

# **DIVERSITY AND PATTERN IN PLANT COMMUNITIES**

edited by H.J. During, M.J.A. Werger & H.J. Willems

SPB Academic Publishing bv, The Hague, 1988

# CHANGES IN SPECIES DIVERSITY DURING SECONDARY FOREST SUCCESSION ON THE NORTH CAROLINA PIEDMONT

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## Abstract

Secondary forest succession can be represented as a four-stage process wherein the stages vary predictably in apparent intensity of competition and in the relative importance of establishment and mortality events (Peet and Christensen 1987; Peet 1988). Based on this four-stage model we hypothesize successional trends in diversity and community structure potentially applicable to many forest systems. We then test these hypotheses using data from forests of the North Carolina piedmont and make the following observations.

1. When averaged over all site conditions, species richness (species per 0.1 ha) is relatively constant during secondary succession. This result contrasts with reports from other regions where richness shows various clear trends during succession.

2. In steady-state stands as well as certain successional stages, species richness is strongly and positively correlated with soil pH and cation availability. This result contrasts with more common reports of richness decreasing or first increasing and then decreasing with increasing fertility. When sites are stratified by cation availability, distinctive, site-specific successional trends in richness can be identified. Infertile sites show a steady increase in richness early in succession followed by a decline with the onset of steady-state conditions, whereas fertile sites show relatively constant richness early in succession, but an increase with the onset of steady-state. Correlations with soil attributes are strong for species richness of the subordinate shrub and herb strata, but weak to nil for the dominant tree stratum.

3. Beta diversity (gradient length) increases and average niche breadth decreases during succession.

These and other data suggest (1) that an understanding of the population dynamics of the dominant tree species can lead to greater ability to predict successional changes in species richness and related aspects of community structure, and (2) that a clear understanding of patterns in species richness will require study of the component plant guilds.

## Introduction

Plant species richness, or species number, has been reported to vary during secondary forest succession in a multiplicity of ways. Some workers have found support for Odum's proposition (1969) that richness increases monotonically toward an asymptote in steady-state (or climax) vegetation (*e.g.*, Tagawa 1964; Brunig 1973; Nicholson and Monk 1974). Others have suggested a steady increase toward a maximum in late successional stands, with a subsequent decline as seral species are lost (*e.g.*, Loucks 1970; Auclair and Goff 1971; Whittaker 1972, 1977; Horn 1974; Bazzaz 1975). Still others have reported a decline after an early post-disturbance peak, followed by an increase coincident with the death of the initial cohort of dominant trees (*e.g.*, Habeck 1968; Peet 1978). Clearly, we are a long way from a general model of change in species richness during forest succession.

What progress has been made in development of more general models of successional change in species richness has come from regional syntheses of variation along environmental gradients. In particular, Auclair and Goff (1971) constructed such a model for forests of the Great Lakes region, and Peet (1978) expanded on this model to fit forests of the Colorado Front Range. In both studies, on favorable sites species richness was seen to climb to a peak shortly after catastrophic disturbance when competitive pressures were relatively low, decline steadily during the highly competitive growth and thinning phase of population development, and then increase with the onset of stable, climax conditions.

In an earlier paper (Christensen and Peet 1984) we examined trends in compositional convergence during succession on the North Carolina piedmont. In that study we found that, for a given site, convergence on climax composition is not monotonic as had been predicted by most previous workers, but instead varies with the stage of forest development. The general pattern is convergence during the intense competition of the thinning phase, divergence (or relaxation) during the transition from thinning to climax when many canopy trees die, and then convergence on the climax composition. This result may apply to changes during secondary succession in many forest systems.

