there is heterogeneity (*i.e.*, beta diversity) within plots as well as among plots. The arbitrariness of the scale of "alpha" and "gamma" diversity means that we cannot expect to deduce a single explanation for variability in either, even if we restrict ourselves to a particular group of species in a particular system.

In this study, I compare patterns of community variation and species richness within tenth hectare plots to variation among these plots and demonstrate that at

least some determinants of species composition and species richness on the landscape scale also exist on a scale less than a tenth hectare.

Methods

Vegetation survey. In the autumn of 1985, I established thirty 20 m×50 m (0.1 hectare) plots in the Duke Forest (Durham and Orange Counties, North Carolina, USA). These plots were located to represent the major compositional gradients in hardwood forest types previously described from the North Carolina piedmont (Peet and Christensen 1980) and to avoid obvious signs of major human disturbance. None of the plots included pine trees, which are indicators of secondary succession in the North Carolina piedmont (Oosting 1942). Forty circular 2 m^2 subplots were randomly located (with the constraint that they be non-overlapping) in each plot. The percent cover of vertical projections of each bryophyte and tracheophyte species under 1 m tall and rooted in each subplot was visually estimated to the nearest 5%. This vegetation survey was done with random plot sequence between April 27 and May 18, 1986. During this period, leaves of seedlings, shrubs, and fall-blooming herbs were fully expanded but the spring ephemerals had not yet disappeared. All plots were visited several times between September 1985 and November 1987 in order to obtain complete species lists (for species of all sizes) for all plots. Voucher specimens were deposited in the Duke University Herbarium for all species common enough to warrant collecting. Twenty species (out of 311 total) were not collected in order that their sparse populations not be further decimated.

Ordination of plots. Two data sets were generated from the plant composition data: 1) the 'floristic' data set, in which species are recorded as present or absent (this includes species which were not in any of the forty subplots), and 2) the 'vegetation' data set, in which the mean cover of each species in each plot was estimated from the forty subplots. Both of these data sets were ordinated, without transformation, using detrended correspondence analysis (DCA, Hill and Gauch 1980) with the polynomial detrending algorithm of the computer package CANOCO (ter Braak 1985). Plot #23 was ordinated passively (ter Braak 1985) because it was found to have plant species indicative of human disturbances (*Glechoma hederacea, Muscari botryoides, Ranunculus abortivus,* and *Stellaria media).* The "passive ordination" here means that plot #23 had no effect on the ordination axis scores of the other plots.

Ordination of subplots. There are two properties of weighted averaging techniques (such as DCA) which make them useful for comparing small-scale plant community patterns with large-scale patterns. The first is that the score w_{jk} of plot j along axis k is the average of the scores v_{ik} of each species i in plot j, where the scores are first weighted by the abundance x_{ij} of the species:

$$w_{jk} = \sum_{i} x_{ij} v_{ik} / \sum_{i,j} x_{ij} \qquad \text{Eq. 1}$$

This property allows one to generate ordination scores for new plots based on the species scores from a previously existing ordination (see, for example, Campbell 1987). I calculated the subplot scores on four DCA axes for subplots within each plot in two ways: 1) the 'floristic' comparison, in which x_{ij} is 1 if species i is present and 0 if absent in subplot j, and v_{ik} is obtained from the floristic ordination of 0.1 ha plots described in the previous section, and 2) the 'vegetation' comparison, in which x_{ij} is the percent cover of species i in subplot j, and v_{ik} is obtained from the vegetation ordination of 0.1 ha plots. Equation 1 ensures that the within-plot species scores are strictly determined by among-plot patterns of species composition. In other words, the within-plot ordinations are in terms of the among-plot ordinations. For example, *subplots* with low ordination scores on the first axis will include species which are typical of *plots* with low first axis scores in the original ordination. Unlike the axes of the plot ordinations, the subplot ordination axes are not necessarily orthogonal.

