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Short-Term Dynamics of Second-Growth Mixed Mesophytic Forest Strata in West Virginia

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ABSTRACT The short-term dynamics of mixed mesophytic forest strata in West Virginia were examined using similarity analysis and linear correlation of shared ordination space. The overstory tree, understory tree, shrub/vine, and herb strata were stable over a six year interval, whereas the tree seedling and sapling strata were unstable. All strata but the shrub/vine and tree seedling strata were correlated with soil pH, elevation, P, K, Fe, Mn, Ca, and Mg, with the latter two variables being the weakest for the overstory tree, understory tree, and sapling strata. The herb stratum was also significantly correlated with the shrub/vine and tree seedling strata. The soil fertility gradient corresponded with a moisture gradient. More xeric plots tended to be less stable than more mesic plots for all strata. Successful forest management may depend on knowledge of the lower tree strata species composition, because such composition will likely vary prior to future disturbance events.

INTRODUCTION The study of forest short-term dynamics provides the baseline data necessary to understand subtle vegetation change that occurs during periods between large disturbance events. The expected disturbance frequency in deciduous forests is every 50–200 years (Runkle 1985) or, specific to the Central Appalachian region, 31 years (Schular and Fajvan 1999). There are examples of even shorter periods (e.g., 2.8 year fire-return interval) in upper slope and ridge top stands prone to fire (Cutter and Guyette 1994), but current management of these forests has resulted in fire rotation periods for as long as 6,000 years (Dey et al. 2002). Vegetation composition may be defined mostly by individual species fitness (survival and reproduction), and changes in composition without a significant disturbance event suggest sensitivity of species fitness to small-scale environmental change.

Mixed mesophytic forests of the eastern United States are relatively diverse in both species and structure (Braun 1950, Muller 1982). Most late-successional deciduous forests in this region commonly have five distinct strata. These strata are the overstory trees, understory trees, saplings, shrubs/vines, and ground vegetation (herbaceous plants and tree seedlings). The herbaceous and suffrutescent species of the ground vegetation may be referred to as the 'resident' group and the tree seedlings as the 'transient' group (Gilliam and Roberts 2003), because the surviving tree seedlings are expected to transfer from one stratum to another. Because of these different roles, separating this ground layer into two strata (herbaceous/suffrutescent species and tree seedlings) may help evaluate short-term vegetation change.

It remains unclear how the forest strata compare in terms of overall stability during shorter time periods and if stable strata are defined by the same environmental variables. Such linkages among strata have been reported for late-successional forests (Gagnon and Bradfield 1986, Host and Pregitzer 1992, Gilliam et al. 1995, McEwan et al. 2005) but not found for younger or disturbance prone forests (Dunn and Stearns 1987, Sagers and Lyon 1997).

Stability over the short-term as well as any linkages among strata may be specific to different land types, such as ridges and upper slopes versus lower slopes, due to differences in species composition (Muller 1982, Small and McCarthy 2002). Upper slopes and ridges within a mixed mesophytic forest area are noted for dominance by oak species (Braun 1950), which are adapted to the more xeric conditions with relatively open canopies. Such oak forests may be self-perpetuating even without frequent disturbance. Overstory oak species may be well-represented on sites other than ridges and upper slopes of mixed mesophytic forests, possibly due to historic logging and fire, but the sapling stratum is often lacking oak species. These forests could eventually lose their oak component un-

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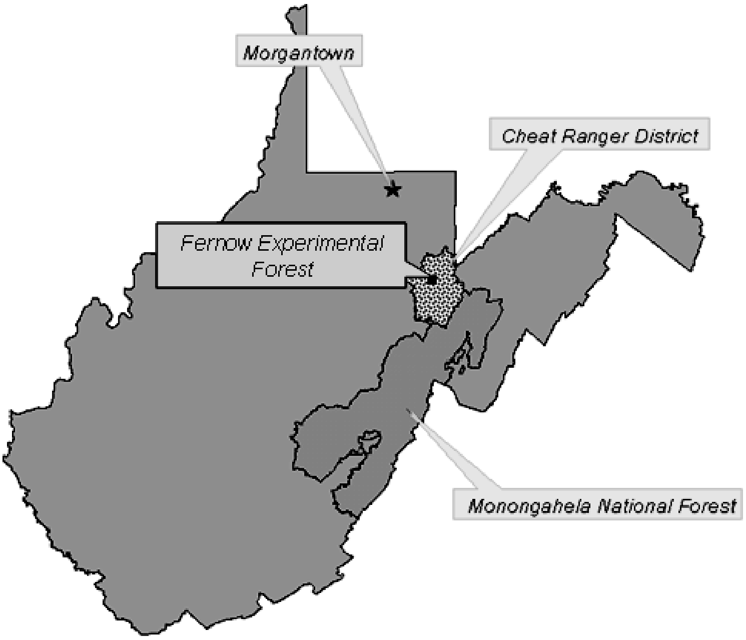

Figure 1. Fernow Experimental Forest in the Cheat Ranger District of the Monongahela National Forest in West Virginia.

less disturbances, such as fire and harvesting, are planned to promote oak regeneration (Lorimer et al. 1994, McCarthy et al. 2001).

We ask the following questions: 1) How do the six strata (separating out the tree seedlings from the herbs) of a second-growth, late-successional forest compare in terms of composition and stability over an interval of six years in the absence of significant disturbance? And 2) Are these strata linked in terms of their response to environmental variables and is any linkage related to the degree of stability? We hypothesize that stable strata will share similar associations with environmental conditions and that the more mesic land types (lower slopes) will show greater instability than the more xeric land types (ridges and upper slopes).

METHODS

Study Area

Our study is located in the Fernow Experimental Forest (39°03 N, 79°41 W; Figure 1) of the Monongahela National Forest in Tucker County, West Virginia. This forest is approximately 1900 ha in area and is part of the Allegheny Mountain Section of the Unglaciated Allegheny Plateau. Most precipitation occurs in the growing season and averages approximately 145 cm yr^{-1}. Soils of this area are typically well-drained, loamy sands, and about 1 m in depth (United States Department of Agriculture, Forest Service 1987; Muzika et al. 1999). Each of the 60 plots is located in second-growth deciduous hardwood stand, approximately 80 years of age, 0.1 ha in size, and devoid of any major natural or anthropogenic disturbances since they were established at the turn of the century. Moreover, the plots were not disturbed between 1994 and 2000 when data were collected. This mixed mesophytic forest consists of vegetation types ranging from more mesic sites that are dominated by sugar maple and beech to more xeric sites that are dominated by oak species (Braun 1950).

Sampling

Vegetation data were collected from June to July in 1994 and again in 2000. At each of the 60 permanently marked 50 m × 20 m plots, species and diameter at breast height (DBH) were recorded for overstory trees (stems $\geq$ 10 cm DBH) and understory trees (2.5 cm $\leq$ stems $<$ 10 cm DBH) in each 0.1 ha plot. Saplings (1 m tall $<$ stems $<$ 2.5 cm DBH) were tallied in each 0.1 ha plot and tree seedlings (stems less than 1 m in height) were tallied in four 25 m^2 subplots and in 10 1-m^2 subplots nested within the 0.1 ha plot. Shrubs and vines were tallied in the same 25 m^2 subplots. Herbaceous species were visually estimated for percent cover in the 10 1-m^2 subplots, using the cover class rating scale described by Daubenmire (1968). Importance values were calculated for overstory trees and understory trees using relative basal area and relative density. For saplings, tree seedlings, shrubs and vines, only relative density was used to calculate the importance values, while for herbs, relative cover was used. Diversity was calculated using the Shannon diversity index (Kent and Coker 1992). Calculations were equivalent for both years of sampling and were averaged per plot. The six measured strata were 1) overstory trees, 2) understory trees, 3) saplings, 4) shrubs/vines, 5) tree seedlings, and 6) herbs. Nomenclature follows Gleason and Cronquist (1993). Voucher specimens of the species reported in this paper are located in the herbaria of West Virginia University (WVA) or of the Northeastern Research Station, United States Department of Agriculture, Forest Service in Parsons, West Virginia.

