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Long-term change in ground-layer vegetation of deciduous forests of the North Carolina Piedmont, USA

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Summary

1 In Southeastern North America residual mature deciduous forests have long been assumed to represent the stable endpoint of succession, with local compositional variation reflecting primarily variation in soils and topographic position. However, the long-term stability of understorey vegetation in this region has rarely been examined due to the lack of reliable baseline data.
2 We resampled a series of permanently marked vegetation plots spanning a range of soil and site conditions in the Piedmont of North Carolina to evaluate compositional change in the understorey of putative 'climax' hardwood forests over a 23-year period. We examined all ground-layer species for change in total and native species richness at 25 m^2 and 1000 m^2, change in species composition and variation in richness and composition with environment.
3 Although native and total species richness remained nearly constant, there was a significant decline in herb richness balanced by a strong increase in tree seedling richness. Species composition changed significantly across all plots with strong evidence of consistency in the direction of plot-level compositional change.
4 Change in herb species richness over time was strongly correlated with environment at 25 m^2. Sites with higher pH, percentage sand and soil cations exhibited less decline in herb species than other sites. Understorey richness tended to increase more over time on low-elevation, mesic sites as opposed to higher, dry sites.
5 The systematic changes in herbaceous species richness and woody seedling abundance do not support the expectation of stability and may be due to the elimination of ground fires and widespread grazing in the early twentieth century, exotic species invasion or increases in white-tailed deer populations.
6 The lack of stability we observed for mature vegetation of the Carolina Piedmont is likely to be representative of temperate forests in general. Our results suggest that the common practice of projecting vegetation change based on contemporary mature vegetation as the expected endpoint is unreliable and results obtained must be viewed with caution.

Key-words: climax, forest dynamics, long-term change, succession, understorey vegetation

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Introduction

Deviation from an expected steady-state forest composition is typically used to assess the successional status of existing forest stands and to provide a target for management and restoration activities. In the Piedmont of the Southeastern United States, as elsewhere in the temperate forest region, remnant hardwood forest stands have long been assumed to represent the stable endpoint of succession (e.g. Ashe 1897; Oosting 1942; Braun 1950; Peet & Christensen 1980; Delcourt & Delcourt 2000), with local compositional variation reflecting primarily variation in soils and topographic position (e.g. Peet & Christensen 1980; Christensen & Peet 1981). However, this assumption of stability has rarely been tested and is open to question. Long-term studies of forest tree composition suggest that broad, region-wide changes are occurring (e.g. Peet & Loucks 1977; Abrams 1992, 2003; McDonald *et al.* 2002,

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2003). Although the exact causes of on-going compositional change in Southeastern forests are uncertain, there are many possible mechanisms. Over the preceding two centuries most of these forests have experienced the elimination of frequent, low-intensity ground fires, the rise and fall of domestic stock and feral hog populations, selective extraction of timber products, exotic species invasions, near extirpation followed by dramatic increases in deer populations to unprecedented levels, progressive landscape fragmentation and anthropogenic climate change. In addition, natural disturbances such as hurricanes are known to have major impacts on forest composition.

Given the changing composition of the forest canopy and the many factors that could be driving it, change might also be expected among ground-layer plants such as herbs, shrubs and tree seedlings. From a biodiversity perspective the ground layer is particularly important as many species are confined to this layer and the remainder must pass through it during their seedling stages. Remarkably, there is little long-term documentation of compositional change in the understorey of the temperate deciduous forests of eastern North America. The limited previous work on understorey change in temperate forests suggests a general pattern of local native species decline with accompanying increases in exotic species (Brewer 1980; Davison & Forman 1982; Drayton & Primack 1996; Rooney & Dress 1997; Rooney *et al*. 2004), but none of these studies have been based on resampling of permanently marked plots. Studies done without plot resampling and multiple site comparisons have limited ability to accurately detect regional changes in understorey species composition. Generalization is further restricted if studies are conducted at only one spatial scale, given the variability of understorey composition and diversity relative to site conditions in temperate deciduous forests (e.g. Palmer 1990; Small & McCarthy 2002).

The Piedmont region of North Carolina has served for many years as a model system for the study of forest succession (e.g. Oosting 1942; Keever 1950; Christensen & Peet 1981). Peet and Christensen established in 1977 a series of multi-scale, permanently marked vegetation plots to document compositional patterns and long-term dynamics across a broad range of soil types and site conditions. We resampled after 23 years as many of the plots as possible to ask three general questions. (1) Is the understorey of mature hardwood forest stands in the study area exhibiting compositional change over time and, if so, is there evidence for consistency in the direction of change across the study area? (2) Which species show the greatest rates of gain, loss and overall variability at different scales, and which species attributes, if any, are typically associated with such trends? (3) Is change in composition or species richness correlated with environment or with richness of the original vegetation? We expected to find that (i) abundance and diversity of herbaceous native species had declined due to recent increases in deer population density and increased woody species density, (ii) the frequency of shade-tolerant woody species had increased in the understorey as a long-term consequence of elimination in the early twentieth century of frequent ground fires and grazing by domestic stock, and (iii) the extent of compositional change has been highest in more productive stands because establishment and growth of new species should be less resource-limited on such sites and deer are known to preferentially graze on sites with more nutrient-rich foliage (Swift 1948).

Materials and methods

STUDY AREA

The study area is in the Piedmont region of the Southeastern United States, in and near the Duke University Forest located in Orange and Durham Counties, North Carolina. The region is characterized by a warm temperate climate, with a mean monthly temperature in July of 26.1 °C and in January of 4.3 °C. Mean annual precipitation is 1.10 m, with July and August the wettest months (National Climatic Data Center 2001). Topography ranges from flatlands of the Durham Triassic Basin to rolling hills and occasional steep slopes and bluffs of the uplands of the Carolina Slate Belt. The elevation within the study area ranges from 75 m to 255 m.

The ancient landscape of the study area is characterized by soils with low nutrient status and high clay content. Soil parent material varies widely and includes areas of sedimentary mudstones and sandstones of the Triassic Basin, metamorphic volcanic ash (Carolina slate) of primarily Cambrian age, and igneous intrusions ranging from acidic granites to mafic diabases (Daniels *et al*. 1999), all of Triassic age or older. The predominant Carolina slate weathers to infertile soil dominated by kaolinitic clays, whereas soils derived from diorite or diabase tend to have higher levels of available nutrients owing primarily to the higher percentage of 2 : 1 lattice clays. Strong soil differences often occur over horizontal distances of less than a metre, reflecting underlying geology, and vegetation composition varies in response to these conditions (Peet & Christensen 1980; Palmer 1990; Daniels *et al*. 1999). Further details on hardwood vegetation variation in relation to soil conditions can be found in Peet & Christensen (1980). The hardwood plots used in this study span a broad range of soil types and are representative of conditions typically found throughout the North Carolina Piedmont.

