Canadian Journal of Forest Research

Research Article

Long-term (17-year) dynamics of herbaceous plant communities after shelterwood regeneration harvests in southern Appalachian cove- and upland hardwood forests

C.H. Greenberg[a], **M. Woodbridge**[a], **T.W. Roof**[b], **and J.L. Adams**[a]

[a]USDA Forest Service, Southern Research Station, Upland Hardwood Ecology and Management Research Work Unit, Asheville, NC 28806, USA; [b]USDA Forest Service, Southern Research Station, Forest Inventory and Analysis, Asheville, NC 28804, USA

Corresponding author: **C.H. Greenberg** (email: Cathryn.greenberg@usda.gov)

Abstract

The southern Appalachians are a "hotspot" of plant diversity. Herbaceous communities are especially rich in mesic cove hardwood forests, compared to drier upland hardwood forests. We evaluated changes in forest structure and herbaceous plant communities over 17 years in mature cove- (CHM) and upland hardwood (UHM) forests, and young 2-age cove- (CHSW) and upland hardwood (UHSW) stands created by shelterwood-with-reserves regeneration harvests (SW). Structure of mature forests was relatively static. In contrast, reduced canopy cover after harvests initiated rapid increases in small tree stem density and blackberry (*Rubus*) cover, followed by dense shade as young trees gained height. We identified 201 herbaceous species including 156 forbs. Species richness was about double in CHM and CHSW than in UHM and UHSW; composition changed little over time within treatments, even as forest structure changed in SW. Among the 79 herbaceous species analyzed, relative abundance of 26 showed a response; most were more abundant in CHM, CHSW, or both compared to UHM, UHSW, or both. Our results indicated that shelterwood harvests had a neutral or positive effect on herbaceous plant richness, diversity, and abundance of most species, and suggested that environmental gradients associated with forest type influenced herbaceous communities much more than SW alone.

Key words: cove hardwood forest, upland hardwood forest, herbaceous plants, herbaceous diversity, shelterwood harvest, southern Appalachians

1. Introduction

The Southern Appalachian Mountains are a "hot spot" of biological diversity due to their biogeographical history and complex topography (Whittaker 1956; Jenkins 2007), with plant diversity among the highest in the temperate forest zone (Wofford 1989; Jenkins 2007). Herbaceous plants comprise less than 1% of total aboveground plant biomass in eastern forests but contribute substantially to total plant diversity and ecosystem function (Gilliam 2007; Wyatt and Silman 2010). Based on six studies, Gilliam (2007) estimated that herbaceous plant species richness in eastern mixed hardwood forests is 2.0–3.4 times greater than overstory tree species richness.

Complex topographic gradients including aspect, elevation, and landform (site concavity or convexity) (e.g., Whittaker 1956) affect temperature and radiation, soil type and development, and moisture at highly local scales (Wyatt and Silman 2010) that in turn provide conditions for different forest types and herbaceous plant communities within a landscape. Soil pH and nutrients (Ulrey 2002; Elliott 2014) and light availability associated with shrub- or tree canopy cover (McEwan and Muller 2011) also influence herbaceous species composition; *Rhododendron maximum* thickets in particular may inhibit tree seedling survival and herbaceous plant diversity by casting dense shade and altering the chemical composition of soils (e.g., Elliott and Miniat 2018). Herbaceous plant communities are especially rich in productive cove hardwood forests associated with mesic, topographically sheltered (concave) landscapes or north-facing slopes, relative to drier upland hardwood forests associated with south or west-facing slopes and flat or convex landscape positions (e.g., Whittaker 1956; Gilliam 2007); even within forest types herbaceous species composition is spatially variable (Schafale and Weakley 1990; Wyatt and Silman 2010; McEwan and Muller 2011). Herbaceous species abundance and occurrence are temporally dynamic, especially within recently harvested, developing stands (Reader and Bricker 1992) but also within mature (Elliott and Knoepp 2005) and old-growth (Brewer 1980) forests.

The southern Appalachians have a long history of natural disturbances, such as wind events of varying types, scales, and severities or rare lightning-ignited wildfires (Greenberg et al. 2016). Humans have also influenced southern Appalachian forests for thousands of years. Anthropogenic

disturbances included frequent burning by Native Americans and (by the 1800s) Euro-American settlers, land clearing for agriculture, poor farming practices that eroded soil, free-range livetock grazing, and the functional extinction of the once-dominant American chestnut (*Castanea dentata*) by a non-native fungus (*Cryphonectria parasitica*) by the mid-20th century (Elliott and Swank 2008; Greenberg et al. 2016). Perhaps most notably, the southern Appalachians were heavily logged in the late 19th and early 20th centuries (Pyle 1988). Heavy disturbances such as regeneration harvests (e.g., methods that create a new age class, such as shelterwood, clearcut, or group selection) alter light and microclimate at the forest floor, and mechanical damage from heavy machinery can potentially alter soil nutrient availability and forest productivity (e.g., Elliott and Knoepp 2005).

Results of studies examining impacts of heavy disturbance associated with regeneration harvests on herbaceous plant communities of eastern hardwood forests are equivocal; some indicate that harvests can reduce species richness and alter species composition—especially in rich cove forests—for decades to centuries (e.g., Duffy and Meier 1992; Fraterrigo et al. 2006; Bunn et al. 2010; Wyatt and Silman 2010; Woodbridge 2020), whereas others report increased diversity (Elliott and Knoepp 2005), or that composition, cover, and diversity return to pre-disturbance levels within 10–20 years (Gilliam et al. 1995; Ford et al. 2000; Gilliam 2007). Many studies used a "retroactive" approach to examine effects of timber harvests by comparing herbaceous plant communities across a chronosequence of post-harvest age-classes (Gilliam et al. 1995; Ford et al. 2000), or between second growth (mature forest that developed after timber harvests) and old growth (presumably never extensively logged) forests (e.g., Duffy and Meier 1992; Jackson et al. 2009; Bunn et al. 2010; Wyatt and Silman 2010; Woodbridge 2020). Such "snapshot" studies, though valuable, may be biased by differences across study sites that are unrelated to disturbance (e.g., conditions associated with soils or topography), or associated with unknown past disturbances (e.g., Johnson et al. 1993), relative to those that track and compare temporal changes in plant communities within the same sites before and after regeneration harvests.

Studies that incorporate pre- and post-harvest herbaceous plant community measurements in southern Appalachian forests are rare; most are short-term (e.g., 1–3 years post-harvest), leaving unanswered questions regarding changes to herbaceous plant communities over time as young forests regrow. Elliott and Knoepp (2005) reported an increase in diversity and no change in species richness within 3 years after shelterwood harvests in dry, high-elevation intermediate mixed-hardwood forests, compared to pre-harvest. Similarly, Benz et al. (in review) reported increased species richness of the groundlayer, including herbaceous species, within 1 year after a shelterwood harvest. In contrast, Elliott et al. (1997) reported that ground flora diversity in cove- and mixed hardwood communities was greater pre- than post-clearcutting and decreased over the next 17 years as early successional species declined and later-successional species were not yet well established.

Several studies focus on species richness, diversity, and evenness, but provide little information on species composition, making it difficult to evaluate how timber harvests affect individual species and communities (Elliott 2014). Further, many studies of the "herbaceous layer" or "ground layer" include both woody (tree and shrub) and herbaceous species, making it difficult to compare studies or understand how timber harvests affect herbaceous plant communities, not confounded by the inclusion of woody species. In addition to variable experimental designs, the suite of species measured, and study longevities, inconsistent results among studies are likely due, at least in part, to the multitude of environmental and anthropogenic drivers that influence plant communities and confound comparisons. This highlights the need for targeted studies of herbaceous response across different forest management activities and forest types.

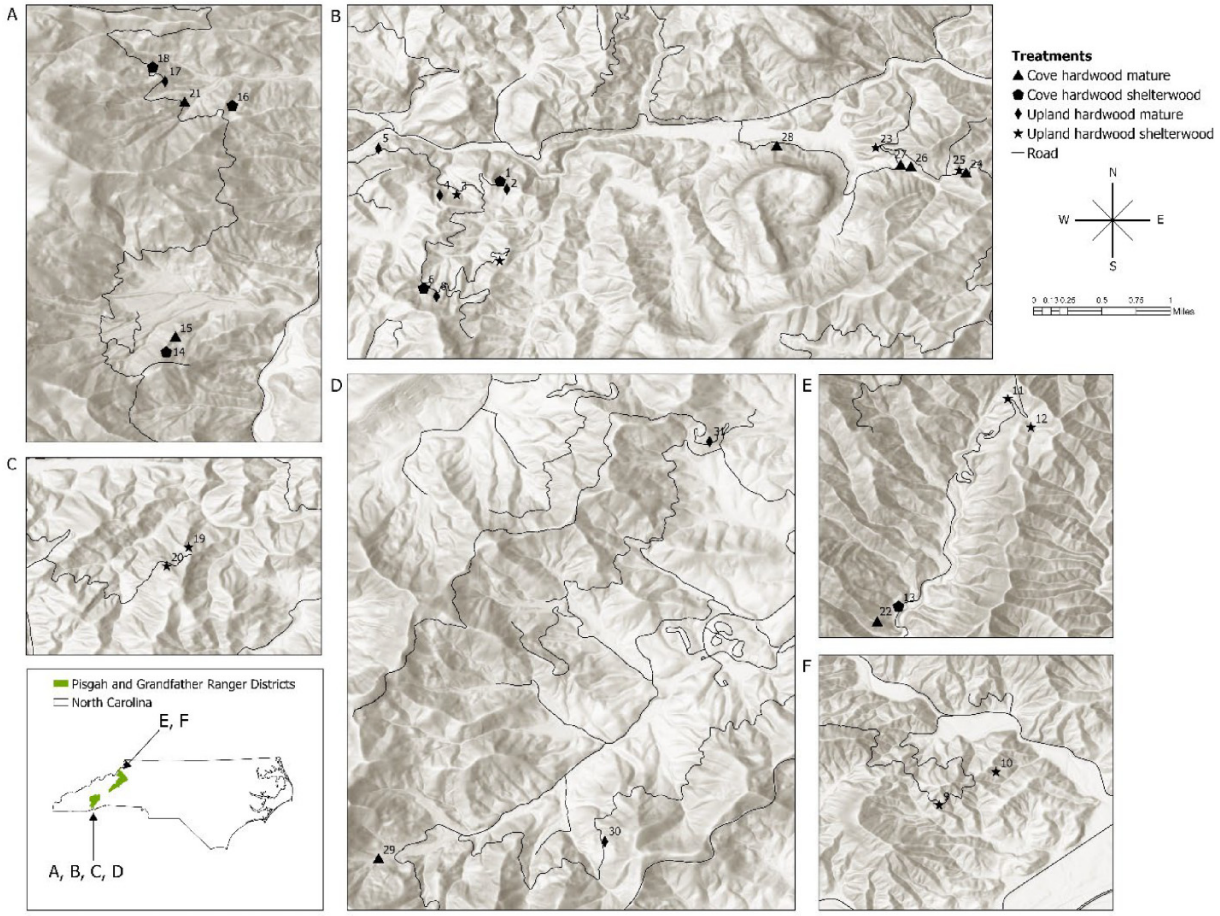
In this study, we evaluated dynamic temporal changes in forest structure, herbaceous plant communities (species richness, diversity, evenness, and composition), and relative abundance of individual species in young 2-age stands created by shelterwood-with-reserves regeneration harvests (termed "shelterwood") and mature forest stands of upland hardwood and cove hardwood forest types over a 17-year period. Our objectives were to compare (1) how herbaceous plant species and communities change through time in response to shelterwood harvests, and; (2) whether herbaceous plant species and community response to shelterwood harvests differs between cove- and upland hardwood forest types. We hypothesized that herbaceous plant communities in cove hardwood forests could be more sensitive to shelterwood harvests than their subxeric upland hardwood forest counterparts that generally support lower species richness and diversity.