Environmental data were collected in the summer of 1994 and included soil physical and chemical characteristics and topographic parameters for each plot. Soil samples were collected from the top 10 cm at four locations on each 0.1 ha plot and mixed. The mixed soil samples were oven-dried and sieved (2 mm mesh). Soils were analyzed for pH, and content (mg g^{-1}) of phosphoric acid (P), calcium (Ca), magnesium (Mg), potassium (K) copper (Cu), aluminum (Al), total nitrogen (N), manganese (Mn), iron (Fe), and boron (B) by the Soil Testing Laboratory at Virginia Polytechnic Institute and State University, using the methods of Donohue and Friedericks (1984). Elevation (m), slope inclination (percent) and aspect (linearalized according to Beers et al. [1966]), were measured at three locations in each plot (the midpoint and two ends of a centrally located 50 m transect that ran parallel with the contour like the plot). Percent cover of moss, rock, and coarse woody debris was visually estimated in each of the 10 1-m^2 plots. All environmental variables were averaged per plot.

Analysis

Importance value was determined for each species in each stratum. Differences in importance values between years provided a stability measure for each stratum determined using squared Euclidean distances (Kent and Coker 1992)

$$D_{ij} = \sqrt{\sum_{K=1}^{m} (X_{ik} - X_{jk})^2}$$

where D_{ij} = the squared Euclidean distance between time periods i and j; m = the number of species; X_{ik} = the importance value of the kth species in year i (1994); X_{jk} = the importance value of the kth species in year j (2000). Values range from 0 to ∞, with larger numbers indicating less similarity. D_{ij} was calculated for each stratum. Any decrease in similarity within a stratum in the six year time span was defined as a decrease in stability. Differences between abundance values for a common species may contribute less to the distance than the same difference of rare species, hence, the species abundance paradox associated with use of Euclidean distances. However, this problem was alleviated by using relative abundance values (i.e., the importance values) for X_{ik} and X_{jk}. Legendre and Gallagher (2001) refer to such a similarity measure as a distance between species profiles. The species abundance paradox is more of a problem when comparing sites that differ in the number of rare species. The latter is not the case in our study because our similarity comparison was temporal, using the same plots within a single stratum. Nonetheless, the herb stratum will be the most likely to suffer from the effects of rare species. If 1994 and 2000 herb abundances are very different, such that one year has more rare species the other year, then the consequent dissimilarity may be an overestimate. Whether or not stability was significantly different among strata was determined by conducting a one-way ANOVA and Tukey's multiple comparisons tests on the mean D_{ij} values of each plot for each stratum, which were $\log_{10}$ transformed (Proc GLM; SAS v. 8.02 2001). The similarity analysis (using $\log_{10}$ transformed data) was also conducted separately on 12 of the 60 plots that were south to southwest facing and located on ridge tops or upper slopes (i.e., more xeric stands) as well as 15 plots that were on north to northeast facing and lower slopes (i.e., more mesic stands).

Significant difference in diversity values among strata was determined using a one-way ANOVA and Tukey's multiple comparison tests; data for the 60 sites met ANOVA assumptions. The subset comparison of mesic and xeric sites required a nonparametric Kruskal-Wallis test (Proc Npar1way; SAS v. 8.02 2001) comparison due to unequal variances.

Canonical correspondence analyses (CCA) with 999 Monte Carlo randomization tests (null hypothesis being no significant relationship between matrices) were run for each stratum using the environmental data (taken in 1994) and both 1994 and 2000 species composition (importance values) matrices (PCORD v. 4; McCune and Mefford 1999). The latter assumes that the measured environmental variables have not changed significantly between 1994 and 2000, because there was no natural or anthropogenic disturbance noted in the stands during this time period. Similar ordination results among strata would indicate that they share environmental variable associations and that the strata may be linked. However, differences in results between years may indicate either a change in species response over this

Table 1. Top 10 tree and shrub species and top 15 herbaceous species (based on 1994 values for all stands) most important species in each stratum and year ranked by importance values (percentages). Nomenclature follows Gleason and Cronquist (1993)

	All (N = 60)		Mesic (N = 15)		Xeric (N = 12)	
Stratum	1994	2000	1994	2000	1994	2000
Overstory tree						
Acer saccharum	17.2	13.5	23.5	13.1	22.9	23.2
Liriodendron tulipifera	15.1	18.9	32.3	39.6	4.8	6.3
Quercus rubra	13.9	18.4	7.4	10.8	21.9	26.8
Acer rubrum	9.6	8.3	0.6	0.3	17.5	16.8
Fagus grandifolia	7.1	5.2	11.9	11.5	2.5	1.3
Tilia americana	5.2	5.2	8.4	8.9	2.8	2.0
Quercus prinus	5.1	5.8	0.0	0.0	4.5	4.6
Prunus serotina	4.4	4.3	2.6	3.6	8.8	8.0
Betula lenta	4.0	3.3	3.1	2.5	2.7	3.1
Tsuga canadensis	3.7	3.7	1.3	1.1	0.6	0.6
Understory tree						
Acer saccharum	41.1	41.7	61.0	62.2	46.6	47.6
Fagus grandifolia	23.4	23.3	24.9	24.4	17.1	17.3
Acer rubrum	7.0	9.1	0.6	0.6	10.0	15.1
Acer pensylvanicum	6.7	3.9	0.9	0.5	10.8	7.2
Hamamelis virginiana	3.0	2.3	5.1	4.2	0.0	0.0
Tsuga canadensis	2.6	2.6	0.1	0.1	0.0	0.0
Amelanchier arborea	2.1	1.4	0.1	0.0	2.6	0.6
Oxydendrum arboreum	2.1	2.0	0.0	0.0	3.1	3.1
Betula alleghaniensis	1.8	3.3	2.6	3.2	0.0	0.0
Tilia americana	1.7	1.9	2.0	1.6	1.2	1.6
Sapling						
Acer saccharum	27.3	26.6	39.8	37.6	44.4	40.2
Fagus grandifolia	24.0	25.5	36.4	37.2	9.8	6.7
Acer pensylvanicum	20.5	24.1	6.7	7.6	21.8	40.8
Acer rubrum	5.0	1.1	0.0	0.0	4.3	0.6
Hamamelis virginiana	4.1	4.0	8.4	7.6	0.0	0.0
Fraxinus americana	1.9	0.4	1.4	0.5	5.9	0.3
Picea rubens	1.4	7.6	0.0	0.0	0.0	0.0
Betula lenta	1.3	1.5	0.2	0.3	5.0	4.5
Tsuga canadensis	1.3	0.6	0.0	0.0	0.1	0.7
Castanea dentata	1.2	0.7	0.0	0.0	0.1	0.1
Tree seedling						
Acer pensylvanicum	18.4	7.7	5.7	6.2	17.3	7.5
Acer rubrum	9.9	29.6	0.4	17.2	7.2	41.0
Acer saccharum	9.5	12.1	31.8	31.6	16.2	8.5
Fraxinus americana	9.1	7.5	15.4	7.6	16.3	6.5
Quercus rubra	8.7	6.6	3.5	8.3	6.1	5.4
Fagus grandifolia	8.7	5.7	17.5	10.8	6.0	1.9
Prunus serotina	7.7	8.2	5.0	2.9	18.9	18.8
Sassafras albidum	4.5	1.4	0.0	0.0	2.2	1.4
Magnolia fraseri	3.5	0.0	0.0	0.1	0.9	0.3
Amelanchier arborea	1.7	1.3	0.0	0.2	1.0	1.2
Shrub/vine						
Rubus spp.	17.0	17.1	8.9	9.8	25.0	25.0
Aristolochia macrophylla	16.3	15.7	72.5	71.1	0.0	0.0
Smilax rotundifolia	7.1	6.8	4.7	5.1	31.3	31.3
Rhododendron maximum	6.3	6.7	0.0	0.0	10.0	11.5
Smilax glauca	4.2	4.1	0.0	0.0	12.5	12.5
Viburnum acerifolium	3.7	3.5	0.0	0.0	15.0	13.5
Kalmia latifolia	3.5	4.1	0.0	0.0	0.0	0.0
Rhododendron sp.	3.3	3.6	0.0	0.0	6.25	6.25
Parthenocissus quinquefolia	2.6	2.5	2.8	2.8	0.0	0.0
Euonymus americanus	1.7	1.7	11.1	11.1	0.0	0.0
Herb						
Laportea canadensis	10.2	13.2	13.2	16.0	20.4	28.2
Dryopteris intermedia	7.3	7.1	4.1	4.5	4.0	4.6
Viola rotundifolia	5.6	5.2	3.7	3.6	8.3	7.4
Viola hastata	4.6	4.6	0.0	0.0	12.2	10.6