The North Carolina Piedmont has a long history of anthropogenic disturbance and much of the current landscape is dominated by successional pine (*Pinus taeda*) forest growing on sites abandoned following agriculture. A number of areas, mostly less suitable for cultivation, have remained as hardwood-dominated forest, and these sites have a history of selective cutting and domestic livestock grazing (Healy 1985). Although

fire has been suppressed since the early 20th century, the original forest understorey vegetation experienced frequent, low-intensity fires set by aboriginal populations, and subsequently by early European settlers, to suppress woody growth and encourage an herbaceous understorey favourable for game and domestic animals (Hatley 1977; Frost 1998). Grazing, which may have mimicked some effects of low-intensity ground fires by suppressing woody growth, persisted in the hardwood forest stands until acquisition for Duke University in the 1920s (McDonald *et al*. 2002). The plots used in this study were originally selected in 1977 for their mature hardwood canopy and were required to show no more than minimal evidence of post-1900 human disturbance (Peet & Christensen 1980; Christensen & Peet 1984). The forest stands all appeared to have retained a hardwood canopy prior to 1900, although livestock grazing and selective timber harvest were likely pervasive during the 19th century.

Although the hardwood stands sampled have remained free of overt anthropogenic disturbance for over 100 years, other forms of disturbance have occurred during this interval. In particular, white-tailed deer (*Odocoileus virginianus*) populations of the northern North Carolina Piedmont more than doubled over the 14-year period of 1985–99 (North Carolina Wildlife Resources Commission, unpublished data). Studies conducted elsewhere in North American temperate forests have found deer to be responsible for significant declines in richness and cover of understorey vegetation (e.g. Waller & Alverson 1997; Rooney *et al*. 2004), so such impacts were to be expected in the Duke Forest, albeit perhaps to a lesser degree owing to the infertile soils causing foliar nutrient contents to be relatively low.

Hurricanes provide an additional source of disturbance. In particular, Hurricane Fran passed through the region in September, 1996. The eye of Fran passed 15 miles east of Duke Forest, and the associated strong north-east winds (up to 35 m s^{-1}) caused severe damage, making it the most destructive natural disaster ever to strike North Carolina (Carpino 1998). Damage in Duke Forest from Fran was patchy and in mature hardwood forests occurred along river bottoms due to flooded soil conditions, as well as on exposed ridge slopes and tops (Carpino 1998).

FIELD METHODS

In 1977, Peet and Christensen established a series of 105 permanent plots in mature hardwood forest as part of a study of secondary succession (Peet & Christensen 1980, 1988; Christensen & Peet 1981, 1984). We resampled the 36 of these that could be precisely relocated and that had not experienced extreme damage during Hurricane Fran, including 5 plots with relatively high levels of hurricane damage, as shown by felled trees and a decline in stand basal area of ≥ 10 m^{-2} ha. Resampling was conducted during the interval of 1999–2001 (referenced as 2000) using the same methodology as in 1977, except for leaf cover scale (see description below). During both sampling periods vegetation was recorded almost exclusively between May 15 and August 15. Spring ephemeral species are typically gone by May 1 and the summer forbs are generally well developed by mid May. The basic sampling unit was a 0.1 ha (20 m × 50 m) plot with a 50 m transect running the length of the plot down the centreline. Frequency and cover (foliage ≤ 1 m high) of all ground-layer vascular plant species were recorded in twenty-five 0.5 × 2 m contiguous subplots arranged along this transect. All species present in the 0.1 ha plot, but absent in the subplots, were also recorded as present. Multiple environmental, soil nutrient and soil texture variables were measured for each plot in 1977 (Table 1; see also Peet & Christensen 1980) and were assumed to have little decade-scale variation.

In the original 1977 survey, leaf cover (below 1 m height) was estimated to the nearest percent for each species per subplot. In the 2000 resurvey, leaf cover was estimated using the protocol of the North Carolina Vegetation Survey, which assigns cover based on a 10-point scale (see Peet *et al*. 1998). To allow comparison across years, the 10-point cover scale was converted to percentages using the geometric mean of each cover class (Oksanen 1976). The average percentage cover for each species per plot was calculated as the average cover across subplots. Species present in the 0.1 ha plot but absent in the subplots were assigned cover values of 0.02% (or half the lowest numerical value possible).

To ensure accurate comparisons of species richness and composition between sample periods, all species

Table 1 Environmental variables recorded for each plot in 1977

Variable	Description	Mean	SD	Min.	Max.
pH	Soil pH in topsoil	4.76	0.586	3.62	5.92
Ca	Ca in topsoil (p.p.m.)	418.59	404.128	37.40	1268.80
Mg	Mg in topsoil (p.p.m.)	101.32	92.633	6.48	306.02
K	K in topsoil (p.p.m.)	67.37	22.911	25.74	117.32
PO_4	PO_4 in topsoil (p.p.m.)	3.38	2.134	0.78	12.98
% sand	Sand in A horizon (%)	56.39	11.015	36.00	75.00
% silt	Silt in A horizon (%)	33.61	7.572	21.00	46.00
% clay	Clay in A horizon (%)	10.56	4.644	4.00	22.00
Slope	Local slope angle (°)	8.78	8.642	0.00	32.00
Elevation	Plot elevation (m)	143.44	36.134	79.30	253.15

nomenclature was standardized to conform to Kartesz (1999). In addition, to control for possible taxonomic inconsistencies across years, separate data sets were created for each year for calculations of species richness and composition. For comparison of species richness, we maintained full species identifications for most taxa and grouped to genera those species considered particularly difficult to split from related taxa based on vegetative characteristics. For comparison of species composition, all potentially problematic species were grouped to genus and all family level and unknown designations were removed. The combined final species list for richness contained 331 taxa with 314 identified to species, 11 to genus, and 6 to family or above. The final species list for comparison of composition contained 302 taxa, with 285 identified to species and 17 to genus. All woody (shrub and tree) species were assigned a shade tolerance value of low, mid or high, following the United States Department of Agriculture designations (USDA 2002).

CHANGE IN FOREST UNDERSTOREY RICHNESS AND COMPOSITION

We compared changes in total understorey species richness and species richness grouped by growth form (tree, shrub or herb) at each site at the cumulative subplot (25 m^2) and full plot (1000 m^2) scales. The significance of change in richness between survey periods (1977–2000) was tested using paired exact randomization tests of the difference in richness over time with 1000 randomizations and plots serving as replicates (H_0: Difference in richness across years is equal to zero; Manly 1997). Change in richness in hurricane-damaged plots (5 out of 36) was qualitatively compared to all other plots.

To assess changes in understorey composition between 1977 and 2000, we ran a block multi-response permutation procedure (MRPP) to test the null hypothesis of no change between survey periods in the understorey composition within plots at 25 m^2 and 1000 m^2. Block MRPP is a multivariate permutation procedure for use with paired-plot compositional data. Tests of significance are based on random permutations across years of within plot differences in species composition, calculated using a Euclidean dissimilarity measure and species presence/absence (Mielke & Berry 1982, 2001). Tests were performed with PC-ORD version 4.24 (McCune & Mefford 1999).