The second useful property of weighted averaging techniques is that the eigenvalue of an ordination axis is equivalent to the squared correlation coefficient between species scores and plot scores (Pielou 1984). Once species and plot scores have been standardized to zero (weighted) mean and unit (weighted) standard deviation, the squared correlation coefficient r_k^2 is readily calculated:

$$r_k^2 = \left[\sum_{i,j} x_{ij} v_{ik} w_{jk} / \sum_{i,j} x_{ij} \right]^2 \qquad \text{Eq. 2}$$

This coefficient is a measure of the strength or importance of an ordination axis. In cases where the plot scores are calculated for a new data set (in this case, the subplots) based on species scores from ordination of another data set (the plots), r_k^2 measures how strongly variation in species composition in the new data set reflects variation in the other data set. If small-scale (among subplot) variation in species composition was quite dissimilar to large-scale (among plot) variation, r_k^2 would be close to zero. If small-scale variation in species composition perfectly matched large-scale variation, r_k^2 would be close to the eigenvalue r_{max}^2 of detrended correspondence analysis calculated from among-subplot species scores for each plot. r_{max}^2 is the maximum possible correlation between species scores and subplot scores, and is not influenced by among-plot patterns.

There is no obvious way to test the significance of the comparisons of small-scale vs. large-scale patterns using standard parametric or nonparametric inferential statistics. As the within-plot subplot scores are calcu-

lated from the among-plot species scores, it would be circular to compare the two by testing the significance of the parameters of a linear (or rank order) model. In addition, the ordination scores and eigenvalues are complex functions of random variables (plant abundances) of unknown underlying statistical distributions. In such confusing cases, it is advisable to devise randomization (or "Monte Carlo") tests of significance (Sokal and Rohlf 1981, chapter 18.3).

To test the significance of r_k^2, I employed a Monte Carlo permutation test similar to that described by ter Braak (1985). In this study, the null hypothesis is that there is no relationship between small-scale and large-scale patterns. I simulated the null model by creating 101 sets of randomized species scores, each consisting of the species scores present in the original ordination of plots, but in a different random order. If r_k^2 calculated using the original species scores was greater than the calculated r_k^2 using the randomized species scores at least 95% of the times, then community variation among subplots was considered to have a significant relationship to community variation among plots at $p<0.05$. The "circularity" alluded to in the previous paragraph is equivalent in the real and the randomized data sets, so significance is not an artifact of calculating r_k^2.

Species richness. The number of species per 0.1 ha plot was regressed against the within-plot means and standard deviations of all the environmental variables (see Palmer 1990 for techniques and discussion related to the environmental variables) with stepwise regression using PROC STEPWISE (SAS Institute 1985), with significance level for entry = 0.05. Stepwise regression is a method of selecting a subset of explanatory variables which maximally explains variation in a dependent variable (Draper and Smith 1981, Chapter 6.4). Stepwise regression is best used as an exploratory technique rather than a hypothesis testing technique, because it does not take multiple comparisons into account. However, the lack of inclusion of a variable in the model is a good indication that it is either unimportant or redundant with variables already in the model (Draper and Smith 1981).

Comparing species richness and environmental variables is more complicated for the 2 m^2 subplots than for the 0.1 ha plots. Palmer (1990) demonstrates that there is much small-scale (within plot) spatial dependence in environmental variables. Spatial dependence compromises the use of least-squares (or any other) regression techniques for statistical inference (Cliff and Ord 1981, Palmer 1988). Although I calculated "significance" of correlations between environmental variables and species richness of subplots, these results must be interpreted with caution. In order to overcome this problem, I calculated the proportion (p) of plots with positive correlations between subplot species richness and the environmental variable of interest. Under the null hypothesis of no correlation between species richness and environment, p is 0.5. An exact test of the difference between the observed p and 0.5 can be readily obtained from the binomial distribution (Freedman et al. 1978 page 234). Such a test is valid even with marked spatial dependence, as long as the species/environment relationship within each plot is independent of the species/environment relationships within all other plots.

It is often informative to test whether species richness of subplots is more variable than one would expect due to chance co-occurrences of species. If there is no significant variation in species richness, it may not be worthwhile to search for determinants or correlates of species richness. The significance of within-plot variation in species richness was obtained using the variance test (Palmer 1987, Schluter 1984).