2. Methods

2.1. Study area

Our study was conducted in the Pisgah and Grandfather ranger districts of the Pisgah National Forest in Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina, USA (Fig. 1). Study sites were located across a wide range of topographic features including aspect, slope position, and % slope; elevations ranged from 500 to 1200 m. Average annual rainfall in the region (Asheville area, 2000–2016) was 119 cm (ranged from 85 to 191 cm) (NOAA National Weather Service). Soils were predominantly Dystrochrepts and Hapludults (Pittillo et al. 1998). Mature forest age was 80–100 years at study establishment. Forests were composed of yellow poplar (*Liriodendron tulipifera*), northern red oak (*Quercus rubra*), magnolia (*Magnolia* spp.), white ash (*Fraxinus americanus*), beech (*Fagus grandifolia*), hemlock (*Tsuga canadensis*), and silverbell (*Halesia carolina*) on moister (cove hardwood) sites; subxeric (upland hardwood) sites were dominated by scarlet oak (*Quercus coccinea*), chestnut oak (*Quercus montana*), black oak (*Quercus velutina*), blackgum (*Nyssa sylvatica*), and sourwood (*Oxydendrum arboreum*), with abundant mountain laurel (*Kalmia latifolia*) in the understory. Red maple (*Acer rubrum*), hickories (*Carya* spp.), flowering dogwood (*Cornus*

Fig. 1. Map of study plot locations in the Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina. Figs was created using ArcGIS Pro version 3.3.0 (ESRI) and assembled from the following data sources: Roads layer and State layer (Pisgah National Forest). Base map—World hillshade DEM from Environmental Systems Research Institute (ESRI).



florida), and white oak (*Quercus alba*) were common throughout (Pittillo et al. 1998).

2.2. Study design

Our herbaceous plant diversity study was part of a long-term "fruit study" (established in 1999) comparing stand dynamics and fleshy fruit, samara, and nut production between mature, closed-canopy forest and two-aged stands with low basal area (BA) retention created by shelterwood-with-reserves regeneration (termed "shelterwoods"; SW) harvests in southern Appalachian upland- and cove hardwood forests (Greenberg et al. 2007). We selected 31 stands of two forest types (upland hardwood (UH) and cove hardwood (CH)) and two silvicultural treatments (harvest types; shelterwood harvests (SW) and mature forest controls (M)) in a 2 × 2 factorial design, for a total of four treatments: upland hardwood shelterwood harvests (UHSW; $n = 9$) and mature forest controls (UHM; $n = 8$), and; cove hardwood shelterwood harvests (CHSW; $n = 6$) and mature forest controls (CHM; $n = 8$). Forest types (cove [type 56] or upland hardwood [type 53]) were determined by the United States Forest Service (USFS; Southern Region Silvicultural Examination and Prescription Field Book, for Continuous Inventory of Stand Conditions version 4.02, unpublished report) based on pre-harvest tree species composition at the stand level. Whereas this method may not reflect within-stand variability in topography and site quality (e.g., Beasley et al. 2022), it is simple and more practical than sampling-intensive or statistically complex methods. Additionally, it is widely used to categorize forest types, making our results more accessible and useful to forest managers. We selected SW study sites based on availability of stands that met our age, forest type, and silvicultural treatment criteria. M and SW stands were not paired, but we attempted to locate them within the same general areas to minimize variability due to location or topography.

Shelterwood harvests were conducted during 1998–1999 using a shelterwood-with-reserves regeneration method. About 15%–20% of the original mature tree BA—mostly scattered oaks and hickories—was retained in both forest types to create a heterogeneous stand structure and maintain hard mast (acorns and hickory nuts) production for wildlife while facilitating the initiation and development of tree regeneration. Shelterwood stands averaged 7.0 ha (range 3.2–10.5 ha) in size and were generally the same age as mature stands when they were harvested. US Forest Service personnel con-

ducted standard site-preparation treatments in regenerated stands within a year of harvesting by cutting all stems 2.5–20 cm diameter at breast height (dbh) (Pisgah district) or 5–25 cm dbh (Grandfather district) and ≥1.4 m tall. The harvested tree stump surfaces of red maple, flowering dogwood, silverbell, sourwood, yellow poplar, sassafras (*Sassafras albidum*), black locust (*Robinia pseudoacacia*), Fraser magnolia (*M. fraseri*), and blackgum, as well as rhododendron (*Rhododendron* spp.), and mountain laurel (*Kalmia latifolia*) were treated with herbicide (Garlon 3A, 50–50 mix; Dow AgroSciences, Indianapolis, IN) to reduce sprouting.

We randomly established one 20 × 50 m (0.1 ha) plot (extending 10 m out along both sides of a 50 m centerline) in each of our 31 study sites, at least 25 m from stand edges. Tree species were quantified in the 0.1 ha plots. We established a 4 × 50 (0.02 ha) sub-transect (extending 2 m out along both sides of the 50 m centerline); this was further subdivided into 20 (10 on each side of the centerline) contiguous 2 × 5 m quadrats for clonal shrub and herbaceous plant community measurements. Trees and clonal shrubs were not included in this study except to characterize forest structure as a possible indicator of light availability for herbaceous plants at the forest floor. We measured forest structure and herbaceous plant communities in 2004 (5 years post-harvest; Y5), 2009 (Y10), 2013 (Y14), and 2016 (Y17).

2.3. Forest structure

In Y5, Y10, Y14, and Y17, we tallied small (≥0.5 m height and <12.7 cm dbh) tree stems of individuals by species within the 0.1 ha plot. Stump sprouts were also tallied for ≤30 randomly selected subset of individuals per species within each plot. Stump sprout count subsamples per species within plots was often low, so we pooled them across SW or M plots (respectively) for each year and applied the average number of sprouts to the number of individuals (by species) to harvest treatment. Thus, total stem counts (individuals + stump sprouts) used in data analyses were crude estimates. Dbh of trees ≥12.7 cm was measured in Y5, Y14, and Y17 and used to calculate BA; BA for Y10 was interpolated based on tree growth Y5–Y14. We visually estimated % cover of each clonal shrub species (e.g., *Gaylussacia*, *Kalmia*, *Rhododendron*, *Rubus*, and *Vaccinium* spp.) in seven cover classes (Daubenmire 1959) within each of the 20, contiguous 2 × 5 m quadrats per transect. Cover classes and midpoints of each were: (class 1—0% midpoint 0%; class 2—0.1%–4.9% midpoint 2.5%; class 3—5%–24.9% midpoint 15.5%; class 4—25%–49.9% midpoint 37.5%; class 5—50%–74.9% midpoint 62.5%; class 6—75%–94.9% midpoint 85%; and class 7—95%–100% midpoint 97.5%). Cover class midpoints were averaged across quadrats for plot-level estimates, then summed across species, thus total clonal shrub cover estimates sometimes exceeded 100%. We estimated % canopy using a spherical densiometer, held at breast height, in a subset of study sites ($n = 3$ per treatment). Measurements were taken at each of five subplots established at a randomly chosen distance along and perpendicular (≤25 m out) to 200 m transects bisecting stands, established to census bird communities (Greenberg et al. 2023), and averaged for a stand-level estimate of canopy cover.

2.4. Herbaceous plant community measurements

Starting in Y5, and again in Y10, Y14, and Y17 we quantified the occurrence (presence/absence) of all herbaceous species including ferns, graminoids, and forbs (including herbaceous vines) within each of the 20, contiguous 2 × 5 m quadrats located along each side of the centerline transect. Surveys were conducted once at each plot during late May through September. *Phytolacca americana* and woody vine species (e.g., *Aristolochia macrophylla*, *Parthenocissus quinquefolia*, *Smilax glauca*, *Smilax rotundifolia*, *Toxicodendron radicans, Vitis rotundifolia*) were recorded in the larger 20 × 50 m plots and are not included in measurements of herbaceous plant communities as part of this study. Plants were identified to species when possible; species nomenclature follows the USDA NRCS Plants Database (http://plants.usda.gov, 01/30/2024).

2.5. Data analysis

We used repeated measures ANOVAs (PROC MIXED; SAS 9.3) in a completely randomized design with compound symmetry covariance structure to compare forest structure variables, herbaceous species community metrics (species richness, diversity, and evenness), and abundance of herbaceous species and life forms among the four treatments (UHSW, UHM, CHSW, and CHM) over the 17 years following harvests in SW. We recognize that alternative statistical approaches could potentially reveal more nuanced relationships among sites but chose a more traditional approach for clear and easily interpreted results. In all ANOVAs we considered treatment, year, and their interaction to be fixed effects, and plot (the replicate unit; 31 total) to be a random effect and the repeated subject factor. We calculated species richness (total number of species per plot) for each survey year based on species' presence within a plot, regardless of the number of quadrats in which it occurred. If a plant could only be identified to genus, we included it in our species richness counts only if no other individuals within that genus occurred on that plot. We used relative frequency within plots as index of each species' relative abundance (termed "abundance"), calculated as the proportion of the 20 quadrats per plot in which it occurred. We calculated species diversity (H') (Shannon 1948) based on species richness and abundance, and species evenness using Pielou's (1966) evenness index. For analyses of individual species, we included only those occurring in ≥5 plots in at least one of our four sample years. Our primary interest was in treatment effects, or treatment × year interaction effects as indicators that plant communities or species were responding differently among the four treatments. A non-significant treatment × year interaction indicated that the impact of treatment did not vary significantly through time. Where significant treatment × year interactions were present, we identified treatments or years warranting further examination ($p < 0.05$ in tests of effect slices) and used the least square means for partitioned F tests (SLICE option) in PROC MIXED (SAS 9.4) to examine the significance of treatment differences within identified years or differences among years within identified treatments. Treatment, year, or treatment × year interaction differences

were considered significant with an overall experimental α of < 0.05; data were log transformed as needed to reduce heteroscedasticity.

