

Losses in understory diversity over three decades in an old-growth cool-temperate forest in Michigan, USA

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Abstract: Diversity in temperate forests is concentrated in the understory, but understory dynamics are poorly understood for old-growth forests. We use repeated measurements of more than eight hundred 1 m² plots over three decades to assess patterns of understory diversity in old-growth mesic and wet forests in northern Michigan, USA. We ask whether diversity changes systematically over time and whether dynamics are related to spatial scale. We find, for all habitats, significant understory diversity loss at square-metre scales but not at coarser scales. Total herbaceous cover, however, remained constant or increased in total and for nearly all frequent species, and no species were lost overall. We explore hypotheses about diversity regulation by exploring correlations with habitat, canopy composition, and properties of understory species. Non-indigenous plants are rare at the study site, earthworm invasion is not apparent, and deer browse is not intense. Diversity changes may be related to ecological guild membership. We suggest that the general loss of fine-scale diversity is driven by either changing canopy composition or competitive dynamics within the understory community. Management for diversity maintenance in temperate forests must address understory communities; if herbaceous diversity is scale dependent and unstable over decadal time frames, management approaches need to account for factors driving changes.

Résumé : Dans les forêts tempérées la diversité est concentrée en sous-étage; mais la dynamique en sous-étage des forêts anciennes est mal comprise. Nous avons utilisé les mesures de plus de 800 placettes échantillons de 1 m² répétées pendant trois décennies pour évaluer les patrons de diversité en sous-étage de forêts anciennes mésiques et humides dans le nord du Michigan, aux États-Unis. Nous nous sommes demandés si la diversité change de façon systématique avec le temps et si la dynamique est reliée à l'échelle spatiale. Il y a une perte importante de diversité en sous-étage de tous les habitats à l'échelle d'un mètre carré, mais pas à des échelles plus grossières. Cependant, le couvert total des plantes herbacées est demeuré constant ou a augmenté au total et pour presque toutes les espèces fréquentes; en général aucune espèce n'est disparue. Nous examinons les hypothèses concernant la régulation de la diversité en étudiant les corrélations avec l'habitat, la composition de la canopée et les propriétés des espèces en sous-étage. Les plantes exotiques sont rares dans la zone d'étude; l'invasion des vers de terre n'est pas apparente et le broutage des chevreuils n'est pas intense. Les changements dans la diversité sont peut-être reliés à l'appartenance à la guild écologique. Nous croyons que la perte générale de diversité à petite échelle est causée soit par le changement de composition de la canopée, soit par la dynamique de compétition au sein de la communauté de sous-étage. L'aménagement qui vise le maintien de la diversité dans les forêts tempérées doit se préoccuper des communautés de sous-étage; si la diversité des plantes herbacées est dépendante de l'échelle et instable sur des horizons de 10 ans, les méthodes d'aménagement doivent tenir compte des facteurs responsables des changements.

[Traduit par la Rédaction]

Introduction

In most temperate forests, understory communities are much more species rich than the canopy, but dynamics of herbaceous communities are comparatively poorly understood (Whigham and Chapa 1999; Gilliam and Roberts 2003; Whigham 2004). This is particularly so in "slow" systems like late-successional forests where studies of understory community dynamics have been largely dependent on chronosequence approaches. Long-term studies based on permanent plots are rare in general but especially so in old-growth forest systems (Bakker et al. 1996; Bekker et al. 2007; but

see Holland 1978). Woods (2007), for the same study site used here, found canopy diversity loss over 70 years in 0.08 ha permanent plots associated with homogenization of canopy communities within patches of uniform habitat and community differentiation among habitat patches. These trends were interpreted as a result of competitive sorting among canopy species and as indicative of long-persistent responses to rare, severe disturbances. By contrast, studies using space-for-time substitution have often been interpreted to support the hypothesis that baseline "gap-phase" dynamics can sustain stable canopy composition and diversity in old-growth forests (Runkle 1981, 2000; Woods 1984).

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Whether such dynamics are at play in understory communities and, if so, at what scales is unknown. Is understory diversity in old-growth forests generally equilibrium at decadal scales, or are these communities more typically experiencing long-persistent reorganization and diversity changes similar to those suggested for canopy communities? How does the answer to this question depend on spatial scale? It is well established that understory species distributions respond to fine-scale edaphic variation such as microtopography created by canopy tree tip-ups (Beatty 1984, 2003; Peterson and Campbell 1993); historical variation in rates of creation of such habitat variation may lead to long-term changes in understory pattern and diversity similar to but at a finer scale than that proposed for canopy trees.

The few multiyear studies available offer ambiguous patterns. A 7 year permanent-plot study in old-growth mesic hardwoods in Quebec (Holland 1978) describes square-metre quadrat richness as “barely changing”, while species turnover was significant, but also showed significant declines in square-metre understory species richness in one of two stands. Understory diversity has declined in unlogged, historically oak-dominated forests in both eastern North America (Davison and Forman 1982) and Europe (Malmer et al. 1978; Kwiatkowska 1994), but this may be attributed to changed fire or grazing regime and consequent loss of species responding to such disturbances. Plot-level understory diversity in a British ancient woodland remained unchanged, while cover decreased over 17 years (Kirby and Thomas 2000), while a 30 year resampling of “ancient” (continuously forested since at least 1775) alluvial forests in Belgium found declining understory diversity (Baeten et al. 2010). Long-term comparisons based on repeated sampling of stands (not the same sample points) show declining diversity in old-growth forests in Pennsylvania (Hough 1965; Rooney and Dress 1997) and in a range of stands in Wisconsin (Wiegmann and Waller 2006) where changes were attributed to deer browse and anthropogenic disturbance.

Comparative studies between stands of different successional status show no clear trends in understory diversity. Some find higher alpha diversity in old-growth stands than in comparable secondary forests (Matlack 1994; D’Amato et al. 2009), others the reverse (Metzger and Schultz 1981; Scheller and Mladenoff 2002) or minimal or inconsistent relationships (Moore and Vankat 1986; Mladenoff et al. 1993; Gilliam 2002).

Differences in spatial scale of sampling and varying interactions among successional status, management history, and environmental conditions make these results difficult to interpret and compare. Nonetheless, forest managers are called upon to maintain diversity, and resulting management practices are frequently designed to mimic natural “gap-phase” disturbance patterns on the assumption that diversity is thus best maintained (see, for example, Attiwill 1994; Hunter 1999).

This study assesses diversity patterns and dynamics using long-term (up to 30 years) remeasurements of over eight hundred 1 m² permanent plots in the understory of a cool-temperate old-growth forest with no history of active management in northern Michigan, USA. While limited to a single area, this data set is unique in combining multidecade temporal span with the old-growth character of the site. We ask, specifically (i) is understory diversity in this old-growth

stand stable over time, (ii) how are observed patterns related to spatial scale and canopy composition or habitat, and (iii) can observed relationships suggest processes regulating or driving understory diversity dynamics?

Study site and methods

Study site

The 100 ha Dukes Research Natural Area (46°02'N 87°09'W), in the Hiawatha National Forest of northern Michigan, has not been logged or otherwise subject to active management. Forests are mixed age, with canopy trees >300 years old (K.D.W., unpublished data). Climate is cool-temperate with annual precipitation averaging >900 mm; cumulative snowfall averages >4000 mm annually. Soils are developed on thick glacial till over Paleozoic sediments. See Woods (2007) for further site description.

In 1935, two hundred and forty-six 0.2 acre (809 m²) inventory plots (“canopy plots”) were established on an approximately 40 m × 100 m grid over the Dukes Research Natural Area with centers marked by steel pipes. Woody stems have been remeasured several times (Woods 2007). Tree species distributions are associated with substrate properties that vary among relatively uniform habitat patches. Woods (2007) assigned habitat patches to five habitat-types: (i) swamp forests on organic soils with generally high Ca and cation-exchange capacity dominated by *Thuja occidentalis* L., *Fraxinus nigra* Marsh., and *Acer rubrum* L., (ii) maple-dominated stands on relatively well-drained uplands with high pH and Ca strongly dominated by *Acer saccharum* Marsh., (iii) mixed upland stands with impeded drainage due to hard-pan and lower pH, supporting more diverse canopy with *Tsuga canadensis* (L.) Carrière, *Betula alleghaniensis* Britton, *Acer rubrum*, and *Fagus grandifolia* Ehrh., (iv) hemlock-dominated patches with coarser soils, deep mor humus, and lower pH and available cation concentrations dominated by *Tsuga canadensis*, and (v) transitional habitats with a fine-scale mixture of upland and wetland substrate within canopy plots. Since 1935, shade-tolerant species (particularly *Thuja*, *Tsuga*, *Fagus*, and *Acer saccharum*) increased in dominance in all habitats and less tolerant species have declined with little or no establishment of new canopy trees; consequently, canopy diversity has decreased at the canopy plot scale and composition within habitat patches has become more homogeneous (Woods 2007). Woods (2004, 2007) interpreted these patterns as evidence of long-term effects of intermediate canopy disturbances with subsequent competitive sorting over several centuries.

Data set

In 1978–1980, J.S. established four 1 m × 1 m understory quadrats per canopy plot ($n = 972$ quadrats) positioned 15 and 35 ft east and west of canopy plot centers and marked with wire stakes and estimated percent cover by quadrat for all vascular species. In 1992–1993, D.J.H. remeasured 448 quadrats in 112 upland canopy plots, and these, along with 304 understory quadrats (76 canopy plots) in swamp forests, were remeasured by K.D.W. in 2002–2007.