Results

Large-scale patterns. For both the flora and vegetation data sets, species with low DCA first axis scores are generally typical of species-rich, cation-rich forests such as alluvial forests (*e.g., Botrychium virginianum, Lonicera japonica, Ulmus rubra, Polystichum acrostichoides, Carpinus caroliniana),* swamp forests *(Fraxinus pennsylvanica, Arisaema triphylla),* or cove forests *(Smilacina racemosa, Viburnum acerifolium, Fagus grandifolia, Cimicifuga racemosa)* (Peet and Christensen 1980). Species with high first axis scores are typical of species-poor, cation-poor forests such as bluff forests *(Vaccinium stamineum, Vaccinium vacillans),* oligotrophic forests *(Quercus velutina),* montmorillonite forests *(Hieraceum venosum),* and mondadnock forests *(Vaccinium stamineum, Quercus prinus, Vaccinium tenellum)* (Peet and Christensen 1980). Plot scores along the first axis are strongly related to the logarithm of calcium concentration ($r = -.815$ for the floristic data set, $r = -.793$ for the vegetation data set, see Palmer (1990) for methods and further discussion). The second and subsequent ordination axes are harder to interpret for both data sets. The only readily discernable pattern is that mosses *(Thuidium delicatulum, Bryoandersonia illecebra, Dicranum scoparium,* and *Leucobryum albidum)* have low second axis scores in the floristic ordination, suggesting that humidity, bare soil, or some other factor which affects bryophyte distribution determines variation along the floristic second axis. The only significant correlations between the plot scores of the two data sets are for the floristic first axis with the vegetation first axis, and the floristic third axis with the vegetation fourth axis (rank correlation $r_s^2 = 0.934$, $p < .001$ and $r_s^2 = 0.580$, $p < .05$, respectively, with Bonferroni correction for multiple comparisons, Morrison 1976). Thus, for the most part, the patterns in the two ordinations require separate in-

Table 1. The ratio r_k^2/r_{max}^2 is used here for comparing small-scale (within plot) vs. large-scale (among plot) community patterns. Values close to one indicate that small-scale patterns are similar to large-scale patterns; those close to zero indicate that small-scale patterns do not reflect large-scale patterns. Significance was tested with a Monte Carlo permutation test described in the text. Numbers in parentheses are the number (out of 101) of random r_k^2 greater than the observed r_k^2.

Floristic Comparison

Plot	Axis 1	Axis 2	Axis 3	Axis 4
1	0.080 (49)	0.094 (25)	0.141 (1) **	0.101 (17)
2	0.467 (10)	0.364 (48)	0.642 (1) **	0.490 (8)
3	0.292 (21)	0.397 (1) **	0.376 (7)	0.383 (5) *
4	0.251 (0) **	0.224 (0) **	0.143 (36)	0.123 (56)
5	0.326 (10)	0.367 (4) *	0.406 (2) *	0.373 (5) *
6	0.412 (13)	0.373 (21)	0.371 (28)	0.241 (88)
7	0.297 (0) **	0.141 (6)	0.038 (101)	0.153 (2) *
8	0.381 (31)	0.449 (3) *	0.388 (23)	0.405 (17)
9	0.375 (0) **	0.503 (0) **	0.229 (11)	0.261 (2) *
10	0.180 (80)	0.361 (3) *	0.307 (8)	0.303 (12)
11	0.237 (49)	0.320 (7)	0.271 (31)	0.261 (41)
12	0.264 (8)	0.294 (4) *	0.232 (14)	0.292 (1) **
13	0.274 (9)	0.262 (13)	0.255 (23)	0.384 (0) **
14	0.206 (49)	0.348 (0) **	0.152 (81)	0.281 (12)
15	0.208 (0) **	0.165 (17)	0.211 (3) *	0.155 (24)
16	0.171 (8)	0.213 (3) *	0.168 (14)	0.132 (46)
17	0.454 (4) *	0.285 (56)	0.641 (3) *	0.571 (4) *
18	0.285 (8)	0.405 (0) **	0.360 (0) **	0.238 (36)
19	0.285 (27)	0.232 (62)	0.375 (3) *	0.277 (38)
20	0.367 (0) **	0.272 (0) **	0.127 (91)	0.156 (64)
21	0.288 (0) **	0.211 (1) **	0.191 (4) *	0.138 (24)
22	0.298 (6)	0.237 (25)	0.227 (36)	0.337 (3) *
23	0.134 (6)	0.170 (1) **	0.108 (35)	0.130 (14)
24	0.302 (32)	0.209 (87)	0.254 (62)	0.261 (64)
25	0.204 (0) **	0.147 (2) *	0.203 (0) **	0.143 (7)
26	0.177 (5) *	0.168 (8)	0.171 (17)	0.098 (76)
27	0.333 (0) **	0.159 (65)	0.267 (4) *	0.198 (36)
28	0.174 (13)	0.191 (13)	0.418 (0) **	0.200 (5) *
29	0.262 (0) **	0.103 (66)	0.128 (37)	0.171 (5) *
30	0.442 (2) *	0.250 (64)	0.391 (10)	0.291 (47)

