Forest Ecology and Management 596 (2025) 123091

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Successional trajectories differ among post-harvest and mature cove and upland hardwood forests

C.H. Greenberg *, M. Woodbridge

USDA Forest Service, Southern Research Station, Upland Hardwood Ecology and Management Research Work Unit, Asheville, NC 28806, USA

ARTICLE INFO

Keywords:
Cove hardwood forest
Upland hardwood forest
Forest succession
Mesophication
Oak regeneration
Regeneration harvest
Shelterwood harvest
Stand development

ABSTRACT

Oak (*Quercus*) dominance in undisturbed eastern hardwood forests is declining as shade-tolerant species (e.g., red maple; *Acer rubrum*) gradually replace them (termed “mesophication”), especially on mesic sites. In contrast, compositional change can be accelerated after regeneration harvests as regeneration responds to overstory removal. We evaluated the tree and sapling strata over 17 years in mesic, mature cove hardwood (CHM) and subxeric upland hardwood (UHM) forests, and young cove hardwood and upland hardwood stands created by shelterwood-with-reserves harvests (CHSW and UHSW) to assess whether compositional shifts were evident or likely over time. In SWs, saplings comprised the dominant canopy. Compositional differences between the tree and sapling strata in mature forests suggested that CHM will become *less* “mesophytic” as red maple (a widespread generalist) replaces oak and yellow-poplar (*L. tulipifera*; a mesophyte) as overstory dominants in the gradual process of forest turnover; UHM will become more “xerophytic-generalist” as red maple and xerophytes (blackgum (*Nyssa sylvatica*), sourwood (*Oxydendrum arboreum*) replace oak trees. In contrast, differences between the sapling strata in SWs and the overstory strata in mature forest controls showed that both mesic (CHSW) and subxeric (UHSW) forest types rapidly transitioned to a “mesophytic-generalist” composition as red maple and mesophytes (yellow-poplar, sweet birch (*Betula lenta*)) quickly dominated the canopy. Interspecific competition may continue to alter successional trajectories as SW stands develop. Our study illustrates strikingly different pathways, rates, and outcomes for shifting species dominance among undisturbed mature and post-harvest stands on mesic and subxeric sites and suggests that changes do not always imply increases in mesophytic species, or “mesophication”.

1. Introduction

In the southern Appalachian Mountains, complex topographic gradients including aspect, elevation, and landform (site concavity or convexity) affect temperature and radiation, soils, and moisture at highly local scales (Wyatt and Silman, 2010) that in turn provide conditions for different forest species and assemblages (“forest types”) across the landscape (e.g., Whittaker, 1956). Tree species composition differs somewhat across a gradient from lower quality xeric sites to higher quality mesic sites due to interspecific differences in “functional traits” including tolerance to drought, temperature, shade, and disturbances such as fire (e.g., Whittaker, 1956; Nowacki and Abrams, 2008; Woodbridge et al., 2022). For example, yellow-poplar (*Liriodendron tulipifera*), northern red oak (*Quercus rubra*), sweet birch (*Betula lenta*), striped maple *Acer pensylvanicum*), white ash (*Fraxinus americana*), American beech (*Fagus grandifolia*), cucumber- (*Magnolia acuminata*) and Fraser magnolia (*M. fraseri*), black cherry (*Prunus serotina*), silverbell (*Halesia carolina*), and eastern hemlock (*Tsuga canadensis*) are characteristic of cove hardwood forests associated with mesic, topographically sheltered (concave) landscapes or north-facing slopes; these species are all considered “mesophytic” because they are strongly associated with mesic sites, despite differences in their tolerance to shade and fire. In contrast, chestnut oak (*Q. montana*), scarlet oak (*Q. coccinea*), black oak (*Q. velutina*), sourwood (*Oxydendrum arboreum*), pignut hickory (*Carya glabra*), mockernut hickory (*C. tomentosa*), and blackgum (*Nyssa sylvatica*) are characteristic of upland hardwood forests associated with subxeric, lower site quality on south or west-facing slopes and flat or convex landscape positions. Red maple (*A. rubrum*) in particular is common across the moisture gradient (e.g., Whittaker, 1956; Burns and Honkala, 1990; McNab, 2011) and can act as both an early and late successional species (Abrams, 1998). These attributes suggest that red maple is not a “mesophytic” (moisture-limited) species

---

* Corresponding author.
E-mail address: Cathryn.greenberg@usda.gov (C.H. Greenberg).

https://doi.org/10.1016/j.foreco.2025.123091
Received 3 July 2025; Received in revised form 11 August 2025; Accepted 13 August 2025

but instead a generalist that, in the absence of limiting factors such as frequent fire, is capable of thriving across a wide range light availability and edaphic conditions.

Natural disturbances (e.g., single-tree mortality, wind, ice, insect pests, lightning-ignited wildfire) that vary in frequency, scale, and severity, also affect forest dynamics (Greenberg et al., 2016). Additionally, humans have influenced southern Appalachian forests for thousands of years. Native Americans and (by the 1800's), Euro-American settlers used frequent (estimated at 2–3 year intervals) fire to maintain more open forests on drier sites across much of the landscape; mesophytic coves burned much less frequently (Lafon et al., 2017; Arthur et al., 2021). In the southern Appalachians, a very low ratio of lightning- to human-ignited wildfires indicates that wildfire is (Greenberg et al., 2021), and historically was (Greenberg et al., 2016; Arthur et al., 2021) rare, and most fires were human-ignited. Frequent fires altered species composition by killing smaller stems of fire-sensitive tree species such as red maple; increased light and reduced litter depth also promoted oak and yellow pine (*Pinus*) regeneration and growth (Grissino-Mayer, 2016; Arthur et al., 2021). Other anthropogenic disturbances included land clearing for agriculture, farming practices that eroded soil, free-range livetock grazing, and the functional extinction of the American chestnut (*Castanea dentata*) by a non-native fungus (*Cryphonectria parasitica*) by the mid-20th century (Elliott and Swank, 2008; Faison and Foster, 2014; Greenberg et al., 2016). Perhaps most notably, the southern Appalachians were heavily logged in the late 19th and early 20th centuries (Pyle, 1988); dry slash piles and sparks from railroad log trains caused frequent post-logging wildfires (Lafon et al., 2017). Today's mature (>100 year old) oak-dominated forests across much of the southern Appalachians were established following this exploitative logging and prior to fire exclusion policies beginning in the 1930s (Lorimer, 1993; Hutchinson et al., 2005).

Abundant research suggests that the species composition of some relatively undisturbed eastern hardwood forests is undergoing a slow transition from dominance by intermediate, fire-tolerant species such as oak and hickory, to shade-tolerant, fire-intolerant species such as red maple (Nowacki and Abrams, 2008; Fei et al., 2011; Chapman and McEwan, 2016; Knott et al., 2019). This process, termed “mesophication” (Nowacki and Abrams, 2008) may be more prominent on higher quality mesic sites where red maples are recruited more strongly than on xeric sites where oak recruitment is stronger (Hilt, 1985; McEwan et al., 2005; Fei and Steiner, 2008; Kabrick et al., 2014; Chapman and McEwan, 2016), but inconsistent results among studies (Chapman and McEwan, 2016; Palus et al., 2018; Dyer and Hutchinson, 2019) indicate that local biotic and abiotic factors modify its rate and severity (Woodbridge et al., 2022).