The North Carolina forests in which we studied convergence showed a pattern of population development quite similar to that seen on favorable sites in the Rocky Mountains and the Great Lakes states (Auclair and Goff 1971; Peet and Christensen 1987). This suggested the possibility that species richness might also show consistent patterns of successional change across these rather divergent forest types. In addition, the changes in intensity of competition indicated by our analysis of piedmont forests suggested additional hypotheses with respect to beta diversity and niche breadth. In this paper we build on our earlier work on convergence to hypothesize successional changes in species richness and related structural attributes for North Carolina piedmont forests. We then test these hypotheses and examine the degree to which our results agree with or expand on the earlier studies of the Rocky Mountain and Great Lakes forests.

### The four-stage model and compositional convergence

Several authors working in different forest types have proposed convergent versions of a general, four-stage model of forest development (e.g., Jones 1945; Bloomberg 1950; Daubenmire and Daubenmire 1968; Bormann and Likens 1979; Peet 1981; Oliver 1981; Peet and Christensen 1987). These models focus on the population dynamics of the dominant trees and appear applicable to most forest types where one or a few species dominate the initial cohort of trees that invades after a catastrophic disturbance.

The first or 'establishment' stage of forest development is characterized by minimal competition and is a period during which many individuals, and often many species, become established. Following canopy closure, a period of intense competition occurs. During this stage, often called the 'thinning' stage, growth by canopy dominants crowds and eventually kills most of the smaller trees. The intense competition largely precludes establishment of new stems. When thin-

ning has progressed to the point where gaps created by deaths of canopy trees can no longer be filled by lateral expansion of existing trees, the forest enters the third or 'transition' stage. During this stage, competition is less intense. The fourth and final stage of succession is the 'steady-state' (or climax) stage where all sizes of trees occur and all of the preceding three stages occur in miniature, less extreme forms scattered at random through the forest (Watt 1947).

The results of our earlier analysis of compositional convergence (Christensen and Peet 1984) can be readily interpreted in terms of the four-stage model. For that study we divided piedmont forests into five age classes or strata: 20–40 yr-old pine stands, 40–60 yr-old pines, 60–80 yr-old pines, pine stands over 80 years old, and uneven-aged hardwood stands. The first three strata represent portions of the thinning stage, the old pine stands correspond to the transitional forests, and the relatively mature hardwood forests correspond roughly to the steady-state stage.

In one analysis we ordinated stands in each age stratum using detrended correspondence analysis (DCA; see Hill and Gauch 1980) and then compared the rank order of species along the primary ordination axes. In a second analysis we compared species positions on the first three axes simultaneously by means of canonical correlation analysis. In both cases we found that during the thinning phase species distributions become increasingly like those in the mature forests, then become markedly less similar to steady-state composition during the transition phase before finally converging on the final climax composition.

In earlier work (Peet and Christensen 1980b; Christensen and Peet 1981) we had shown the first ordination axis in the mature forests to correlate strongly with soil cation status as indicated by pH, available Ca, available Mg, or total available cations. When we examined convergence in terms of species sorting along this gradient, we obtained essentially the same results as with pure compositional gradients derived using ordination methods. There was strong convergence during the thinning phase, relaxation or even divergence during the transitional phase, and then convergence to the climax composition.

### Hypotheses

Our work on compositional convergence (Christensen and Peet 1984) led us to the conclusion that the intensity of competition changes in a predictable fashion during secondary succession with peaks during the thinning and steady-state phases. This result, in turn, led us to make the following four sets of predictions about successional changes in species diversity and related aspects of community structure (see Fig. 1).

1. Species richness should increase during the initial establishment phase when competition is low, decline during the highly competitive thinning phase, and then increase again during the transition phase. During the climax phase species richness should either decline slightly due to the loss of noncompetitive successional species, or reach a new peak as poorly dispersed climax-specialist species slowly invade.