Vegetation Comparison

Plot	Axis 1	Axis 2	Axis 3	Axis 4
1	0.456 (48)	0.222 (86)	0.302 (76)	0.646 (6)
2	0.406 (48)	0.446 (26)	0.332 (73) **	0.450 (26)
3	0.405 (64)	0.572 (11)	0.367 (65)	0.455 (48)
4	0.456 (4) *	0.246 (56)	0.284 (54)	0.322 (39)
5	0.452 (19)	0.508 (9)	0.313 (62)	0.487 (17)
6	0.616 (5) *	0.637 (6)	0.332 (48)	0.513 (15)
7	0.397 (0) **	0.187 (76)	0.419 (0) **	0.201 (50)
8	0.395 (68)	0.601 (10)	0.311 (82)	0.543 (18)
9	0.352 (39)	0.579 (4) *	0.265 (64)	0.191 (98)
10	0.624 (22)	0.486 (57)	0.437 (86)	0.487 (73)
11	0.464 (71)	0.557 (29)	0.466 (64)	0.533 (52)
12	0.472 (20)	0.257 (76)	0.396 (46)	0.518 (17)
13	0.502 (1) **	0.402 (24)	0.345 (50)	0.291 (79)
14	0.454 (90)	0.489 (67)	0.368 (95)	0.637 (30)
15	0.249 (76)	0.178 (94)	0.230 (82)	0.331 (37)
16	0.368 (16)	0.247 (57)	0.286 (55)	0.462 (5) *
17	0.244 (98)	0.456 (32)	0.298 (79)	0.267 (88)
18	0.182 (96)	0.327 (21)	0.474 (8)	0.750 (0) **
19	0.535 (37)	0.471 (38)	0.220 (101)	0.535 (38)

Table 1 - continued

Plot	Axis 1	Axis 2	Axis 3	Axis 4
20	0.558 (7)	0.254 (50)	0.622 (3) *	0.325 (46)
21	0.296 (2) *	0.161 (42)	0.190 (27)	0.178 (24)
22	0.485 (38)	0.592 (8)	0.438 (60)	0.473 (44)
23[+]	0.200 (71)	0.298 (16)	0.155 (96)	0.156 (92)
24	0.305 (84)	0.232 (93)	0.449 (26)	0.219 (100)
25	0.183 (31)	0.276 (3) *	0.128 (63)	0.224 (6)
26	0.248 (21)	0.114 (90)	0.137 (97)	0.214 (49)
27	0.448 (10)	0.335 (44)	0.309 (57)	0.310 (54)
28	0.518 (1) **	0.224 (83)	0.349 (28)	0.357 (28)
29	0.332 (57)	0.397 (25)	0.246 (82)	0.282 (67)
30	0.399 (59)	0.497 (19)	0.212 (98)	0.595 (10)

*$p < .05$
**$p < .01$
[+]Plot 23 was not included in among-plot ordinations

terpretations.

Comparison of small-scale and large-scale patterns. Almost a third of the comparisons between small-scale and large-scale floristic patterns were significant (Table 1). Furthermore, only five plots did not have significant within-plot variation along any of the among-plot floristic ordination axes. Thus, floristic patterns observed on the landscape (among-plot) scale are here reflected in floristic patterns on a scale smaller than one tenth hectare. In contrast, only twelve (10%) of the vegetation comparisons are significant. This does not greatly exceed the number of erroneous significant results we would expect (six; that is, 5% of the total number of comparisons) if the null hypothesis were true. The results of the vegetation comparison should therefore be interpreted with caution, if at all.

Plots with low first axis scores have a slightly higher tendency to vary significantly with respect to the first axis than plots with high first axis scores (Fig. 1a). Similarly, plots with high second axis scores vary significantly with respect to the second axis (Fig. 1b). Plots with significant variation along the third and fourth floristic axes did not exhibit any obvious patterns with respect to position along any floristic axes. No pronounced patterns were observed with respect to significance of within-plot variation along any of the vegetation axes.