In 1978–1979, 79 upland plots were sampled early enough for reliable detection of spring ephemeral species (*Allium tricoccum* Aiton, *Claytonia caroliniana* Michx., *Cardamine*

concatenata (Michx.) Sw., *Cardamine diphylla* (Michx.) Alph. Wood, *Dicentra canadensis* (Goldie) Walp., *Dicentra cucullaria* (L.) Bernh., and *Erythronium americanum* Ker Gawl.). Sampling from 1992 to 2007 was too late in the season to capture spring ephemerals; in June 2009, K.D.W. conducted a resampling for spring ephemerals only in 78 upland plots (312 quadrats). *Allium tricoccum* flowering scapes were present in some summer samples but did not allow meaningful cover estimates and may have been unreliable indicators of presence; *Allium tricoccum* is therefore grouped with ephemerals in analysis.

Enough wire stakes remained from initial measurements to allow subjective estimation of the accuracy of quadrat relocation by measurement from canopy plot centers. Placement rarely varied more than 0.5 m from original stakes, so “relocated” quadrats typically overlap by more than 50%.

In 1978–1980, cover was estimated as 0.1%, 0.4%, 1%–5%, 6%–15%, 16%–35%, 36%–65%, and >65%. From 1992 forward, cover was assigned to 10% intervals with a <1% category. For analysis, the first two categories for 1978–1980 and the first category for 1992 forward were recoded to 0.4% and other estimates to category midpoint.

Beginning in 1992, understory species occurrences were tabulated at least once for the four quadrants (northeast, southeast, southwest, and northwest) of each resampled canopy plot (quadrant = 200 m²). Species lists by quadrant from the most recent available measurement were used to assess richness patterns at coarser spatial scales.

Taxonomy and floristics

Taxonomy is according to the USDA Plants Database (<http://plants.usda.gov/java/>), February 2010 (see Appendix A, Table A1 for a list of all common species). In analysis, we pool some *Carex* species to the section level where species discrimination may have been inconsistent across measurements. However, the few other ambiguous taxa, some vegetative grasses, ferns, and *Carex* species, were confidently distinguishable as different from other taxa in a particular sample unit and date and are retained in calculation of diversity indices. Tree seedlings and bryophytes were not consistently recorded and are excluded from analyses here.

Understory diversity and cover patterns

We compared three community properties across sample periods and at different spatial scales: species richness (S), Shannon’s index ($H = -\sum p_i \ln p_i$, where p_i is relative cover for species i), and total cover (cover estimates summed for all understory species recorded by quadrat). Some of these measures were not available for all comparisons.

We assessed changes in understory community characteristics at three spatial scales. First, we compared cover and diversity measures across sample periods for individual 1 m² quadrats (referred to as quadrat diversity and cover) disregarding, initially, potential spatial autocorrelation among the four quadrats in each canopy plot. Second, we pooled the four 1 m² quadrats within each canopy plot to obtain diversity indices, treating the four 1 m² quadrats as a single 4 m² quadrat distributed over a linear distance of about 20 m (referred to as canopy plot diversity). Third, we used species lists for canopy plot quadrants to examine one-time patterns in S only at coarser scales. Comparing diversity and cover

over time, between measurement periods, was complicated by differences in sampling frequency among habitats and for irregular sampling for spring ephemerals in upland habitats. Analyses using data from 1 m² quadrats can be grouped into three sets of comparisons as follows.

(i) For all remeasured quadrats ($n = 752$), both individually and pooled within canopy plots, we compared both diversity measures and cover between the first sample period (1978–1980) and the most recent period (2002–2007).

(ii) For upland habitat types (448 quadrats), we compared diversity and cover across all three sample periods: 1978–1980, 1992–1994, and 2002–2007. Two intervals of comparable length allowed some assessment of consistency in trends. This is particularly valuable given that measurements were conducted by different researchers using slightly different protocols across dates; consistency in trends for the two intervals may give some assurance that apparent changes are not methodological artifacts.

(iii) For spring ephemerals (six species listed above), we conducted independent comparisons of S and total cover for ephemerals alone using only quadrats sampled early in 1978–1980 and in the dedicated spring 2009 measurement ($n = 280$). Nearly all of these quadrats were in maple-dominated and mixed upland habitat types. Occurrences of ephemerals elsewhere were extremely sparse; consequently, we did not test for habitat type effects on diversity in this comparison. Because only ephemerals were measured in 2009, these measurements were combined with understory data from 2004 to 2007 for the same quadrats to develop estimates of total S for quadrats. Because samples from different years and different dates were combined for the recent period, we did not attempt to analyze changes in cover-based measures (H and total cover).

We used repeated-measures ANOVA to explore effects of habitat type (as a categorical variable) and canopy composition (as covariates) on understory cover and diversity and their change over time. As discussed above, we use habitat type as an indicator of complex patterns in substrate properties (Woods 2007). Canopy effects were represented in ANOVA models by (i) plot-level basal area for individual dominant tree species (*Acer saccharum*, *Acer rubrum*, *Betula alleghaniensis*, *Fagus grandifolia*, *Fraxinus nigra*, *Thuja occidentalis*, and *Tsuga canadensis*) and total plot basal area and (ii) for upland plots where individual trees were mapped, a distance-weighted canopy influence index ($CI = \sum (\text{tree diameter at breast height}) / (\text{distance from quadrat})$) (Lorimer 1983) for trees within 8 m of each understory quadrat calculated for total canopy influence and separately for each dominant species. We did not use quadrats pooled by plot in this analysis, since CIs could not be used meaningfully. Repeated-measures ANOVAs for upland quadrats used all three measurement periods; all other treatments involved two measurements. We incorporated Greenhouse–Geisser correction factors for departure from sphericity in assessing “within-subject” results of ANOVAs, but their use caused no changes in significance of factors in any test.

Since the four quadrats within each canopy plot are much closer together than distances between canopy plots, we explored spatial autocorrelation among individual quadrats at the canopy plot scale for further insight into scaling effects on diversity patterns. Repeated-measures ANOVAs, con-

ducted separately for each habitat type, allowed assessment of influence of plot, as a categorical variable, on diversity and cover and their changes over time. Differences in results between quadrat-scale analysis and analyses of quadrats pooled by canopy plot afford further insight into scaling effects

We used paired *t* tests with Bonferroni corrections for post hoc comparisons of understory diversity and cover among habitat types and between measurement periods.

Finally, we constructed species accumulation curves for each habitat type using both 1 m² quadrats (for the earliest and latest sample period) and canopy plot quadrants (recent only) to obtain further understanding of spatial structure of *S*. We bootstrapped species accumulation curves (PC-ORD 5.06 (McCune and Mefford 2006)) within each habitat type by pooling understory quadrats (subsamples of 500 for each sample size; ephemerals not included). These curves do not offer a diversity measure directly comparable with direct measurement within specified sample areas, but they measure a rate of species accumulation with increasing area that can be compared across sample periods.

Comparing patterns among species and groups

We compared temporal changes in abundance and frequency of selected species and species groups to explore possible causal hypotheses for observed changes in diversity. To assess whether changes in species abundance were related to initial abundances, we calculated correlations (nonparametric Spearman's ρ) between relativized changes in frequency and cover and initial values for these measures for all species with more than 20 occurrences. We also correlated changes in frequency and cover with initial values of Fridley's Θ (Fridley et al. 2007), a co-occurrence-based index of niche breadth; this comparison allows indirect assessment of whether changes in species cover and frequency were correlated with specialist (low values of Θ) or generalist (high values of Θ) life histories.

Finally, we compared trends in species documented to be particularly sensitive or insensitive to deer browsing (Anderson 1994; Balgooyen and Waller 1995; Kraft et al. 2004; Wiegmann and Waller 2006; Heckel et al. 2010; Holmes and Webster 2010). Sensitive species with >20 quadrat occurrences included *Aralia nudicaulis* L., *Clintonia borealis* (Aiton) Raf., *Maianthemum canadense* Desf., *Maianthemum racemosum* (L.) Link, *Polygonatum pubescens* (Willd.) Pursh, *Streptopus lanceolatus* (Aiton) Reveal, and *Trillium grandiflorum* (Michx.) Salisb.. Species considered less palatable to deer were *Arisaema triphyllum* (L.) Schott, *Athyrium filix-femina* (L.) Roth, *Botrychium virginianum* (L.) Sw., *Carex intumescens* Rudge, *Carex pauciflora* Lightf., *Carex* sect. *Heleonastes*, *Carex* sect. *Montanum*, and *Huperzia lucidula* (Michx.) Trevis.

All statistical analyses used Systat v.11 software (Systat Inc., Chicago, Illinois).

Results

Full data set, two measurements, individual quadrats

Repeated-measures ANOVAs for all quadrats (upland and wetland) for two measurement periods (1978–1980 and 2004–2007) without ephemeral species found between-quad-

rat variation in *S* to be significantly related to habitat type ($F_{[4,739]} = 10.12$, $P < 0.001$), *Acer saccharum* basal area ($F_{[1,739]} = 13.93$, $P < 0.001$), and *Acer rubrum* basal area ($F_{[1,739]} = 3.89$, $P = 0.05$). *Acer saccharum* dominated plots had lower *S* in general (Fig. 1; Table 1), while *Acer rubrum* basal area was negatively correlated with *Acer saccharum* basal area. Differences within quadrats (between measurements) were significant overall ($F_{[1,739]} = 23.35$, $P < 0.001$), but there were no significant interactions with habitat type or canopy composition. (See Appendix A, Table A2 for full ANOVA results.)