2. The predictability of species richness from site variables should be low dur-

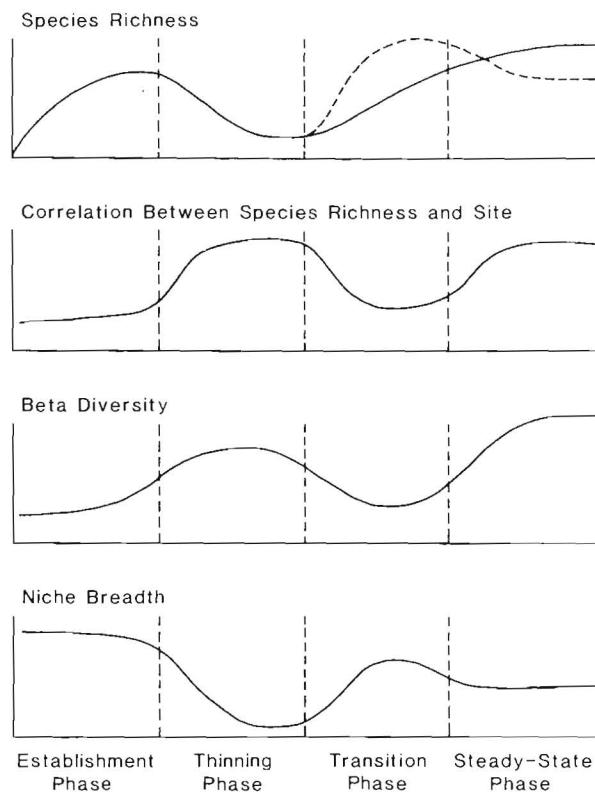


Fig. 1. Hypothesized changes in diversity and community structure during forest stand development.

ing the establishment phase when ample resources allow almost any species to invade, increase during the thinning phase due to competitive sorting (Peet 1988), decline again during the transition phase due to a relaxation in competition, and then increase again to an asymptote in the more competitive steady-state phase.

3. Initially, average niche breadth should be high because there is little competitive limitation on where species can grow. During the thinning phase niche breadth should decline due to competition limiting species to those habitats where they are best adapted. During the transition phase niche breadths should increase again as competition is relaxed, only to decline in the steady-state phase when the intensity of competition increases again.

4. Given a constant number of species, niche breadth and beta diversity should be negatively correlated, because if niches are broad they overlap more resulting in lower compositional turnover along a gradient. Thus, for the same reasons described in (3) above, beta diversity should be low during the establishment phase, increase during the thinning phase, and decrease during the transition phase. In the steady-state phase beta diversity should increase to an asymptote higher than the peak during the thinning phase because, not only are those species previously present more competitively restricted in distribution, but also many narrowly distributed, mature-phase specialist species are present here but not in the thinning phase.

### The study area

All field work was conducted in or near the Duke University Forest, in Orange, Durham, and Wake Counties, North Carolina. The Duke Forest is located in the northeastern portion of the North Carolina piedmont, a region of rolling hills, ancient soils, and a diverse range of parent rock types. Climatic records for nearby Raleigh indicate an annual precipitation of 1145 mm and a mean annual temperature of 15.5°C. Additional information can be found in Peet and Christensen (1981b) and Christensen and Peet (1981, 1984).

For this study we confine our analysis to forest stands growing on sites abandoned from agriculture, and to relatively mature hardwood forests with little evidence of human disturbance during the past 80 years. The great majority of post-disturbance forests of the study area are dominated by one or a combination of *Pinus taeda* and *Pinus echinata*. (Botanical nomenclature follows Radford, Ahles and Bell 1968). To a lesser extent *Liquidambar styraciflua*, *Liriodendron tulipifera*, and *Pinus virginiana* act as post-disturbance invaders. Composition of the mature forests varies greatly in response to site conditions, particularly soil chemistry and texture. On typical upland sites *Quercus alba* and other species of *Quercus* and *Carya* dominate with an understory of smaller tree species such as *Oxydendron arboreum* and *Cornus florida*. (Details of species composition and its successional change can be found in Peet and Christensen 1980b and Christensen and Peet 1981, 1984; also see Oosting 1942).