Species richness. Stepwise regression revealed that more than half of the variation in species richness of 0.1 ha plots can be explained by mean magnesium concentration (partial R^2 -0.602, $p < 0.0001$). The residual variation in species richness in this study is negatively related to mean potassium concentration (partial

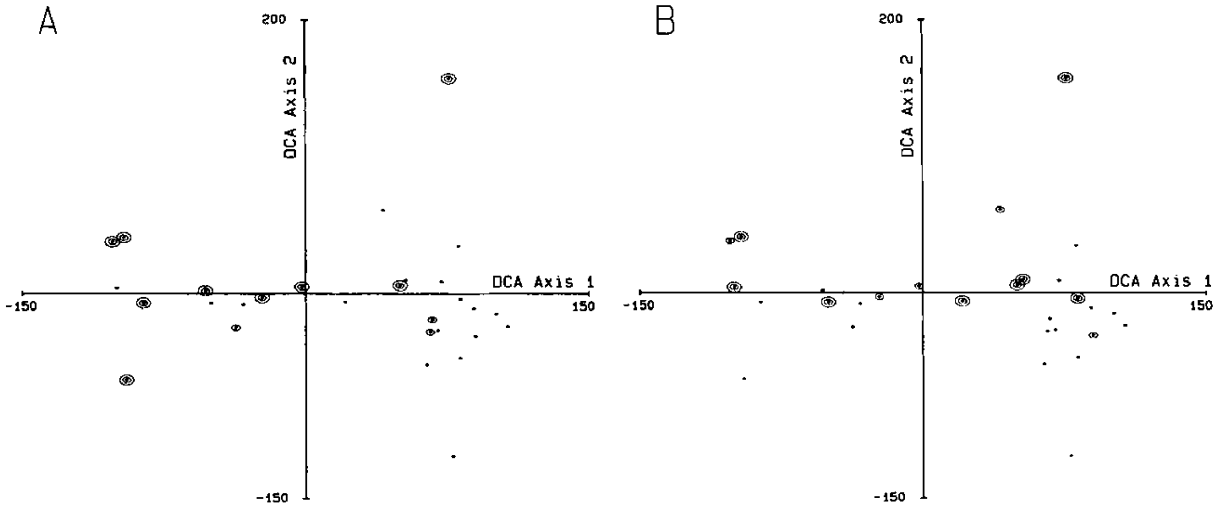

Fig. 1. Plot scores on the first and second floristic DCA axes. A) Circled plots have significant within-plot variation with respect to the first among-plot floristic axis. B) Circled plots have significant within-plot variation with respect to the second among-plot floristic axis. Single circle: $p < 0.05$; Double circle: $p < 0.01$. Significance is determined by a Monte Carlo procedure for r_k^2 described in the text.

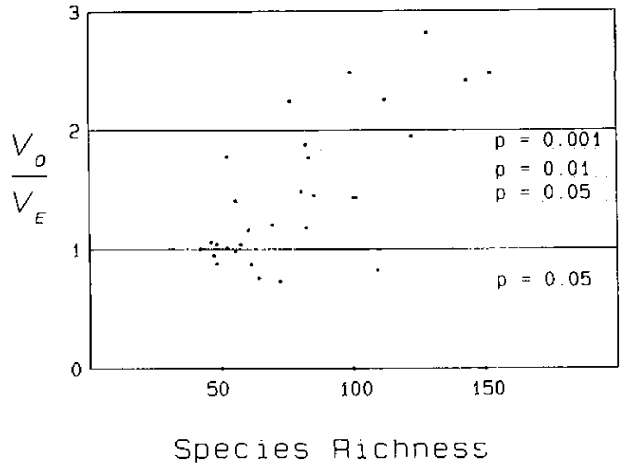

Fig. 2. The results of the variance test for subplots, as a function of total plot species richness. On the y - axis is the ratio of observed variance of species richness (V_O) to expected variance of species richness (V_E), calculated assuming random co-occurrences of species. The dashed horizontal lines are critical p values of this ratio, and were obtained from the chi squared distribution (Schluter 1984).