Results for *H* were similar. Variables affecting between-quadrat variation were habitat type ($F_{[4,739]} = 6.65$, $P < 0.001$), *Acer saccharum* basal area ($F_{[1,739]} = 12.24$, $P < 0.001$), and *Acer rubrum* basal area ($F_{[1,739]} = 4.13$, $P = 0.05$). Changes in *H* over time within quadrats were significant ($F_{[1,739]} = 17.69$, $P < 0.001$), but there were no significant interactions with habitat type or canopy composition.

In all cases, diversity changes within quadrats were negative (*S* decreased by about 20% overall) and decreases were significant for each habitat type except maple-dominated stands (post hoc *t* tests with Bonferroni correction, $P = 0.05$) (Fig. 1; Table 1). ANOVAs for total understory cover found no significant effects of habitat type or of canopy composition on differences between quadrats. Cover changed over time within quadrats ($F_{[1,739]} = 6.69$, $P = 0.01$), and the interactions with change within quadrats were significant for habitat type ($F_{[4,739]} = 3.19$, $P = 0.01$) and *Acer rubrum* basal area ($F_{[1,739]} = 5.28$, $P = 0.02$).

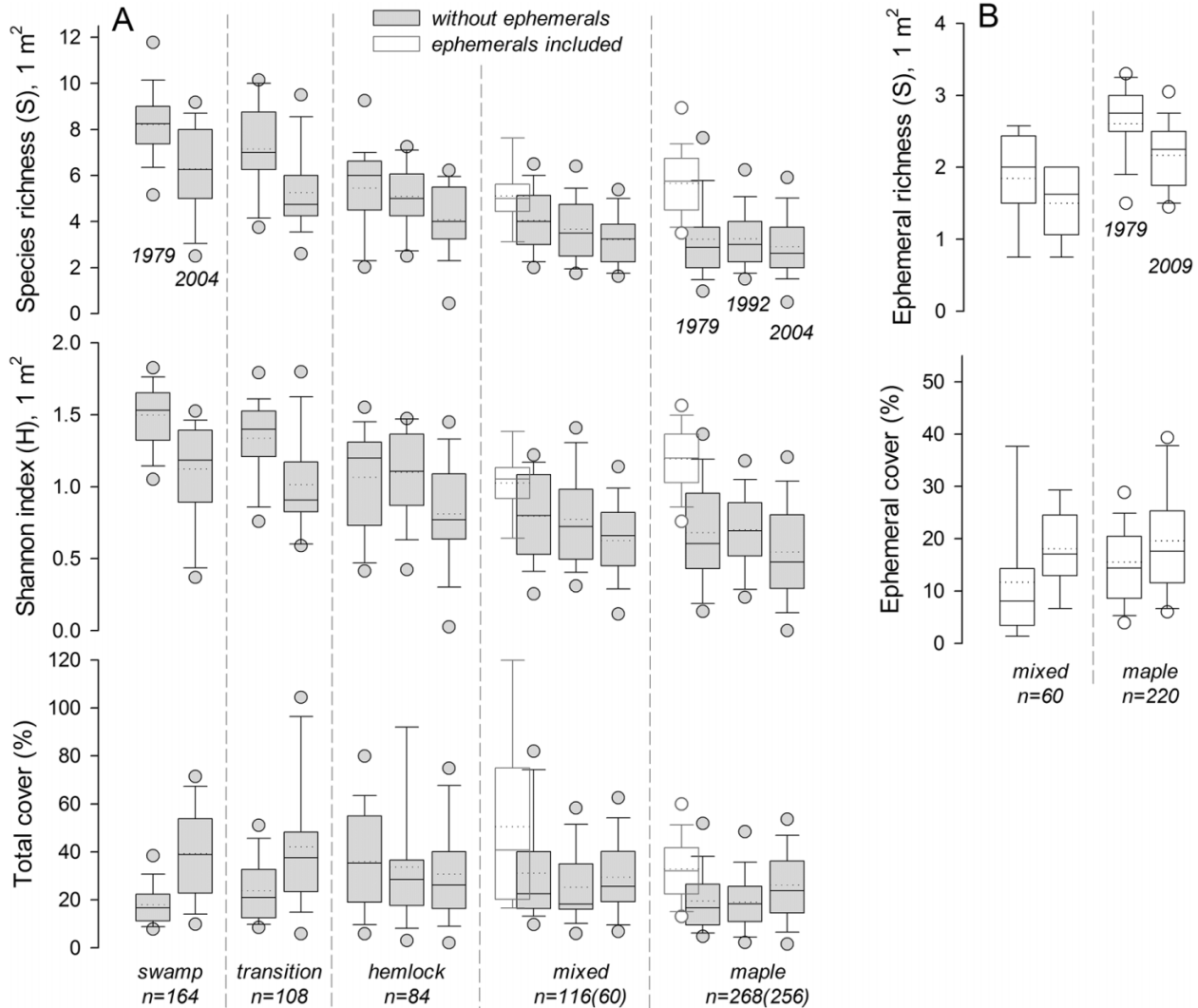
Changes in total cover, all increases, were significant overall ($P < 0.05$) and for swamp and transitional habitats ($P < 0.01$) but not for any upland habitats in this comparison (Fig. 1; Table 1). Cover change estimates could be biased due to the different categories used for cover estimates in the first compared with later sample intervals; for example, species with cover of 1%–5% would have been assigned a value of 3% for 1978–1980 and 6% for subsequent samples, and a high frequency of such instances could produce a spurious apparent increase in cover. We assessed this possibility by two reanalyses. First, we recoded all such records for 1978–1980 to 5% and recalculated cover estimates; changes in total cover estimates were minor, and there were no changes in results of statistical comparisons. Second, we conducted a separate analysis of cover changes using only species with >10% cover; changes in average cover for most species and for quadrats remained positive (total cover increases were about 85% of those observed when all species were incorporated).

Within habitat type, ANOVAs also showed effects of plots on variation among quadrats and variation within quadrats over time for both diversity measures for upland habitats but not for transitional or wetland forest habitats. Plot effects indicate spatial autocorrelation at the scale of 5–10 m (distance between quadrats within canopy plots) but are smaller than habitat type effects in the overall analysis. Plot effects were significant in analysis of total understory cover only for the maple-dominated habitat type without ephemerals.

Full data set, two measurements, quadrats pooled by plot

Results of repeated-measures ANOVAs for diversity measures calculated for four pooled quadrats per canopy plot showed similar but less pronounced changes in diversity and

Fig. 1. Changes in understory cover and diversity in 1 m² quadrats over time by habitat. Box plots show median (solid line) and mean (broken line), middle two quartiles (box), 10th and 90th percentiles (whiskers), and 5th and 95th percentiles (circles). Years indicate the midpoint of the sampling period. Boxes are grouped by habitat types as indicated at the bottom (two periods for swamp and transitional forests and three for upland habitats). (A) Total understory diversity and cover not including six species of spring ephemerals (see text) in gray. For the 1978–1980 sampling period, unshaded boxes show figures including spring ephemerals. Sample sizes are quadrat numbers (in parentheses for sample size with ephemerals). All changes between sampling intervals for *S* and *H* are significant (*t* tests, $P < 0.05$) except in maple-dominated habitats. Cover increases are significant in swamp and transitional habitats. (B) Similar to Fig. 1A, for spring ephemerals only. Sample size refers to quadrats sampled for spring ephemerals in both 1978–1980 and dedicated sampling in 2009. Decreases in *S* and increases in cover are significant ($P < 0.05$).



cover. Again, significant direct effects on *S* were due to habitat type ($F_{[4,176]} = 5.72$, $P < 0.001$) and *Acer saccharum* basal area ($F_{[1,176]} = 7.58$, $P = 0.01$). Within-plot (between-measurement) differences were significant overall ($F_{[1,176]} = 16.38$, $P < 0.001$), but there were no significant interactions with basal area. Results for *H* were similar; between-plot effects were significant for habitat type and *Acer saccharum* basal area ($F_{[4,176]} = 4.88$, $P = 0.001$ and $F_{[1,176]} = 7.67$, $P = 0.01$). Within-plot changes in *H* were significant ($F_{[1,176]} = 12.06$, $P < 0.001$) with no interactions.

Post hoc comparisons of *S* and *H* showed significant decreases for all plots combined but only for hemlock-dominated and swamp habitat types treated separately.

Upland habitats only, three measurements, quadrat comparisons

Species richness differences among plots were significantly related to habitat type ($F_{[3,437]} = 13.88$, $P < 0.001$) and to *Acer rubrum* CI ($F_{[1,437]} = 9.4$, $P = 0.001$), *Acer saccharum* CI ($F_{[1,437]} = 5.39$, $P = 0.02$), and *Fagus grandifolia* CI ($F_{[1,437]} = 4.12$, $P = 0.04$). Within quadrats, over the three measurements, differences in *S* were significantly related to measurement period ($F_{[2,874]} = 8.92$, $P < 0.001$), with significant interaction with *Acer saccharum* CI ($F_{[2,874]} = 4.24$, $P = 0.02$) and total canopy CI ($F_{[2,874]} = 4.49$, $P = 0.01$).

Significant main effects for differences in *H* between quadrats were habitat type ($F_{[3,437]} = 10.28$, $P < 0.001$) and *Acer*

Table 1. Diversity and cover statistics by habitat-type (mean with standard error in parentheses).