Consistency in the direction of compositional change among plots at 1000 m^2 was assessed using non-metric multidimensional scaling (NMS) with varimax rotation (Kruskal 1964; Mather 1976) as implemented in PC-ORD version 4.24 (McCune & Mefford 1999). Species occurring in fewer than two plots were deleted from the data set prior to the NMS ordination. Compositional dissimilarity between plots was assessed using the Bray–Curtis dissimilarity measure and average species cover. Appropriate dimensionality for the ordination was assessed using a Monte Carlo test. The direction of compositional change between the two observations of each plot was examined by constructing vectors between plot pairs on the two-dimensional ordination (McCune & Grace 2002). The length of each vector represents the amount of compositional change based on dissimilarity between plot observations. The relative positions of the 1977 and 2000 observations on an ordination axis were compared with a two-sample *t*-test (Peterson & McCune 2001). Plots that experienced hurricane damage were identified separately in the ordination diagram to examine the direction and extent of compositional change in relation to other hardwood plots.

An indicator species analysis (Dufrêne & Legendre 1997) was performed in PC-ORD to examine relationships of individual species to the 1977 and 2000 sample periods. The test provides a method for assessing which species have the strongest affinities to one time period, thereby emphasizing species with the strongest influence on compositional change over time in the NMS ordination. The indicator value for each species was calculated by combining the relative abundance and relative frequency of each species in each year, and the highest indicator value (IV_{max}) across years was used as the overall indicator value for each species. The statistical significance of IV_{max} for each species was evaluated using a Monte Carlo test with 1000 randomizations.

CHANGE IN SPECIES RICHNESS AND COMPOSITION WITH ENVIRONMENT

Spearman's rank correlation was used to test the correlation of environmental factors (Table 1) with change in richness at 25 m^2 and 1000 m^2 for species grouped by growth form (herb, shrub or tree). A correlation analysis was also used to examine the change in richness for each growth form in relation to the original 1977 richness at each scale.

To assess whether change in species composition varied with environment, the lengths of the paired plot vectors in the NMS ordination were compared to the primary environmental ordination axis. Individual environmental variables were first overlaid on the NMS ordination with a vector biplot as implemented in PC-ORD. The angles of each environmental vector in the ordination indicate the direction of highest correlation, and the lengths represent the strength of the correlation. A varimax rotation was used to maximize the alignment of environmental variables with one primary ordination axis (Mather 1976). Correlations between the ordination axes and environmental variables were calculated with Pearson's r^2. The lengths of the paired-plot vectors were correlated with 1977 plot positions on the primary environmental ordination axis using Spearman's rank correlation to test whether the extent of compositional change between plots varied with environment.

Results

CHANGE IN UNDERSTOREY SPECIES RICHNESS

Total species richness (across all plots) decreased over time with much of the loss driven by a decrease in herb species. Peet & Christensen (1980) recorded a total of 272 species throughout the hardwood plots in 1977, whereas the 2000 resurvey recorded 252 species for a net loss of 20 (see Appendix S1 in Supplementary Material). Total loss of native species was 70, with 83% of the decline due to a loss in herbs (58 species). Forty-two new native species occurred in 2000 (35 herb species), and 7 new exotic species were recorded (1 tree, 1 shrub, and 5 herbs; Appendix S1). In addition to overall herb loss, the number and abundance of the less common native herb species declined over time. Sixty-one percent (89 out of 145) of the herb species that occurred in 10 or fewer plots in 1977 declined in plot frequency, and more than half of those that declined (52 species) were not recorded at all in 2000.

The loss in overall diversity contrasts with the change observed at the subplot (25 m^2) and plot (1000 m^2) scales for paired plots. At 25 m^2 there was no significant change in total or native species richness (Table 2). Total and native species richness increased at 1000 m^2 across a majority of the plots (22 out of 36), but only total species richness showed significant increases ($P \leq 0.05$) likely due to the new exotic species recorded in 2000 (Table 2). Plots that incurred significant damage from Hurricane Fran showed some of the greatest increases in total species richness; all five plots increased in total richness by 12–25 species at 1000 m^2 and four increased in total species richness at the 25 m^2 scale.

Richness showed significant declines at both 25 m^2 and 1000 m^2 for all herbs and native herbs (Table 2). This contrasts with the change in tree richness, which showed strong increases at the subplot and plot scales (Table 2), but no increases in total tree richness across all plots (net loss of two species, Appendix S1). The same assemblage of tree species dispersed across all plots, thereby increasing mean plot-level richness in the context of overall species loss. Shrub richness did not significantly change at 25 m^2, but there were significant increases in both total and native richness at 1000 m^2. All hurricane plots increased in richness at 1000 m^2 across all growth forms (results vary for 25 m^2), and the greatest increases were for trees (5–11 species per plot) and herbs (2–13 species per plot).

CHANGE IN UNDERSTOREY COMPOSITION

Understorey composition exhibited significant change between 1977 and 2000 at both 25 m^2 and 1000 m^2 (blocked MRPP 25 m^2: $P = 0.001$, $R = 0.003$; 1000 m^2: $P = 0.013$, $R = 0.002$; R measures within-group agreement). There is also strong evidence of consistency in direction of change in composition across all plots at 1000 m^2 based on the orientation of the NMS paired-plot vectors (Fig. 1). Plots show significant separation by year ('group') along axis 2 of the ordination with plots sampled in 2000 located lower on axis 2 ($n = 36$, $t = 5.00$, $P < 0.001$; Fig. 2). These results imply that there was a consistent trend among plots in species compositional change between 1977 and 2000. Hurricane-damaged plots showed a similar direction and extent of compositional change to that of non-hurricane plots (Fig. 1). The final coefficients of determination (r^2) for the correlations between the NMS ordination distances and distances in the original plot × species space are 0.392 for axis 1, 0.108 for axis 2, and 0.222 for axis 3. The varimax rotation maximized the alignment of environmental variables with axis 1 (Table 3), relegating the temporal trend to axis two. Axis 3 is not displayed

Table 2 Summary statistics for change in species richness at the subplot (25 m^2) and plot (1000 m^2) scale, 1977 vs. 2000 ($n = 36$ paired plots). Data listed are for all ground-layer species (Total), species separated by growth form (herb, shrub or tree), and native species of each species group

	All Species		Herbs		Shrubs		Trees	
	Total	Native	Total	Native	Total	Native	Total	Native
25 m^2								
Plots with increase*	19	15	11	10	12	13	26	26
Plots with decrease†	15	15	21	22	16	17	6	6
Mean richness difference	0.14	−0.06	−1.50	−1.80	−0.30	−0.25	1.97	1.97
Permutation test statistic	93	86	40	33	26	28	86	86
P-value	0.460	0.530	0.036	0.014	0.227	0.290	0.0001	0.0001
1000 m^2								
Plots with increase	22	22	12	9	22	21	30	30
Plots with decrease	13	13	22	24	10	10	5	5
Mean richness difference	3.17	2.11	−2.06	−2.86	1.11	0.97	4.11	4.00
Permutation test statistic	204	173	61	44	62	57	161	157
P-value	0.030	0.093	0.041	0.006	0.011	0.019	0	0

*Plots with increase = Total number of plots (out of 36) that increased in species richness.
†Plots with decrease = Total number of plots (out of 36) that decreased in species richness.