In mature eastern hardwood forests, mesophication began decades ago, likely in part due to fire exclusion policies that favored development of shade-tolerant species in the low-light understory (e.g., Lorimer, 1984; Abrams, 1992, 1998; Hutchinson et al., 2005; Nowacki and Abrams, 2008). In turn, heavy shade cast by a denser midstory suppresses oak regeneration, as it requires 20–30 % full sunlight (Gottschalk, 1994) to develop into sapling-sized advance regeneration – a prerequisite for successfully competing with faster-growing species such as yellow-poplar after their release by overstory reduction (Johnson et al., 2009). Thus, oak seedlings may be abundant within a forest understory but are nonetheless undergoing regeneration failure (e.g., Lorimer, 1993; Hutchinson et al., 2005; Nowacki and Abrams, 2008; Schweitzer and Dey, 2011; Palus et al., 2018) as they fail to attain a canopy position and are gradually replaced by shade-tolerant, non-oak species in the natural process of forest turnover (Beasley et al., 2022). The loss of overstory oak is concerning to forest managers and ecologists due to its commercial timber value, and food value of their protein-rich seed – acorns – to wildlife (Brooke et al., 2019).

Shifts in species' dominance and forest composition can be accelerated after regeneration harvests (e.g., treatments that create a new age class, such as shelterwood, clearcut, or group selection) where heavy overstory removal dramatically increases light at the forest floor. Harvests initiate rapid increases in woody stem density as seedlings germinate and harvested tree stumps resprout. This forest structure is short-lived as young stands progress from the stem initiation into the stem exclusion stages of stand development (Oliver and Larson, 1996; Johnson et al., 2009; Loftis et al., 2011). Young tree sprouts and seedlings gain height and girth, with the newly regenerated strata of saplings often reaching canopy closure with concomitant reductions in light and stem densities within 15 years (Loftis et al., 2011). Whereas these harvest methods can regenerate fully stocked stands of commercial tree species, composition of the developing overstory can rapidly transition from oak and hickory, to faster-growing shade-intolerant early successional species such as yellow-poplar, sweet birch, black cherry, and black locust (*Robinia pseudoacacia*) as well as shade-tolerant species such as red maple, and sugar maple (*A. saccharum*) (Trimble, 1973; Tift and Fajvan, 1999; Nyland et al., 2006; Shure et al., 2006; Vickers and Fox, 2015; Ryan et al., 2024). This can be especially problematic in mesic, cove hardwood forests on higher-quality sites where these species may be more abundant, hence providing onsite sources of regeneration by seed rain, seed bank, and stump sprouting (Keyser et al., 2012; Keyser and Zarnoch, 2014).

In this study, we evaluated dynamic temporal changes in forest structure and species composition of trees ($\geq$12.7 cm diameter at breast height (dbh)) and saplings (2.54–12.6 cm dbh) in recently harvested 2-aged stands created by shelterwood-with-reserves regeneration harvests (termed "shelterwood") and undisturbed mature stands of cove- and upland hardwood forest types over a 17-year period. We focused on the tree and sapling size classes to assess whether shifts in species dominance (based on importance values) were evident or likely to occur over time in mature and (or) recently harvested cove- and upland hardwood forests. We hypothesized that (1) shifts in overstory species dominance would be negligible in mature forests, but low oak regeneration (saplings) and increasing, or abundant regeneration of other species would suggest that future forests will be dominated by non-oak species, and; (2) shelterwood harvests in cove- and upland hardwood forest types would promote rapid shifts in species' dominance compared to the overstories (trees) of their mature forest type counterparts, as regeneration (saplings of stump sprout and seedling origin) of fast growing, shade-intolerant or generalist species responded to increased light.

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 conditions including aspect, slope position, and percent slope; elevations ranged 500–1200 m. Average annual rainfall in the region (Asheville area, 2000–2016) was 119 cm (ranged 85–191 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.

2.2. Study design

We selected 31 stands of two forest types (upland hardwood (UH) and cove hardwood (CH)) and two age classes (shelterwood harvests (SW) and relatively undisturbed 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

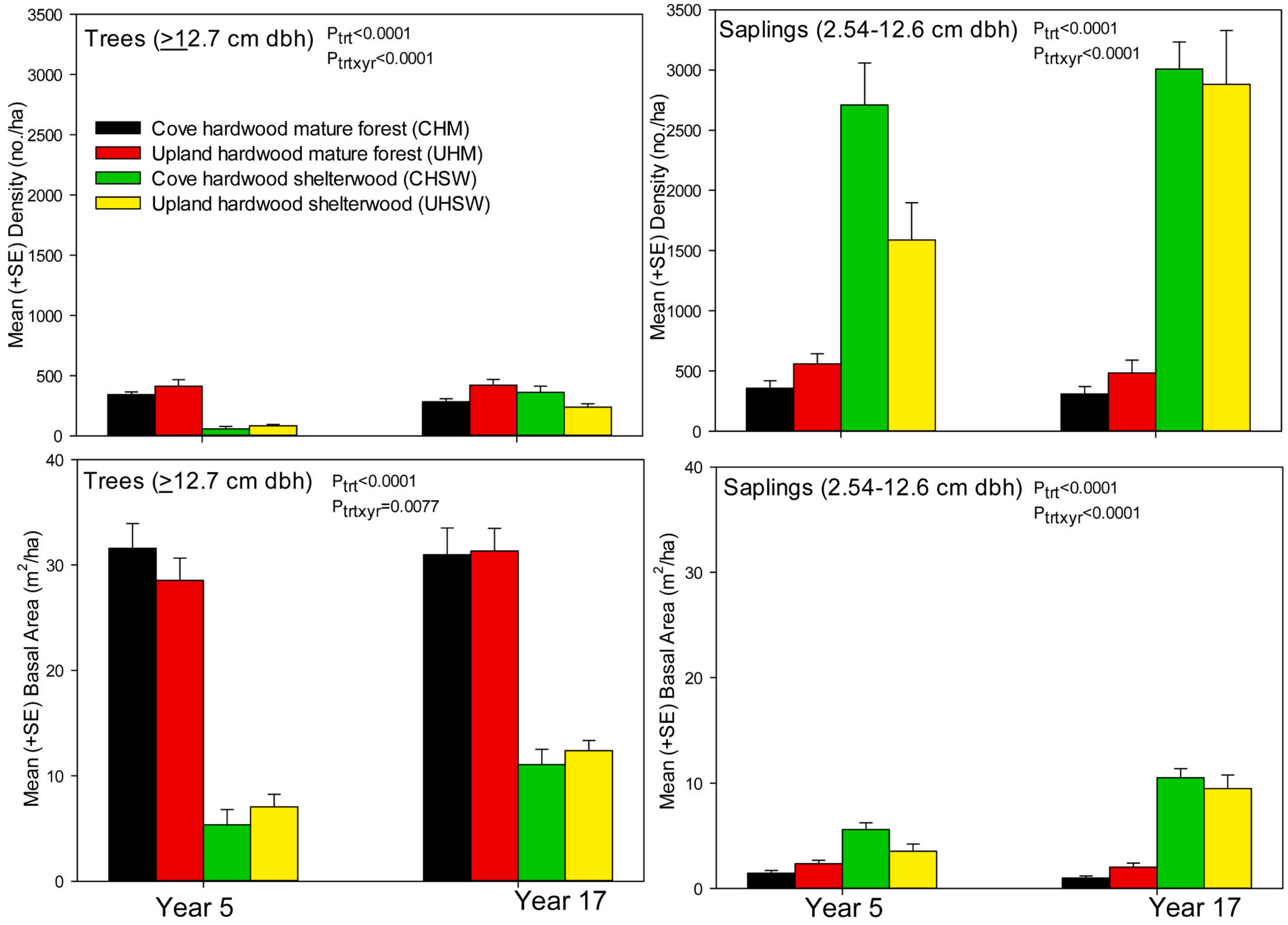

Fig. 1. Mean density and BA of trees (≥12.7 cm dbh) and saplings (2.54–12.6 cm dbh) in mature cove- (n = 8) and upland hardwood (n = 8) forests, and young cove- (n = 6) and upland hardwood (n = 9) shelterwood harvests (harvested ca. 1999) 5 and 17 years post-harvest, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.