Habitat	<i>n</i>	<i>S</i>		<i>H</i>		Total cover (%)	
		1978–1980	2002–2007	1978–1980	2002–2007	1978–1980	2002–2007
By quadrat (1 m²)							
Maple-dominated	272	3.2 (2.1)	2.9 (2)	0.7 (0.5)	0.6 (0.5)	20 (19)	26 (26)
Maple-dominated with ephemerals	220	5.5 (2.1)	3.9 (1.6)	1.2 (0.4)	0.6 (0.4)	32 (21)	35 (27)
Mixed upland	116	4.0 (2.1)	3.2 (1.7)	0.8 (0.5)	0.6 (0.4)	31 (28)	29 (23)
Mixed upland with ephemerals	56	5.4 (2.4)	3.4 (1.4)	1.1 (0.5)	0.7 (0.4)	53 (43)	38 (24)
Hemlock-dominated	72	5.5 (2.3)	3.9 (1.9)	1.1 (0.5)	0.8 (0.4)	32 (31)	28 (28)
Transition	108	7.1 (2.9)	5.2 (2.7)	1.3 (0.5)	1.0 (0.5)	24 (21)	41 (34)
Swamp	162	8.3 (2.9)	6.6 (2.7)	1.5 (0.4)	1.2 (0.4)	18 (16)	42 (33)
All plots	730	5.2 (3.2)	4.2 (2.7)	1.0 (0.6)	0.8 (0.5)	23 (22)	32 (29)
Quadrats pooled by canopy plot (4 m²)							
Maple-dominated	68	7.3 (3.6)	7.0 (3.7)	1.3 (0.4)	1.2 (0.6)		
Maple-dominated with ephemerals	55	10.6 (3.4)	8.0 (2.2)	1.8 (0.3)	1.4 (0.3)		
Mixed upland	29	8.1 (2.6)	6.9 (2.8)	1.2 (0.5)	1.2 (0.4)		
Mixed upland with ephemerals	15	10.6 (4.9)	6.7 (2.0)	1.6 (0.6)	1.3 (0.3)		
Hemlock-dominated	18	10.7 (4.2)	8.3 (3.4)	1.6 (0.4)	1.3 (0.5)		
Transition	27	16.0 (4.3)	13.4 (5.1)	2.0 (0.4)	1.9 (0.5)		
Swamp	41	18.2 (3.7)	15.9 (4.8)	2.2 (0.3)	2.0 (0.4)		
All plots	183	5.3 (2.7)	4.2 (2.2)	1.0 (0.5)	0.8 (0.4)		

rubrum CI ($F_{[1,437]} = 5.73$, $P = 0.02$). Changes within quadrats over measurement intervals were significant generally ($F_{[2,874]} = 4.28$, $P = 0.01$), as were interactions with *Acer saccharum* CI ($F_{[2,874]} = 4.41$, $P = 0.04$) and total canopy CI ($F_{[2,874]} = 3.99$, $P = 0.02$); habitat type did not contribute significantly to explaining changes in *H* within quadrats.

Cover varied significantly with habitat type in between-plot analysis for uplands ($F_{[3,437]} = 9.02$, $P < 0.001$), but no other variables had significant effects. The main effect of within-plot variation over time was significant ($F_{[2,874]} = 3.31$, $P = 0.04$), as was the interaction with habitat type ($F_{[6,874]} = 2.36$, $P = 0.03$).

Post hoc comparisons showed both *S* and *H* decreasing significantly for all habitat types for both intervals (*t* test with Bonferroni correction, $P < 0.05$), except for maple-dominated habitats in the first interval where decreases were not significant (Fig. 1; Table 1). Trends from the first to the second and from the second to the third measurements were similar for all variables.

Upland quadrats with ephemerals, two measurements

For the reduced data set used to estimate total richness including ephemerals (combining species counts for 2009 and 2002–2007 samples for second measurement), ANOVAs found significant main effects on differences among quadrats only for *Fagus grandifolia* CI ($F_{[1,273]} = 4.71$, $P = 0.03$). The main effect for variation within quadrats over time was significant ($F_{[1,273]} = 23.76$, $P < 0.001$) but showed no interactions with CI for individual species or overall.

Post hoc comparisons found significant decreases in total *S* for both mixed upland habitats and maple-dominated habitats when ephemerals were included (*t* test, $P < 0.05$) (without ephemerals, this habitat type was the only one that showed no significant change).

When richness and cover for ephemerals alone were compared between 1978–1980 and 2009, *S* of ephemerals de-

clined significantly in maple-dominated habitats and ephemeral cover increased in both mixed upland and maple-dominated habitat (*t* test, $P < 0.05$).

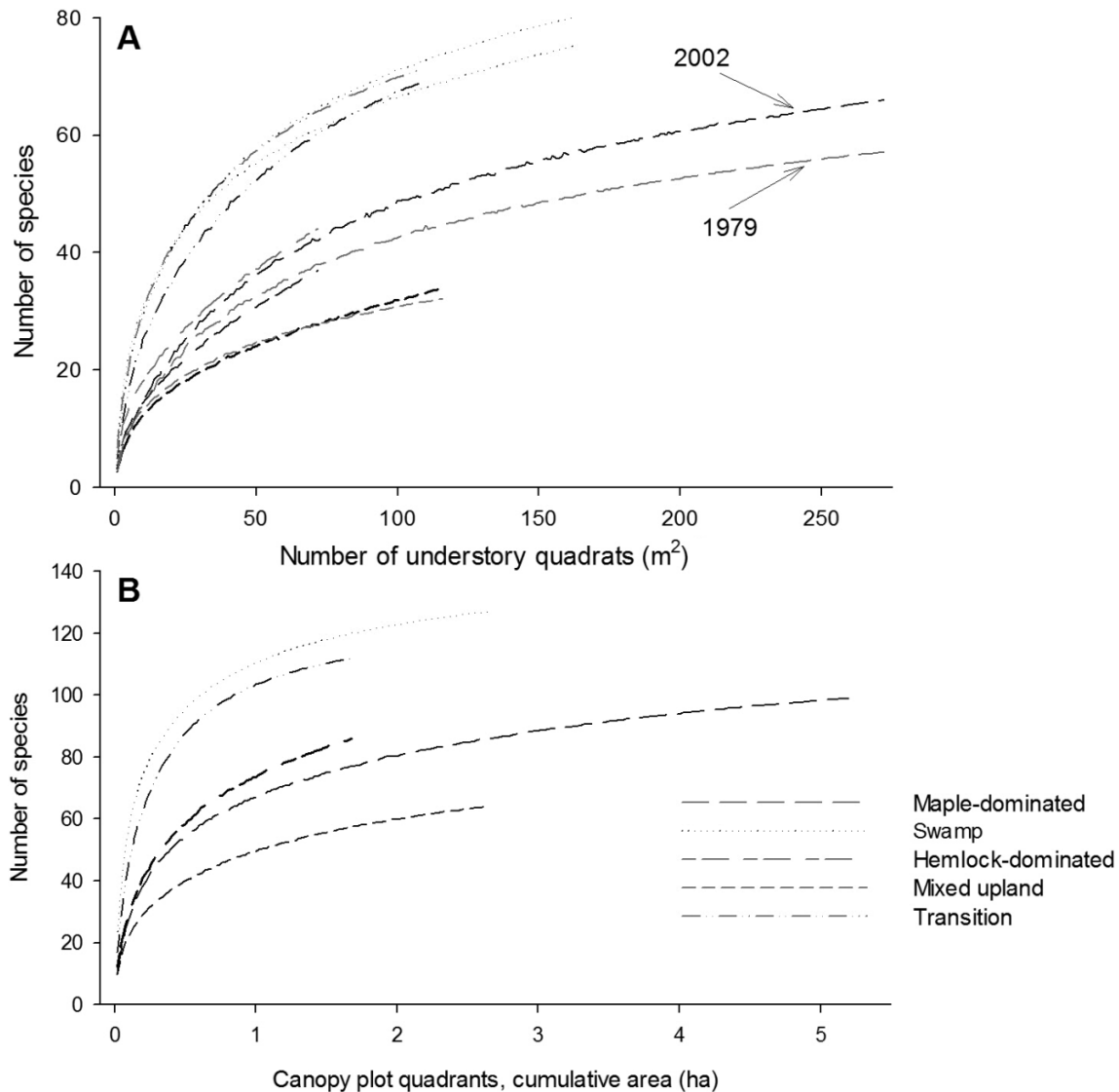
Larger-scale patterns: species accumulation curves

Species accumulation curves whether for square-metre quadrats or canopy plot quadrants (Fig. 2) were steepest and higher for all cumulative areas for swamp and transitional habitats, curves were similar and intermediate for maple-dominated and hemlock-dominated habitats, and mixed upland habitats were consistently lowest in richness at cumulative areas >5 m². The 95% confidence bands (± 2 SD) for swamp habitats do not overlap with those for upland habitat types at any cumulative area. For areas >30 – 45 m², mixed upland curves were significantly lower than others. For quadrat-based curves (Fig. 2A), despite general decreases in quadrat-scale diversity over time, there are no significant differences in species accumulation curves between 1978–1980 and 2002–2007 for any habitat type at areas of more than about 5 m²; in fact, in some instances, species counts are higher for more recent samples at larger cumulative areas. Swamp and transitional habitats, with the highest quadrat-scale diversity loss, showed very little change in curves between sampling periods. For plot quadrant based curves, diversity ranking among habitat types does not change at the maximum scale examined (approximately 2 ha for all but maple-dominated habitat).