$R^2 = 0.214$, $p < 0.0001$). No other variables met the 0.05 significance level for entry into the model. If magnesium is omitted from the pool of variables, calcium (which is strongly correlated with magnesium) is the first variable entered (partial $R^2 = 0.514$, $p < 0.0001$).

The results of the variance test are demonstrated in Figure 2. Species richness is significantly more variable in half of the plots than the random expectation. In addition, the degree of departure from random expectation is positively related to total plot species richness. The significant variation in species richness indicates that it may be fruitful to seek relationships between environment and species richness.

The third column of Table 2 shows that species richness is negatively correlated with soil phosphorus concentration and positively related to soil pH more often than expected due to chance. The numbers in this column, as stated in methods, are valid despite spatial dependence. To correct for multiple comparisons using Bonferroni significance levels, the p values in Table 2 should be multiplied by 11, the number of comparisons. Only pH is significantly related to species richness by this more conservative test. As previously stated, we must be cautious while interpreting the significance of within-plot regressions (the numbers in parentheses in Table 2). Therefore the word "significant" is in quotation marks below. When one examines the correlations for individual plots in Table 2, the number of plots with "significant" positive correlations does not exceed six for any environmental variable, while the number of plots with "significant" negative correlations does not exceed four.

Species richness of subplots was positively correlated with calcium concentration in only two-thirds of the plots. Only two of the four "significant" correlations were in plots in which the variance test detected significant variation in species richness. There were even fewer positive correlations ("significant" or not) between magnesium and subplot species richness. Thus it appears that species richness within plots is not strongly determined by soil cation concentrations.

Discussion

Ordination of 0.1 ha hardwood forest plots reveals patterns that are consistent with the literature (Peet and Christensen 1980). These patterns are visible along the first ordination axis of both the floristic and the vegetation data sets, and are strongly related to soil calcium and species richness. The difficulty of interpreting ordination axes after the first is reflected in the companion paper to this one (Palmer 1990), which shows that there are no significant relationships between a plot's species composition and eleven measured environmental variables once calcium concentration is factored out. However, it must be stressed that unmeasured but potentially important factors such as nitrogen, sulfur, temperature, water, biotic factors (*e.g.* predation, disease), and stochastic factors (*e.g.* disturbance, historical accidents) may contribute to variation in species composition.

Although the second through fourth floristic ordination axes are difficult to interpret, they are not merely results of random patterns of species occurrences. The significant variation *within* plots in terms of these flo-

Table 2. The number of plots with positive and negative correlations between environmental variables and species richness. The values in parentheses are the number of statistically significant ($p < 0.05$) correlations, under the flawed assumption that subplots are independent replicates. The 2-tailed p values were obtained from the binomial distribution; they test whether the plots could have arisen from a population of plots in which 50% of the correlations between species richness and environment are positive. These values are valid despite spatial dependence.

Variable	# positive correlations	# negative correlations	2-tailed p
Phosphorus	7 (1)	23 (3)	0.005
Potassium	17 (3)	13 (1)	0.584
Calcium	20 (4)	10 (0)	0.098
Magnesium	17 (1)	13 (2)	0.584
Weight/Volume	18 (4)	12 (0)	0.361
pH	24 (4)	6 (0)	0.001
Buffered acidity	10 (0)	20 (4)	0.098
Cation exchange capacity	14 (1)	16 (2)	0.855
Manganese	20 (4)	10 (0)	0.098
Copper	18 (6)	12 (2)	0.361
Humic acid	11 (1)	19 (0)	0.200
Canopy openness	15 (2)	15 (1)	1.000

ristic axes demonstrates that the same patterns observed on the large-scale are repeated on a much smaller scale. Common patterns indicate common causes, even in the absence of *post hoc* rationalizations or interpretations of the patterns. If species placement along floristic axes was random, we would not expect parallel patterns to develop at any scale.

Small-scale patterns of floristic variation strongly depend on position along major gradients. As displayed in Table 1, the small-scale floristic patterns within many plots are significantly similar to large-scale floristic patterns. Figure 1 indicates that these plots are not a random sample of all plots. Small-scale variation along the community gradient represented by each of the first two axes is more likely at one end of the gradient than the other.