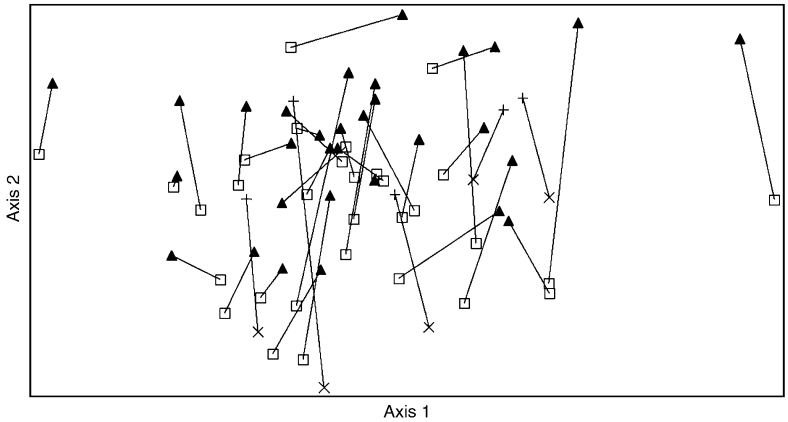

Fig. 1 NMS ordination of plots in species space with paired-plot vectors from the 1977 to the 2000 plot observation. Symbols are plots coded for year: ▲ = 1977, □ = 2000, + = 1977 hurricane plot, × = 2000 hurricane plot.

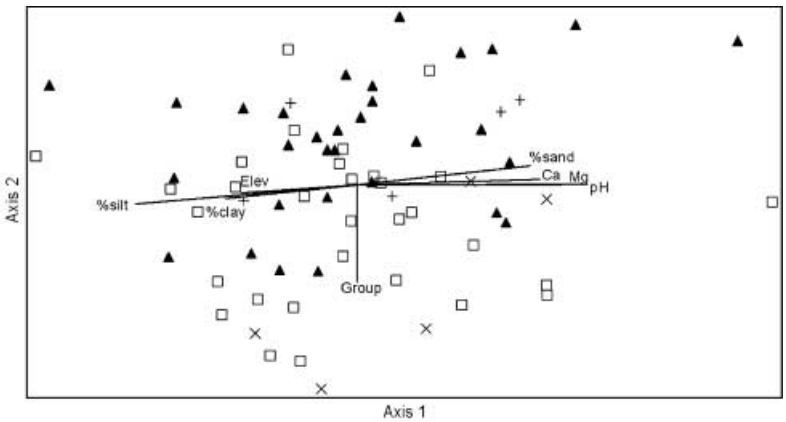

Fig. 2 NMS ordination of plots in species space with correlation vectors of environmental variables (radiating from centre). Ordination represents same plot configuration as Figure 1. All correlation vectors have $r^2 = 0.250$. Length of correlation vectors represents the strength of the correlation and angle indicates direction of highest correlation. Symbols are plots coded for year: ▲ = 1977, □ = 2000, + = 1977 hurricane plot, × = 2000 hurricane plot. Group is a categorical variable for year (1977, 2000). All other environmental variables are defined in Table 1.

in Figs 1 and 2 due to low correlation with all measured environmental variables.

The results of the indicator species analysis show that the strong directional change in species composition evident in the NMS ordination across nearly all plots (Fig. 1) is predominantly due to decreases in herb frequency and abundance and increases in tree frequency and abundance (Table 4). Fourteen species are highly indicative of plot composition in 1977 ($P < 0.05$), and nearly all (10 out of 14) decreased in both subplot and plot frequency over time (Table 4). Among the herbs, only one, *Polygonatum biflorum*, showed an increase in frequency at either scale (+1 increase in plot frequency) whereas several exhibited high declines in plot frequency (≥ 4 plots) (e.g. *Prenanthes altissima*, *Chrysogonum virginianum*, *Chamaelirium luteum*, *Silene virginica*, *Epifagus virginiana*, *Tephrosia virginiana*, *Agrimonia pubescens*, *Ruellia caroliniensis* and *Viola* spp., Appendix S1). In contrast only four tree species, *Celtis laevigata*, *Quercus coccinea*, *Quercus michauxii*

Table 3 Coefficients of determination (r^2) for the correlations between NMS ordination axes and measured environmental variables. Group is a categorical variable for year (1977 or 2000). Vector length is the length of the paired-plot vectors between corresponding 1977 and 2000 plots. All other environmental variables are defined in Table 1

	NMS axis		
	1	2	3
Group (year)	0.001	0.263	0.039
Vector length	0.103	0.006	0.089
pH	0.624	0.001	0.027
Ca	0.497	0.016	0.085
Mg	0.554	0.000	0.039
K	0.149	0.009	0.002
PO_4	0.018	0.012	0.018
% sand	0.470	0.052	0.000
% silt	0.602	0.053	0.000
% clay	0.355	0.038	0.003
Slope	0.023	0.011	0.078
Elevation	0.312	0.022	0.025

Table 4 Indicator values (percentage of perfect indication) and frequency statistics of species associated with 1977 or 2000 plots, listed in order of statistical significance (*P*-value) by year. The *P*-value is based on the proportion of 1000 randomized trials (Monte Carlo test) with indicator value equal to or exceeding the observed indicator value

		Indicator value			Change in frequency	
Species name	Growth form	1977	2000	*P*-value	25 subplots	Plot
1977						
Chimaphila maculata	Herb	72	18	0.001	−52	−4
Desmodium spp.	Herb	82	11	0.002	−66	−4
Viburnum rafinesquianum	Shrub	72	24	0.002	−3	−2
Vitis aestivalis	Shrub	52	4	0.013	−28	−8
Goodyera pubescens	Herb	35	4	0.014	−9	−7
Euphorbia corollata	Herb	39	5	0.015	−7	−9
Euonymus americana	Shrub	56	16	0.027	10	−1
Aureolaria virginica	Herb	35	1	0.029	−8	−8
*Lonicera japonica**	Shrub	53	7	0.038	−12	−2
Polygonatum biflorum	Herb	57	24	0.038	−13	1
Carya glabra	Tree	59	27	0.039	−37	0
Nyssa sylvatica	Tree	66	10	0.044	−14	4
Sambucus nigra	Shrub	14	0	0.044	−16	−5
Houstonia caerulea	Herb	14	0	0.046	−3	−5
2000						
Rubus spp.	Shrub	2	47	0.003	29	13
Phytolacca americana	Herb	0	22	0.004	7	8
Vitis rotundifolia	Shrub	22	74	0.015	150	2
Quercus falcata	Tree	3	30	0.026	18	11
Carpinus caroliniana	Tree	5	40	0.028	102	8
Liriodendron tulipifera	Tree	16	55	0.037	105	6
Fraxinus americana + *pennsylvanica*	Tree	18	54	0.041	88	9

*Introduced species

and Crataegus flava, exhibited declines in plot frequency of ≥ 4 plots. One exotic species, *Lonicera japonica*, declined in subplot and plot frequency over time (–12 and –2, respectively).