Differences among species and species groups

Fifty-three taxa occurred in >20 quadrat samples in the earliest and most recent samples combined (Appendix A, Table A1). Of these, eight showed proportional increases in frequency (quadrat occurrences) of $>20\%$, while 31 decreased by $>20\%$. Twelve species decreased in average cover by more than 20% of original values, while 30 showed proportional increases of $>20\%$ and 16 more than doubled in cover (Appendix A, Table A1; Fig. 3).

Fig. 2. Species accumulation curves by habitat for (A) 1 m² quadrats and (B) 200 m² canopy plot quadrants. Line type indicates habitat; in Fig. 2A, curves for initial sampling (1978–1980) are in gray and for the most recent sampling period are in black. In Fig. 2A, changes within habitat are not significant (curves for 2002 are within 95% confidence bands for the initial sample). The 95% confidence bands for swamp and transition habitat do not overlap with bands for upland habitats and curves; for mixed upland habitat, confidence bands do not overlap with other types for areas >50 m². Relationships among habitats in Fig. 2B are similar.



Proportional changes in frequency and cover were not correlated with initial frequency or cover. Changes were not correlated with Fridley's Θ , providing no suggestion that increasing or decreasing species were more likely to be generalists or specialists. Cover and frequency were strongly positively correlated. Fridley's Θ was negatively correlated with both total cover ($\rho = -0.47$ for 1978–1979 and -0.37 for recent samples for Θ estimated from initial samples, $P < 0.05$) and frequency (corresponding values -0.22 , -0.30 , and $P < 0.05$). Species with higher "generalist" scores occurred less frequently across quadrats and tended to have lower cover than more specialized species; in other words, within individual quadrats, more specialized species tended to be dominant in recent samples.

Changes in cover and frequency for species reported as particularly sensitive or resistant to deer browse were not distinct; both groups showed dynamics consistent with general

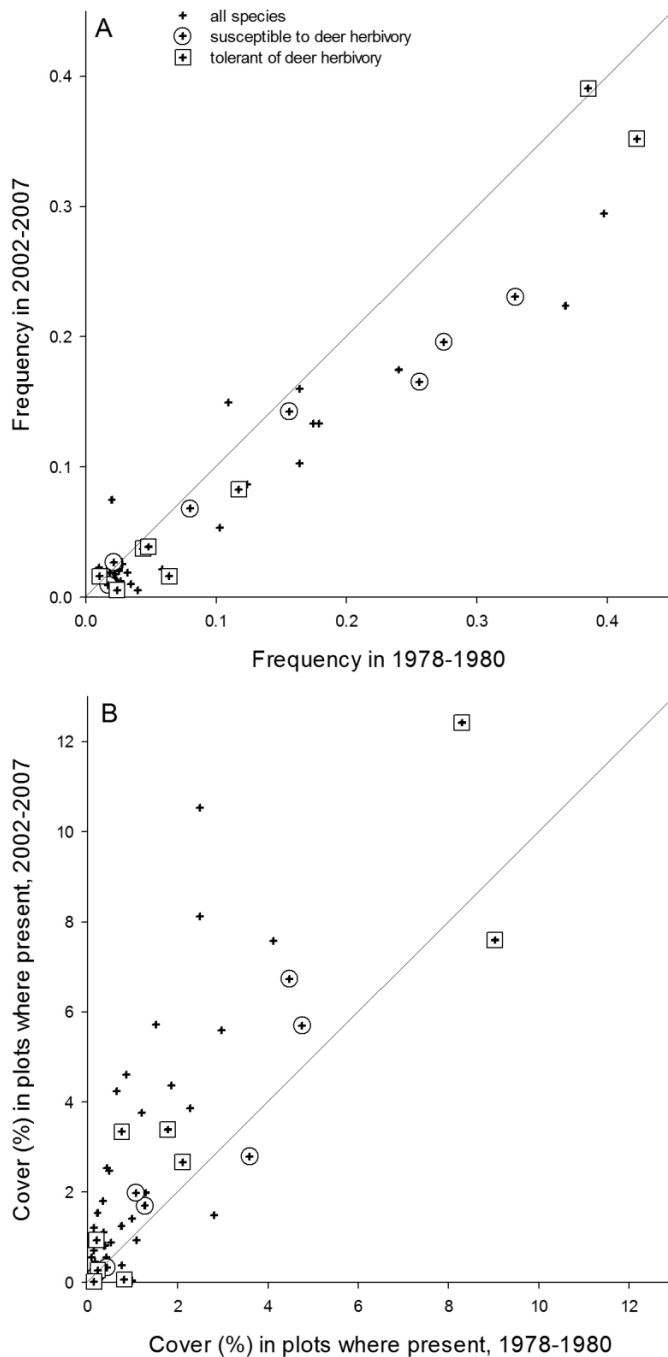
trends (Fig. 3). *Polygonatum* decreased in cover, *Trillium grandiflorum* and *Clintonia* decreased in frequency, and *Aralia* and *Maianthemum canadense* increased in average cover; no other changes in either group were significant (t tests, $P = 0.05$).

Discussion

We focus on four general patterns in diversity in the herbaceous understory of these forests as follows.

(i) Diversity is habitat dependent, with markedly higher diversity, at all spatial scales in swamp forest. Despite pronounced differences in habitat properties and canopy composition among upland areas (Woods 2007), understory diversity differences among upland habitats are minor and generally insignificant.

Fig. 3. Changes in (A) frequency and (B) cover for 52 common understory species in square-metre quadrats. Frequency is the proportion of all quadrats in which species were present. Cover values are the average for quadrats in which species occurred in the indicated sample periods. Circles indicate species documented as sensitive to deer browse and squares species that are thought to be resistant to deer (see text). Large majorities of common species decreased in frequency but increased in local cover where they occurred; patterns for deer-sensitive and deer-tolerant species were not distinctive.



(ii) In all habitats, over the three decades of this study, understory alpha diversity (at the scale of 1 m² quadrats) has declined by about 20% for species richness. This does not appear to be a methodological artifact. Inconsistent field taxon-

omy would contribute to this trend only if more species were differentiated in earlier samples, but the reverse applied; no taxa from 1978–1980 were absent in later samples, but several species were added. Because of small quadrat size, failures of detection (cf. Kéry 2004) are unlikely to influence results. Small errors in quadrat relocation should not introduce bias in terms of diversity changes over time. Losses were greatest for wetland habitats and lowest for maple-dominated habitats and plots with high *Acer saccharum* basal area or canopy influence index generally (and evident only in the spring ephemeral guild for maple-dominated stands) (Fig. 1; Table 1).

(iii) Diversity loss is scale dependent, becoming less pronounced at the scale of canopy plots (quadrats pooled over a linear distance of about 20 m) and not apparent at all, for any habitat-type, in species accumulation curves at coarser scales (Fig. 2).

(iv) Finally, patterns of abundance changes among species are more consistent with changes in diversity being competition driven rather than due to mammalian herbivory or invasive species (Fig. 3).

Despite changes in diversity, total herbaceous cover increased overall. Increases were predominantly in wetland habitats and were minor, often not statistically significant in uplands. Wetland habitats, in more recent samplings, tended to have higher total cover than other habitats, but otherwise, total cover was not strongly habitat dependent (Fig. 1; Table 1).

Diversity is highest for all spatial scales in swamp and transitional habitats where organic soils dominate. Higher canopy openness in swamp forests could permit persistence of more light-demanding species, but this is not readily evident from species lists, and old-growth swamp forests here frequently have very high canopy basal area (Woods 2007). We suspect that high microtopographic diversity is important in maintaining understory diversity in swamp forests but are unable to assess this hypothesis using current data. Relationships between understory diversity and substrate differences among habitat types are not straightforward. For example, high-diversity swampy forests here are generally high in pH and cation availability (Woods 2007), but among upland types, *Acer saccharum* is a strong indicator of cation availability but is generally associated with relatively low understory diversity at least at the square-metre scale. However, understory diversity (with spring ephemerals included) varied only slightly across the range of substrate properties and canopy compositions represented. While *Acer* canopy dominance was important in a number of ANOVAs, other dominant canopy species rarely had significant explanatory power. This was particularly surprising in the case *Tsuga* dominance, as it contrasts with reports of relatively low diversity in hemlock-dominated stands elsewhere (Daubenmire 1930; Black and Mack 1976). Rogers (1980) found little compositional difference between late-successional *Tsuga* and mixed stands but did not address diversity differences. D'Amato et al. (2009) reported species richnesses at the 1 m² scale in Massachusetts old-growth *Tsuga* stands similar to those reported here, with significantly lower richness in secondary stands. The low diversity reported for some *Tsuga* forests may be due to management history combined with relatively slow recolonization or recovery of herbaceous species tolerant of

low light levels and distinctive soil properties associated with *Tsuga* canopy.

Declines in diversity within 1 m² quadrats for all habitats were unexpected. Declines are also significant but less pronounced for quadrats pooled within canopy plots. We also observed positive spatial autocorrelation in diversity patterns and dynamics within canopy plots (over 5–15 m between individual quadrats within plots), but the overall result of large, square-metre-scale diversity declines cannot be attributed to autocorrelation, nor can the less pronounced diversity loss observed when quadrats are pooled by canopy plot. No decline is evident at yet larger scales in species accumulation curves, and no species present in early samples are lost in later samples. The pronounced quadrat-scale diversity loss is apparently a scale-related phenomenon. Over the same three-decade interval, total herbaceous cover has remained constant or increased. Simultaneously, several common species decreased in frequency (Fig. 3; Appendix A, Table A1), while a large majority showed increases in cover in quadrats where they occur.