### Methods

We used the same data set as in Christensen and Peet (1984). In brief, 238 forest stands were sampled using 0.1 ha plots. Tree importance values were calculated as the average of relative density and relative basal area of all woody stems over 1 m tall. Herb importance values were calculated as the average of relative frequency and relative cover in 25 0.5 × 2 m subplots. Each 0.1 ha plot was searched for additional species of vascular plants which were given token importance values of .01. Soil A (0–10 cm) and B (~ 40 cm) horizons were sampled and analyzed as described in Christensen and Peet (1981, 1984).

Stands were selected to represent the range of soil and topographic conditions over which typical old field succession occurs. In addition, samples were stratified by the five age strata we used in 1984 and which are described above. Samples representing unusual environmental conditions such as alluvial forests, swamps, and rocky bluffs were excluded to assure consistent coverage of site conditions within the five age strata. For meaningful comparisons of some measures of beta diversity and niche breadth it is necessary to have a fixed reference gradient. Because in earlier work we found soil pH (followed by the closely correlated cation availability) to have the highest correlation with the first DCA ordination axis, we used soil pH as the primary reference gradient. Sites with extreme soil pH values were deleted to assure that each stratum represented the same range of soil pH.

Species richness was defined as number of vascular plant species per 0.1 ha

*Table 1.* Species richness (species / 0.1 ha) and diversity ( $e^{H'}$ ; Simpson's index  $-^1$ ) for four age groups of successional pines and near-climax hardwood forests on the North Carolina piedmont. No statistically significant differences were found within a column.

| Stand age              | N  | Richness | $e^{H'}$ | Simpson's index $-^1$ |
|------------------------|----|----------|----------|-----------------------|
| Pines: 20–40 yrs       | 20 | 51.0     | 15.3     | 9.6                   |
| Pines: 40–60 yrs       | 35 | 48.8     | 15.7     | 10.3                  |
| Pines: 60–80 yrs       | 34 | 49.5     | 17.0     | 10.9                  |
| Pines: > 80 yrs        | 30 | 52.7     | 17.7     | 11.5                  |
| Hardwoods: uneven-aged | 72 | 52.5     | 18.0     | 11.8                  |

(1000 m<sup>2</sup>). In addition, we calculated two standard diversity indices for comparative purposes; the exponentiated form of  $H'$  and the reciprocal of Simpson's index (Peet 1974). Correlation between the various measures of species diversity and the physical environment was assessed using Spearman's rank correlation coefficient.

Two measures of beta diversity were calculated for each age stratum. The first measure was the length of the first DCA axis as computed using the DECORANA algorithm (Hill 1979; Hill and Gauch 1980). The results are presented in units of standard deviations of species abundance. These units are roughly equivalent to half-changes in species composition multiplied by .84 (Hill 1979). For the second measure we calculated percent difference in species composition for each stand as compared to the stand with the lowest soil pH, and then used linear regression to calculate the slope of the relationship between compositional change and change in soil pH. We repeated the analysis using the stand with highest pH as the reference stand and obtained essentially identical results. The results are presented in units of half-changes.

As previously described in Christensen and Peet (1984), two measures of niche breadth along the pH gradient were calculated for each of the five age-strata for both herb data and tree data. The first measure, a direct measure of spread, used McNaughton and Wolf's index (1970), which is essentially the importance-weighted standard deviation of the mean species location. The second index, called stand heterogeneity, is the within stand importance-weighted standard deviation of species' importance-weighted pH preference.

## Results

Mean species number per 0.1 ha is shown in Table 1 for each age stratum. Means for all strata fell within the narrow range of 48.8 – 52.7 sp/0.1 ha, thus failing to reveal any trend with age. The two diversity indices both show a small but steady increase with age. Thus, we fail to find support for our hypothesized bimodal trend in richness.