Table 1. Continued

Stratum	All (N = 60) 1994	All (N = 60) 2000	Mesic (N = 15) 1994	Mesic (N = 15) 2000	Xeric (N = 12) 1994	Xeric (N = 12) 2000
Polystichum acrostichoides	3.6	4.2	6.0	6.7	0.8	0.5
Gaultheria procumbens	3.4	3.7	0.0	0.0	0.0	0.0
Disporum lanuginosum	3.4	3.1	4.4	3.8	4.0	5.2
Viola canadensis	2.9	2.1	5.8	5.0	1.9	1.4
Thelypteris noveboracensis	2.8	3.2	2.5	2.9	2.1	1.5
Dennstaedtia punctilobula	2.7	3.4	0.1	0.0	5.8	6.6
Dioscorea quaternata	2.7	1.5	0.4	0.2	2.9	3.6
Medeola virginiana	2.6	2.7	0.9	1.2	2.2	1.7
Stellaria pubera	2.5	2.4	4.3	3.8	0.9	0.5
Mitchella repens	1.6	2.5	0.0	0.0	5.2	7.7
Osmorhiza claytonii	1.2	1.5	2.9	3.9	0.0	0.0

short time period or a change in unmeasured environmental variables to which certain strata and/or species may be more sensitive.

Simple linear correlations comparing the linear combination scores (from CCA results) for each stratum were run to determine which strata were most similar in terms of their response to the measured environmental variables (Proc Corr; SAS v. 8.02 2001). Weak multicollinearity existed among some environmental variables (pH and several of the nutrients), but removal of these variables (either pH alone or all the correlated nutrients) did not change the results. The degree of importance of each environmental variable was determined using the CCA intraset correlations (Pearson) from axes 1 and 2. Intraset correlations show the relative magnitudes and importance of the environmental variables in structuring the ordination. They are correlations of the environmental variables and the ordination axes.

RESULTS

Composition and stability

There has been some change in composition in all strata over the six year time span (Table 1), with the change being greatest for the tree seedling stratum followed by the sapling, overstory tree, herb, understory tree, and shrub/vine strata. For the overstory tree stratum, *Quercus rubra* and *Liriodendron tulipifera* increased in importance by 4.5 and 3.8%, respectively in 2000 while most other species decreased in importance, especially *Acer saccharum*, which decreased by 3.7% (Figure 2a). Understory trees of *Acer rubrum* and *Betula alleghaniensis* increased in importance by 2.1 and 1.5%, respectively, while *Acer pensylvanicum* decreased in importance by 2.8%. Saplings of *Picea rubens* and *A. pensylvanicum* increased in importance by 6.3 and 3.5%, respectively, while *A. rubrum* decreased in importance by 3.9%. Shrub/vine changes showed a 0.6% increase in importance for *Kalmia latifolia* and a 0.6% decrease in importance for *Aristolochia macrophylla* (Figure 3). *Laportea canadensis* showed the most change in terms of herbaceous species, increasing by 3% in importance, while most other more common herbs showed little change (Figure 4). In contrast, seedlings of *A. rubrum* increased in importance by 20% and seedlings of *A. pensylvanicum* decreased by 11% (Figure 2a). Based on the most important overstory species, it appears that while overstory trees of *Q. rubra* and *L. tulipifera* increased in importance slightly over the six years, there was little regeneration of these species (i.e., they did not maintain or increase in importance in the 2000 tree seedling, sapling, or understory tree strata), and they may be eventually replaced by *A. rubrum* or other species.

Changes in species composition between 1994 and 2000 did not result in significant differences in diversity within each stratum. However, the overstory tree stratum was significantly more diverse than the understory tree and sapling strata in both years and the seedling stratum in 1994 (Figure 5a; $F = 16.1$, df = 7, $P = <0.0001$ for diversity comparisons of all sites). Understory trees (in 2000) and saplings (in both years) were both significantly less diverse than seedlings. The herb stratum was the most diverse while the shrub/vine stratum was the least diverse of all strata.

When comparing the 15 mesic stands with the 12 xeric stands, *Acer saccharum* exhibited a 10% reduction in overstory stratum importance in the 15 mesic stands (Figures 2b and c, Table 1). The increase in the importance of *Liriodendron tulipifera* as an overstory tree is also stronger in the mesic stands, whereas the increase in importance of *Quercus rubra* as an overstory tree is close to 3% in the mesic stands and 6% in the xeric stands. An increase in importance of *Acer rubrum* as an understory tree was noted only in the xeric stands. In the sapling stratum, *Acer pensylvani-*