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, 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 class and forest type criteria. Mature 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. We assumed that prior to harvests, CHSW stands were similar to CHM, and UHSW stands were similar to UHM in species composition and productivity, and that if CHM or UHM stands were harvested, they would regenerate similarly to CHSW and UHSW, respectively (Vickers and Fox, 2015).

Shelterwood harvests were conducted during 1998–1999 using a shelterwood-with-reserves regeneration method. About 15–20 % of the original mature tree basal area (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 M stands when they were harvested. US Forest Service personnel conducted standard site-preparation treatments in regenerated stands within a year of harvesting by cutting all stems 2.5–20 cm 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, Fraser magnolia, and blackgum, as well as rhododendron (*Rhododendron* spp.), and mountain laurel (*Kalmia latifolia*) were treated with herbicide (Garlon 3 A, 50–50 mix; Dow AgroSciences, Indianapolis, IN) to reduce sprouting.

2.3. *Forest structure and composition measurements*

We quantified density and BA of trees (≥12.7 cm dbh) and saplings (2.54–12.6 cm dbh) in Y5 and Y17 post-harvest for all tree species within a 20 × 50 m (0.1 ha) plot randomly placed within each study stand. Individuals (defined as single stems or the largest-dbh stem within a cluster of stump sprouts) were counted by species in four size classes: Class 1 = stem < 2.54 cm diameter and ≥ 0.5 m height (not evaluated here); Class 2 = 2.54–7.5 cm dbh; Class 3 = 7.6–12.6 cm dbh, and Class 4 ≥ 12.7 cm dbh. Stump sprouts were tallied by size class for ≤ 30 randomly selected subset of individuals per species within each plot. Stump sprout count subsamples – especially when partitioned by species and size class – was often low within plots, so we pooled them across plots within each treatment for each year and applied the average number of sprouts to the number of individuals with sprouts (by species and size class) per plot, by treatment. The dbh of trees (≥ 12.7 cm dbh) was measured in Y5 and Y17 and used to calculate BA. Sapling BA was calculated using the dbh midpoint of size class 2 or 3 dbh ranges, respectively.

2.4. *Data analysis*

We used repeated measures 2-way ANOVAs (PROC MIXED; SAS 9.3) in a completely randomized design with compound symmetry covariance structure to compare species richness, diversity, and evenness, total stem density (number/ha) and total BA (m^2/ha) of saplings (2.54–12.6 cm dbh) and (separately) trees (≥12.7 cm) among UHSW, UHM, CHSW, and CHM over the 17 years following harvests in SW. We focused on changes in importance values (IV) of sapling and tree species as indicators of shifts in species dominance within and among treatments. We calculated IVs for saplings and trees of each species as relative density (%) + relative BA (%)/2. We used 2-way ANOVAs to analyze IVs for individual species if either saplings, trees, or both occurred in ≥ 6 plots and IV averaged ≥ 15 in at least one treatment and year, for a total of 8 focal species (or genera; *Quercus*). We calculated species diversity (H′) (Shannon, 1948) based on species richness and BA, which better reflects the level of site occupancy than density (McMinn, 1992). 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. Our primary interest was in treatment effects, or treatment × year interaction effects as indicators that sapling or tree communities or species were responding differently among the four treatments over time; a non-significant treatment x year interaction indicated that the impact of treatment did not significantly change over our 17-year study period. Where significant treatment x 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 x year interaction differences were considered significant with an overall experimental α of < 0.05.

Plot-level community composition was evaluated and results were visualized using non-metric multidimensional scaling ordination (NMS) based on IVs. 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 were evaluated across harvest type (SW and M), forest type (CH and UH), strata (saplings and trees), and year (Y5 and Y17), including all two-way interactions. The NMS was run at the species level (all *Quercus* species were included individually). To aid in interpretation and better illustrate the effects of treatment and time on species composition, we additionally added species codes for the 7 focal species meeting our criteria (see Section 2.4) and the averaged species code for all *Quercus* species combined (“QUERCUS”) to the NMS figures.

Significant differences in composition, based on the IVs of all species sampled, was evaluated using distance-based multivariate analysis of variance (perMANOVA) in the R package vegan, blocked by plot to account for repeated sampling (Oksanen et al., 2015; R Development R Core Team, 2025). The test statistic is the pseudo F-ratio, where a large value indicates that plots within different age classes (M or SW) or forest types (CH or UH) (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 another category). 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-category variation (dispersion), differences in mean values of the categories, or both (Anderson, 2001). We calculated average dispersion values (average distances to category centroids) within our categories using the betadisper function in the R package vegan and used diagnostic plots to evaluate dispersion vs. location effects when dispersion was significantly different based on Tukey’s Honest Significant Differences (Anderson et al., 2006).

3. Results

3.1. *Forest structure and community composition*

Tree density was greater in both M than SW treatments, and greater in UHM than CHM (Fig. 1). A treatment x year interaction effect indicated that tree density increased over time within both SW treatments as saplings grew into the tree size class. By Y17 tree density remained greater in UHM than CHM and UHSW and was additionally greater in CHSW than UHSW. Tree BA was also greater in both M than SW treatments; tree BA increased over time within UHM, CHSW, and UHSW but remained greater in both M than both SW treatments in Y17. Sapling density and BA were greater in both SW than both M treatments (Fig. 1). Initially (Y5), sapling density was greater in CHSW than UHSW but increased over time in UHSW, and by Y17 no differences between the SW treatments were detected. Sapling BA was greater in both SW than M treatments and increased over time; in Y5 it was greater in both SW treatments than CHM, and greater in CHSW than UHM; by Y17 it was greater in CHSW and UHSW than CHM and UHM (Fig. 1).

We recorded a total of 38 species in our study, including 30 tree- and 37 sapling species (Appendix, Table A1). ANOVAs indicated that both tree species richness and diversity were greater in CHM and UHM than CHSW and UHSW but increased over time within both SW treatments as saplings grew into the tree size class; by Y17 no differences were detected among treatments (Fig. 2). Sapling species richness was greater in both SW than both M treatments. Sapling richness increased slightly over time within CHM, and substantially in UHSW, as small stump sprouts and seedlings of multiple species grew into the sapling size class; by Y17 sapling richness was greatest in UHSW (Fig. 2). Sapling species diversity was greater in UHSW than in M of either forest type but did not change over time (Fig. 2). Species evenness of both trees and saplings did not differ among treatments and no treatment x year interaction effects were detected (Fig. 2). NMS showed that community composition (e.g., the species makeup of the community, based on IVs that account for density and BA) varied by strata (tree and sapling), forest type (CH versus UH), harvest type (SW versus M), and, to a lesser extent, year (Table 1; Fig. 3).