In earlier studies (Peet and Christensen 1980b; Christensen and Peet 1984) we found a high correlation between species richness and soil cation availability in steady-state forests. The second set of hypotheses, that predictability of species number based on site conditions increases during the thinning phase, decreases

Table 2. Spearman rank correlations of soil cation availability (sum of Ca, Mg, K) with species richness (species / 0.1 ha), and with diversity ( $e^{H'}$ ; Simpson's index  $^{-1}$ ) for four age classes of successional pine and near-climax hardwood forests.

| Stand age              | Richness  | $e^{H'}$  | Simpson's index $^{-1}$ |
|------------------------|-----------|-----------|-------------------------|
| Pines: 20–40 yrs       | 0.485*    | 0.656***  | 0.669***                |
| Pines: 40–60 yrs       | 0.508**   | 0.213     | 0.204                   |
| Pines: 60–80 yrs       | 0.595**** | 0.350*    | 0.226                   |
| Pines: 80+ yrs         | 0.272     | 0.202     | 0.155                   |
| Hardwoods: uneven-aged | 0.505**** | 0.441**** | 0.279**                 |

\* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ ; \*\*\*\* =  $p < 0.0001$ .

Table 3. Spearman rank correlations of soil cation availability (sum of Ca, Mg, K) with tree, shrub, herb, and total species richness (species / 0.1 ha) for four age classes of successional pine and near-climax hardwood forests.

| Stand age              | Trees  | Shrubs    | Herbs     | Total     |
|------------------------|--------|-----------|-----------|-----------|
| Pines: 20–40 yrs       | 0.368  | 0.487*    | 0.461*    | 0.485*    |
| Pines: 40–60 yrs       | 0.354* | 0.482**   | 0.481**   | 0.508**   |
| Pines: 60–80 yrs       | 0.109  | 0.522***  | 0.483**   | 0.595**** |
| Pines: 80+ yrs         | -0.003 | 0.221     | 0.294     | 0.272     |
| Hardwoods: uneven-aged | 0.101  | 0.474**** | 0.489**** | 0.505**** |

\* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ ; \*\*\*\* =  $p < 0.0001$ .

during the transition phase, and increases again to an asymptote in the steady-state, was motivated by this result. To test these ideas we calculated the rank correlation between available soil cations (sum of available Ca, Mg and K) and species richness for each of the age strata (see Table 3). We found, as predicted, a steady increase in the magnitude and significance of the correlation during the thinning phase, a marked reduction in magnitude and significance during the transition phase, and another increase in the steady-state phase.

The two diversity indices showed maximum correlations and significance in the first and last age strata (Table 2). This suggests that there is a strong relationship between concentration of dominance in a few species and soil cation availability for the youngest and also the most mature stands, but not those of intermediate age.

To examine whether trends in species richness with soil cation availability are related to plant stature or growth form, we divided the species present into three groups: trees, shrubs, and herbs. Spearman rank correlations between species richness and soil cation availability are shown in Table 3 for each of these three groups. For both herbs and shrubs the trends are the same as for the complete species pool. Specifically, the magnitude and significance of the correlation increases during the thinning phase, declines during the transition phase, and then increases again in the steady-state phase. However, the trees failed to show this pattern, except that the correlation did decline markedly (to near zero) in the transition phase.

To better visualize the complex relationships between soil cations, stand age, and species number, we plotted species richness as a two-dimensional response