Plot-level community composition was evaluated across treatments and results were visualized using non-metric multidimensional scaling ordination (NMS) based on Raup-crick distances. NMS was performed using the metaMDS function in the vegan package in R (Oksanen et al. 2015). To select dimensionality, stress values from two, three, four, and five dimensional solutions were compared. MetaMDS uses an iterative approach with random starts and transforms data with large ranges using square root and Wisconsin double standardization. The final solution minimizes stress and is rotated so that the first axis explains the most variance. We initiated 250 independent runs (Peck 2016). Compositional differences across treatments were examined using distance-based multivariate Analysis of variance (ANOVA) (perMANOVA) in the R package vegan, blocked by plot to account for repeated sampling (Oksanen et al. 2015; R Development Core Team 2019). The Raup-Crick metric was used based on the significant differences in richness (Chase et al. 2011) observed in our data. The test statistic is the pseudo *F* ratio, where a large value indicates that plots within different categories differ in their species composition (i.e., plots within one category are closer to one another in multivariate space than they are to plots in the comparison group). Interactions that were not significant ($p < 0.05$) were removed from the final model. PerMANOVA is less sensitive to dispersion effects than other similar tests (Anderson and Walsh 2013), but may still confound location and dispersion effects. In other words, significant differences may be caused by differences in within-group variation (dispersion), differences in mean values of the groups, or both (Anderson 2001). We calculated average dispersion values (average distances to group centroids) within our groups using the betadisper function in the R package vegan and used diagnostic plots to evaluate dispersion versus location effects when dispersion was significantly different based on Tukey's honest significant differences (Anderson et al. 2006).

3. Results

3.1. Forest structure

Small tree (≥0.5 m ht and <12.7 cm dbh) stem density was greater in UHSW and CHSW than in CHM and UHM (Fig. 2); density in UHSW and CHSW decreased each year from Y5 through Y17. Density of large (≥12.7 cm dbh) trees was greater in UHM than all other treatments and greater in CHM than UHSW and CHSW. Within CHSW and UHSW, large tree density increased over time; within CHM it decreased slightly over time. Large tree BA was greater in UHM and CHM than in UHSW and CHSW and increased over time within UHM, UHSW, and CHSW. Total clonal shrub cover was greater in UHM and UHSW than CHM, and greater in UHM than CHSW (Fig. 2); within UHSW and CHSW total shrub cover was greater in Y5 than any subsequent year. Percent canopy cover (measured at breast height) did not differ among treatments; within both UHSW and CHSW canopy cover was lower in Y5 than all subsequent years, and in Y5 it was greater in UHM and CHM than UHSW and CHSW.

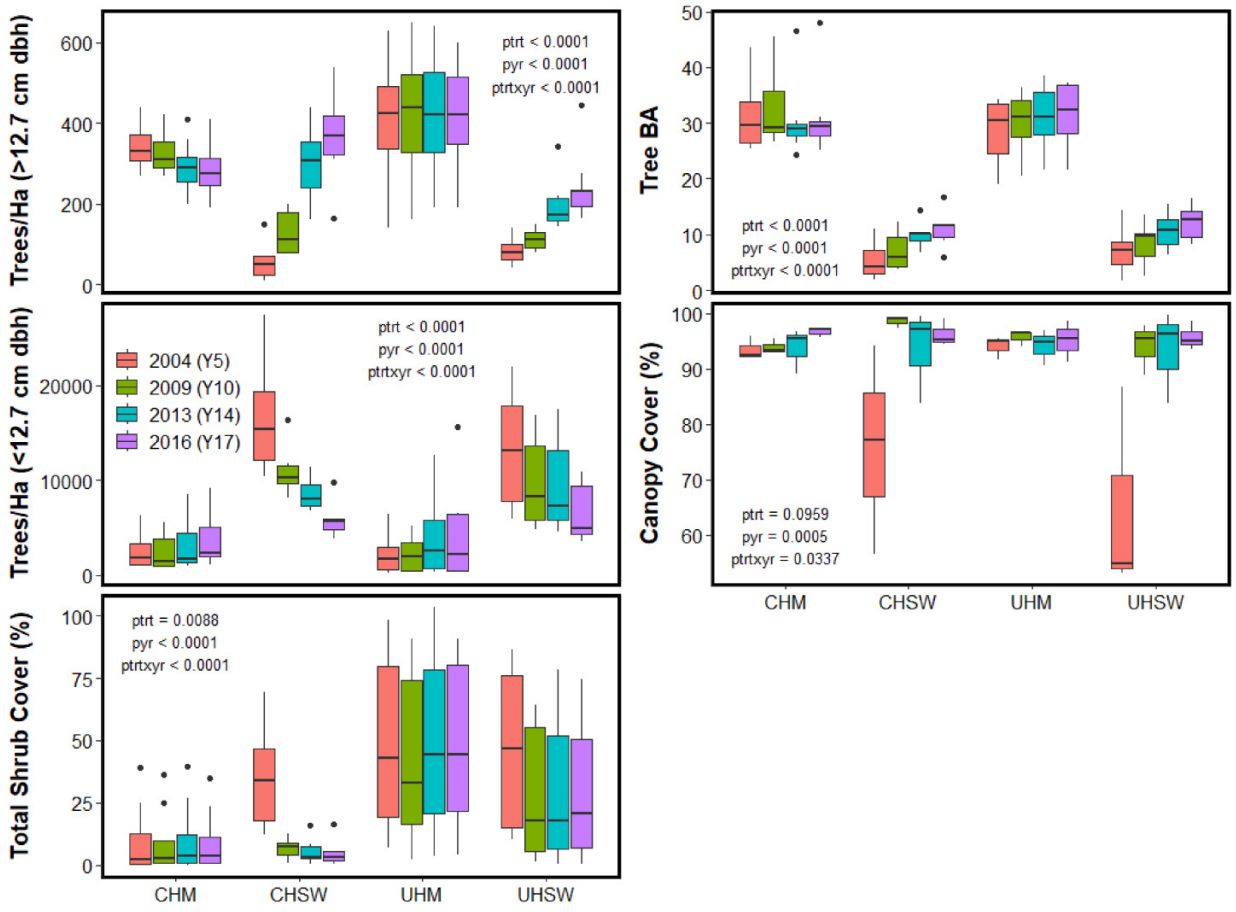
3.2. Herbaceous plant communities

We identified 201 herbaceous species (or unique genera) across all 31 plots within our study period including 17 fern, 28 graminoid, and 156 forb species (Table 1). Total herbaceous plant species richness was greater in CHM and CHSW (average range across years 36–41, both treatments) than UHM (range 16–17), and greater in CHM than UHSW (range 22–25) (Fig. 3). Species diversity was greater in CHM (average range across years 3.16–3.26) and CHSW (range 3.16–3.31) than UHM (range 2.08–2.24; UHSW range 2.65–2.73). Species evenness did not differ among treatments (average range across all treatments and years 0.75–0.92) (Fig. 3).

Among herbaceous life forms, fern species richness was greater in CHM (average range across years range 5.5–5.8) and CHSW (range 5.2–5.7) than UHM (range 1.6–1.9), and greater in CHM than UHSW (range 2.8–4.7). Abundance of ferns was greater in CHSW (average range across years 87.5–89.2) than in UHM (range 31.3%–39.3%), CHM (79.4% all years), and UHSW (range 55.6%–58.3%); within CHSW abundance of ferns was greater in Y5 than all subsequent years (Fig. 4). Graminoid species richness did not differ among treatments (average range across years and treatments 1.1–5.3). Abundance of graminoids did not differ among treatments (average range across years and treatments 29.4%–70.0%); within CHM abundance of graminoids was lower in Y5 than all subsequent years; within UHSW it was greater in Y5 than all subsequent years (Fig. 4). Forb species richness was greater in CHM (average range across years 28.3–30.1) and CHSW (range 27.7–33.4) than in UHM (range 11.9–13.1) and UHSW (range 15.9–17.2). Abundance of forbs was greater in CHM (average range across years 93.1%–98.8%) and CHSW (range 96.7%–99.2%) than UHSW (range 70.0%–73.3%) and marginally ($p < 0.10$) greater in CHSW than UHM (range 69.4%–80%) (Fig. 4).

Among the 79 species that were sufficiently common for statistical analysis, abundance of 26 showed a significant treatment and (or) treatment × year interaction effect indicating that abundances varied among years within treatments, or among treatments within years (Table 1; Fig. 5). Among these, most showed greater abundance in CHM, CHSW, or both compared to UHM, UHSW, or both. Seven species showed both treatment and treatment × year interaction effects. *Ageratina altissima* abundance was greater in CHSW and lower in UHM than all other treatments, and greater in CHM than UHSW; within both UHSW and CHSW, abundance was greater in Y5 than all subsequent years and differences among treatments varied among years. *Asplenium platyneuron* abundance was greater in CHM and CHSW than UHM, greater in CHM than CHSW, and greater in CHSW than UHSW; within CHM, abundance was greater in Y5 and Y10 than all subsequent years. *Conopholis americana* abundance was greater in CHM than UHM and UHSW. Within CHM *C. americana* abundance varied among years; within CHSW it was lower in Y5 than all subsequent years. *Eurybia macrophylla*

Fig. 2. Boxplots of density and BA of large (≥12.7 cm dbh) trees and small (<12.7 cm dbh) tree stem density, % canopy cover (measured at breast height), and % total shrub cover (based on the midpoint of 7 cover classes) in shelterwood harvests (harvested ca. 1999) and mature forests within upland hardwood forest or cove hardwood forest types 5, 10, 14, and 17 years post-harvest, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina. Middle value represents the mean.



abundance was greater in CHSW than all other treatments; within CHSW, abundance was greater in Y5 than all subsequent years, and greater in Y10 and Y14 than Y17. *Galax urceolata* abundance could not be analyzed due to highly skewed abundances among plots where it occurred. *Maianthemum racemosa* abundance was greater in CHM than UHSW and CHSW, greater in CHSW than UHM and UHSW, and greater in UHM than UHSW; within CHM abundance was greater in Y5 than Y17. *Phegopteris hexagonoptera* abundance was greater in CHM than UHM and UHSW; within CHSW abundance was greater in Y5 than all subsequent years, and greater in Y17 than Y10. *Sanguinaria canadensis* abundance was greater in CHSW than all other treatments, and greater in CHM than UHM and UHSW; within CHSW abundance varied among years.

Eleven species showed a treatment effect but no treatment × year interaction effect. *Arisaema triphyllum* abundance was greater in CHM and CHSW than UHM and UHSW. *Cypripedium acaule* abundance was greater in CHM than all other treatments. *Eurybia divaricata* abundance was greater in CHSW than UHM and UHSW. *Galium triflorum* abundance was greater in CHM than all other treatments and greater in CHSW than UHM and UHSW. *Medeola virginiana* abundance was greater in CHM than all other treatments, greater in CHSW than UHM and UHSW, and greater in UHM than UHSW. *Phryma leptostachya* abundance was greater in CHM than CHSW, greater in CHSW than UHSW and lower in UHM than all other treatments. *Polystichum acrostichoides* abundance was greater in CHSW than UHM and UHSW. *Potentilla canadensis* abundance was greater in CHSW than all other treatments, and greater in UHSW than CHM and UHM. *Prosartes lanuginosa* was greater in CHSW than UHM and UHSW. *Uvularia perfoliata* abundance was greater in CHSW than UHM and UHSW. Only one species, *Dennstaedtia punctilobula*, showed greater abundance in an upland hardwood treatment; abundance was greater in UHSW than UHM and CHM.