Small-scale floristic variation is *significantly* related to large-scale floristic variation, but it is not *strongly* related. 96.7% of the ratios of r_k^2 to r_{max}^2 for the floristic comparison are less than 0.5, indicating that large scale patterns generally account for less than half of the maximum possible correlation between species scores and subplot scores. This suggests that there are important small-scale causes of species occurrence which are unimportant or absent on the large scale. Thus, floristic variation in piedmont hardwood forests is not strongly self-similar (*sensu* Mandelbrot 1983): small-scale floristic variation is not a miniature version of large-scale floristic variation.

The lack of pattern along the small-scale (subplot) vegetation axes suggests that variation in species cover on the small scale is unrelated to variation on the large scale. Small-scale variation in species cover may result from differential growth caused by localized stochastic events such as deposition of animal excreta, establishment of ant colonies, death of individual canopy trees, or decay of coarse woody debris. Stochastic events relating to the establishment, growth and death of understory plants are most likely seen on scales not much larger than individuals. The greater number of plants at larger spatial scales would tend to cancel out such effects. Some of the variation in small-scale patterns may be related to the interactions between individuals or the "morphological pattern" of Kershaw (1973). The potential causes of stochastic small-scale variation in cover are so numerous and complex that they are unlikely to result in consistent, easily interpretable patterns.

Species richness of 0.1 ha plots is strongly related to soil calcium and magnesium, indicating that richness is not a result of random associations. Likewise, the variance test reveals that species richness patterns among 2 m^2 subplots are also not results of random associations. Despite this, within-plot variation in richness is not a miniature version of among-plot variation in richness. Calcium and magnesium are not as consistently related to within-plot species richness patterns as they are to among-plot species richness patterns. These results imply that there are different determinants of species richness at different scales.

Surprisingly, the within-plot standard deviations of calcium or magnesium concentrations did not significantly explain species richness of plots. Since calcium and its correlates are strongly related to species composition of plots (see above and Palmer 1990), I expected plots with variable calcium concentrations to contain species from many parts of the calcium gradient. These plots would be expected to have more species than would plots with little variation in calcium. The inability of within-plot standard deviations of environmental variables to explain plot species richness suggests that the habitat diversity hypothesis (Shmida and Wilson 1985) does not account for variability in species richness at the 0.1 ha scale in North Carolina piedmont hardwood forests.

Why is the strong correlation between species richness and cations among plots not reflected within plots? One possible (partial) explanation is that calcium and magnesium are extremely variable at a scale smaller than subplots (Palmer 1990, Figure 2). Approximately one half of the within-plot variation in calcium (as well as magnesium) is present within a subplot. Subplots are thus not extremely distinct from each other with respect to concentrations of these cations. Any relationship between species richness and these cations would be somewhat obscured at this scale. This explanation is not complete because species richness is not consistently related to the substantial variability in cations which remains among plots.

Soil pH, which is positively related to calcium and magnesium, has about one third of the within-plot variability represented within a subplot (Palmer 1990, Figure 2). This indicates that subplots are more distinct with respect to pH than they are with respect to calcium and magnesium. This distinctness of subplot pH may explain why pH has more positive correlations with species richness than do the cations. However, the relationships between pH and richness are still quite weak.

Table 2 suggests that there may be a negative correlation between species richness and phosphorus within plots. This is particularly interesting because there is no suggestion of such a negative correlation among plots. However, the observed patterns may have been an artifact of performing multiple correlations. Independent small-scale studies of phosphorus would be needed to evaluate the presence of a negative relationship with species richness. In any case, phosporus cannot be considered a primary determinant of species richness: correlations were generally weak, and only four of the plots exhibited "significant" patterns.

Summary

The same patterns of presence and absence of species among 0.1 ha plots are often observed among 2 m^2 subplots within these plots. The common patterns imply that species distributions have common causes at both scales. Even though some common causes exist, it must be noted that much variation among subplots does not parallel large-scale patterns. This suggests that small-scale floristic variation is not merely a "scaled down" version of large-scale floristic variation. Small-scale variation in species abundance does not reflect large-scale patterns, so variation in abundance must have specific small-scale causes which are unimportant on the large scale. Small-scale patterns of species richness are only weakly related to large-scale patterns of species richness. We therefore must consider species composition as well as species richness to be caused by a multitude of factors, including some that are scale-specific, and some that operate across a wide domain of spatial scales.

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