3.2. *Trees*

NMS illustrated that the initial (Y5) composition of the tree (≥12.7 cm dbh) strata in both SW treatments (where trees were mostly residual oaks selected for retention during harvests) was similar to their M forest type counterparts (CHM and UHM, respectively) but more variable, especially in CHSW (Fig. 3a). Notable changes in the tree composition of both SW treatments were evident between Y5 and Y17, including decreased variability and a shift away from oak in CHSW, and a shift in UHSW away from UHM and towards the CHM composition over time (Fig. 3a,b). In CHM, the tree stratum was dominated by oak (mainly northern red oak), yellow-poplar, and red maple throughout the study period (Fig. 3a,b); eastern hemlock was also moderately important (IV=14) in Y5, but most were dead by Y17 due to infestation by the hemlock wooly adelgid (*Adelges tsugae*; Appendix, Table A1; Fig. 4). In UHM the tree stratum was dominated by oak (mainly chestnut oak) and red maple in both Y5 and Y17; sourwood was also moderately important. In SWs, the tree strata were initially (Y5) composed primarily of residual trees that were intentionally retained during harvests. In CHSW oak (mainly northern red oak) was the dominant tree species in Y5; hickory and red maple were moderately important. In UHSW oak (mainly white- and chestnut oak) and red maple were the dominant tree species in Y5 (Appendix, Table A1; Fig. 4). In both SW treatments, shifts

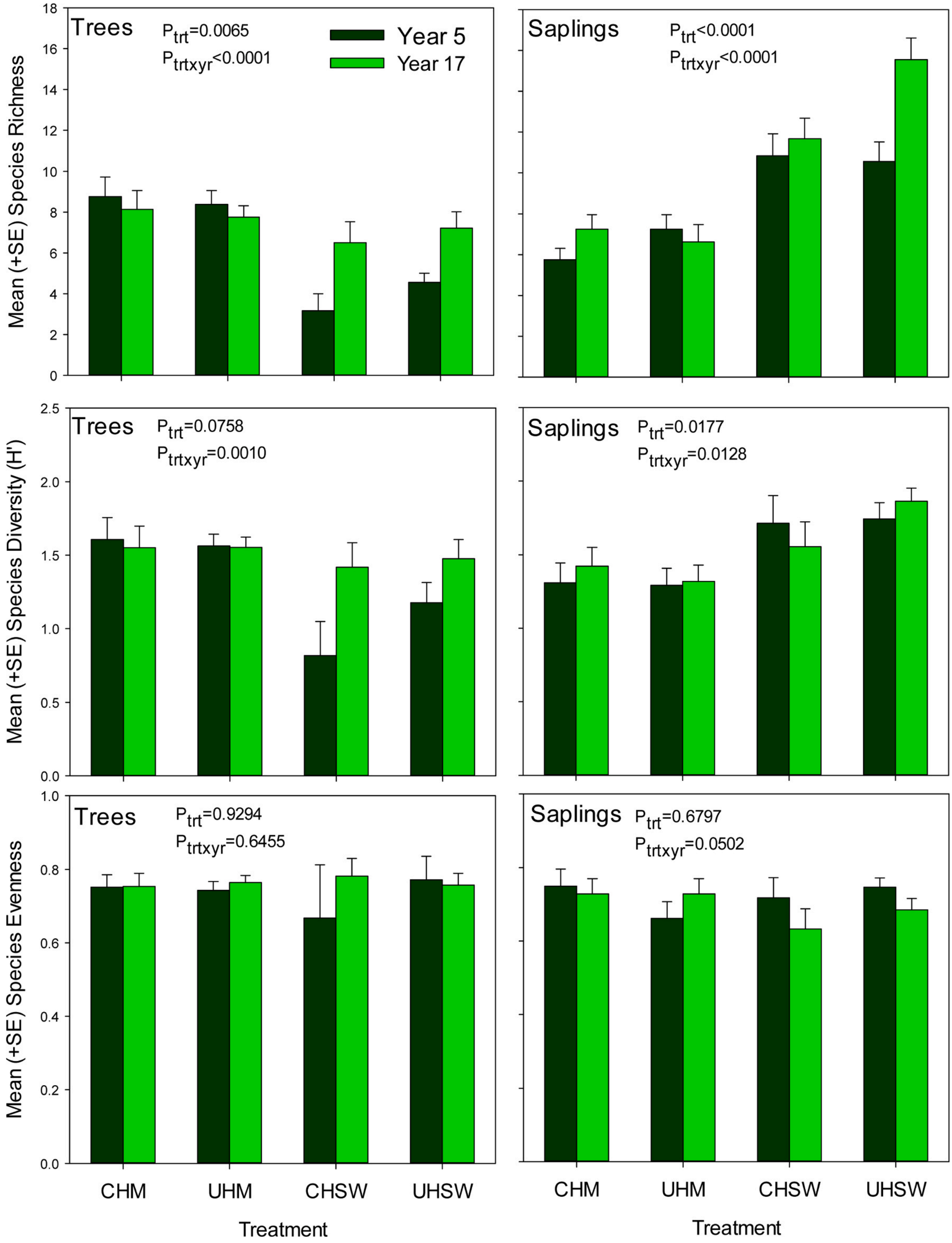

Fig. 2. Mean (+SE) species richness, and diversity (H') (based on BA) and evenness of trees (≥12.7 cm dbh) and saplings (2.54–12.6 cm dbh) in mature cove- (n = 8) and upland hardwood (n = 8) forests, and young cove- (n = 6) and upland hardwood (n = 9) shelterwood harvests (harvested ca. 1999) 5 and 17 years post-harvest, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina.

in tree IVs were evident for some species by Y17 (Appendix Table A1; Fig. 4). Oak tree IV decreased between Y5 (Fig. 3a) and Y17 (Fig. 3b) in both SW treatments (from 41.9 to 13.6 in CHSW; from 44.4 to 27.6 in UHSW) as oak saplings failed to recruit into the tree size class whereas saplings of some other species did. In Y5 oak tree IV was greater in UHM and UHSW than CHM; by Y17 it was greater in UHM than CHSW and UHSW. Yellow-poplar tree IV increased substantially over time in both SW treatments (from 7.1 to 32.2 in CHSW; from 7.6 to 20.7 in UHSW); by Y17 yellow-poplar tree IV remained lower in UHM than all other treatments but did not differ among CHSW, UHSW and CHM. Red maple tree IV ranged from 11.9 to 23.6 across treatments and years but did not differ among them, and no treatment x year interaction effects were detected (Appendix Table A1; Fig. 4).