Eight species showed a treatment × year interaction effect but no treatment effect. *Eutrochium purpureum* abundance within CHSW was greater in Y5 than all subsequent years. *Lysimachia quadrifolia* abundance within CHSW was greater in Y5 than all subsequent years, and within UHSW it was greater in Y5 and Y10 than Y17. *Polygonatum* spp. abundance within CHSW was greater in Y5 than all subsequent years, and lower in Y10 than Y17. *Prenanthes* spp. abundance within UHSW was

Table 1. Total number of plots where each species occurred each year, and results of repeated measures mixed-model ANOVAs comparing relative abundance (proportion of the 20 quadrats per plot in which it occurred) of sufficiently common (occurred in ≥5 plots in ≥1 year)[a] species among shelterwood harvests (harvested ca. 1999) and mature forests within upland hardwood forest or cove hardwood forest types 5, 10, 14, and 17 years post-harvest, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina[b].

Species	Y5[a]	Y10	Y14	Y17	P_{trt}	P_{yr}	P_{trtxyr}
FERNS							
*Adiantum pedatum**	4	5	5	5	0.0951	0.1591	0.3037
*Asplenium platyneuron**	5	3	2	2	**<0.0001**	<0.0001	**0.0117**
Athyrium filix-femina	12	12	13	13	0.7865	0.5109	0.6172
Botrychium biternatum	4	5	4	5	0.2326	0.2952	0.5258
*Botrychium virginianum**	6	6	6	7	0.9551	0.6715	0.9155
Dennstaedtia punctilobula	13	13	13	14	**0.0304**	0.2474	0.4202
Huperzia lucidula	6	8	11	10	0.2362	0.1489	0.3832
Osmunda spp.[c]	11	12	12	12	0.7293	0.0360	0.5285
*Phegopteris hexagonoptera**,[d]	6	5	5	6	**0.0012**	0.0472	**<0.0001**
Polystichum acrostichoides#,[d]	16	19	19	19	**0.0194**	0.1895	0.2458
Thelypteris noveboracensis	19	20	20	20	0.1260	0.1695	0.8480
GRAMINOIDS							
Arundinaria gigantea+	5	7	7	7	0.5452	0.2872	0.9225
Brachyelytrum erectum	10	10	12	10	0.0559	0.4229	0.0895
Carex digitalis	0	16	21	17	0.3209	<0.0001	0.2712
Carex pensylvanica	3	13	15	14	0.3096	0.0039	0.7110
Carex swanii	1	9	2	2	0.6448	0.5623	0.3843
Carex virescens	2	3	6	6	0.7946	0.9800	0.5880
Danthonia compressa	1	5	6	2	0.0556	0.0609	0.4129
Dichanthelium boscii	3	8	7	7	0.4298	0.0620	0.3789
Dichanthelium commutatum	2	4	8	8	0.1605	0.7433	0.9789
Dichanthelium dichotomum	3	11	11	9	0.2276	0.0486	0.5960
FORBS							
Actaea racemosa#	6	6	6	7	0.3098	0.0092	0.0804
Ageratina altissima@	13	10	8	9	**<0.0001**	<0.0001	**<0.0001**
Amphicarpaea bracteata	2	6	5	9	0.3336	0.0148	0.8377
Anemone quinquefolia	4	4	4	5	0.3975	0.1162	0.2272
Arisaema triphyllum#	13	14	15	14	**0.0026**	0.0699	0.2863
*Caulophyllum thalictroides**	5	5	5	6	0.1020	0.2210	0.4002
Chamaelirium luteum	1	1	3	6	0.6731	0.0196	0.7430
Chelone lyonia	5	5	3	2	0.1589	0.2573	0.1032
Chimaphila maculata&	13	15	18	19	0.0972	0.2144	0.4224
Clintonia umbellulata	5	5	5	6	0.1165	0.3377	0.3040
Conopholis americana	9	12	12	9	**0.0382**	0.4507	**0.0024**
Cypripedium acaule	5	5	5	3	**0.0157**	0.1662	0.1228
Desmodium nudiflorum	11	5	6	6	0.2554	0.7523	0.9945
Dioscorea quaternata	11	12	16	18	0.1607	<0.0001	0.3403
Eurybia divaricata	19	18	18	18	**0.0335**	0.0341	0.2337
Eurybia macrophylla@	5	4	4	1	**0.0083**	0.0001	**<0.0001**
Eutrochium purpureum@	13	11	11	12	0.5521	0.0132	**<0.0001**
Galium circaezans	6	7	8	9	0.7162	0.5541	0.4739
Galium latifolium	13	12	11	10	0.2061	0.0020	0.3723
*Galium triflorum**	5	5	5	5	**<0.0001**	0.9795	0.7243
Gentiana spp.[e]	9	12	7	4	0.1556	0.0105	0.2134
Goodyera pubescens	22	25	25	28	0.8113	0.5300	0.6448
Hieracium paniculatum	8	5	5	4	0.8819	0.0425	0.4166
Houstonia purpurea	14	19	17	14	0.1235	0.3097	0.0859
Iris cristata	6	5	2	2	0.1311	0.5015	0.4179

Table 1. (*concluded*).

Species	Y5[a]	Y10	Y14	Y17	P_{trt}	P_{yr}	P_{trtxyr}
*Laportea canadensis**	5	5	5	6	0.1985	0.0124	0.1992
Lilium michauxii	9	12	13	11	0.4172	0.7393	0.2733
Lysimachia quadrifolia@	17	19	17	17	0.1722	<0.0001	**<0.0001**
*Maianthemum racemosum**	12	13	8	9	**<0.0001**	0.5455	**0.0046**
Medeola virginiana[d]	16	18	18	19	**<0.0001**	0.4773	0.1148
Mitchella repens	4	6	6	8	0.2703	0.0517	0.3962
Monotropa uniflora	7	5	2	4	0.1355	0.4392	0.4757
Muhlenbergia tenuiflora	0	6	4	4	0.8900	0.0625	0.8483
Phryma leptostachya	1	2	3	6	**<0.0001**	0.7108	0.9079
Polygonatum spp.*,[f]	16	19	16	18	0.1411	0.0004	**0.0232**
Potentilla canadensis	10	9	9	7	**<0.0001**	0.0001	0.8538
Prenanthes spp.	14	19	16	18	0.2756	0.0831	0.0328
*Prosartes lanuginosa**	8	9	8	7	**0.0233**	0.1652	0.6445
Pycnanthemum montanum	9	7	5	6	0.2829	0.0353	0.0568
*Sanguinaria canadensis**	7	8	7	7	**<0.0001**	<0.0001	**<0.0001**
Sanicula sp.	4	5	5	6	0.3183	0.3050	0.2317
Smilax biltmoreana	4	10	11	10	0.9924	<0.0001	**<0.0001**
Smilax herbacea	7	2	2	4	0.1276	<0.0001	**0.0101**
Solidago arguta	3	5	4	4	0.9020	0.0890	0.3946
Solidago curtisii	15	16	16	15	0.0816	0.0001	**<0.0001**
Solidago puberula	2	5	4	3	0.7677	0.0898	0.2803
*Stellaria pubera**	0	0	8	5	0.0645	0.0139	0.0588
Stenanthium gramineum	5	5	4	3	0.9580	0.7971	0.2158
Symphyotrichum cordifolium	4	5	7	6	0.2291	0.5107	0.4838
Trillium spp.*,[d]	7	7	8	7	0.0671	0.7387	0.2078
Uvularia perfoliata[d]	5	5	6	5	**0.0335**	0.4541	0.6357
Uvularia puberula	12	12	12	12	0.4308	0.1257	0.0401
Veratrum parviflorum	7	8	8	9	0.8551	0.3466	0.5073
Viola blanda	13	16	16	17	0.9852	0.9992	0.9962
Viola hastata	19	19	22	22	0.9013	0.0003	0.4339
Viola rotundifolia[d]	12	13	14	14	0.0681	0.7842	0.4387
Viola sororia	20	20	17	19	0.1433	0.8257	0.0943
Zizia trifoliata	7	8	7	6	0.9651	0.9016	0.1974

Note: Also see Fig. 5.

[a]Species occurring in <5 plots in all years included *Actaea pachypoda*, *Agrimonia* sp., *Agrostis perannens*, *Ambrosia artimisiifolia*@, *Andropogon virginicus*, *Anemone virginiana*, *Angelica* sp., *Arabis laevigata*, *Aralia nudicaulis*, *Aralia racemosa*, *Aristolochia serpentaria*, *Arnoglossum reniformis*, *Aruncus dioicus*, Asteraceae sp., *Astilbe biternata*, *Aureolaria laevigata*, *Botrichium dissectum*, *Bromus* sp., *Calystegia* sp., *Carex aestivalis*, *C. blanda*, *C. communis*, *C. debilis*, *C. laxiflora*, *C. plantaginea*, *C. radiata*, *Campanula divaricata*, *Chrysogonum virginianum*, *Circaea lutetiana*, *Collinsonia canadensis*∗, *Coreopsis major*, *Cypripedium parviflorum*, *Cystopteris* sp., *Deparia acrostichoides*∗, *Desmodium glutinosum*, *Dichanthelium acuminatum*, *D. clandestinum*, *Doellingeria infirma*, *Dryopteris intermedia*∗, *D. marginalis*∗, *Epifagus virginiana*, *Epigaea repens*, *Erechtites hieraciifolia*, *Erigeron pulchellus*, *Euonymus obovatus*, *Euphorbia corollata*, *Fragaria virginiana*, *Galearis spectabilis*, *Galium pilosum*, *Geranium maculatum*, *Gillenia trifoliata*, *Helianthus microcephalus*, *Helianthus* sp., *Heliopsis helianthoides*, *Hexastylis shuttleworthii*, *Hexastylis* sp., *Houstonia serpyllifolia*, *Hydrophyllum* sp.∗, *Hypericum hypericoides*, *H. punctatum*, *Hypoxis hirsuta*, *Impatiens capensis*∗, *Ipomoea* sp., *Iris verna*, *Lactuca* sp., *Lespedeza cuneata*, *L.* repens, *Lespedeza* sp., *Ligusticum canadense*, *Lilium superbum*, *Lobelia inflata*, *L. puberula*, *Luzula acuminata*, *L. echinata*, *Microstegium vimineum*, *Malaxis unifolia*, *Melampyrum lineare*, *Monarda clinopodia*, *Monarda* sp., *M. hypopitys*, *Osmorhiza claytonii*∗, *Oxalis dillenii*@, *O. grandis*, *O. stricta*@, *Packera aurea*, *Panax quinquefolius*∗, *Passiflora lutea*, *Physalis* sp., *Poa autumnalis*, *P. cuspidata*, *Poa* sp., *Podophyllum peltatum*, *Polypodium virginianum*, *Potentilla simplex*, *Pycnanthemum incanum*, *Ranunculus hispidus*, *Ranunculus* sp., *Sabatia angularis*, *Scleria triglomerata*, *Scutellaria elliptica*, *S. serrata*, *Silene stellata*, *S. virginica*, *Solidago bicolor*, *S. caesia*, *S. nemoralis*, *S. roanensis*, *S. rugosa*, *Solidago* sp., *Stachys* sp., *Symphyotrichum dumosum*, *S. lateriflorum*, *S. lowrieanum*, *S. prenanthoides*, *S. undulatum*, *Thalictrum dioicum*, *T. thalictroides*, *Thaspium barbinode*, *Tiarella cordifolia*, *Tipularia discolor*, *Tradescantia subaspera*, *Veratrum hybridum*, *Verbena urticifolia*, *Viola canadensis*∗, *V. pubescens*. Unknown *Carex* spp. and *Dichanthelium* spp., occurred in >8 plots in ≥1 year but were not analyzed separately, except in life form analyses. *Galax urceolata* occurred in ≤6 plots each year but could not be analyzed due to highly skewed abundance among plots.