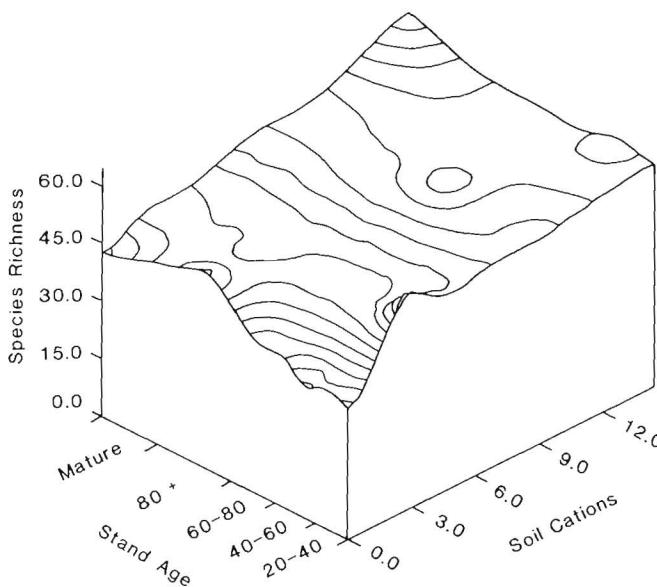


Fig. 2. Variation in species richness during secondary forest succession on the North Carolina piedmont as related to soil cation availability (sum of Ca, Mg, K in meq). Species richness is shown as species per 1000 m<sup>2</sup> with contour intervals of three species.

surface. The resulting figure (Fig. 2) shows quite different successional trends for different levels of soil cations. On infertile sites there is a steady increase in species number through the transition phase, after which there is a decline. The decline likely represents the loss of seral species as predicted by Loucks (1970). On high cation sites species number is roughly constant up to and through the transition phase, but shows an increase in the steady-state. The constant richness during stand development likely reflects the ability of most rapidly dispersed species to become established early in these favorable sites. The richness increase in the steady-state phase corresponds to the establishment of a suite of mature forest specialists characteristic of fertile sites with long-established hardwood forest. It is unclear to what extent their late arrival corresponds to poor dispersal, making them equivalent with the 'ancient woodland species' described for British woodlands (see Peterken 1974; Rackham 1980), versus poor success in forests dominated by pines.

There is no consensus as to how to best measure beta diversity (see Wilson and Mohler 1983; Wilson and Shmida 1984). In studies where several alternative measures have been employed, the results have not been strikingly consistent and sometimes have been markedly divergent (*e.g.*, Whittaker *et al.* 1984). As described in the methods section, we selected variants on two of the more popular approaches. With both the DCA and percentage difference methods, tree data showed peak beta diversity during the thinning phase, a decline during the transition phase, and an increase again in the steady-state (Table 4). Herb data showed the same pattern when using the percentage difference measure, but not for the DCA method. For all four measures beta diversity reached its absolute maximum

*Table 4.* Beta Diversity, or compositional differentiation along the soil pH gradient for four age classes of successional pine and near-climax hardwood forests.

| Stand age              | DCA axis length |       | Percent difference slope |                    |
|------------------------|-----------------|-------|--------------------------|--------------------|
|                        | Trees           | Herbs | Trees                    | Herbs              |
| Pines: 20–40 yrs       | 1.78            | 2.32  | 6.94 <sup>a</sup>        | 6.92 <sup>a</sup>  |
| Pines: 40–60 yrs       | 2.32            | 2.35  | 7.08 <sup>a</sup>        | 7.36 <sup>a</sup>  |
| Pines: 60–80 yrs       | 2.25            | 2.13  | 5.68 <sup>a</sup>        | 10.93 <sup>b</sup> |
| Pines: 80+ yrs         | 1.57            | 2.53  | 5.44 <sup>a</sup>        | 5.38 <sup>a</sup>  |
| Hardwoods: uneven-aged | 2.50            | 2.73  | 11.28 <sup>b</sup>       | 10.80 <sup>b</sup> |

Beta diversity is measured as (A) the length of the first detrended correspondence analysis axis (from Christensen and Peet 1984), and (B) as the slope of percentage compositional difference versus the pH difference. Indices within a column with shared superscripts are not statistically different ( $p < 0.01$ ) based on pairwise comparisons (Sokal and Rohlf 1981).