Table 1

Tree (≥12.7 cm dbh) and sapling (2.54–12.6 cm dbh; “Strata”) community composition within shelterwood harvests (harvested ca. 1999) and mature forests (“Harvest type”) of cove- or upland hardwood forest types (“Forest type”) 5- and 17 years post-harvest (“Year”), Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina. The table shows the effects of the individual drivers of species composition from perMANOVA based on Bray-Curtis distances of species importance values.

	df	Sum of Sqs	R^2	F	p-value
Harvest type	1	1.339	0.03878	6.3556	< 0.001
Forest type	1	2.786	0.08069	13.2257	< 0.001
Strata	1	3.178	0.09205	15.0872	< 0.001
Year	1	0.327	0.00948	1.5533	0.026
Harvest type: Forest type	1	0.595	0.01723	2.8240	< 0.001
Harvest type: Strata	1	1.303	0.03774	6.1852	< 0.001
Forest type: Strata	1	0.562	0.01627	2.6664	< 0.001
Harvest type: Year	1	0.273	0.00792	1.3011	0.059
Residual	115	24.164	0.69984		
Total	123	34.528	1.00000		

3.3. Saplings

NMS illustrated that sapling composition changed little over time in both M forest types (CHM and UHM), with only a slight convergence between Y5 and Y17 (Fig. 3c,d). In CHM the sapling stratum was dominated by red maple and eastern hemlock; red maple sapling IV did not change, but hemlock sapling IV decreased over time, (Appendix Table A1; Fig. 4). In UHM the sapling stratum was dominated by red maple, blackgum, and (moderately) sourwood; no changes in IVs between Y5 and Y17 were detected. Notably, oak and yellow-poplar sapling IVs were negligible in both CHM and UHM and did not change over time. In contrast to M, sapling composition in SW treatments was slightly more dynamic (Fig. 3c,d); especially notable was the increased difference in composition between UHSW and UHM over time (Fig. 3c, d). Initially, (Y5) saplings were dominated by red maple, yellow-poplar, and silverbell in CHSW, and by red maple and sourwood in UHSW (Appendix Table A1; Fig. 4). Yellow-poplar sapling IV was greater in CHSW and UHSW than CHM and UHM; within UHSW it increased between Y5 and Y17 (from 7.8 to 14.4). Sweet birch sapling IV was also greater in CHSW and UHSW than CHM and UHM; it increased in both SW treatments between Y5 and Y17 (from 8.5 to 20.5 in CHSW; from 11.7 to 22.0 in UHSW), and by Y17 it was greater in both SW treatments than M of either forest type (also see Fig. 3d). Blackgum sapling IV was greater in UHM than CHM and CHSW, and IV did not change over time in any treatment. Sourwood sapling IV was greater in UHM and UHSW than CHM and CHSW; within UHSW IV decreased between Y5 and Y17, and by Y17 IV was greater in UHM than CHM and CHSW, and greater in UHSW than CHSW. Oak sapling IV was negligible in all treatments (0.0 – 6.9 across all treatments and years) but nonetheless was greater in CHSW and UHSW than CHM and UHM and did not change over time. Red maple and silverbell sapling IV did not differ among treatments or change over time in any treatment (Appendix Table A1; Fig. 4).

3.4. Visualizing successional trajectories in mature forests and shelterwoods

NMS indicated that within both M forest types (CHM and UHM) the composition of saplings differed from the composition of trees (Table 1; Fig. 5). Overall, the sapling composition in both CHM and UHM was more similar to the tree composition in CHM compared to UHM, and this difference slightly increased over time (Fig. 5; also see Fig. 4). Sapling composition in mature forests showed decreased importance of oak over time compared to the overstory composition, particularly in UHM. In CHM, oaks were consistently less important in the sapling strata compared to the tree strata (Fig. 5). In SWs, saplings were the dominant strata and were likely better indicators of the potential future mature forest overstory than the few remaining, intentionally-selected residual mature trees. NMS showed that the species composition of saplings in both CHSW and UHSW differed substantially from the overstory (tree) composition in both CHM and UHM throughout the 17-year study period, and differences increased over time (Fig. 6; also see Fig. 4). Notably, the species composition of saplings in UHSW was more similar to the overstory (trees) composition in CHM than UHM, likely driven in part by large increases in yellow-poplar saplings in UHSW over time (Fig. 6).

4. Discussion

Our long-term study allowed us to examine how forest structure, species composition, and the relative importance of trees and regeneration (saplings) differed, or changed over time, within and among undisturbed mature- and recently harvested cove- and upland hardwood forest types. Changes in the structure of both mature forest types (CHM and UHM) were few and relatively minor over the 17-year study period. Total BA increased slightly in UHM but not in CHM stands, likely due to offsets in growth by heavy mortality of eastern hemlock trees associated with hemlock wooly adelgid. Total density and BA of saplings in both M forest types, where closed canopies cast heavy shade, showed no change over the 17-year study period. In contrast, forest structure in SWs was highly dynamic and differed substantially from M stands. Most overstory trees were removed during harvests; increased post-harvest light initiated rapid increases in sapling densities as seedlings germinated and harvested tree stumps resprouted, rapidly gaining height and girth as young stands progressed from the stem initiation into the stem exclusion stages of forest stand development (Oliver and Larson, 1996; Johnson et al., 2009; Loftis et al., 2011). In our study, sapling densities – largely driven by yellow-poplar – increased more rapidly in mesic (CHSW) than subxeric (UHSW) SWs, but by year 17 post-harvest no differences were evident. Few studies compare post-harvest stand structure across moisture gradients, but some suggest that initially, density of post-harvest regeneration is greater on higher- than lower-quality sites (Johnson et al., 1998).

Many studies (e.g., Lorimer, 1993; Hutchinson et al., 2005; Nowacki and Abrams, 2008; Schweitzer and Dey, 2011; Palus et al., 2018) show a widespread failure of oak to successfully regenerate in undisturbed mature hardwood forests; small seedlings may be present, or even abundant, but heavy shade inhibits their growth and likelihood of eventually attaining a canopy position (Loftis et al., 2011). Additionally, abundant research indicates that red maple and other shade-tolerant, fire-intolerant species are gradually increasing in hardwood forest understories, creating dense shade that further suppresses the development of oak regeneration. Some studies indicate that mesic sites are more susceptible than drier sites to “mesophication” and oak regeneration failure (McEwan et al., 2005; Fei and Steiner, 2008; Nowacki and Abrams, 2008; Kabrick et al., 2014; Chapman and McEwan, 2016; Arthur et al., 2021; but see Palus et al., 2018).

We found large compositional differences between the tree and sapling strata within both cove- and upland hardwood M treatments. Most notably, oak was dominant in the tree strata, but virtually absent in the sapling strata of both mesic (CHM) and subxeric (UHM) forest types; additionally, yellow-poplar was dominant in the overstory of CHM but sapling IV was negligible. Initially (Y5) eastern hemlock was moderately important in the overstory of CHM and an important component of the sapling strata, but IVs in both strata decreased over time – likely due to hemlock wooly adelgid infestation – and saplings seem unlikely to grow into the tree strata. Regeneration (saplings) in both mature forest types was dominated by red maple; in UHM blackgum and (moderately) sourwood were additionally important. Although the importance of these shade-tolerant sapling species did not increase over time, they were nonetheless poised to replace overstory oaks and other species as they senesce and die over time. Our results additionally indicate that oak regeneration failure was apparent in both mature forest types (CHM and UHM) throughout the 17-year study period. Compositional differences