[b]In 2004 (Y5) only 7 of 8 plots measured in UHM and 5 of 6 plots in CHSW in 2004 for logistical reasons.

[c]*Osmunda* spp. included *O. cinnamomea* and *O. claytoniana*.

[d]Log-transformed for analysis.

[e]*Gentiana* spp. lumped; included *G. decora*, *G. saponaria*, *G. villosa*.

[f]*Polygonatum* spp. lumped; predominantly *P. biflorum*, but *P. pubescens*∗ occurred in 4 plots (2 CHSW; 2 CHM). *P. pubescens* is a rich cove indicator species; *P. biflorum* is an acidic cove indicator species (Ulrey 2002).

*Rich cove indicator species (Ulrey 2002).

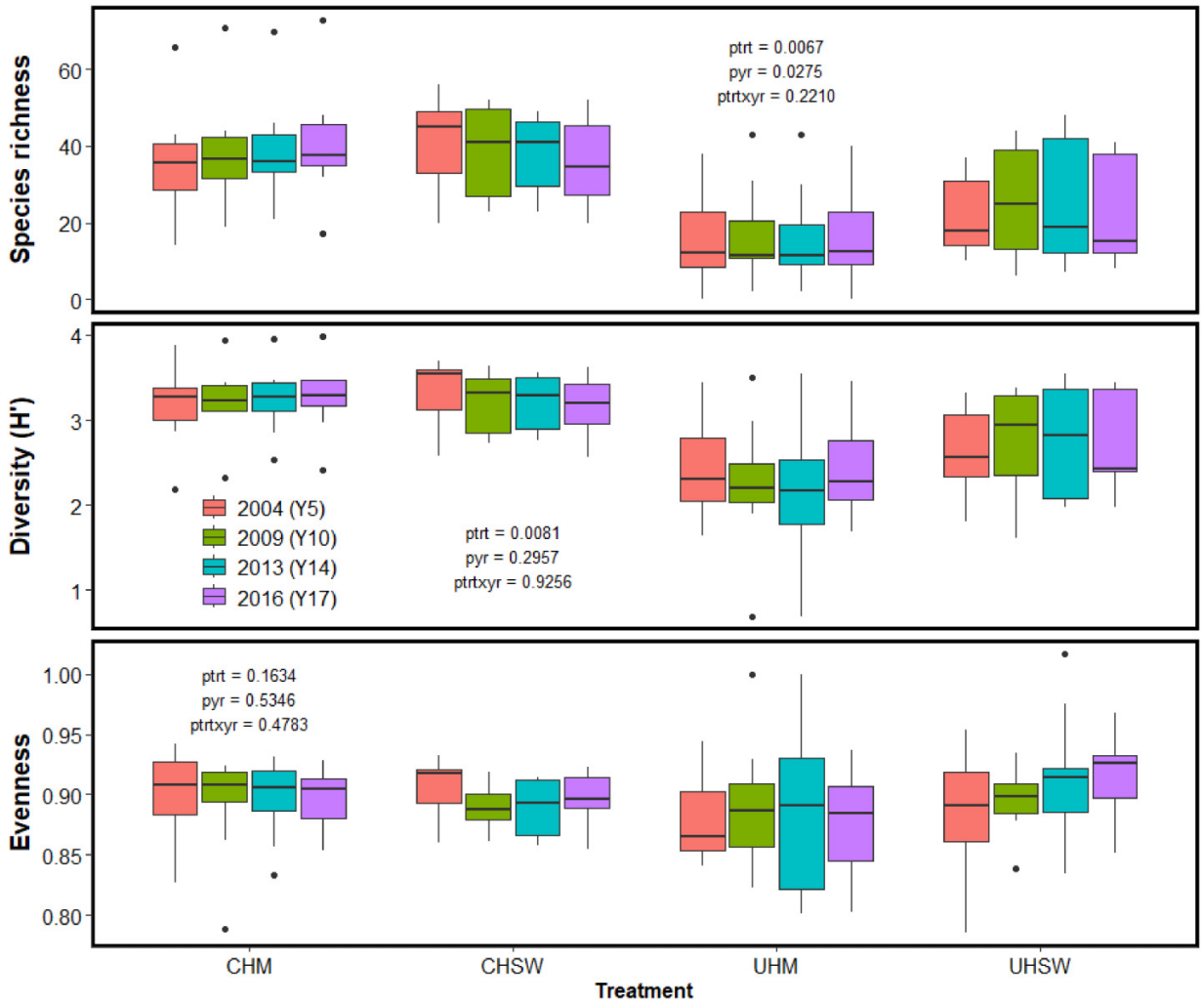
#Common in rich cove forest but not an indicator species (Ulrey 2002).

+Dry-mesic oak hickory forest indicator species (Ulrey 2002).

&Common in dry-mesic oak hickory forest but not an indicator species (Ulrey 2002).

@Considered to be ruderal or "early successional".

Fig. 3. Boxplots of total herbaceous species richness, diversity (H') (calculated using relative frequency—or the proportion of the 20 quadrats per plot in which each species occurred—for abundance; middle value represents the mean), and evenness in shelterwood harvests (harvested ca. 1999) and mature forests within upland hardwood forest or cove hardwood forest types 5, 10, 14, and 17 years post-harvest, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.



lower in Y5 than all subsequent years, and within CHSW it was lower in Y5 than Y14 and Y17 and lower in Y10 than Y17. *Smilax biltmoreana* abundance within CHSW was lower in Y5 than all subsequent years, and lower in Y10 and Y14 than Y17. *Smilax herbacea* abundance within CHSW was greater in Y5 than all subsequent years; in Y5 it was greater in CHSW than all other treatments, and greater in CHM than UHSW. *Solidago curtisii* abundance within CHSW decreased each successive year; in Y5 it was greater in CHSW than UHM and UHSW, and in Y10 it was greater in CHSW than UHM. *Uvularia puberula* abundance within CHSW was greater in Y5 and Y10 than Y14 and Y17.

We also looked at potential differences in the herbaceous community as a whole. We found significant compositional differences between forest types ($p < 0.0005$; Table 2; Fig. 6) and years ($p < 0.0005$; Table 2; Fig. 6). The effect of SW varied by forest type ($p = 0.0095$; Table 2; Fig. 6), but the interaction between forest type and year ($p = 0.9855$; Table 2; Fig. 6) and harvest type and year ($p = 0.8196$; Table 2; Fig. 6) were not significant, and the associated interactions were therefore removed from the final model. For the NMS, we plotted final stress values against the number of dimensions and choose the 4-dimensional solution (stress = 12.1), as the reduction in final stress was minimal (0.02) and based on a visual inspection of stressplots. Stability was evaluated based on the best solution being repeated twice in 20 runs. We display the compositional differences by treatment and year in Fig. 6. However, our significant differences were potentially confounded by significantly greater dispersion in multivariate space in the SW treatments, most noticeable in UHSW, which was more variable than the other treatments (Figs. A1 and A2). Based on the visualization of the multivariate dispersions (Fig. A2), we found evidence of dispersion (e.g., variation) treatment effects, and location (e.g., composition) effects for forest type (Fig. A2). We found no differences in dispersion among years.

Fig. 4. Boxplots of species richness and relative abundance (proportion of the 20 quadrats per plot in which they occurred; middle value represents the mean) of fern, graminoid, and forb life forms in shelterwood harvests (harvested ca. 1999) and mature forests within upland hardwood forest or cove hardwood forest types 5, 10, 14, and 17 years post-harvest, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.

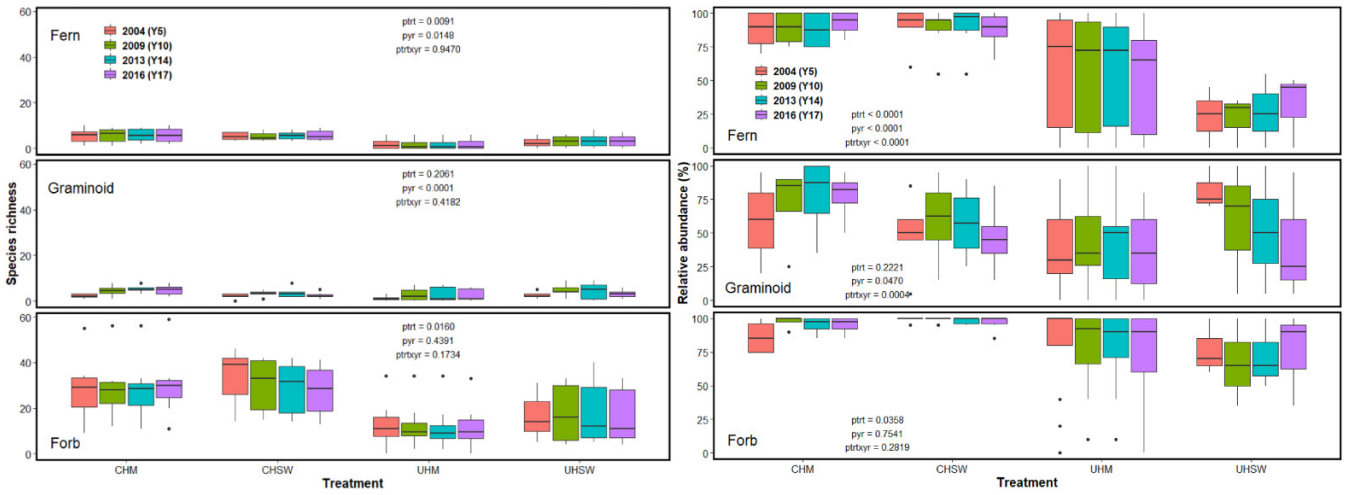


Fig. 5. Boxplots of relative abundance (proportion of the 20 quadrats per plot in which it occurred; middle value represents the mean) of herbaceous species in shelterwood harvests (SW; harvested ca. 1999) and mature forest (M) within upland hardwood (UH) or cove hardwood (CH) forest types 5, 10, 14, and 17 years post-harvest, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina. Only species showing a significant ($p < 0.05$) treatment and (or) treatment × year effect are displayed.