*Table 5.* Niche breadth along the soil pH gradient, and within stand heterogeneity of species pH preference, for four age classes of successional pine and near-climax hardwood forests (after Christensen and Peet 1984).

| Stand age              | Niche breadth     |                   | Stand heterogeneity |                   |
|------------------------|-------------------|-------------------|---------------------|-------------------|
|                        | Trees             | Herbs             | Trees               | Herbs             |
| Pines: 20–40 yrs       | 2.10 <sup>a</sup> | 2.40 <sup>a</sup> | 0.91 <sup>a</sup>   | 0.68 <sup>a</sup> |
| Pines: 40–60 yrs       | 1.55 <sup>b</sup> | 1.93 <sup>b</sup> | 0.86 <sup>b</sup>   | 0.57 <sup>b</sup> |
| Pines: 60–80 yrs       | 1.51 <sup>b</sup> | 1.86 <sup>b</sup> | 0.84 <sup>b</sup>   | 0.54 <sup>b</sup> |
| Pines: 80+ yrs         | 1.61 <sup>b</sup> | 1.98 <sup>b</sup> | 0.82 <sup>b</sup>   | 0.54 <sup>b</sup> |
| Hardwoods: uneven-aged | 1.47 <sup>b</sup> | 1.81 <sup>b</sup> | 0.74 <sup>c</sup>   | 0.49 <sup>c</sup> |

Indices within a column with shared superscripts are not statistically different ( $p < 0.01$ ) based on pairwise comparisons (Sokal and Rohlf 1969).

in the steady-state phase, probably because of the presence of numerous poorly dispersed ancient woodland specialists.

We calculated two measures of niche breadth. The first is a direct measure of niche breadth based on the standard deviation of species distributions along the pH gradient. The second, an indirect measure, is the average within stand variation in species pH preference. The second index differs from the first in that if stands have all their species with roughly equivalent pH preferences, a low value will be returned, even if the stands occur on quite different pH soils than would be indicated by mean species position. Both tree and shrub data show widest niche breadths (both measures) in the youngest stands with a decline in niche breadths during the thinning phase (Table 5). Both measures with both tree and herb data show narrowest niche breadths to occur in the steady-state phase, the situation where the plants have presumably had the longest period to be sorted through competition. The two measures give different results for the transition phase, and in no case is the transition phase significantly different from that observed during the late thinning phase. Thus, our results support our hypotheses that niches are broadest early in succession and narrowest in the steady-state, but there is no clear support for the hypothesized increase in niche breadth during the transition phase.

## Discussion and conclusions

### *Successional trends in species richness*

The results of this study at first seemed disappointing in that the successional patterns in richness we found did not lend themselves to explanation through a simple extension of the graphical model proposed earlier for Rocky Mountain and Lake States forests (Auclair and Goff 1971; Peet 1978). Because forest development on most sites in our study area, like that on favorable sites in the Rocky Mountains, appeared to conform to the four-phase model, we expected that changes in species richness would similarly show a negative correlation with the inferred intensity of competition (see Peet 1978). Specifically, we expected richness to be maximal late in the establishment phase and then again in the transition phase. Instead, we found species number to be essentially constant during succession when averaged across all sites.

Environmental control of species richness appears too strong for the successional pattern to be apparent without multi-dimensional representation or stratification by site characteristics. However, the fact that successional change in richness varies with site quality is consistent with forest development in the Rocky Mountains and the Great Lake states. Further, the correlation with and perhaps the degree of control by environmental factors does appear to change during succession in a manner consistent with the intensity of competition suggested by the four-phase forest development model.

Our success in using the four-phase model to predict beta diversity to be lowest in the establishment phase and highest in the steady-state, along with our success in predicting niche breadth to be high in the establishment phase, low during thinning and steady-state, and somewhat higher during transition does offer hope that a unified model for changes in richness during stand development might be developed by focusing on the population interactions of the dominant plants (see Peet and Christensen 1980a). The correspondence between the inferred intensity of competition and the level of correlation between species richness and soil cation content supports this suggestion. Further, the success of Pineda *et al.* (1981a, b) in correlating niche breadth with lack of competitive dominance during grassland succession bodes well for extension to nonforested systems.