These results may be interpreted to imply a trend towards stronger dominance by fewer species at scales of one to a few square metres. Maintenance of diversity at the plot scale and beyond suggests development of a more distinct patchy structure at coarser scales. These patterns mirror longer-term changes in canopy composition in the same stand (Woods 2007). Since 1935, tree diversity within 0.08 ha canopy plots has declined across the study area, with increasing dominance within habitat patches but increasing differentiation among patches. At the stand scale, all originally common tree species have remained abundant in some habitats (with the exception of *Ulmus americana* L., affected by introduced disease), but differentiation of community composition between habitats has increased. A similar process may be at work in herbaceous understory communities but at spatial scales differing by two to three orders of magnitude. Contrary to this pattern, Naaf and Wulf (2010) described increasing homogeneity (decreasing beta diversity) across a wide array of late-successional forests in Germany, but this study addresses a wide range of habitats over a regional scale and it is difficult to compare it with the current study.

Whittaker et al. (2001) noted the necessity of specifying scale in analyses of “inventory diversity”, and our findings both emphasize this point and further suggest that scale dependence can be strongly divergent for different components of plant communities. Whittaker et al. (2001) also recognized common scale-related confusions between “inventory” and “differentiation” (alpha and beta) diversity. Although we do not measure differentiation diversity directly, increasing dominance at the square-metre scale without concurrent loss of diversity at scales of tens to hundreds of square metres suggests that enhanced differentiation diversity over these coarser scales may be associated with declines in alpha diversity at finer scales.

Diversity declines in late-successional, old-growth forests raise theoretical and practical questions. Can declines be reconciled with understanding of late-successional systems? Are they due to endogenous successional processes or to external forcings or particular historical events? To the extent that management and conservation priorities include maintenance of diversity at particular scales (Falk et al. 2008), answers to

these questions, particularly for understory communities, should be important for applied ecologists.

While our data do not permit rigorous tests of hypotheses for diversity decreases, we use observed patterns to weigh six mechanisms that have been invoked in explaining diversity loss as follows.

(i) Competition with nonindigenous plant species

Diversity declines have been linked to competition with aggressive, nonindigenous species (Yurkonis et al. 2005; Mason et al. 2009), but this mechanism does not apply here; nonindigenous plants are extremely rare in the study area, present only as a few sparsely scattered individuals.

(ii) Changed trophic interactions

Diversity loss in eastern North American forest understories has been attributed to direct and indirect effects of faunal change, especially increased deer browse (e.g., Alverson et al. 1988; Rooney 2001; Horsley et al. 2003; Côté et al. 2004; Rooney et al. 2004) and invasion by earthworms (Bohlen et al. 2004; Hale et al. 2005, 2006; Frelich et al. 2006; Holdsworth et al. 2007) (however, other workers (Royo et al. 2010) have suggested that moderate deer browse can enhance species richness). While we cannot exclude influence of trophic interactions on observed dynamics, these usual suspects are unlikely to be primary drivers. We have not observed earthworms or earthworm activity in the study area and presence of deep, multiyear litter layers throughout the stand is inconsistent with presence of at least the most destructive species, *Lumbricus terrestris* L. Diversity loss is most pronounced in unlikely earthworm habitat (saturated organic soils), and herbaceous species noted as reduced in worm-invaded sites (Holdsworth et al. 2007) did not show distinctive changes here. Intense herbivory by white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) is regionally well documented, but the Dukes Research Natural Area appears to experience only moderate deer herbivory (Holmes et al. 2008). *Tsuga* regeneration, typically an early casualty (Anderson and Loucks 1979; Tilghman 1989; Krueger and Peterson 2006; but see Mladenoff and Stearns 1993), is abundant and healthy (K.D.W., unpublished data). Herbaceous species known to be particularly vulnerable to deer herbivory (Anderson 1994; Balgooyen and Waller 1995; Kraft et al. 2004) do not show distinctive declines in frequency or cover compared with other understory species, including those thought to be unpalatable to deer (Fig. 3). Deer herbivory can have a homogenizing effect on understory communities and leads to decreasing total cover (Rooney et al. 2004; Holmes and Webster 2010), but our data show increased total cover and suggest enhanced community differentiation.

(iii) Climate change

Ongoing climatic warming is likely to produce significant floristic turnover and could lead to local diversity declines, particularly if population and range expansions of warmer-climate species lag contractions for cooler-climate species. Some of the species declining in frequency here have northerly distributions, but a climate change cause may not be consistent with unchanged or increased average cover for most of these. Our data do not allow strong assessment of this hypothesis.

(iv) Interactions with canopy

Understory diversity patterns show no consistent or strong linkage to canopy composition, but substantial changes in canopy and sapling strata may still be a contributing factor in observed dynamics (Miller et al. 2002). In swamp forests, where diversity decline is greatest, evergreen *Thuja occidentalis* has increased substantially with commensurate declines in deciduous *Fraxinus nigra* (Woods 2007). In upland stands, evergreen *Tsuga canadensis* increased in dominance in hemlock-dominated and mixed-composition habitats. Increasing *Fagus grandifolia* populations include high densities of saplings and subcanopy trees. All of these changes would decrease light availability at the forest floor, potentially enhancing dominance of species most tolerant of light limitation. Barbier et al. (2008) noted lower diversity in evergreen-dominated forests generally. Only maple-dominated habitats are likely to have experienced no reduction in forest floor light intensity due to changing canopy composition, and in these stands, diversity declined only among spring ephemerals.

(v) Competitive interactions within the understory

Competition without major disturbance may be sufficient to drive local diversity losses among canopy trees, even centuries after major disturbance (Harcombe et al. 2002; Woods 2007). Competition among long-lived herbaceous species (and with tree seedlings not included in this analysis) may drive similar dynamics in the understory. Local canopy alpha diversity can decline in late-successional forests without the effects of rare intermediate disturbances (Woods 2004; Bouchard et al. 2006; Nagel and Diaci 2006; Nagel et al. 2006); a similar mechanism, acting at finer scales for herbaceous species, is consistent with our observations. Our data do not allow analysis of types of disturbance that might be implicated, but very localized phenomena that might have little or no effect on canopy composition might be important. Pit-mound topography created by tree fall is known to influence the understory community pattern (Bratton 1976; Beatty 1984), but how such habitat structures change with time since disturbance is not well understood. Degen et al. (2005) found increased understory diversity after storm disturbances in European forests and Falk et al. (2008) documented increased understory diversity following selection harvests in southern Ontario. However, even if competitive sorting following disturbance is driving diversity declines, so little is known about life expectancies and demography of forest understory species that we are unable to estimate required intensity or frequency of disturbance for maintenance of diversity.

(vi) Changed competitive regime due to N deposition

Competitive interactions may be affected as well by anthropogenically enhanced N deposition, leading to decreased plant diversity. While this phenomenon has been most intensively studied in grasslands, the mechanisms invoked may affect forest understories as well (Bobbink et al. 1998; Gilliam 2006; but see Lu et al. 2010). We are unable to assess this hypothesis directly, but most models predict increased homogeneity among habitats (decreased differentiation diversity) as the most likely result, and this is not apparent in our results. Our study area is subject to comparatively moderate increases in N position compared with base-

line fluxes (Bobbink et al. 2010). Analysis of life history characteristics of increasing and decreasing species may help assess this hypothesis.

These hypotheses are not mutually exclusive, but we judge the fourth and fifth to be most consistent with our data. Both invoke direct or indirect effects of moderate disturbance in late-successional or primary forests as important in maintaining and structuring diversity (Collins and Pickett 1987; Scheller and Mladenoff 2002). Scheller and Mladenoff (2002) found only two species, both ferns, with higher frequency in old-growth forests compared with forests with some logging; one of those species, *Gymnocarpium dryopteris*(L.) Newman, increased markedly here and the other, *Dryopteris intermedia* (Muhl. ex Willd.) Gray, maintained frequency (Appendix A, Table A1). Both hypotheses predict greater declines among species with generalist life histories as interspecific competition or intensifying canopy effects refine distributions. This may be consistent with the increased relative dominance here of species with narrow realized niche (low Fridley's Θ), but closer analysis of life history distributions is needed for more rigorous assessment.

More generally, our results highlight the critical value and rarity of long-term, permanent-plot studies at appropriate scales for understanding dynamics of slow systems. One other multidecade study of understory composition in North American old-growth forests (Taverna et al. 2005) found declining diversity in forests of the Piedmont of North Carolina, attributing the trend primarily to anthropogenic changes (fire suppression, exotic competitors, livestock grazing). Declining understory diversity has also been documented in multidecade studies in late-successional European forests (Malmer et al. 1978; Kwiatkowska 1994; Baeten et al. 2010; Durak 2010) and is variously interpreted as a direct or indirect result of changes in historical grazing or other changed management practices. Forests classified as "ancient" in these studies may have been subject to active management as recently as a few centuries ago (within the life spans of dominant species) and so might still be undergoing changes driven by past disturbances. Our study site has no history of active management.