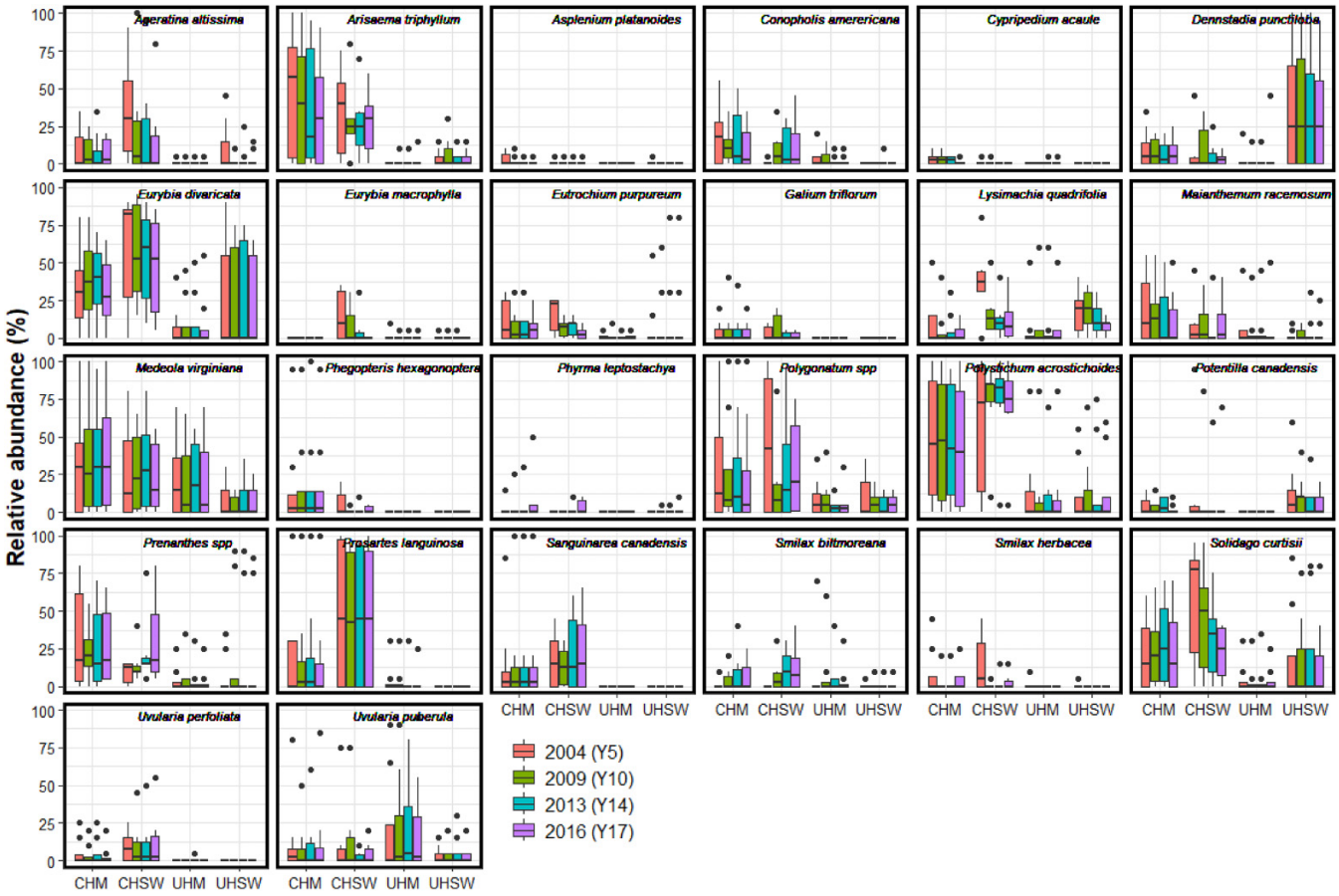
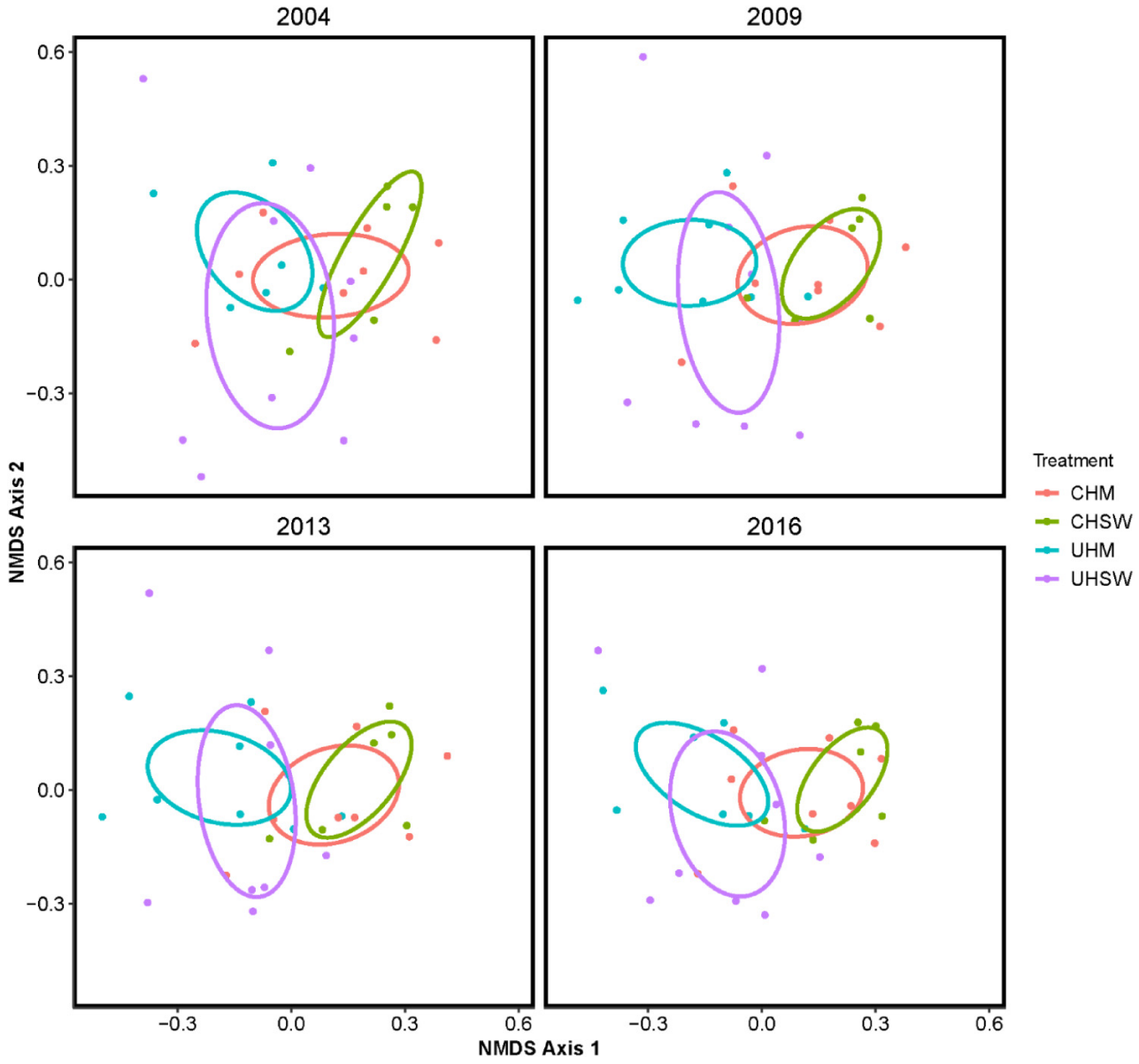


Table 2. Herbaceous community composition within shelterwood harvests (SW; harvested ca. 1999) and mature forests (M) of upland hardwood (UH) forest or cove hardwood (CH) forest types 5, 10, 14, and 17 years post-harvest, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.

Predictor	Df	Sum of sqs	R^2	pseudo-*F*	*p* value
Harvest type	1	00976	0.02845	5.1736	≤0.0005
Forest type	1	06932	0.20207	36.7509	≤0.0005
Year	1	01847	0.05385	9.7939	≤0.0005
Harvest type: forest type	1	02859	0.08334	15.1569	0.0095
Residual	115	21692	0.6323		
Total	119	34306	1		

Note: The table shows the effects of the individual drivers of species composition from perMANOVA based on Raup-Crick distances.

Fig. 6. Herbaceous community composition within shelterwood harvests (SW; harvested ca. 1999) and mature forests (M) of upland hardwood (UH) forest or cove hardwood (CH) forest types 5, 10, 14, and 17 years post-harvest, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina. Figs displays nonmetric multidimensional scaling ordination based on Raup-Crick distances. The two axes that explain the most variation are displayed. Ellipses are 95% confidence ellipses for the average composition (weighted centroids).



4. Discussion

Our long-term study allowed us to examine how herbaceous plant communities and species composition differed between upland- and cove hardwood forest types, and how they responded to shelterwood harvests and dynamic changes in forest structure for 17 years post-harvest, compared to uncut mature forest controls. Our results suggested that microclimatic conditions and environmental gradients associated with forest type exerted a much stronger influence on herbaceous plant diversity and composition than shelterwood harvests alone. Shelterwood harvests had a neutral or positive effect on these community-level metrics, especially in upland hardwood forests where a trend of greater richness and diversity was evident for SW compared to M, as also observed in the greater compositional variation in the UHSW. Additionally, we found that the composition of upland hardwood herbaceous communities was more variable following shelterwood harvest, suggesting that beta diversity increased following harvest in this forest type. Although abundances of some species differed within and among treatments, our species evenness results indicated that herbaceous plant communities were not dominated by one or a few species in any treatment. Finally, more of the variation in composition was explained by forest type than harvest type, suggesting composition is most strongly controlled by forest type.

In our study, forest structure in both upland- and cove hardwood mature stands was relatively static throughout the study period, with similar BA but greater shrub cover (*K. latifolia* in particular; unpubl. data) in UHM than CHM throughout the study period. Unsurprisingly, forest structure was highly dynamic in SW treatments as young forests progressed from the "stem initiation" into the "stem exclusion" stages of stand development following regeneration harvests (e.g., Oliver and Larson 1996). Increased light after heavy overstory removal in SW initiated rapid increases in small tree stem densities as harvested stumps resprouted and new seedlings germinated. In Y5, spikes in total clonal shrub cover in both SW treatments (UHSW and CHSW) were driven primarily by *Rubus* responding to the recently disturbed, high-light environment (Ricard and Messier 1996; Widen et al. 2018; Greenberg et al. 2023; unpubl. data). Young, competitive trees in SW treatments grew rapidly in girth and height, shading out and killing many of their cohorts with concomitant reductions in both small tree stem density and *Rubus* cover by Y10. Despite dramatic changes in forest structure within shelterwood, our results indicated that effects on herbaceous plant communities (species richness, diversity, evenness, and composition) and most species were relatively minor.

Among the 79 species that were sufficiently abundant for statistical analysis, most (69%) showed no response to treatment. Among tested species responding to treatment, only one, *Dennstaedtia punctilobula*, showed a greater abundance in the UH forest type (UHSW) than mature CH or UH forests. Most species were more abundant in CHM, CHSW, or both compared to UHM, UHSW, or both, further indicating that both mature and recently harvested mesic cove hardwood forests supported more species in greater abundance than drier upland hardwood forests. Elliott et al. (1997) reported that some shade tolerant genera such as *Viola*, *Galium*, *Sanguinaria*, *Uvularia*, and *Veratrum* were not yet well established within 17 years after a clearcut. In contrast, our results suggested similar (e.g., *Uvularia puberula*, *Veratrum parviflorum*; most *Viola* species) or greater (e.g., *Sanguinaria canadensis*, *U. perfoliata*, in SW) abundances of these species between SW and M, at least within the same forest type (usually CH). In our study, abundances of nearly all tested species in CHSW remained similar to or greater than abundances in CHM throughout our 17-year study period, consistent with our analyses showing similarity in species composition of cove hardwood plots between treatments. Our results corroborate those of Ford et al. (2000) and Gilliam et al. (1995), who also found few differences in the abundances of herbaceous flora among different age-classes of Appalachian hardwood forests and suggest that many species are resilient to heavy disturbances such as shelterwood harvests.