### *Competition and the unimodal response curve for species richness*

The strong positive correlation between species richness and soil cation status which we found for both the thinning and steady-state phases of forest development contrasts with the prevailing wisdom that richness shows a unimodal response along a fertility gradient and that the curve is sufficiently positively skewed that an increase in soil fertility will usually have the result of a decrease in species richness (see Grime 1973; Huston 1979, 1980; Tilman 1982; Peet *et al.* 1983). Separate analysis for the tree, shrub and herb strata showed no trend for trees, but strong trends for herbs and shrubs. This result is consistent with Grubb's (1987) observation that woodland herb vegetation is generally depauperate in species on infertile, acidic sites and increases steadily in richness with in-

creasing fertility, at least through the range of soil pH and herb standing crop typically found in natural vegetation. (Grubb does not report a similar pattern for shrubs). Certainly there are productive forest herb communities dominated by a single species, such as *Mercurialis perennis* or *Urtica dioica* in Europe or *Laportia canadensis* or *Impatiens pallida* in eastern North America. However, these cases of monospecific dominance appear to be exceptional.

In contrast to forest herbs, grassland herbs have frequently been shown to exhibit a decline in species richness with increasing fertility (e.g., Vries and Kruijne 1960; Harper 1971; Auclair *et al.* 1976; Kirchner 1977; Peet *et al.* 1983). This appears to be a rather frequent phenomenon and has been termed 'the paradox of enrichment' (see Rosenzweig 1971; Riebesell 1974). The fact that forest herbs generally increase in richness with increasing fertility while grassland herbs decline suggests that the skew of the unimodal response curve for richness along a fertility gradient is generally negative for woodland herbs and positive for grassland herbs.

Perhaps the explanation for this apparent difference in the relationship between richness and soil fertility for grassland and woodland herbs lies in the nature of the competition for resources. Among the dominant trees in a forest, competition is typically asymmetric, with individual trees capturing resources at levels disproportionate to their size (Weiner and Thomas 1986; Knox *et al.* 1988). Such asymmetric competition is generally associated with competition for light; where competition is largely for soil resources it is more likely to be symmetric (Weiner 1985; Weiner and Thomas 1986). Asymmetric competition should lead to decreased species richness as, through time, the most successful species gain a progressively greater share of the available resources, and the more fertile the site the faster this process should take place. In contrast, where competition is for soil resources and thus more nearly symmetric, extinction rates are much lower. Under such conditions an increase in available resources (typically soil nutrients or water) can be expected to provide more opportunities for new species to grow and exploit the available resources.

Various theories have been proposed to account for the unimodal curve of species richness along a fertility gradient (e.g., Grime 1979; Huston 1979; Tilman 1982). To these we add a new alternative. We propose that the left or ascending portion of the curve represents symmetric competition where community structure is controlled primarily by competition for soil resources. In contrast, the right or descending portion of the curve represents the domain where asymmetric competition, or competition for light, dominates. In the understory of a forest where light is universally low, the guilds of subordinate species (herbs and shrubs) show little asymmetric competition among themselves. Light and soil resources are too scarce for these species to interact much, but any increase in soil nutrients should provide new opportunities for growth. Thus, we hypothesize that species richness increases along the nutrient gradient until those few extreme sites are reached where soil resources are sufficiently abundant for competition for light between herbs to be important.

This model provides an alternative explanation for the observed trends in correlation between herb and shrub species richness and site quality during succession. The correlations are high when there is intense asymmetric competition be-

tween the trees resulting in low levels of light penetrating to the forest floor. In contrast, the correlation is low where there is less competition for light among the trees, specifically during the establishment and transition phases. Since the sign of the correlation with substrate should vary with canopy density, we expect reduced correlation during the transition phase when canopy density is heterogeneous.

The overall strong correlation between species richness and soil cations is a result of the numerical dominance of herb and shrub species over tree species and suggests that a clear understanding of patterns in species richness will require a division of communities into at least guilds of dominant and subordinate species. This supports arguments by Peet (1978), Colwell (1979), and Grubb (1987) that ultimately determination of the mechanisms responsible for variation among communities in species richness will need to focus on component guilds.

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