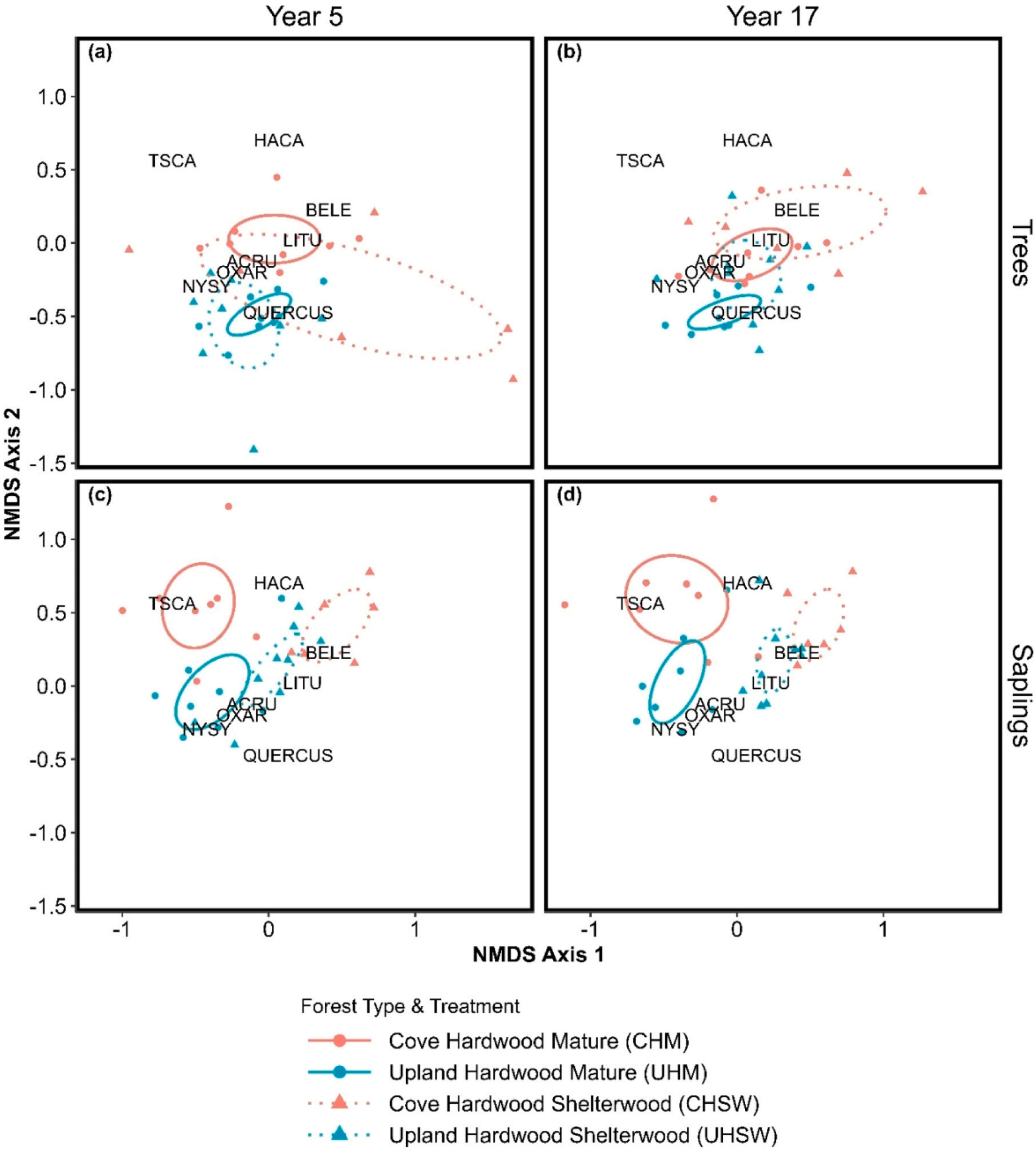

Fig. 3. Community composition of trees (≥12.7 cm dbh) and saplings (2.54–12.6 cm dbh) in mature cove- and upland hardwood forests, and young cove- and upland hardwood shelterwood harvests (harvested ca. 1999) 5 and 17 years post-harvest, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina. The figure visualizes differences in composition through time from nonmetric multidimensional scaling ordination based on Bray-Curtis distances of species importance values. In other words, stands closer to one another are more similar in composition than stands that are farther apart. Species scores, the approximate location where each species is most abundant across all plots and years (weighted average), are represented by species codes: ACRU (*A. rubrum*), BELE (*B. lenta*), HACA (*H. carolina*), LITU (*L. tulipifera*), NYSY (*N. sylvatica*), OXAR (*O. arboreum*), TSCA (*T. canadensis*), and QUERCUS (all *Quercus* spp.).

between the tree and sapling strata within M forest types suggest that, if left undisturbed, overstory oak-yellow-poplar dominance in CHM will gradually transition toward dominance by red maple, and oak dominance in UHM will transition toward dominance by red maple, blackgum, and sourwood.

In sharp contrast to the apparent slow successional trajectory from oak to red maple and other shade-tolerant species in undisturbed mature forests, our study showed a rapid post-harvest shift in species dominance in both mesic (CHSW) and subxeric (UHSW) SWs as the regeneration strata (stump sprouts and seedlings) responded to overstory removal. In SWs of both forest types this transition was driven by rapid increases in mesophytic shade-intolerant (Burns and Honkala, 1990) yellow-poplar and sweet birch saplings, and an abundance of shade-tolerant red maple; whereas SW harvests did not promote the expansion of red maple (e.g., Fei and Steiner, 2008; but see Vickers and Fox, 2015) relative to mature stands, our results suggest that it will nonetheless remain dominant as young SW forests mature. Shifts in the relative importance of species in SWs were also evident in the tree strata by 17 years after harvests. Because many mature oak trees were retained during SW harvests their relative importance did not initially (Y5) differ among treatments. However, oak tree importance (a relative metric) decreased substantially over time in both CHSW and UHSW as saplings of other species – especially yellow-poplar – grew into the tree size class.