Some studies report that herbaceous species composition within forests is dynamic; species can disappear or colonize, leading to shifts in species richness, diversity, and composition (e.g., Brewer 1980; Elliott and Knoepp 2005). This can be more pronounced after disturbances such as timber harvests (Elliott and Knoepp 2005), but also occurs in mature forest. For example, Reader and Bricker (1992) reported that 3%–12% of herbaceous species disappeared from plots within two years of timber harvests, whereas 9%–13% disappeared from mature forest plots; furthermore, the percentage of species occurring less frequently within 2 years of cutting was lower in harvested (23%–36%) than unharvested (33%–37%) plots. Elliott and Knoepp (2005) suggested that interannual differences in climatic variables, such as rainfall could affect herbaceous plant species composition and diversity even in the absence of disturbances. In our study, abundances of several species fluctuated among years overall, or within some treatments, but for most, trends of increase or decrease were not evident. This is consistent with our finding that composition fluctuated through time, but these temporal changes did not vary by either forest type or harvest treatment.

Disturbed sites, such as roadsides and timber harvests can become infested by non-native invasive species (herbaceous and woody plants or vines) where they are already established, or if abundant seed sources are nearby or already present in the soil prior to disturbance (e.g., Greenberg et al. 2001). Non-native invasive plants may in fact contribute to greater plant diversity in uplands (Brown and Peet 2003) but nonetheless degrade intact native plant communities. However, our observed increases in richness or fluctuations in composition were mainly driven by native species. Our study plots exhibited minimal problems with non-native invasive herbaceous species (only *Microstegium vimineum*, recorded in one plot), likely because many of our sites were not near seed sources such as heavily infested roadsides or ruderal sites.

In our study, we likely missed some "early successional" or ruderal species because we did not quantify herbaceous plant communities until 5 years post-harvest. However, temporal trends in abundance were evident for some, with abundance peaking by Y5 and decreasing over time in CHSW (e.g., *Eurybia macrophylla*, *Eutrochium purpureum*) or in both

CHSW and UHSW (e.g., *Ageratina altissima*, *Lysimachia quadrifolia*). *Phytolacca americana* was not measured in our herbaceous species quadrats (it was measured in the larger 0.1 ha plot) but proliferated after shelterwood harvests, and virtually disappeared within 5 years as high densities of young trees gained height, creating dense shade (Perry et al. 1999; Greenberg et al. 2007). Elliott et al. (1997) also reported decreases in early successional species (e.g., *Aster*, *Erichtites*, *Solidago*, *Eupatorium*, and *Panicum* (Radford et al. 1968)) over 17 years following a clearcut. In our study, several other species generally not considered to be early successional also peaked in Y5, mainly in CHSW, and decreased over time (e.g., *Phegopteris hexagonoptera*, *Polygonatum* spp., *Smilax herbacea*, *Uvularia puberula*). In contrast, *Prenanthes* spp. increased over time in both CHSW and UHSW, and *Smilax biltmoreana* increased over time in CHSW. These dynamic changes in abundance by both early successional- and several shade-tolerant herbaceous species in SW suggest that increased light or other post-harvest resources promoted germination by newly-colonizing or banked seeds, or growth from pre-existing roots or rhizomes, with abundances declining to levels similar to those in M as young SW forests progressed from the stem initiation into the stem exclusion phases of stand development (e.g., Oliver and Larson 1996).

We did not measure herbaceous plant communities until 5 years post-harvest, and thus were unable to compare pre- to post-harvest response or directly examine immediate post-harvest effects. Additionally, because we conducted our surveys primarily during summer, we may have missed spring ephemerals that senesce soon after flowering and thus cannot address possible effects of shelterwood harvests on them. Further, like many other studies we used second-growth mature (once-logged; 80–100 years old at study establishment) forests as our benchmark for comparisons with recent shelterwood harvests (twice-logged; 80–100 years prior to, and again just prior to study establishment). Thus, we cannot draw inferences about effects of multiple harvests across longer-term timber rotations (e.g., hundreds of years) on herbaceous plant communities. Similarly, our study cannot address how herbaceous plant communities in shelterwood harvests might compare with those in old growth forests that never experienced extensive logging.

Studies comparing southern Appalachian second growth mature forest to old growth forest suggest they may differ in herbaceous species richness, abundance, and (or) composition, although the magnitude of differences varies greatly among studies and functional groups (e.g., slow dispersing spring ephemerals; Bunn et al. 2010). Bunn et al. (2010) reported differences in understory community composition between old growth and 55-year post-logged southern Appalachian forests but concluded that overall community composition and among-community similarity was more closely associated with environmental gradients and community attributes than logging history. Similarly, Jackson et al. (2009) reported high community similarity and no difference in herbaceous species richness or diversity between old growth and second growth mature rich cove forest across scales (0.01–1000 m^2), although total herbaceous cover and 10% of tested species had lower abundance in second- than in old-growth stands. In contrast, Duffy and Meier (1992) reported about 50% lower species richness and 30% lower % cover of early-spring herbaceous plants in second- than in old growth mixed mesophytic forest, with no relationship between stand age (est. age 45–87 years) and total herbaceous cover or species richness in second growth forests. Their study was limited by a sampling protocol that excluded areas with extensive shrub cover and focused on early spring species, making their results limited in spatial and temporal scale (Elliott et al. 1993; Johnson et al. 1993). Woodbridge (2020) reported that groundlayer species richness in southern Appalachian cove hardwood forests was lower in second growth mature (70+ years post-clearcut) than old-growth cove hardwood forests but did not differ between those age-classes in low-elevation xeric forests. Wyatt and Silman (2010) reported differences in herbaceous species composition, higher richness, and greater individual abundances in old growth than in mature, 100–150 years post-logged rich cove forests, concluding that the herbaceous layer requires more than 150 years after timber harvesting to recover to old growth levels. These studies suggest that second growth mature forests could potentially support species that persisted or re-colonized after heavy logging in the early 1900s but support reduced abundances of some sensitive species, compared to old growth forests.

Although we cannot compare post-harvest recovery rates in our study to old-growth, our comparisons between SW and M indicate that herbaceous community species richness, diversity, evenness, and species composition in shelterwood harvests were similar to that in mature forest within 5 years post-harvest. Our results corroborate those of several other studies showing few differences in herbaceous species richness, diversity, or composition between recent regeneration harvests to second growth mature forest (Fredericksen et al. 1999; Elliott and Knoepp 2005; Benz et al. in review) or across second growth age classes (Gilliam et al. 1995; Ford et al. 2000; Gilliam 2002). Our study further indicates that shelterwood harvests did not adversely affect abundance of individual herbaceous species. Similarly, Ford et al. (2000) reported that species richness, diversity, and evenness in southern Appalachian cove hardwood forests did not differ among stand ages 15, 25, 50, and >85 year post-logging; abundances of four species differed among stand ages but none showed a trend (increase or decrease) corresponding with stand age. Gilliam et al. (1995) found no difference in herbaceous species richness and diversity between 20-year-old clearcut stands and second growth 70+ year old forests in West Virgina, but soil nutrients affected species diversity within younger stands (Gilliam 2002).

Our study elucidates important differences in herbaceous plant communities between upland- and cove-hardwood forests, showing that both mature and recently harvested mesic cove hardwood forests generally support greater species richness and diversity than their subxeric upland hardwood forest counterparts. Our results suggest that many herbaceous plant species in mature cove- and upland hardwood forests, including several shade tolerant species, are resilient to forest floor disturbances and to the temporally

transient changes in light and microclimate associated with shelterwood regeneration harvests.

Acknowledgements

This study was funded by the United States Department of Agriculture Forest Service, Southern Research Station, Bent Creek Experimental Forest. D.J. Levey assisted with vegetation plot design as part of an earlier companion study of native fleshy fruit production at the Savanna River Site, Georgia. We thank the staff at the Pisgah National Forest, especially T. Oprean and J. Blanton, for their assistance in finding study sites and logistical support. L. Smith-Moody, T. Roof, K. Frick, T. Hayes, P. Craig, V. Gibbs, J. O'Shields, G. Graeter, M. Duncan, and many other staff members and volunteers provided invaluable field assistance. Any opinions, findings, conclusions, or recommendations expressed in the material are the authors and do not necessarily reflect the views of the USDA.

Article information

History dates

Received: 21 October 2024
Accepted: 10 March 2025
Accepted manuscript online: 20 March 2025
Version of record online: 11 April 2025

Notes

This paper is one of a selection of papers from the North American Forest Ecology Workshop (NAFEW), Asheville, NC, June 24 27, 2024.

Copyright

Data availability

Data will be made available on request.

Author information

Author ORCIDs

C.H. Greenberg https://orcid.org/0000-0002-2831-0989

Author contributions

Conceptualization: CHG
Formal analysis: CHG, MW
Investigation: CHG, TWR, JLA
Methodology: CHG
Project administration: CHG
Supervision: CHG
Writing – original draft: CHG, MW
Writing – review & editing: CHG

Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. **26**(1): 32–46.

Anderson, M.J., and Walsh, D.C.I. 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? Ecol. Monogr. **83**(4): 557–574. doi:10.1890/12-2010.1.

Anderson, M.J., Ellingsen, K.E., and McArdle, B.H. 2006. Multivariate dispersion as a measure of beta diversity. Ecol. Lett. **9**(6): 683–693. PMID: 16706913.

Beasley, C., Carter, D.R., Coates, T.A., Keyser, T.L., and Greenberg, C.H. 2022. Impacts of oak-focused silvicultural treatments on the regeneration layer nine years posttreatment in a productive mixed-oak southern Appalachian forest. J. Torr. Bot. Soc. **149**(2): 166–180.

Benz, B.L., Forrester, J.A., Keyser, T.L., and Greenberg, C.H. in review. Changes in ground-layer plant species assemblages and successional patterns following a decade of oak restoration. Submitted to Rest. Ecol. 2/2024.

Brewer, R. 1980. A half-century of changes in the herb layer of a climax deciduous forest in Michigan. J. Ecol. 823–832.

Brown, R.L., and Peet, R.K. 2003. Diversity and invasibility of southern Appalachian plant communities. Ecology, **84**(1): 32–39.

Bunn, W.A., Jenkins, M.A., Brown, C.B., and Sanders, N.J. 2010. Change within and among forest communities: the influence of historic disturbance, environmental gradients, and community attributes. Ecography, **33**(3): 425–434.