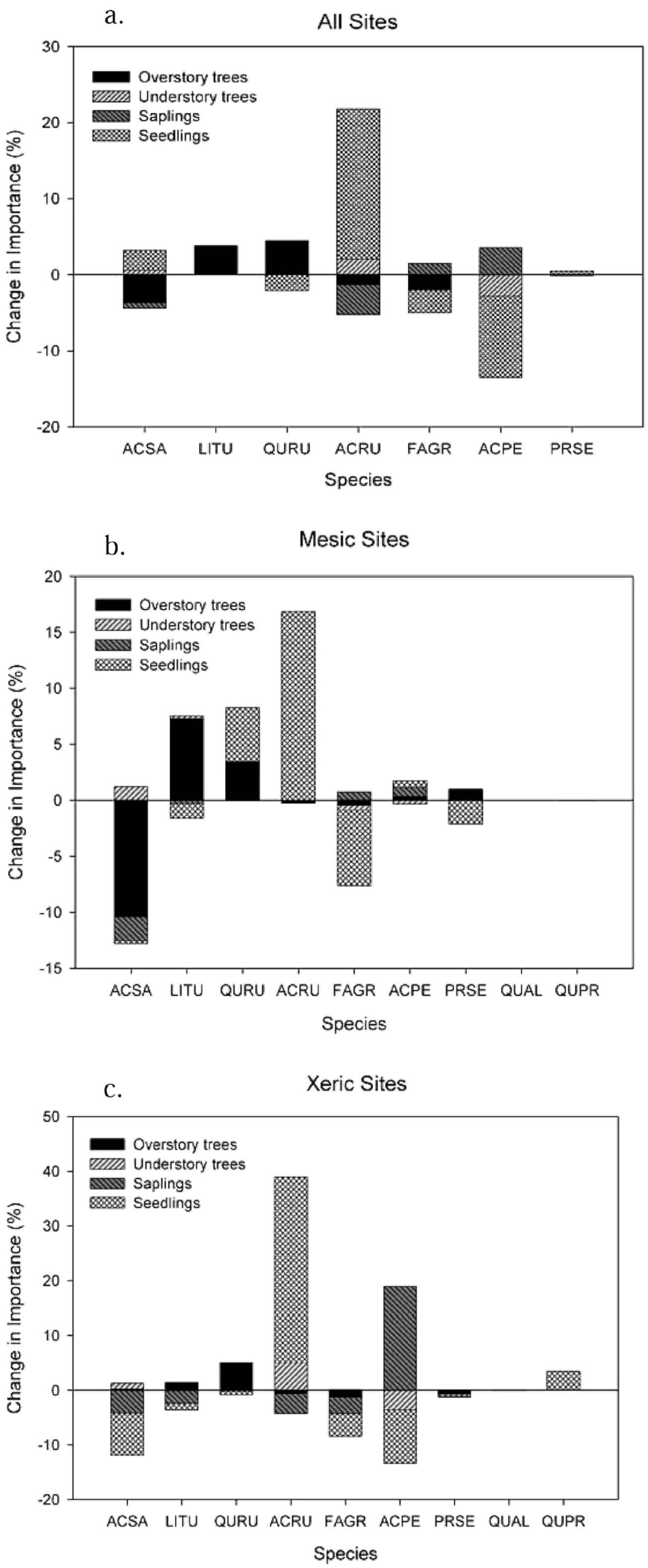

Figure 2. Change in importance value (%) of dominant species for each tree stratum between 1994 and 2000 for a: all sites, b: xeric sites, and c: mesic sites. Species names are represented with the first two letters of the genus and the species epithet as listed in Table 1.

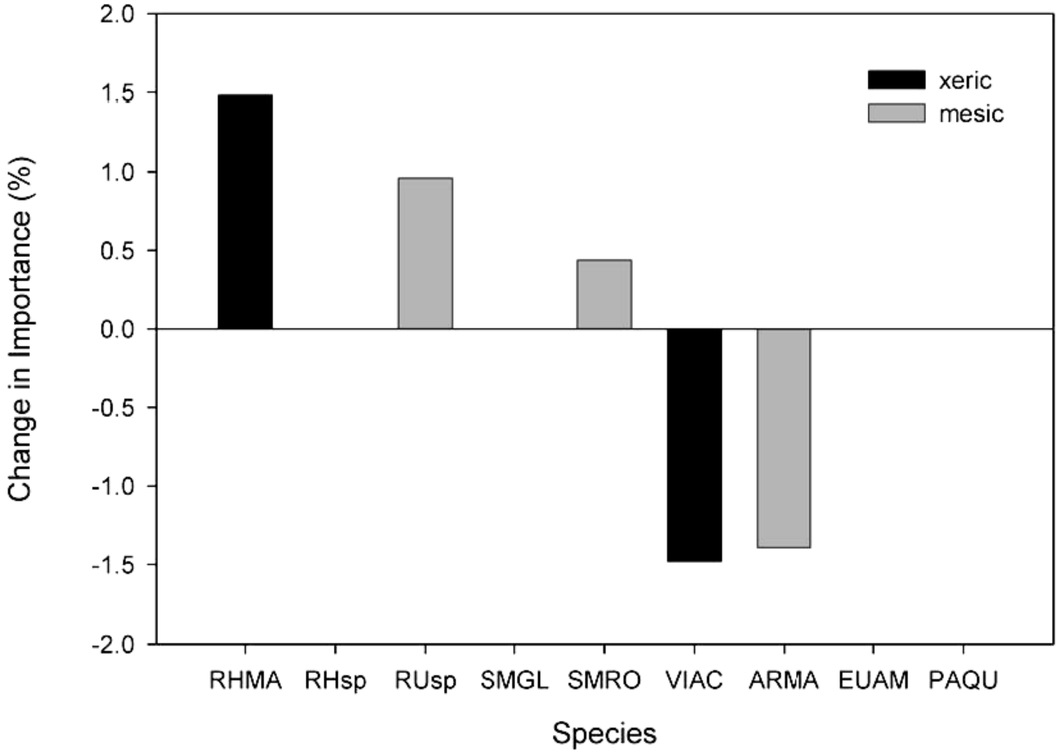

Figure 3. Change in importance values (%) for shrub and vine species between 1994 and 2000 for the most mesic only and most xeric only stands.

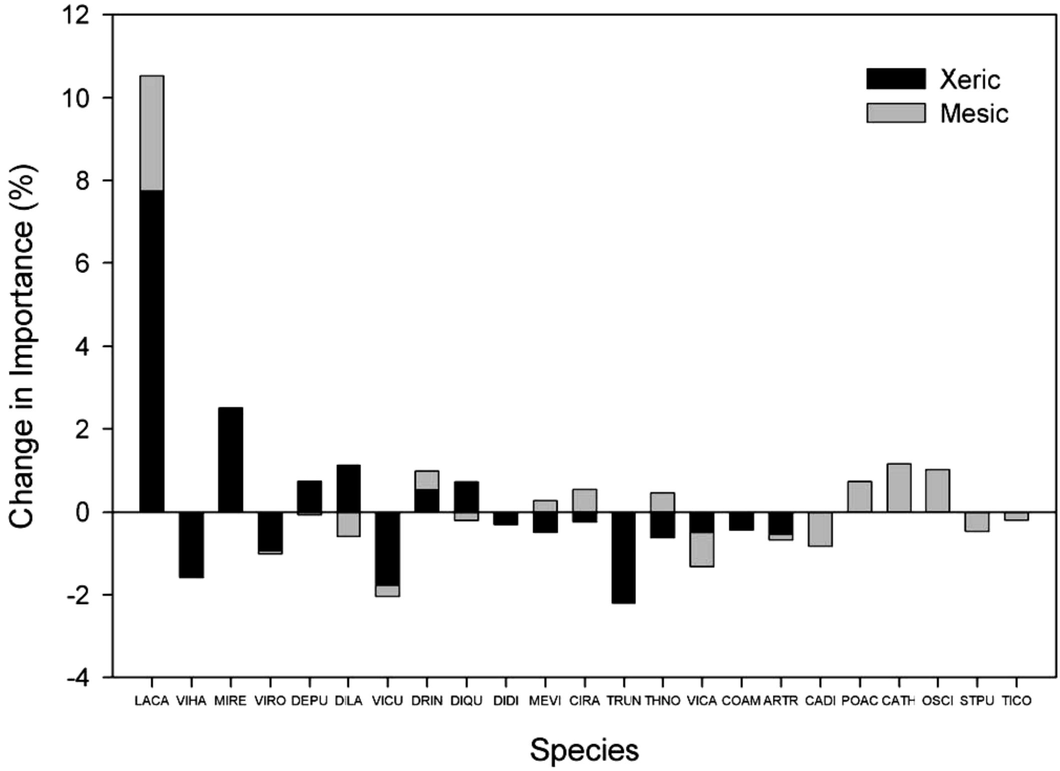

Figure 4. Change in importance values (%) between 1994 and 2000 for herbaceous species using only the most mesic and most xeric stands.