Seven species are highly indicative of plot composition in 2000 ($P < 0.05$; Table 4), including four trees but only one herb, *Phytolacca americana*, which is commonly found in disturbed sites throughout North Carolina (Radford *et al.* 1968). *Phytolacca* was not found in 1977 and it exhibited the highest increase in total plot frequency for herbs (+8 plots), occurring in all five hurricane-damaged plots. *Microstegium vimineum*, an exotic species found in low woods of the Piedmont (Radford *et al.* 1968), had the next highest increase in plot frequency for herbs (+7 plots), two of which were hurricane plots. Nineteen tree species increased in plot frequency by ≥ 4 plots, including the exotic species, *Paulownia tomentosa*, which did not occur at all in 1977 (Appendix S1). In contrast, only four herb species, in addition to *Phytolacca* and *Microstegium*, increased in plot frequency by ≥ 4 plots; *Danthonia spicata*, *Polystichum acrostichoides*, *Phryma leptostachya* and *Uvularia perfoliata*.

Of the tree species that increased in plot frequency by more than one plot, 10 are classified as highly shade tolerant, 18 are mid-shade tolerant, and 3 have low shade tolerance (Appendix S1). The highly shade-tolerant tree species showing the greatest increases in subplot and plot frequency include *Acer barbatum*, *Carpinus caroliniana*, *Fagus grandifolia* and *Ostrya virginiana*. Some historically dominant (and less shade tolerant) oak and hickory species also exhibited increases in subplot and plot frequency, with *Quercus falcata*, *Quercus alba* and *Carya ovata* showing the greatest increases over time (Appendix S1). The oak or hickory species that declined in plot frequency or had strong declines in subplot frequency were *Quercus coccinea*, *Quercus marilandica*, *Quercus michauxii*, *Carya glabra*, and *Carya pallida* (Appendix S1).

The only shade intolerant tree species that increased in subplot and plot frequency were *Liriodendron tulipifera*, *Liquidambar styraciflua* and *Quercus phellos*. *Liriodendron* is highly indicative of plot composition in 2000 (IV_{max} $P < 0.05$; Table 4) and it had the highest increase in subplot occurrences (+105; +6 in plot frequency) across all tree species. Liquidambar increased in subplot frequency by 26 and plot frequency by 2, *Quercus phellos* increased by 1 and 8 for subplot and plot frequency, respectively (Appendix S1). Both *Liriodendron* and *Liquidambar* are well known to increase in abundance following modest canopy damage such as many plots sustained during Hurricane Fran, although the increases in these species were not restricted to hurricane-damaged plots.

CHANGE IN SPECIES RICHNESS AND COMPOSITION WITH ENVIRONMENT

Relationships between change in species richness and environmental variables varied with growth form at

Table 5 Environmental variables correlated with change in species richness at 25 m^2 from 1977 to 2000. Data listed are for species separated by growth form (herb, shrub or tree). Only correlations with $P < 0.05$ are shown below. No factors were significantly correlated with change in richness at 1000 m^2. $*P < 0.01$

Variables	Tree	Shrub	Herb
pH			0.44*
Ca			0.52*
Mg			0.54*
K			0.41
PO_4			
Sand			0.47*
Silt	−0.35		−0.42*
Clay			−0.39
Slope			
Elevation	−0.46*		−0.49*
Full 1000 m^2 richness			0.43*

25 m^2, but no significant relationships were found at 1000 m^2 (Table 5). Herb species had the strongest correlations with environment, with positive correlations (increased richness over time) associated with pH and soil cations (Ca, Mg, K) (Table 5). Change in herb species richness is positively correlated with percentage sand and negatively correlated with percentage silt and percentage clay. Note that collinearity of the soil attributes makes inferences with respect to causation problematic; soil cation variables and pH are generally positively correlated ($0.0001 < P < 0.01$), and percentage sand varies inversely with percentage silt and percentage clay as all three together add to 100.

Change in tree species richness showed no relationship with pH or soil cations and was only moderately correlated with percentage silt (Table 5). The changes in tree and herb richness are both negatively correlated with elevation (Table 5). This relationship likely reflects soil variation as there is only moderate variation in elevation within the study area (80–250 m), but soil moisture and nutrient availability vary with topographic position and thus elevation (Peet & Christensen 1980). Low, mesic, nutrient-rich sites tended to increase in tree and herb species richness over time, while higher, infertile, drier sites generally decreased in richness. Change in shrub richness was not correlated with any examined environmental variables. Only change in herb richness was significantly correlated (positively) with the original (1977) plot richness, indicating that plots with higher richness in 1977 tended to increase in herb richness to a greater extent over time.

Change in overall species composition at 1000 m^2 is moderately correlated with environment (Spearman's rank correlation: $r = 0.38$, $P = 0.023$), based on the analysis of paired-plot vector length with 1977-plot position along axis 1 of the NMS ordination (Fig. 1). The positive correlation means that vector length increased from left to right along axis 1, and thus that plots with higher soil cations, pH, and percentage sand exhibited greater compositional change (Figs 1 and 2). Nonetheless, it is important to note that the overall coefficient of determination (r^2) of plot vector length with axis 1 is low (0.103, Table 3), which implies that although there is some relationship with environment, compositional change at 1000 m^2 occurred across all plots, largely independent of the measured environmental factors. This is also represented by the nearly orthogonal position of the 'group' (year) vector relative to the primary environmental vectors in the NMS vector biplot (Fig. 2).

Discussion

The understorey composition of mature hardwood forests in Duke Forest does not provide support for the 'steady-state' expectation. Although species fluctuations are to be expected in late-successional stands due to natural dynamics (Pickett & White 1985), the larger directional change that appears to be occurring across all hardwood plots is not consistent with expected late succession stability. The traditional interpretation of the mature hardwood forests of the Piedmont of the Southeastern United States as the regional end point of succession and the goal for restoration is, at best premature, as they represent a moving target.

We found a decline in overall understorey native species richness with herbaceous species showing the strongest decreases. These results are consistent with studies that show widespread regional losses of species diversity (e.g. Tilman *et al.* 1994; Pimm *et al.* 1995) and highlight a potential trend towards increased species loss in mature hardwood forests over time (Jolls 2003). Our results differ from other studies of temperate forests in that a similar pattern of overall understorey species loss is not yet observed at smaller scales (Davison & Forman 1982; Kwiatkowska 1994; Drayton & Primack 1996; Rooney *et al.* 2004). The Duke Forest hardwood plots did not exhibit significant change in understorey native species richness at either the subplot (25 m^2) or plot (1000 m^2) scale, apparently due to the combined effect of decreasing herb richness and increasing tree seedling richness at both scales.