In our study, oak sapling IVs were greater in both SW than M

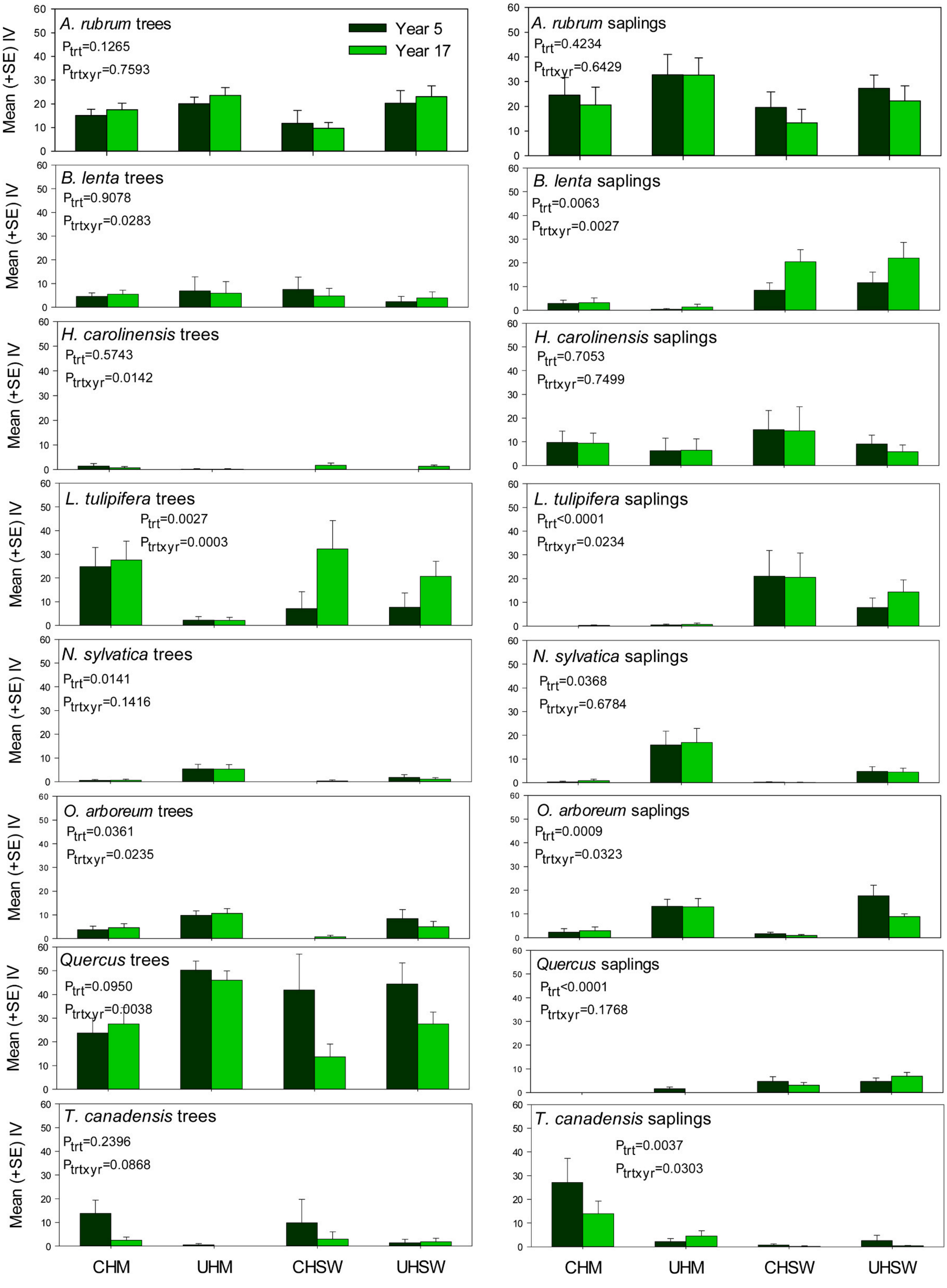

Fig. 4. Mean (±SE) importance value (IV) of dominant tree (≥12.7 cm dbh) and sapling (2.54–12.6 cm dbh species in mature cove- (n = 8) and upland hardwood (n = 8) forests, and young cove- (n = 6) and upland hardwood (n = 9) shelterwood harvests (harvested ca. 1999) 5 and 17 years post-harvest, and results of repeated measures mixed-model ANOVAs comparing treatments and treatment x year interactions, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina. Species were included if saplings, trees, or both occurred in ≥ 6 plots with an average IV ≥ 15 in any treatment and year.

treatments but were nonetheless very low. This was likely due to a paucity of *in situ* oak saplings prior to harvests (as in both M treatments), as well as a dearth of stump sprout regeneration. Many oak trees were intentionally, preferentially retained during SW harvests, resulting in relatively few oak stumps as potential sources of regeneration. In contrast, the clearcut regeneration method, whereby all trees, including oak are harvested, can promote heavy stump sprouting by oaks, along with other species (Cook et al., 1998; Johnson et al., 2009; Vickers and

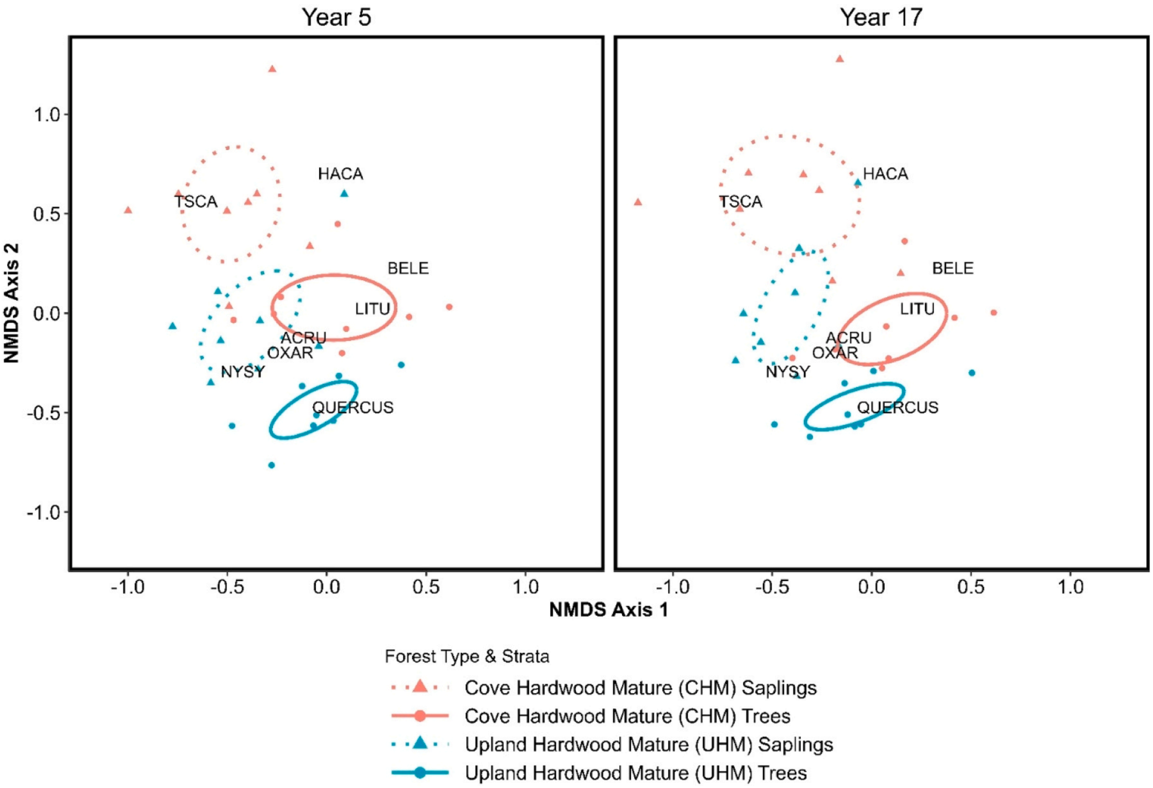

Fig. 5. Community composition of trees (≥12.7 cm dbh) and saplings (2.54–12.6 cm dbh) in mature cove and upland hardwood forests 5 and 17 years post-harvest, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina. The figure visualizes differences in composition through time from nonmetric multidimensional scaling ordination based on Bray-Curtis distances of species importance values. In other words, stands closer to one another are more similar in composition than stands that are farther apart. Species scores, the approximate location where each species is most abundant across all plots and years (weighted average), are represented by species codes: ACRU (*A. rubrum*), BELE (*B. lenta*), HACA (*H. carolina*), LITU (*L. tulipifera*), NYSY (*N. sylvatica*), OXAR (*O. arboreum*), TSCA (*T. canadensis*), and QUERCUS (all *Quercus* spp.).

Fox, 2015). Thus, oak regeneration could potentially be enhanced, at least initially, by stump sprouting if more mature oak trees were included in regeneration harvests (e.g., Vickers and Fox, 2015). However, successful recruitment of oaks into the tree size class would nonetheless be uncertain due to low sprouting potential for some species of larger-dbh oak trees (Keyser and Zarnoch, 2014) and fierce post-harvest competition with abundant, faster-growing species such as yellow-poplar and red maple.