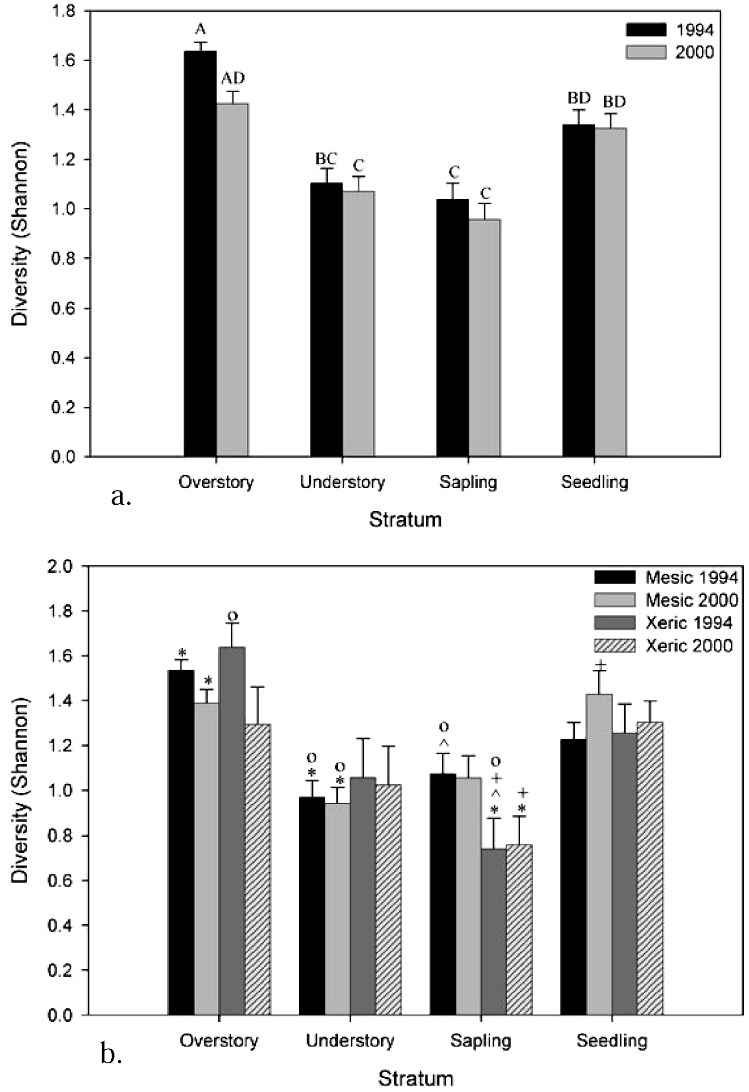

Figure 5. Comparison of diversity (Shannon) both within and among forest strata for a: all sites and b: only the mesic and xeric sites. Strata that share one or more signs (*,^, +, o) are significantly different from each other.

cum increased by over 20% in the xeric stands and less than 5% in the mesic stands. Overall tree vegetation composition changes were greater in the xeric stands. This was especially notable for *A. rubrum* tree seedlings, which increased in importance by 17% on the mesic sites and 34% on the xeric sites. Though there was comparatively little change in shrub and vine species, there was a difference in species changes by land type. *Rhododendron maximum* increased while *Viburnum acerifolium* decreased over the six years and neither was found on mesic sites. *Rubus* sp. and *Smilax rotundifolia* increased over this time period but only on mesic sites, though both were found more abundantly in xeric sites (Figure 3, Table 1). While changes in individual species composition of the herbs within the six years was greater in the xeric sites, with an increase in *Dennsteadstia punctilobula* and *Mitchella repens* and a decrease in two violet species and *Trillium undulatum*, the differences between the sites were better defined by presence or absence of particular species (Figure 4, Table 1). Eighteen xeric site species, including *Mitchella repens*, *Trillium undulatum*, *Conopholis americana*, and *Diphasiastrum digitatum* did not occur on the mesic sites. However, far more species on the mesic sites (60 species) were not found on the xeric sites. Prominent examples were *Hydrophyllum canadense*, *Asarum canadense*, *Actea pachypoda*, *Meehania cordata*, *Lilium superbum*, and *Uvularia grandiflora*.

The 1994 overstory tree stratum on xeric sites was significantly more diverse than understory tree and sapling strata on both xeric and mesic sites in the same year (F = 5.57, df = 15, P =

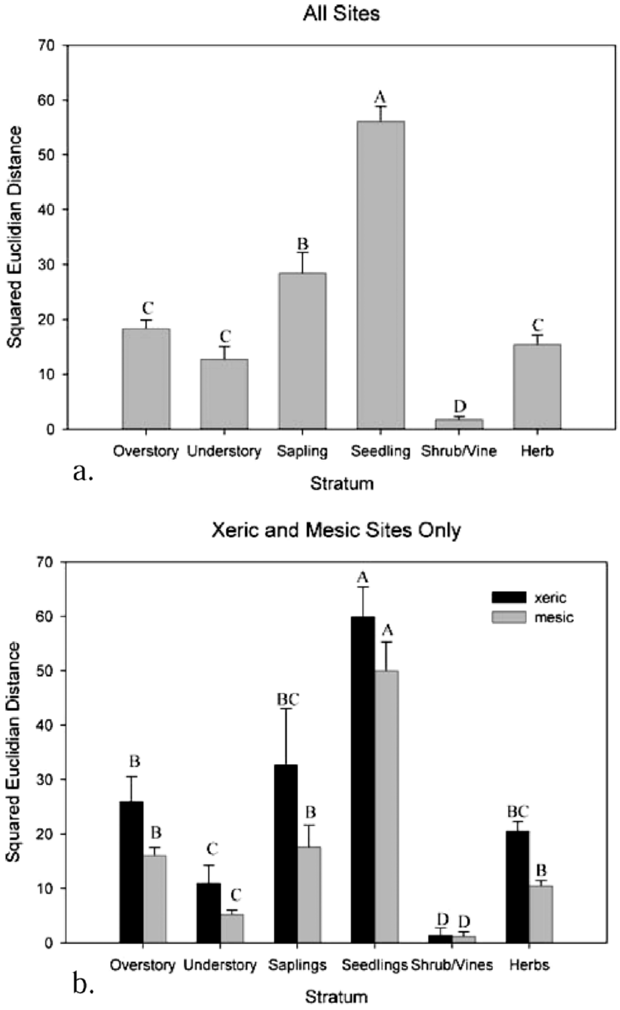

Figure 6. Squared Euclidean distance averages for each stratum for a: all sites and b: xeric and mesic sites only. Those with different letters are significantly different at a p-value ≤ 0.05.

<0.0001 for all diversity comparisons between the xeric and mesic sites). The overstory tree stratum on mesic sites was significantly more diverse than understory trees on mesic sites and saplings on xeric sites in both 1994 and 2000. The sapling stratum on xeric sites was significantly less diverse than the sapling stratum on mesic sites in 1994 and the seedling stratum on mesic sites in 2000 (Figure 5b). Sapling species diversity appears to be the most sensitive to the moisture gradient.

Squared Euclidean distance analysis ($F = 34.8$, df = 5, $P < 0.001$) of overall composition showed the tree seedling stratum had the greatest change in composition between 1994 and 2000, followed by the sapling, overstory tree, herb, understory tree, and shrub/vine strata (Figure 6a). The herb, overstory tree, and understory tree strata did not differ significantly and were the most stable strata after the shrub/vine stratum. Stability patterns for the separate mesic plots ($F = 60.8$, df = 5, $P < 0.001$) showed that the sapling stratum was not significantly different from the overstory tree, understory tree, or herb strata, though the seedling stratum was still the significantly most unstable stratum and the shrub/vine stratum was still the significantly most stable. For the xeric plots, the overstory stratum was significantly less stable than the understory tree and shrub/vine strata and only significantly more stable than the seedling stratum ($F = 34.8$, df = 5, $P < 0.001$). The xeric plots tended to be less stable in all strata compared to the mesic plots, though the differences were not significant (Figure 6b).