Our expectation of declines in herb diversity and abundance was based on the growing evidence of the detrimental impacts of white-tailed deer populations on forest understorey vegetation (Anderson 1994, 1997; Kelley 1994; Rooney & Dress 1997; Waller & Alverson 1997; Rooney *et al.* 2004). Although we did not specifically test for deer effects, the significant decline in herbs and the estimated > 100% increase in white-tailed deer populations in the northern Piedmont of North Carolina since 1985 provide support for herbivory as a possible causal factor of decline. Kelley (1994) found that deer browsing on forest herbs is generally concentrated in the spring (April and May) when many understorey plants are available and before agricultural crops begin to provide food (see also Roberts & Gilliam 2003). Nearly all of the herb species that exhibited relatively high decreases in plot frequency (≥ 4 plots) are woodland

herbs present in the spring (Radford *et al*. 1968). Additional changes potentially linked to deer herbivory include the decline of legumes (e.g. *Desmodium* spp. and *Lespedeza* spp.), which are known to have particularly nutritious foliage and to be preferentially browsed (Swift 1948; Osborne 1993), and the decline of wintergreen herbs (e.g. *Chimaphila maculata* and *Goodyera pubescens*). Deer herbivory could also be a reason for the decline in the exotic vine *Lonicera japonica* as it is considered a regional food item for white-tailed deer (Osborne 1993). *Lonicera japonica* is the only exotic species that decreased in frequency at the subplot and plot level between 1977 and 2000.

Increases in white-tailed deer populations have also been suggested to contribute to the decline of oak and hickory species in hardwood forests due to their preference for browsing on *Quercus alba* (white oak) and *Carya ovata* (shagbark hickory) seedlings and saplings (Strole & Anderson 1992; see also Marquis *et al*. 1976; Tilghman 1989). Such a factor would further exacerbate the oak and hickory decline often attributed to fire suppression and competition with shade-tolerant species (Lorimer 1985; Abrams 1992; Lorimer *et al*. 1994; McDonald *et al*. 2002, 2003). Our results run contrary to this expectation as over half of the oak and hickory species plot occurrences in 1977 had increased in subplot and plot frequency in 2000, including *Quercus alba* and *Carya ovata*. Oak and hickory species are reproducing in the understorey, but other factors appear to be preventing them from surviving into older age-classes in Duke Forest (see McDonald *et al*. 2002) and the Piedmont region in general (Abrams 2003). The overall increase in tree seedling richness and the significant declines in herbaceous species richness highlight the need for further research on deer effects in the Piedmont region.

Although not supporting a deer effect, the strong increase in tree seedling richness across nearly all plots provides support for our expectation of increases in woody species abundance due to recovery from past fire and grazing disturbance associated with land use. The cessation of low-intensity fires and understorey grazing in hardwood forests since the early 1900s has facilitated the recruitment of woody species throughout Eastern forests (Abrams 2003). This recruitment has largely supported shade-tolerant species, such as *Acer rubrum*, *Acer barbatum* and *Fagus grandifolia*, as they tend to be faster growing and more competitive in the understorey, and numerous studies have documented their increase in hardwood forest canopies (Christensen 1977; Anderson & Adams 1978; Lorimer 1984; Lorimer *et al*. 1994; McDonald *et al*. 2002). We observed strong increases in the frequency of shade-tolerant species at both the subplot and plot scale, but the overall increase in tree seedlings was not restricted to species with high shade-tolerance.

The increase in abundance of the shade-intolerant species *Liriodendron tulipifera* and *Liquidambar styraciflua* at both scales suggests localized plot disturbances, such as from Hurricane Fran, as an additional factor effecting woody species density in the mature forests of Duke Forest. White (1999) found that *Liriodendron* and *Liquidambar* seedlings had greatly increased in damaged Piedmont hardwood forests one year following Hurricane Fran. Additional species that significantly increased in White's (1999) study plots and which also showed increases in the present analysis include *Pinus* spp., *Paulownia tomentosa*, *Phytolacca americana* and *Erechtites hieraciifolia*. All of these species are known to colonize disturbed sites with high-light conditions and three (*Paulownia*, *Phytolacca* and *Erechtities*) did not occur at all in 1977. The consistent increase in richness across all growth forms (at 1000 m^2) in hurricane-damaged plots runs contrary to the larger trends in the data and suggests that plot-level effects from the hurricane persisted over the 3–4 years following the storm. Yet it is important to note that increases in shade-intolerant species were not restricted to hurricane-damaged plots, and therefore this trend cannot be explained by the hurricane effect alone. Other isolated disturbances (ranging from individual tree-falls to large ice storms) throughout the forest likely helped facilitate the recruitment of shade-intolerant species. As none of the studied plots experienced large-scale hurricane damage, we expect that with time the early successional species will decline and be replaced by the mid- and late-successional species (Pickett & White 1985).

The creation of forest patches by Hurricane Fran also could have contributed to the moderate increase in exotic species abundance and diversity. Each of the five exotic species that occurred in greater than one plot in 2000 (*Ligustrum sinense*, *Microstegium vimineum*, *Verbascum thapsus*, *Paulownia tomentosa* and *Glechoma hederacea*) invaded one or more of the hurricane damaged plots. These species are easily dispersed and are commonly found on roadsides and in disturbed sites throughout much of North Carolina (Radford *et al*. 1968). We initially did not expect the hardwood forests of Duke Forest to experience strong increases in exotic species as they have remained relatively intact and isolated from regional anthropogenic disturbances, such as habitat fragmentation, over at least the last 70 years. However, given the predominant trend towards increased exotic species presence throughout Eastern forests (Luken 2003; Rooney *et al*. 2004) and the habitat disturbance that continues surrounding Duke Forest, we anticipate that their abundance and diversity will continue to increase (see also Bickel 2001).

The significant correlations between change in herb richness and environmental variables at 25 m^2 suggest that there are local patterns of species change along primary environmental gradients. In general, drier, less fertile sites showed little change (or loss) in small-scale herb richness and mesic, fertile sites the greatest increases over time. These results add a temporal perspective to the earlier work by Peet & Christensen (1980) where they found that herbs show stronger variation in richness in response to local edaphic variation than do shrubs

and trees. Some authors have also suggested that the rate of succession is a function of site conditions (Peet & Loucks 1977; Fralish *et al*. 1991). Our results (for herbs and trees) suggest that change in late-successional stands will likely be greater in mesic, fertile sites.

The moderate positive correlation between change in overall species composition (as represented by plot vector length in Fig. 1) and environmental variables provides support for our expectation of greater overall species change in areas of relatively higher soil fertility and low topographic position. This result differs from the above discussion of species richness in that it pertains to change based on the entire species assemblage within a plot, rather than just number of species. The result suggests that change in overall species composition is greater in mesic, low-elevation, fertile plots (due primarily to loss of herbs and an increase in tree seedling richness), whereas drier, less fertile sites do not exhibit as much compositional change.