Old-growth, primary forests are often taken as baselines in development of management and conservation strategies and goals. This is likely rooted in long-standing assumptions of relative stability of such communities and the corollary that community patterns reflect underlying environmental patterns with little influence of historical variables. However, we speculate that natural disturbance interacting with competitive filtering may drive very long-persistent community changes without invoking recent exogenous influences. If processes involved in the fourth and fifth hypotheses above are, in fact, primary drivers of changes observed here, assumptions of baseline stability must be reconsidered; old-growth systems are not necessarily inherently stable and may be, generally, in continuous, dynamic response to historical events (Woods 2004). If this is the case, management targeting maintenance or restoration of native plant diversity becomes more complex, and it becomes necessary to clearly define scales of interest and to obtain more precise understanding and management of disturbance regimes in light of their long-persistent effects on fine-scale pattern and diversity.

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Appendix A

Tables A1 and A2 appear on the following pages.

Table A1. Frequency (proportional occurrence in 1 m² quadrats) and average cover in quadrats where present for all taxa with >20 occurrences in 1978–1980 or 2001–2009, with proportional change in both variables.

Species	1978–1980		2001–2009		Proportional change	
	Frequency	Average cover (%)	Frequency	Average cover (%)	Frequency	Cover
* <i>Allium tricoccum</i>	0.05	0.57	0.20	4.24	2.80	6.39
<i>Aralia nudicaulis</i>	0.16	0.85	0.14	1.22	-0.09	0.43
<i>Arisaema triphyllum</i>	0.04	0.05	0.04	0.06	-0.15	0.07
<i>Athyrium filix-femina</i>	0.05	0.59	0.04	0.63	-0.19	0.07
<i>Botrychium virginianum</i>	0.02	0.03	0.01	0.01	-0.78	-0.94
<i>Brachyelytrum erectum</i>	0.03	0.02	0.02	0.08	-0.42	3.76
<i>Caltha palustris</i>	0.03	0.23	0.02	0.27	-0.21	0.19
<i>Carex intumescens</i>	0.01	0.02	0.02	0.05	0.50	1.64
<i>Carex pauciflora</i>	0.02	0.02	0.01	0.01	-0.78	-0.91
<i>Carex</i> sect. <i>Heleonastes</i>	0.06	0.20	0.02	0.22	-0.75	0.10
<i>Carex</i> sect. <i>Montanae</i>	0.12	0.11	0.08	0.41	-0.30	2.78
<i>Chrysosplenium americanum</i>	0.04	0.28	0.01	0.07	-0.87	-0.76
<i>Circaea alpina</i>	0.06	0.12	0.02	0.07	-0.64	-0.45
<i>Cirsium muticum</i> and <i>Cirsium palustre</i>	0.02	0.18	0.01	0.14	-0.41	-0.20
* <i>Claytonia caroliniana</i>	0.85	3.22	0.55	3.87	-0.36	0.20
<i>Clintonia borealis</i>	0.33	2.02	0.23	1.69	-0.30	-0.17
<i>Coptis trifolia</i>	0.24	0.27	0.17	0.98	-0.27	2.66
<i>Cornus canadensis</i>	0.16	0.28	0.10	0.35	-0.37	0.24
<i>Corylus cornuta</i>	0.02	0.23	0.01	0.21	-0.47	-0.08
* <i>Dicentra canadensis</i> and <i>Dicentra cucullaria</i>	0.62	6.17	0.33	2.78	-0.46	-0.55
<i>Dryopteris intermedia</i>	0.39	3.35	0.39	5.05	0.01	0.51
* <i>Erythronium americanum</i>	0.88	4.51	0.91	8.23	0.03	0.83
<i>Galium triflorum</i>	0.12	0.10	0.09	0.31	-0.30	2.26
<i>Gaultheria hispidula</i>	0.03	0.01	0.01	0.04	-0.55	3.22
<i>Gymnocarpium dryopteris</i>	0.11	0.34	0.15	1.82	0.37	4.44
<i>Impatiens capensis</i>	0.03	0.13	0.01	0.07	-0.88	-0.47
<i>Linnaea borealis</i>	0.05	0.01	0.04	0.08	-0.25	4.21
<i>Listera convallarioides</i>	0.03	0.02	0.03	0.02	0.16	0.14
<i>Lonicera canadensis</i>	0.02	0.21	0.07	0.72	2.73	2.45
<i>Huperzia lucidula</i>	0.42	4.78	0.35	3.87	-0.17	-0.19
<i>Impatiens capensis</i>	0.03	0.13	0.01	0.07	-0.88	-0.47
<i>Linnaea borealis</i>	0.05	0.01	0.04	0.08	-0.25	4.21
<i>Listera convallarioides</i>	0.03	0.02	0.03	0.02	0.16	0.14
<i>Lonicera canadensis</i>	0.02	0.21	0.07	0.72	2.73	2.45
<i>Huperzia lucidula</i>	0.42	4.78	0.35	3.87	-0.17	-0.19
<i>Lycopus uniflorus</i>	0.02	0.04	0.02	0.08	-0.24	0.90
<i>Maianthemum canadense</i>	0.27	0.81	0.20	1.30	-0.29	0.60
<i>Matteuccia struthiopteris</i>	0.01	0.07	0.02	0.33	1.33	4.10
<i>Mitchella repens</i>	0.10	0.11	0.05	0.17	-0.48	0.52
<i>Mitella nuda</i>	0.17	0.13	0.13	0.68	-0.24	4.41
<i>Onoclea sensibilis</i>	0.03	0.19	0.03	0.38	-0.10	1.00
<i>Osmorhiza longistylis</i>	0.02	0.09	0.01	0.07	-0.36	-0.20
<i>Osmunda cinnamomea</i>	0.02	0.20	0.02	0.37	0.00	0.88
<i>Oxalis montana</i>	0.40	1.87	0.29	2.69	-0.26	0.44
<i>Phegopteris connectilis</i>	0.02	0.05	0.01	0.09	-0.50	0.72
<i>Polygonatum pubescens</i>	0.08	0.22	0.07	0.13	-0.15	-0.41
<i>Prunella vulgaris</i>	0.02	0.05	0.01	0.08	-0.31	0.65
<i>Pyrola secunda</i>	0.03	0.03	0.02	0.13	-0.16	3.37
<i>Ribes triste</i>	0.01	0.02	0.02	0.08	4.67	3.92
<i>Rubus pubescens</i>	0.18	0.50	0.13	1.48	-0.25	1.99
<i>Scutellaria lateriflora</i>	0.03	0.05	0.00	0.00	-0.89	-0.98
<i>Maianthemum racemosum</i>	0.02	0.08	0.03	0.07	0.25	-0.13
<i>Maianthemum trifolium</i>	0.02	0.07	0.02	0.29	0.21	3.08
<i>Streptopus lanceolatus</i>	0.26	1.05	0.17	0.59	-0.35	-0.44
<i>Trientalis borealis</i> Raf.	0.16	0.22	0.16	0.28	-0.02	0.27
<i>Trillium grandiflorum</i>	0.02	0.05	0.01	0.04	-0.46	-0.22
<i>Viola</i> (stemless)	0.37	0.61	0.22	1.49	-0.39	1.43
<i>Viola pubescens</i>	0.02	0.09	0.01	0.04	-0.65	-0.55

Note: Spring ephemerals are indicated by an asterisk preceding the species name. Total sample size is 752 quadrats (in 188 canopy plots); spring ephemeral statistics are for 284 quadrats in 71 canopy plots (all upland canopy plots sampled in both intervals early enough to detect spring ephemerals).

Table A2. Full results for repeated-measures ANOVAs.

I. All quadrats, two measurements (1978–1980 and 2004–2007)

A. Species richness (S)

1. Between subjects (quadrat or plot)

Individual quadrats			Pooled by canopy plot			
Variable	df	F	P	df	F	P
Habitat type	4	10.12	0.00	4	5.72	0.00
Plot basal areas:						
<i>Acer rubrum</i>	1	3.89	0.05	1	1.81	0.18
<i>Acer saccharum</i>	1	13.93	0.00	1	7.58	0.01
<i>Betula alleghaniensis</i>	1	0.26	0.61	1	0.05	0.61
<i>Fagus grandifolia</i>	1	3.01	0.08	1	1.28	0.82
<i>Fraxinus nigra</i>	1	0.00	0.98	1	0.04	0.84
<i>Thuja occidentalis</i>	1	0.89	0.35	1	0.51	0.48
<i>Tsuga canadensis</i>	1	1.96	0.16	1	0.74	0.39
All canopy species	1	0.01	0.91	1	0.04	0.84
Error	739			176		

2. Within subjects

	df	F	P	df	F	P
Main effect within (time)	1	23.35	0.00	1	16.38	0.00
Interactions with:						
Habitat-type	4	1.92	0.11	4	0.92	0.46
Plot basal areas:						
<i>Acer rubrum</i>	1	1.68	0.20	1	2.00	0.16
<i>Acer saccharum</i>	1	0.84	0.36	1	1.72	0.19
<i>Betula alleghaniensis</i>	1	1.40	0.24	1	1.17	0.28
<i>Fagus grandifolia</i>	1	0.51	0.48	1	0.30	0.58
<i>Fraxinus nigra</i>	1	0.01	0.92	1	0.20	0.65
<i>Thuja occidentalis</i>	1	0.21	0.65	1	0.10	0.75
<i>Tsuga canadensis</i>	1	0.04	0.85	1	0.07	0.80
All canopy species	1	0.69	0.41	1	0.02	0.90
Error	739			176		