Linkages among the strata

The 1994 overstory tree plots were arranged in ordination space along a topographically-based mesic to xeric stand gradient, though clearly several other sites not as strictly defined by topography also followed this gradient. Five

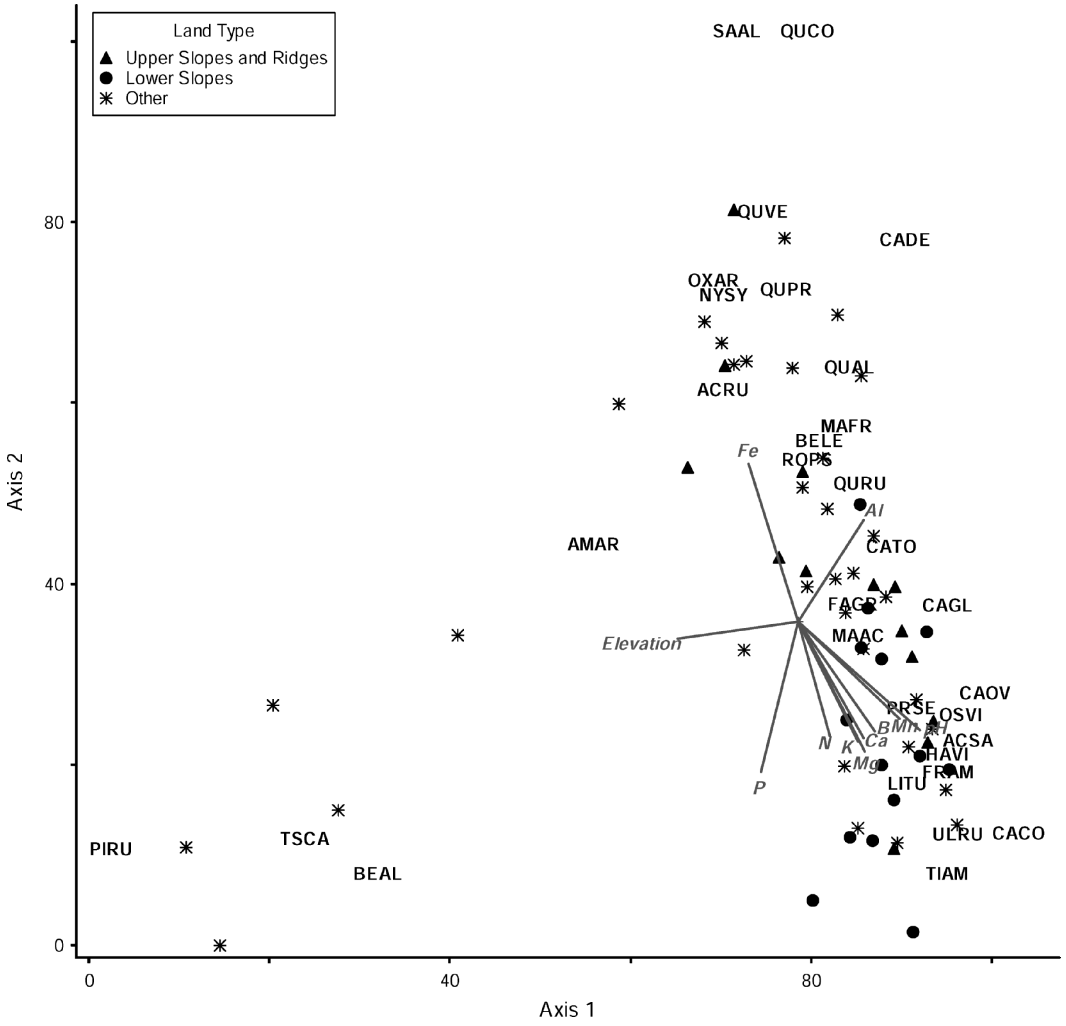

Figure 7. CCA for 1994 overstory stratum. Other strata showed a similar separation of sites and are not presented.

higher elevation stands characterized by *Picea rubens*, *Ilex montana*, and *Tsuga canadensis* also were even better separated along the second axis (Figure 7). The same general trends in ordination space arrangement were found with the other strata and in 2000 and are not presented. For the herb stratum, the first axis was a reversed parallel to the second axis, with its soil fertility and moisture gradient reflected on the first axis, which suggests these gradients may be most important for this stratum or that the elevation gradient is more important for the tree species than the herbaceous species. However, the second axis eigenvalues for all strata were relatively strong for all but the tree seedling and shrub/vine strata (Table 2). The species-environment correlations of Axis 1 and 2 were determined to be significantly different from randomized data, $p \leq 0.01$ for all strata except the seedling and shrub/vine strata (Table 2). The seedling stratum was significantly correlated only with environmental variables related to Axis 1 using 1994 data, and the shrub/vine stratum was significantly correlated only with variables related to Axis 1 in both years. The environmental variables most strongly associated with the overstory tree and understory tree, sapling, and herb strata were pH, elevation, P, K, Mg, Fe, Ca, Mn, B, N, and Al (Table 3), with Fe and Al at the opposite end from the other nutrients and the more mesic stands defined by higher pH, P, K, Mg, Ca, Mn, B, and N values than the more xeric stands. Both the mesic and xeric stands were separated from five higher elevation stands along an elevation gradient (Figure 7). The variables correlated with both the herb and shrub/vine Axes 1 or 2 included pH and Mn.

Simple linear correlations of the CCA ordination Axis 1 showed that all strata except the shrub/vine and sapling strata were significantly linked in 1994 (Table 4). However, the overstory tree, understory tree, sapling and, to a lesser

Table 2. CCA eigenvalues, Monte Carlo-derived *p*-values (999 iterations) for axes 1 and 2, and percent cumulative variance explained for axes 1 and 2 for each stratum using 1994 and 2000 vegetation and 1994 environmental data. ns = Monte Carlo test was not significantly different from what would be expected at random

Stratum	Year	Axis 1	*p*	Axis 2	*p*	Cumulative Variance Explained (%)
Overstory tree	1994	0.606	0.01	0.438	0.01	28.7
	2000	0.648	0.01	0.460	0.01	24.6
Understory tree	1994	0.576	0.01	0.444	0.01	31.0
	2000	0.645	0.01	0.453	0.01	31.5
Sapling	1994	0.546	0.01	0.430	0.02	17.8
	2000	0.876	0.01	0.402	0.01	31.6
Tree seedling	1994	0.517	0.01	ns	ns	8.6
	2000	0.790	0.01	0.439	0.01	21.9
Shrub/vine	1994	0.898	0.01	ns	ns	21.6
	2000	0.894	0.01	ns	ns	10.3
Herb	1994	0.745	0.01	0.566	0.02	14.6
	2000	0.799	0.01	0.739	0.01	12.2

extent, the herb strata also had strong r (Pearson's coefficient) values (above 60% explained variation), whereas the r values were relatively weak for all correlations for the tree seedling and shrub/vine strata. Using 2000 data, the overstory tree and understory tree strata were significantly linked with all other strata except the shrub/vine stratum. The accompanying r values were above 90% for all but the herb stratum. The 2000 sapling stratum was significantly linked with the overstory tree, understory tree, and seedling strata and all associations had very high r values. Likewise, the 2000 seedling stratum was significantly linked with the overstory tree, understory tree, and sapling strata with high r values. Thus, the seedling stratum in terms of Axis 1 became more similar to the other tree strata in 2000 and less similar to the herb and shrub/vine strata, which both became less similar to all tree strata and to each other in 2000 compared to 1994 (Table 4). However, the seedling stratum shared more variables with the herb stratum defined by Axis 2 in 2000 than it did in 1994, but a correlation analysis comparing the two strata using Axis 2 scores did not show a significant correlation.

DISCUSSION

Question 1: How do the six strata of a second-growth, late-successional forest compare in terms of composition and stability over an interval of six years?