Conclusion

The systematic declines in herbaceous species richness, directional changes in composition, and dramatic increases in woody seedling abundance signal important on-going shifts in mature hardwood forests of the Piedmont. Both the past legacy of human disturbance in these forest stands and the current disturbance regimes continue to prevent establishment of the dynamic equilibrium long thought to exist in these mature *Quercus–Carya* (oak–hickory) hardwood forests (e.g. Oosting 1942; Braun 1950; see also Foster *et al*. 1992). Some authors have suggested that the current shift toward a more mesic-appearing hardwood forest is typical of late-successional stands and that the historic dominance of oak–hickory forests was primarily a consequence of the higher fire frequencies of past centuries (Abrams 1992, 2003; White & White 1996; McDonald *et al*. 2002). Whether fires should be reintroduced to the ecosystem is a matter of debate, but needs consideration in development of strategies for protecting hardwood stands from future species loss. Exclusion of fire could explain some of the species losses, but these losses are likely to have largely run their course prior to 1977, with the persistence of fire-maintained species restricted to road verges and other artificially maintained openings. Many losses are of species typically associated with mesic closed forest, and these are more likely the victims of the increased deer pressure. The loss of herbaceous species highlights yet another alarming trend: their decline in the protected forest stands of Duke University Forest cannot be attributed to the mechanisms commonly associated with species extinction, such as habitat fragmentation and invasive species (Wilcove *et al*. 1998; Jolls 2003). This implies a strong need for control of local deer populations until their impact can be adequately assessed, coupled with more research to better understand the mechanisms responsible for herb species declines.

Fire-suppression, deer population increases, increased habitat fragmentation, climate change, anthropogenic changes in precipitation chemistry and many other factors potentially influencing composition of mature hardwood forests are likely to be widespread in eastern North America (e.g. Abrams 1992, 2003; Anderson 1997; Frost 1998). Consequently, the lack of stability we observed for mature vegetation of the Carolina Piedmont is likely to be representative of temperate forests in general. Our results suggest that to project vegetation change based on contemporary mature vegetation as the expected endpoint is risky at best and results obtained must be viewed with caution.

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Supplementary material

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/JEC/JEC965/JEC965sm.htm

Appendix S1 Changes in species frequency for Duke Forest hardwood plots, North Carolina, USA, from 1977 to 2000.

References

Abrams, M.D. (1992) Fire and the development of oak forests. *Bioscience*, **42**, 346–353.

Abrams, M.D. (2003) Where has all the white oak gone? *Bioscience*, **53**, 927–939.

Anderson, R.C. (1994) Height of white-flowered trillium (*Trillium grandiflorum*) as an index of deer browsing intensity. *Ecological Applications*, **4**, 104–109.

Anderson, R.C. (1997) Native pests: the impact of deer in highly fragmented habitats. *Conservation in Highly Fragmented Landscapes* (ed. M.W. Schwartz), pp. 117–134. Chapman & Hall, New York, NY.

Anderson, R.C. & Adams, D.E. (1978) Species replacement patterns in central Illinois white oak forests. *Proceedings of the Central Hardwoods Conference II* (ed. P.E. Pope), pp. 285–301. Purdue University, West Lafayette, Indiana.

Ashe, W.W. (1897) Forest of North Carolina. Timber trees and forests of North Carolina. *North Carolina Geological Survey, Bulletin No. 6* (eds G. Pinchot & W.W. Ashe), Winston, North Carolina.

Bickel, K.A. (2001) *Land use, disturbance, and the spread of non-native plant species in a Piedmont forest ecosystem. M.E.M.* Thesis, Duke University, Durham, North Carolina.

Braun, E.L. (1950) *Deciduous Forests of Eastern North America*. Hafner Publishing Co, New York.

Brewer, R. (1980) A half-century of changes in the herb layer of a climax deciduous forest in Michigan. *Journal of Ecology*, **68**, 823–832.

Carpino, E.A. (1998) *Ecological determinants of hurricane damage in a Southeastern Piedmont forest. M.E.M*. Thesis, Duke University, Durham, North Carolina.

Christensen, N.L. (1977) Changes in structure, pattern, and diversity associated with climax forest maturation in Piedmont, North Carolina. *American Midland Naturalist*, **97**, 176–188.

Christensen, N.L. & Peet, R.K. (1981) Secondary forest succession on the North Carolina piedmont. *Forest Succession: Concept and Applications* (eds D. West, H. Shugart & D. Botkin), pp. 230–245. Springer-Verlag, New York.

Christensen, N.L. & Peet, R.K. (1984) Convergence during secondary forest succession. *Journal of Ecology*, **72**, 25–36.

Daniels, R.B., Buol, S.W., Kleiss, H.J. & Ditzler, C.A. (1999) *Soil Systems in North Carolina*. Technical Bulletin 314. North Carolina State University, Raleigh, North Carolina.

Davison, S.E. & Forman, R.T.T. (1982) Herb and shrub dynamics in a mature oak forest: a thirty-year study. *Bulletin of the Torrey Botanical Club*, **109**, 64–73.

Delcourt, H.R. & Delcourt, P.A. (2000) Deciduous forests. *North American Terrestrial Vegetation*, 2nd edn (eds M.G. Barbour & W.D. Billings), pp. 357–395. Cambridge University Press, Cambridge.

Drayton, B. & Primack, R.B. (1996) Plant species lost in an isolated conservation area in Metropolitan Boston from 1894 to 1993. *Conservation Biology*, **10**, 30–39.

Dufrêne, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**, 345–366.

Foster, D.R., Zebryk, T., Schoonmaker, P. & Lezberg, A. (1992) Post-settlement history of human land-use and vegetation dynamics of a *Tsuga canadensis* (hemlock) woodlot in central New England. *Journal of Ecology*, **80**, 773–786.

Fralish, J.S., Crooks, F.B., Chambers, J.L. & Harty, F.M. (1991) Comparison of presettlement, second-growth and old-growth forest on six types in the Illinois Shawnee Hills. *American Midland Naturalist*, **125**, 294–309.

Frost, C.C. (1998) Presettlement fire frequency regimes of the United States: a first approximation. *Fire in Ecosystem Management: Shifting the Paradigm from Suppression to Prescription. Tall Timbers Fire Ecology Conference Proceedings, No. 20* (eds F.L. Teresa, L. Pruden & L.A. Brennan), pp. 70–81. Tall Timbers Research Station, Tallahassee, Florida.

Hatley, M.T. (1977) *The dividing path: the direction of Cherokee life in the eighteenth century*. MS Thesis, University of North Carolina, Chapel Hill, North Carolina.

Healy, R.G. (1985) Competition for land in the American South: agriculture, human settlement, and the environment. Conservation Foundation, Washington, DC.

Jolls, C.L. (2003) Populations of and threats to rare plants of the herb layer. *The Herbaceous Layer in Forests of Eastern North America* (eds F.S. Gilliam & M.R. Roberts), pp. 105–159. Oxford University Press, New York.

Kartesz, J.T. (1999) *A Synonymized Checklist and Atlas with Biological Attributes for the Vascular Flora of the United States, Canada and Greenland*, 1st edn. Synthesis of the North American Flora, Version 1.0 (eds J.T. Kartesz & C.A. Meacham). North Carolina Botanical Garden, Chapel Hill, North Carolina.

Keever, C. (1950) Causes of succession on old fields of the Piedmont, North Carolina. *Ecological Monographs*, **20**, 229–250.

Kelley, T.M. (1994) *Effect of white-tailed deer on the understory vegetation of an oak-hickory forest and growth of trees in a white pine plantation*. MS Thesis, Illinois State University, Normal, Illinois.