B. Shannon's index (H)

1. Between subjects (quadrat or plot)

Individual quadrats			Pooled by canopy plot			
Variable	df	F	P	df	F	P
Habitat type	4	6.65	0.00	4	4.88	0.00
Plot basal areas:						
<i>Acer rubrum</i>	1	4.13	0.04	1	1.63	0.20
<i>Acer saccharum</i>	1	12.24	0.00	1	7.67	0.01
<i>Betula alleghaniensis</i>	1	0.00	1.00	1	0.01	0.92
<i>Fagus grandifolia</i>	1	2.83	0.09	1	0.51	0.48
<i>Fraxinus nigra</i>	1	0.03	0.86	1	0.00	0.95
<i>Thuja occidentalis</i>	1	0.36	0.55	1	0.28	0.60
<i>Tsuga canadensis</i>	1	0.90	0.34	1	0.45	0.50
All canopy species	1	0.02	0.88	1	0.01	0.91
Error	739			176		

2. Within subjects

	df	F	P	df	F	P
Main effect within (time)	1	17.69	0.00	1	12.06	0.00
Interactions with:						
Habitat type	4	0.62	0.65	4	0.29	0.89
Plot basal areas:						
<i>Acer rubrum</i>	1	3.82	0.06	1	2.77	0.10
<i>Acer saccharum</i>	1	2.40	0.12	1	1.59	0.21
<i>Betula alleghaniensis</i>	1	3.00	0.08	1	1.59	0.21
<i>Fagus grandifolia</i>	1	1.27	0.26	1	1.63	0.20
<i>Fraxinus nigra</i>	1	0.01	0.94	1	0.06	0.82
<i>Thuja occidentalis</i>	1	0.00	0.95	1	0.00	0.98

Table A2 (continued).

I. All quadrats, two measurements (1978–1980 and 2004–2007)							
	<i>Tsuga canadensis</i>	1	0.22	0.64	1	0.06	0.82
	All canopy species	1	0.11	0.74	1	0.12	0.74
	Error	739			176		
C. Total understory cover							
1. Between subjects (quadrat or plot)							
Individual quadrats							
	Variable	df	<i>F</i>	<i>P</i>	Pooled by canopy plot		
	Habitat type	4	2.21	0.07	4	1.62	0.17
	Plot basal areas:						
	<i>Acer rubrum</i>	1	0.78	0.38	1	0.61	0.44
	<i>Acer saccharum</i>	1	1.53	0.22	1	1.44	0.23
	<i>Betula alleghaniensis</i>	1	1.43	0.23	1	1.73	0.19
	<i>Fagus grandifolia</i>	1	0.66	0.42	1	1.12	0.29
	<i>Fraxinus nigra</i>	1	1.07	0.30	1	0.53	0.47
	<i>Thuja occidentalis</i>	1	1.19	0.28	1	0.81	0.37
	<i>Tsuga canadensis</i>	1	1.35	0.25	1	0.90	0.35
	All canopy species	1	1.35	0.25	1	1.22	0.27
	Error	739			176		
2. Within subjects							
		df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
	Main effect within (time)	1	6.69	0.01	1	3.80	0.05
	Interactions with:						
	Habitat type	4	3.20	0.01	4	2.16	0.08
	Plot basal areas:						
	<i>Acer rubrum</i>	1	5.28	0.02	1	2.27	0.13
	<i>Acer saccharum</i>	1	1.35	0.25	1	0.55	0.46
	<i>Betula alleghaniensis</i>	1	2.80	0.10	1	1.08	0.30
	<i>Fagus grandifolia</i>	1	0.90	0.34	1	0.00	0.98
	<i>Fraxinus nigra</i>	1	0.21	0.65	1	0.04	0.84
	<i>Thuja occidentalis</i>	1	0.22	0.64	1	0.05	0.83
	<i>Tsuga canadensis</i>	1	0.15	0.70	1	0.02	0.89
	All canopy species	1	0.31	0.58	1	0.08	0.78
	Error	739			176		
II. Upland quadrats, three measurements (1978–1980, 1992–1994, and 2004–2007) (<i>P</i> values include Greenhouse–Geisser correction)							
A. Species richness (<i>S</i>)							
1. Between subjects (quadrat or plot)							
Individual quadrats							
	Variable	df	<i>F</i>	<i>P</i>			
	Habitat type	3	13.88	0.00			
	Canopy influence index:						
	<i>Acer rubrum</i>	1	9.40	0.00			
	<i>Acer saccharum</i>	1	5.39	0.02			
	<i>Betula alleghaniensis</i>	1	2.30	0.13			
	<i>Fagus grandifolia</i>	1	4.12	0.04			
	<i>Thuja occidentalis</i>	1	3.12	0.10			
	<i>Tsuga canadensis</i>	1	0.80	0.37			
	All canopy species	1	2.01	0.16			
	Error	437					
2. Within subjects							
		df	<i>F</i>	<i>P</i>			
	Main effect within (time)	2	8.90	0.00			
	Interactions with:						
	Habitat type	6	1.87	0.09			
	Canopy influence index:						
	<i>Acer rubrum</i>	2	0.23	0.79			
	<i>Acer saccharum</i>	2	4.24	0.02			
	<i>Betula alleghaniensis</i>	2	3.63	0.03			

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Table A2 (continued).

II. Upland quadrats, three measurements (1978–1980, 1992–1994, and 2004–2007) (<i>P</i> values include Greenhouse–Geisser correction)				
	<i>Fagus grandifolia</i>	2	0.27	0.76
	<i>Thuja occidentalis</i>	2	3.00	0.06
	<i>Tsuga canadensis</i>	2	1.00	0.37
	All canopy species	2	4.49	0.01
	Error	874		
B. Shannon's index (<i>H</i>)				
1. Between subjects (quadrat or plot)				
Individual quadrats				
	Variable	df	<i>F</i>	<i>P</i>
	Habitat type	3	10.28	0.00
	Canopy influence index:			
	<i>Acer rubrum</i>	1	5.73	0.02
	<i>Acer saccharum</i>	1	2.74	0.10
	<i>Betula alleghaniensis</i>	1	0.92	0.34
	<i>Fagus grandifolia</i>	1	0.94	0.33
	<i>Thuja occidentalis</i>	1	3.22	0.12
	<i>Tsuga canadensis</i>	1	0.00	0.98
	All canopy species	1	0.57	0.45
	Error	437		
2. Within subjects				
		df	<i>F</i>	<i>P</i>
	Main effect within (time)	2	4.28	0.01
	Interactions with:			
	Habitat type	6	0.51	0.80
	Canopy influence index:			
	<i>Acer rubrum</i>	2	0.58	0.56
	<i>Acer saccharum</i>	2	4.54	0.01
	<i>Betula alleghaniensis</i>	2	3.00	0.06
	<i>Fagus grandifolia</i>	2	0.11	0.90
	<i>Thuja occidentalis</i>	2	0.35	0.70
	<i>Tsuga canadensis</i>	2	1.75	0.18
	All canopy species	2	3.99	0.02
	Error	874		
C. Total understory cover				
1. Between subjects (quadrat or plot)				
Individual quadrats				
	Variable	df	<i>F</i>	<i>P</i>
	Habitat type	3	9.02	0.00
	Canopy influence index:			
	<i>Acer rubrum</i>	1	0.69	0.41
	<i>Acer saccharum</i>	1	0.73	0.39
	<i>Betula alleghaniensis</i>	1	1.02	0.31
	<i>Fagus grandifolia</i>	1	0.03	0.86
	<i>Thuja occidentalis</i>	1	0.99	0.32
	<i>Tsuga canadensis</i>	1	2.00	0.16
	All canopy species	1	2.17	0.14
	Error	437		
2. Within subjects				
		df	<i>F</i>	<i>P</i>
	Main effect within (time)	2	3.31	0.04
	Interactions with:			
	Habitat type	6	2.36	0.03
	Canopy influence index:			
	<i>Acer rubrum</i>	2	2.67	0.07
	<i>Acer saccharum</i>	2	0.59	0.56
	<i>Betula alleghaniensis</i>	2	0.52	0.59
	<i>Fagus grandifolia</i>	2	3.62	0.03
	<i>Thuja occidentalis</i>	2	4.57	0.01

Table A2 (concluded).

II. Upland quadrats, three measurements (1978–1980, 1992–1994, and 2004–2007) (<i>P</i> values include Greenhouse–Geisser correction)				
	<i>Tsuga canadensis</i>	2	1.85	0.16
	All canopy species	2	0.54	0.58
Error		874		
III. Upland quadrats with ephemerals, two measurements (1978–1980, combined 2009 and 2004–2007 data)				
A. Species richness (<i>S</i>)				
1. Between subjects (quadrat or plot)				
Individual quadrats				
Variable		df	<i>F</i>	<i>P</i>
Canopy influence index:				
	<i>Acer rubrum</i>	1	0.77	0.38
	<i>Acer saccharum</i>	1	2.59	0.11
	<i>Betula alleghaniensis</i>	1	2.45	0.12
	<i>Fagus grandifolia</i>	1	4.71	0.03
	<i>Tsuga canadensis</i>	1	2.69	0.10
	All canopy species	1	2.25	0.14
Error		273		
2. Within subjects				
		df	<i>F</i>	<i>P</i>
Main effect within (time)				
		1	23.76	0.00
Interactions with:				
Canopy influence index:				
	<i>Acer rubrum</i>	1	1.09	0.30
	<i>Acer saccharum</i>	1	0.21	0.65
	<i>Betula alleghaniensis</i>	1	0.28	0.60
	<i>Fagus grandifolia</i>	1	0.03	0.87
	<i>Tsuga canadensis</i>	1	0.00	0.97
	All canopy species	1	0.26	0.61
Error		273		