Not surprisingly, the tree seedling stratum showed the most change in composition and the least stability within the six year time period. Rarely is this stratum included in analyses of forest dynamics, because it is considered so transient and consequently a poor predictor (Jones and Sharitz 1998, Clark et al. 1998). Our study cannot address whether this change is due to differential transition into the sapling layer, mortality, or fecundity. However, Jones and Sharitz (1998) found that in eight years most surviving seedlings of a floodplain forest in South Carolina grew 30 cm in height or less, suggesting little recruitment into the sapling stratum. Our data show that after six years, *Acer rubrum* is the dominant tree seedling species, switching places with *Acer pensylvanicum* on xeric sites and *Fagus grandiflora* on mesic sites. Both *A. rubrum* and *A. pennsylvanicum* are capable of saturating the forest with seed (Clark et al. 1998). Beckage and Clark (2003) found *A. rubrum* was not favored in any particular microenvironments when compared to *Quercus rubra* and *Liriodendron tulipifera* and concluded that the success of *A. rubrum* is due primarily to demographic stochasticity dependent on high seed production. Thus, based on other studies focusing on the population dynamics of these two species, the instability of our seedling stratum is most likely due to episodic changes in fecundity and not to differential survival or transition into the sapling stratum.

In contrast, the instability of the sapling layer is most likely due to a relatively high rate of mortality, if our study site is similar to other studies. According to Pinero et al. (1984) and Shelton and Cain (1999), juvenile (sapling) mortality has a greater effect on the finite rate of population increase of particular species in a sensitivity analysis than either large tree mortality or overall seed production. For saplings, the relatively high mortality of certain species is most likely due to a lack of shade-tolerance and an inability to survive suppressed growth (Smallidge and Leopold 1994, Kobe et al. 1995). In this six-year time period, *Acer rubrum* and *Acer pensylvanicum* appear to be alternating in terms of relative importance within the tree seedling stratum (where *A. rubrum* dominates) to the sapling stratum (where *A. pensylvanicum* dominates) back to the understory tree stratum (where *A. rubrum* dominates). Attributing the sapling stratum's instability to high mortality (of

Table 3. Most important environmental variables by stratum in years 1994 and 2000 ranked using the CCA intraset correlations from axes 1 and 2. All correlations shown are 0.5 or above in value. Signs indicate the direction of correlation. Axis 1 was the only axis significantly different from random for tree seedling (1994 only) and shrubs/vines (both years). Rock cover and Cu were not significant for any stratum and are not shown. ns = not significant (intraset correlation is not ≥ 0.5). CWD = coarse woody debris

		Overstory tree		Understory tree		Sapling		Seedling		Shrub/vine	Herb	
	Year	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 1	Axis 2
Bryophyte	1994	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
	2000	ns	ns	−0.52	ns	ns	ns	ns	ns	ns	ns	ns
CWD	1994	ns	ns	ns	ns	ns	+0.57	ns	ns	ns	ns	ns
	2000	ns	ns	ns	+0.50	ns	+0.54	ns	ns	ns	ns	ns
Elevation	1994	−0.72	ns	−0.70	ns	−0.71	ns	ns	ns	ns	ns	ns
	2000	−0.73	ns	−0.71	ns	−0.82	ns	−0.77	ns	ns	ns	ns
Slope Aspect	1994	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
	2000	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	−0.51
Slope Inclination	1994	ns	ns	ns	ns	ns	ns	ns	ns	+0.59	ns	ns
	2000	ns	ns	ns	ns	ns	ns	ns	ns	+0.69	ns	ns
Ca	1994	ns	−0.64	ns	ns	ns	ns	ns	ns	ns	+0.84	ns
	2000	ns	ns	ns	−0.50	ns	−0.70	ns	−0.69	ns	+0.50	−0.50
Mg	1994	ns	−0.66	ns	ns	ns	ns	ns	ns	ns	+0.80	ns
	2000	ns	ns	ns	−0.51	ns	−0.76	ns	−0.68	ns	+0.50	−0.50
P	1994	ns	−0.83	ns	−0.74	ns	−0.60	ns	ns	ns	ns	ns
	2000	ns	ns	ns	−0.70	ns	−0.69	ns	−0.81	ns	ns	ns
K	1994	ns	−0.72	ns	−0.55	ns	−0.56	ns	ns	ns	+0.55	ns
	2000	ns	ns	ns	−0.64	ns	−0.69	ns	−0.74	ns	+0.58	−0.50
Mn	1994	+0.60	−0.54	+0.63	ns	+0.55	ns	ns	ns	+0.52	+0.61	ns
	2000	+0.58	−0.55	+0.50	−0.61	ns	−0.68	ns	−0.54	+0.51	+0.57	−0.56
Zn	1994	ns	−0.52	ns	−0.56	ns	−0.53	ns	ns	ns	ns	ns
	2000	ns	−0.51	ns	−0.54	ns	−0.58	ns	−0.57	ns	+0.71	ns
Fe	1994	ns	+0.87	ns	+0.82	ns	+0.86	ns	ns	ns	−0.63	ns
	2000	ns	+0.86	ns	+0.90	ns	+0.88	ns	+0.74	ns	−0.65	+0.54
Al	1994	ns	+0.56	ns	ns	ns	ns	ns	ns	ns	ns	ns
	2000	ns	+0.56	ns	ns	ns	ns	ns	ns	ns	ns	ns
B	1994	ns	−0.61	ns	ns	ns	ns	ns	ns	ns	+0.87	ns
	2000	ns	−0.65	ns	−0.50	ns	−0.70	ns	−0.61	ns	+0.50	−0.52
N	1994	ns	−0.63	ns	−0.53	ns	ns	ns	ns	ns	ns	ns
	2000	ns	−0.63	ns	−0.56	ns	−0.70	ns	−0.69	ns	+0.56	ns
pH	1994	+0.71	−0.63	+0.71	ns	+0.55	−0.51	ns	ns	+0.55	+0.78	ns
	2000	+0.69	−0.63	+0.62	−0.60	+0.54	−0.70	+0.57	−0.66	+0.59	+0.63	−0.67

Table 4. Simple linear correlation of CCA linear combination scores of each stratum for axis 1 for years 1994 and 2000. Highlighted values are those with $p \leq 0.01$ and r above 0.50

		Overstory tree		Understory tree		Sapling		Tree Seedling		Shrub/Vine		Herb	
	Year	r	*p*	r	*p*	r	*p*	r	*p*	r	*p*	r	*p*
Overstory Tree	1994	–	–										
	2000	–	–										
Understory tree	1994	**0.99**	**<0.01**	–	–								
	2000	**0.98**	**<0.01**	–	–								
Sapling	1994	**0.93**	**<0.01**	**0.92**	**<0.01**	–	–						
	2000	**0.96**	**<0.01**	**0.96**	**<0.01**	–	–						
Seedling	1994	0.42	<0.01	0.42	<0.01	0.47	<0.01	–	–				
	2000	**0.97**	**<0.01**	**0.96**	**<0.01**	**0.98**	**<0.01**	–	–				
Shrub/vine	1994	0.29	0.02	0.31	0.02	0.24	0.07	0.33	0.01	–	–		
	2000	0.19	0.15	0.12	0.34	0.09	0.48	0.13	0.32	–	–		
Herb	1994	**0.78**	**<0.01**	**0.82**	**<0.01**	**0.74**	**<0.01**	**0.66**	**<0.01**	0.50	<0.01	–	–
	2000	0.34	0.01	0.30	0.02	0.21	0.11	0.20	0.12	0.22	0.09	–	–

multiple species, including *A. pensylvanicum*) is further supported by our finding that the sapling stratum was the least diverse of all the strata and that this lower diversity was most pronounced in the more xeric stands. Future small-scale disturbance events forming canopy gaps may change this six-year trend, allowing potential coexistence of shade-tolerant and shade-intolerant species on mesic sites as found in one steep, talus slope old-growth forest in West Virginia in which deer pressure was low (Abrams et al. 1998).