Kruskal, J.B. (1964) Nonmetric multidimensional scaling: a numerical method. *Psychometrika*, **29**, 115–129.

Kwiatkowska, A.J. (1994) Changes in species richness, spatial pattern and species frequency associated with the decline of oak forest. *Vegetatio*, **112**, 171–180.

Lorimer, C.G. (1984) Development of the red maple understory in northeastern oak forests. *Forest Science*, **30**, 3–22.

Lorimer, C.G. (1985) The role of fire in the perpetuation of oak forests. *Challenges in Oak Management and Utilization* (ed. J.E. Johnson), pp. 8–25. Cooperative Extension Service, University of Wisconsin, Madison.

Lorimer, C.G., Chapman, J.W. & Lambert, W.D. (1994) Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. *Journal of Ecology*, **82**, 227–237.

Luken, J.O. (2003) Invasions of forests in the Eastern United States. *The Herbaceous Layer in Forests of Eastern North America* (eds F.S. Gilliam & M.R. Roberts), pp. 283–301. Oxford University Press, New York.

Manly, B.F.J. (1997) *Randomization and Monte Carlo Methods in Biology*, 2nd edn. Chapman & Hall, London.

Marquis, D.A., Eckert, P.L. & Roach, B.A. (1976) Acorn weevils, rodents, and deer all contribute to oak regeneration difficulties in Pennsylvania. Research Paper NE-356. USDA Forest Service, Northeastern Forest Experiment Station.

Mather, P.M. (1976) *Computational Methods of Multivariate Analysis in Physical Geography*. J.Wiley & Sons, London.

McCune, B. & Grace, J.B. (2002) Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon.

McCune, B. & Mefford, M.J. (1999) *PC-ORD. Multivariate Analysis of Ecological Data*, Version 4.24. MjM Software, Gleneden Beach, Oregon.

McDonald, R.I., Peet, R.K. & Urban, D.L. (2002) Environmental correlates of oak decline and red maple increase in the North Carolina Piedmont. *Castanea*, **67**, 84–95.

McDonald, R.I., Peet, R.K. & Urban, D.L. (2003) Spatial pattern of *Quercus* regeneration limitation and *Acer rubrum* invasion in a Piedmont forest. *Journal of Vegetation Science*, **14**, 441–450.

Mielke, P.W. Jr & Berry, K.J. (1982) An extended class of permutation techniques for matched pairs. *Communications in Statistics. Part A – Theory and Methods*, **11**, 1197–1207.

Mielke, P.W. Jr & Berry, K.J. (2001) *Permutation Methods: A Distance Function Approach*. Springer Series in Statistics. Springer.

National Climatic Data Center (2001) *Monthly Station Normals of Temperature, Precipitation, and Heating and Cooling Degree Days 1971–2000, North Carolina*. No. 81. National Oceanic and Atmospheric Administration, US Department of Commerce.

Oksanen, L. (1976) On the use of Scandinavian type class system in cover estimation. *Annales Botanici Fennici*, **13**, 149–153.

Oosting, H.J. (1942) An ecological analysis of the plant communities of Piedmont, North Carolina. *American Midland Naturalist*, **28**, 1–126.

Osborne, J.S. (1993) *The White-Tailed Deer in North Carolina*. North Carolina Wildlife Resources Commission, Raleigh, North Carolina.

Palmer, M.W. (1990) Spatial scale and patterns of species-environment relationships in hardwood forests of the North Carolina piedmont. *Coenoses*, **5**, 79–87.

Peet, R.K. & Christensen, N.L. (1980) Hardwood forest vegetation of the North Carolina Piedmont. *Veröffentlichungen Geobotanik Institut ETH. Stiftung Rübel*, **69**, 14–39.

Peet, R.K. & Christensen, N.L. (1988) Changes in species diversity during secondary forest succession on the North Carolina piedmont. *Diversity and Pattern in Plant Communities* (eds H.J. During, M.J. Werger & J.H. Willems), pp. 233–245. SPB Academic Publishing, The Hague.

Peet, R.K. & Loucks, O.L. (1977) A gradient analysis of southern Wisconsin upland forests. *Ecology*, **58**, 485–499.

Peet, R.K., Wentworth, T.R. & White, P.S. (1998) A flexible, multipurpose method for recording vegetation composition and structure. *Castanea*, **63**, 262–274.

Peterson, E.B. & McCune, B. (2001) Diversity and succession of epiphytic macrolichen communities in low-elevation managed conifer forests in Western Oregon. *Journal of Vegetation Science*, **12**, 511–524.

Pickett, S.T.A. & White, P.S. (1985) *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando, Florida.

Pimm, S.L., Russell, G.J., Gittleman, J.L. & Brooks, T.M. (1995) The future of biodiversity. *Science*, **269**, 347–350.

Radford, A.E., Ahles, H.E. & Bell, C.R. (1968) *Manual of the Vascular Flora of the Carolinas*. University of North Carolina Press, Chapel Hill, North Carolina.

Roberts, M.R. & Gilliam, F.S. (2003) Response of the herbaceous layer to disturbance in Eastern forests. *The Herbaceous Layer in Forests of Eastern North America* (eds F.S. Gilliam & M.R. Roberts), pp. 302–320. Oxford University Press, New York.

Rooney, T.P. & Dress, W.J. (1997) Species loss over sixty-six years in the ground layer vegetation of Heart's Content, an old-growth forest in Pennsylvania USA. *Natural Areas Journal*, **17**, 297–305.

Rooney, T.P., Weigmann, S.M., Rogers, D.A. & Waller, D.M. (2004) Biotic impoverishment and homogenization in unfragmented forest understory communities. *Conservation Biology*, **18**, 787–798.

Small, C.J. & McCarthy, B.C. (2002) Spatial and temporal variability of herbaceous vegetation in an eastern deciduous forest. *Plant Ecology*, **164**, 37–48.

Strole, T.A. & Anderson, R.C. (1992) White-tailed deer browsing species preferences and implications for central Illinois forests. *Natural Areas Journal*, **12**, 139–144.

Swift, E. (1948) Deer select most nutritious forages. *Journal of Wildlife Management*, **12**, 109–110.

Tilghman, N.G. (1989) Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *Journal of Wildlife Management*, **53**, 424–453.

Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. (1994) Habitat destruction and the extinction debt. *Nature*, **371**, 65–66.

USDA, N.R.C.S. (2002) *The PLANTS Database*, Version 3.5 (http://plants.usda.gov). National Plant Data Center, Baton Rouge, Louisiana.

Waller, D.M. & Alverson, W.S. (1997) The white-tailed deer: a keystone herbivore. *Wildlife Society Bulletin*, **25**, 217–226.

White, R.D. (1999) *The impacts of Hurricane Fran on a North Carolina Piedmont woodland*. MA Thesis, University of North Carolina, Chapel Hill, North Carolina.

White, P.S. & White, R.D. (1996) Old growth oak and oak-hickory forests. *Eastern Old-Growth Forests* (ed. M.B. Davis), pp. 178–198. Island Press, Washington DC.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. (1998) Quantifying threats to imperiled species in the United States. *Bioscience*, **48**, 607–615.

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