Chase, J.M., Kraft, N.J., Smith, K.G., Vellend, M., and Inouye, B.D. 2011. Using null models to disentangle variation in community dissimilarity from variation in α-diversity. Ecosphere, **2**(2): 1–11.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Sci. **33**: 43–64.

Duffy, D.C., and Meier, A.J. 1992. Do Appalachian herbaceous understories ever recover from clearcutting? Conserv. Biol. **6**(2): 196–201.

Elliott, K.J. 2014. Herbaceous species composition and richness of mesophytic cove forests in the southern Appalachians: synthesis and knowledge gaps. J. Torrey Bot. Soc. **141**(1): 39–71.

Elliott, K.J., and Knoepp, J.D. 2005. The effects of three regeneration harvest methods on plant diversity and soil characteristics in the southern Appalachians. For. Ecol. Manage. **211**(3): 296–317.

Elliott, K.J., and Miniat, C.F. 2018. Herbaceous-layer diversity and tree seedling recruitment are enhanced following *Rhododendron maximum* shrub removal. For. Ecol. Manage. **430**: 403–412.

Elliott, K.J., and Swank, W.T. 2008. Long-term changes in forest composition and diversity following early logging (1919–1923) and the decline of American chestnut (*Castanea dentata*). Plant Ecol. **197**(2): 155–172.

Elliott, K.J., Boring, L.R., Swank, W.T., and Haines, B.R. 1997. Successional changes in plant species diversity and composition after clearcutting a southern Appalachian watershed. For. Ecol Manage. **92**(1-3): 67–85.

Elliott, K.J., Loftis, D.L., and Steinbeck, K. 1993. Vegetation diversity after logging in the southern Appalachians. Letter to the editor, Conserv. Biol. **7**: 220–221.

Ford, W.M., Odom, R.H., Hale, P.E., and Chapman, B.R. 2000. Stand-age, stand characteristics, and landform effects on understory herbaceous communities in southern Appalachian cove-hardwoods. Biol. Conserv. **93**(2): 237–246.

Fraterrigo, J.M., Turner, M.G., and Pearson, S.M. 2006. Interactions between past land use, life-history traits and understory spatial heterogeneity. Landscape Ecol. **21**: 777–790.

Fredericksen, T.S., Ross, B.D., Hoffman, W., Morrison, M.L., Beyea, J., Johnson, B.N., et al. 1999. Short-term understory plant community responses to timber-harvesting intensity on non-industrial private forestlands in Pennsylvania. For. Ecol. Manage. **116**(1-3): 129–139.

Gilliam, F.S. 2002. Effects of harvesting on herbaceous layer diversity of a central Appalachian hardwood forest. For. Ecol. Manage. **155**: 33–43.
Gilliam, F.S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. BioScience, **57**(10): 845–858.
Gilliam, F.S., Turrill, N.L., and Adams, M.B. 1995. Herbaceous-layer and overstory species in clear-cut and mature central Appalachian hardwood forests. Ecol. Applic. **5**(4): 947–955.
Greenberg, C.H., Collins, B.S., McNab, W.H., Miller, D.K., and Wein, G.R. 2016. Introduction to natural disturbances and historic range of variation: type, frequency, severity, and post-disturbance structure in central hardwood forests. *In* Natural disturbances and historic range of variation: type, frequency, severity, and post-disturbance structure in Central Hardwood Forests USA. *Edited by* C.H. Greenberg and B.S. Collins. Springer, New York, USA. pp. 1–32.
Greenberg, C.H., Levey, D.J., and Loftis, D.L. 2007. Fruit production in mature and recently regenerated forests of the Appalachians. J. Wildl. Manage. **71**(2): 321–335.
Greenberg, C.H., Smith, L.M., and Levey, D.J. 2001. Fruit fate, seed germination and growth of an invasive vine—an experimental test of 'sit and wait' strategy. Biol. Invas. **3**: 363–372.
Greenberg, C.H., Whitehead, M., Lanham, J.D., and Tomcho, J. 2023. Shelterwood harvests promote high breeding bird diversity and shrubland species for less than 10 years in hardwood forests. For. Ecol. Manage. **545**: 121257.
Jackson, B.C., Pittillo, J.D., Allen, H.L., Wentworth, T.R., Bullock, B.P., and Loftis, D.L. 2009. Species diversity and composition in old growth and second growth rich coves of the southern Appalachian Mountains. Castanea, **74**(1): 27–38. doi:10.2179/07-017.1.
Jenkins, M.A. 2007. Vegetation communities of Great Smoky Mountains National Park. Southeast. Nat. **6**(sp2): 35–56. doi:10.1656/1528-7092(2007)6[35:VCOGSM]2.0.CO;2.
Johnson, A.S., Ford, W.M., and Hale, P.E. 1993. The effects of clearcutting on herbaceous understories are still not fully known. Conserv. Biol. **7**(2): 433–435. doi:10.1046/j.1523-1739.1993.07020433.x.
McEwan, R.W., and Muller, R.N. 2011. Dynamics, diversity, and resource gradient relationships in the herbaceous layer of an old-growth Appalachian forest. Plant Ecol. **212**: 1179–1191. doi:10.1007/s11258-011-9896-0.
Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., et al. 2015. Vegan: Community Ecology Package. R package version 2.3-4. Available from http://CRAN.R-project.org/package=vegan [accessed May 2024].
Oliver, C.D., and Larson, B.C. 1996. Forest stand dynamics. Updated ed. John Wiley and Sons.
Peck, J.E. 2016. Multivariate analysis for ecologists: step-by-step. *In* MjM software design. 2nd ed. Gleneden Beach, OR.
Perry, R.W., Thill, R.E., Peitz, D.G., and Tappe, P.A. 1999. Effects of different silvicultural systems on initial soft mast production. Wildl. Soc. Bull. 915–923.
Pielou, E.C. 1966. Species-diversity and pattern-diversity in the study of ecological succession. J. Theor. Biol. **10**(2): 370–383. PMID: 5964400.
Pittillo, J.D., Hatcher, R.D., Jr, and Buol, S.W. 1998. Introduction to the environment and vegetation of the Southern Blue Ridge Province. Castanea, 202–221.
Pyle, C. 1988. The type and extent of anthropogenic vegetation disturbance in The Great Smoky Mountains before National-Park-Service acquisition. Castanea, **53**(3): 183–196.
R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org [accessed May 2024].
Radford, A.E., Ahles, H.E., and Bell, C.R. 1968. Manual of the vascular flora of the Carolinas. University of North Carolina Press, Chapel Hill.
Reader, R.J., and Bricker, B.D. 1992. Value of selectively cut deciduous forest for understory herb conservation: an experimental assessment. For. Ecol. Manage. **51**(4): 317–327. doi:10.1016/0378-1127(92)90331-3.
Ricard, J.P., and Messier, C. 1996. Abundance, growth and allometry of red raspberry (*Rubus idaeus* L.) along a natural light gradient in a northern hardwood forest. For. Ecol. Manage. **81**(1-3): 153–160. doi:10.1016/0378-1127(95)03643-1.
Schafale, M.P., and Weakley, A.S. 1990. Classification of the natural communities of North Carolina. Third approximation. North Carolina Department of Environment, Health, and Natural Resources, Division of Parks and Recreation, Natural Heritage Program, Raleigh.
Shannon, C.E. 1948. A mathematical theory of communication. Bell Syst. Tech. J. **27**: 379–423. doi:10.1002/j.1538-7305.1948.tb01338.x.
Ulrey, C.J. 2002. The relationship between soil fertility and the forests of the Southern Appalachian region. PhD dissertation, North Carolina State University.
Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecol Monogr. **26**(1): 1–80. doi:10.2307/1943577.
Widen, M.J., O'Neil, M.A.P., Dickinson, Y.L., and Webster, C.R. 2018. *Rubus* persistence within silvicultural openings and its impact on regeneration: the influence of opening size and advance regeneration. For. Ecol. Manage. **427**: 162–168. doi:10.1016/j.foreco.2018.05.049.
Wofford, B.E. 1989. Guide to the vascular plants of the blue ridge. University of Georgia Press.
Woodbridge, M. 2020. Long-term landscape-scale impact of early 20th century logging on plant communities in The Southern Appalachians. PhD dissertation, State University of New York College of Environmental Science and Forestry.
Wyatt, J.L., and Silman, M.R. 2010. Centuries-old logging legacy on spatial and temporal patterns in understory herb communities. For. Ecol. Manage. **260**(1): 116–124. doi:10.1016/j.foreco.2010.04.010.

Appendix A

Fig. A1. Differences in dispersions between herbaceous communities within shelterwood harvests (SW; harvested ca. 1999) and mature forests (M) of upland hardwood (UH) forest or cove hardwood (CH) forest types 5, 10, 14, and 17 years post-harvest, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina. The UHSW treatment is more variable than the other three, which do not significantly differ from one another.

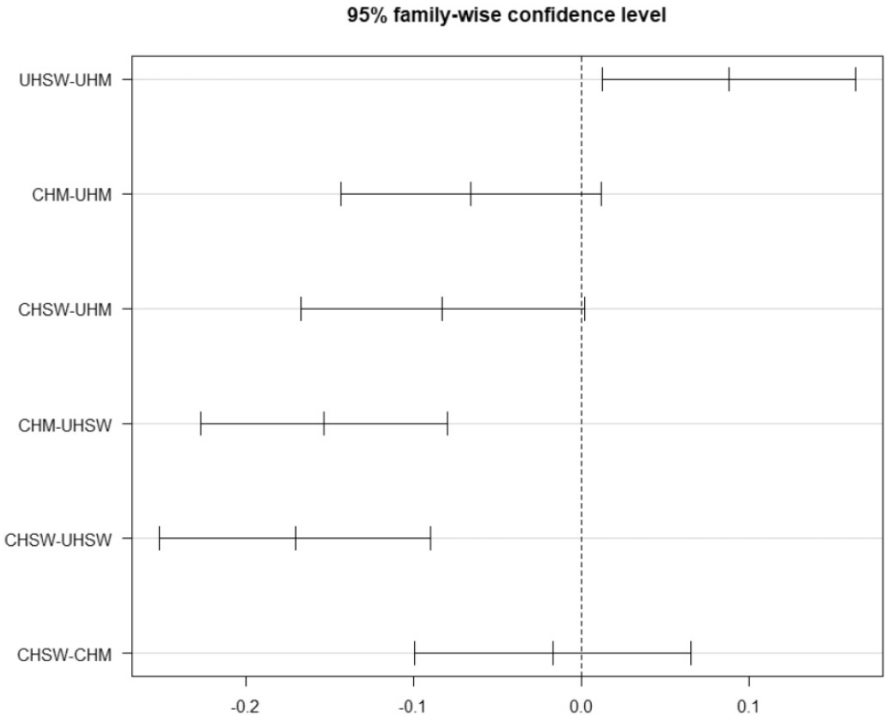


Fig. A2. Standard deviation ellipses around the group centroids of herbaceous species within shelterwood harvests (SW; harvested ca. 1999) and mature forests (M) of upland hardwood- (UH) or cove hardwood (CH) forest types post-harvest, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina. The ellipse around the UHSW treatment is noticeably larger than the others, suggesting the significant perMANOVA results could be due to differences in homogeneity of dispersions.