Stable perennial species dominate both the shrub/vine and herb strata. Nonetheless, some perennial herbaceous plants are noted for responding rapidly to increasing light and nutrients with greater vegetative productivity and increased sexual reproduction (Muller 1990, Marino et al. 1997, John and Turkington 1997). A stable herbaceous layer may equate to a lack of disturbance when light and nutrients are relatively stable. The small amount of potential tree mortality (mainly *Acer saccharum*) evident in the stable overstory tree stratum appears to be unimportant for the herb stratum in terms of disturbance-caused environmental change. Moreover, the decrease in the importance of *A. saccharum* during this time period is more likely a reflection of faster growing trees of *Quercus rubra* and *Liriodendron tulipifera* and not mortality of *A. saccharum*. Many of the *A. saccharum* overstory trees are very old remnants of harvesting operations in the early 1900s when this species was not a valued commodity and recruitment was high, especially compared to shade-intolerant species such as oak (Schular and Fajvan 1999).

Based on the understory stratum, the more xeric stands are more likely to have canopies dominated by *Acer rubrum* over time (conditions being equal) while the more mesic sites are more likely to be dominated by *Acer saccharum*. Several other studies have found similar patterns in mixed-mesophytic forests in Ohio (McCarthy et al. 2001) and in West Virginia (Tift and Fajvan 1999), a *Quercus prinus*-dominated forest in southeastern Pennsylvania (Mikan et al. 1994), mixed oak forests in central Pennsylvania (Nowacki and Abrams 1991), and in upland oak forests of Massachusetts and New York (Lorimer 1984). Likewise, xeric stands are more likely to be represented by *Rhododendron maximum* for shrubs and *Dennstaedtia punctilobula* or *Mitchella repens* for herbs over time, whereas the mesic sites are more likely to be represented by *Rubus* sp. or *Smilax rotundifolia* for shrubs and *Medeola virginiana* or *Thelypteris noveborancensis* for herbs. Other research has associated *R. maximum* with north-facing slopes or more mesic sites (Nilsen et al. 1999, Lei et al. 2002, Clinton 2003), but Dobbs (1998) concluded that *R. maximum* is colonizing less mesic sites due to fire suppression and a lack of grazing (ie., cattle), which supports our findings. *Dennstaedtia punctilobula* has been documented as colonizing relatively acidic soils (Sharpe and Halofsky 2004) and xeric sites (Hill and Silander 2001) in northeastern deciduous forests, but is also known to colonize wide gradients of edaphic conditions (Cody et al. 1977). The ability of species such as *R. maximum* and *D. punctilobula* to out-compete other native species, especially in drier, less fertile sites, may help explain the high levels of sapling mortality found in our study. The reduction in abundance of *Trillium undulatum* during this time period in the xeric stands may be indicative of high levels of deer herbivory (Augustine and Frelich 1998). *Trillium* species could also be negatively responding to soil acidity, though *T. undulatum* is known to colonize more acidic sites than other *Trillium* species (Thompson and Sharpe 2005).

It is important to note that different land types are likely to follow different successional trajectories unless a disturbance event, such as fire or harvesting, is introduced, such that the current species composition is disrupted. Such a disruption did occur in the early 1900s, thus allowing *Quercus rubra* to become significant component of the overstory stratum of more mesic sites in our study area (Schular and Fajvan 1999). Because of a lack of such disturbance, we predicted that the mesic plots would be less stable than the xeric plots, but our results showed the opposite trend. The xeric plots may suffer more than the mesic plots from combined effects of lower fecundity and survivorship in a more stressful environment possibly exacerbated by competition from associated species or deer herbivory (Lyon and Sharpe 1996, Buckley et al. 1998, Martin and Baltzinger 2002).

Question 2: Are these strata linked in terms of their response to environmental variables and is any linkage related to the degree of stability?

Some of the strata do respond similarly to our measured environmental variables, and this linkage is strongest with the overstory tree and understory tree strata (both relatively stable) and the sapling stratum (relatively unstable) for both years (Table 4, Figure 6). The tree seedling stratum, which was the least stable stratum, was linked to the other tree strata in 2000, switching from a link with the herb stratum in 1994. The stable herb stratum is correlated most with the understory and overstory tree strata, and is also influenced by several other variables found more closely associated with the shrub/vine stratum, another stable stratum, but these correlations do not hold in 2000. Because linkages among the overstory tree, understory tree, and herb strata do exist, our results agree in part with those of Gilliam et al. (1995) and Berger and Puettmann (2000). However, while linkages (i.e., shared responses to the environment) in the sapling, understory tree and overstory tree strata remained relatively stable over six years, the response of the ground layer (herb, shrub/vine, and tree seedlings) to its environment appears to be more dynamic within the same time period.

The linked strata appear to be responding similarly to both a moisture and soil fertility gradient. Muller (1982) found similar results in both an old-growth and second-growth forest in southeastern Kentucky in which *Fagus grandifolia* and *Acer saccharum* dominated stands were characterized by intermediate soil fertility and high soil moisture while *Quercus prinus* and *Acer rubrum* dominated stands were characterized by low soil fertility and low soil moisture. Small and McCarthy (2005) and Hutchinson et al. (1999) also found a relationship between high species richness and both high soil moisture and soil fertility. Additionally, both of the previous studies documented a connection between these two gradients such that more xeric sites (topographically defined) also tended to be less fertile. We did not take direct measures of moisture or light in our study, which may have made determination of the relative importance of the moisture and fertility gradient possible.

This difference in response between the upper strata and the lower strata may be due to undetected small-scale disturbance, stress, or biological processes that resulted in an unmeasured change in our focus environmental variables or other unmeasured microclimatic variables between 1994 and 2000. Inter-strata competition may explain the apparent fickleness of the tree seedling layer. For instance, there are several studies that show a negative influence of the shrub layer on herbs and seedlings (Maguire and Forman 1983, Berkowitz et al. 1995, Hedman and Van Lear 1995, Wagner and Radosevich 1998) as well as studies that show the herb and tree seedling layers may be competing (Huebner et al. 1995, Buckley et al. 1998). Other studies show a facilitatory effect of shrubs or herbs on tree seedlings (Berkowitz et al. 1995, Callaway et al. 1996). Differences between the upper and lower strata also may be because the herb and shrub/vine strata in our study area are less influenced by elevation than soil fertility and moisture when compared to the upper strata. Soil moisture and fertility are more likely to change than elevation over a short period due to year-to-year precipitation differences and species composition of the leaf litter (Vesterdal and Raulund-Rasmussen 1998, Knoepp et al. 2005) and, certainly, over a long period due to disturbance events or land use history (Fraterrigo et al. 2005). At coarser scales than our study, it is likely that there is also a connection between an elevation gradient and soil moisture and fertility gradients, which may in turn reveal a stronger link between the upper and lower strata (Reed et al. 1993).

The dynamic nature of the seedling stratum over the short term reveals how predictions of successional trends without such data are problematic. This may appear to support management that disregards this stratum. However, species compositional changes in response to treatments or disturbances that affect the upper strata, especially the saplings, will be dependent on the tree seedling composition just prior to the event. Given the variable influences of the tree seedlings, herbs, shrubs, and vines on each other, these results further support the importance of the ground strata. Because successional trajectories depend on starting conditions, we argue that ignoring these strata is not a sound management strategy when prescribing and scheduling disturbance events. Moreover, because disturbances (i.e., tornadoes and hurricanes) are often unpredictable it may be wise to monitor and manage these strata at least as often as the upper tree strata.

Summary

The stable strata of this mixed mesophytic forest did tend to be linked in terms of response to the chosen environmental variables. However, linkages among strata were weaker for the tree seedling, shrub/vine, and herb strata, while the relatively unstable sapling stratum appeared closely linked to the overstory tree and understory tree strata. The latter suggests it would be unwise to assume a similar response to environmental change caused by a disturbance event for the upper and lower strata. Moreover, because tree seedling composition is likely to vary over the short-term, successional trajectories, which are dependent on starting conditions, are only possible if monitored and managed at least as often as the other layers.

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