Many studies indicate that species dominance can rapidly shift after regeneration harvests, from mixed oak forests (pre-harvest) to shade-intolerant early successional species and shade-tolerant species – many of which are also mesophytic – (Trimble, 1973; Johnson et al., 1998; Tift and Fajvan, 1999; Nyland et al., 2006; Shure et al., 2006; Loftis et al., 2011; Ryan et al., 2024). Oak is often out-competed, particularly on higher quality mesic sites where the abundance and growth rates of competitors, such as yellow-poplar, are likely to be greater. Our results also show that shelterwood harvests promoted rapid shifts in species dominance from oak (pre-harvest) to mesophytic (e.g., tulip-poplar and sweet birch) and generalist (e.g., red maple) species, and further show that this post-harvest “mesophication” can occur on both mesic cove- and subxeric upland hardwood forest sites.

Despite striking differences in species dominance between SWs and mature forest controls, it is important to note that the composition of regeneration following SWs is likely to vary according to onsite pre-harvest species composition and tree dbh’s that can affect levels of stump sprouting (Keyser and Zarnoch, 2014), and onsite or nearby species that can affect the composition of seed rain and buried seed banks (Keyser et al., 2012). Additionally, interspecific differences in growth rates, drought tolerance (Oliver and Larson, 1996; Elliott et al., 2015), and probability of survival (Keyser and Zarnoch, 2014) could continue to alter successional trajectories as SW stands develop. For example, in our study yellow-poplar recruited rapidly into the sapling and (by Y17) tree size classes in SWs, whereas sweet birch appeared slower to recruit into the sapling size class and remained a minor component of the tree strata, suggesting its slower growth and the possibility that it will be largely outcompeted by yellow-poplar as SW forests continue to develop. Similarly, sporadic drought could kill or reduce the competitive ability of fast-growing, mesophytic yellow-poplar, especially on subxeric sites (Hilt, 1985; Morrissey et al., 2008), resulting in reduced importance over time. Nonetheless, given the magnitude of differences in species composition between SWs and mature forest controls, our results suggest that large differences will persist as young stands continue to develop.

The term “mesophication” is loosely used in the scientific literature to describe an ongoing increase in shade-tolerant non-oak species – often characterized as “mesophytic” – in the understories of mature eastern oak-dominated forests, that will likely replace overstory oak trees in the gradual course of forest turnover (Nowacki and Abrams, 2008; Alexander et al., 2021). We suggest that the term “mesophication” is misleading, largely because it conflates tree characteristics including close affinity to mesic sites (the original criteria for defining “mesophytic” species; Schimper, 1903), shade-tolerance, and fire-intolerance as “mesophytes” when categorizing non-oak species implicated in this process. However, the suite of traits associated with “winners and losers” in mature forest succession, and the conditions that favor some species over others are complex, and often not strongly tied to one another (Woodbridge et al., 2022). For example, red maple – often considered an indicator of mesophication (Nowacki and Abrams, 2008) – is by no means strictly mesophytic or closely associated with mesic sites. Rather, it is a generalist species that can thrive across a wide moisture gradient,

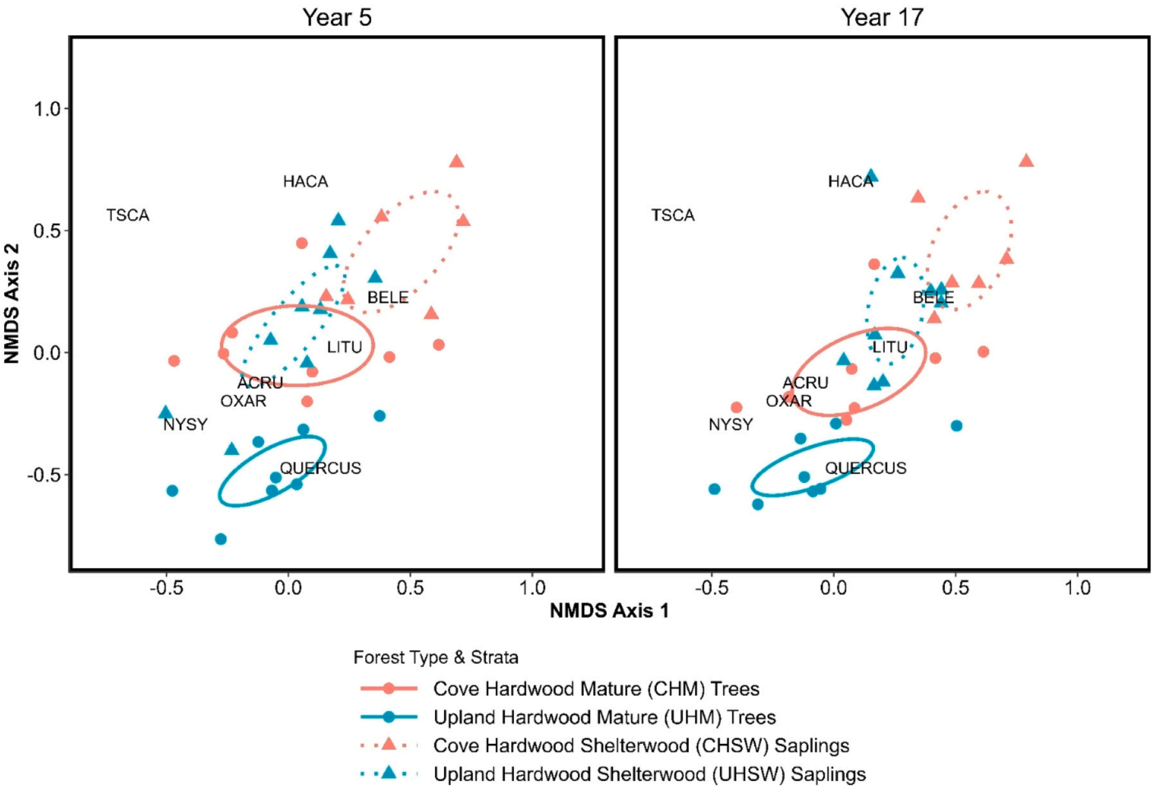

Fig. 6. Comparison of sapling (2.54–12.6 cm dbh) community composition in shelterwood harvests to tree (≥12.7 cm dbh) community composition in mature forests of cove- and upland hardwood forest types 5 and 17 years post-harvest, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina. The figure visualizes differences in composition from nonmetric multidimensional scaling ordination based on Bray-Curtis distances of species importance values. In other words, stands closer to one another are more similar in composition than stands that are farther apart. Species scores, the approximate location where each species is most abundant across all plots and years (weighted average), are represented by species codes: ACRU (*A. rubrum*), BELE (*B. lenta*), HACA (*H. carolina*), LITU (*L. tulipifera*), NYSY (*N. sylvatica*), OXAR (*O. arboreum*), TSCA (*T. canadensis*), and QUERCUS (all *Quercus* spp.).

including even the driest sites (e.g., Abrams, 1998; Iverson et al., 2017; Palus et al., 2018); further, although it is shade-tolerant, it also thrives in high light environments following disturbances as varied as timber harvests, land clearing, agricultural abandonment, and windthrow (Abrams, 1998). We suggest that the fire exclusion policies enacted in the 1930s, that virtually eliminated the practice of frequent, widespread burning by humans, provides the simplest explanation for the subsequent increase of fire-intolerant red maple (Abrams, 1998; Arthur et al., 2021) - even without invoking its (dubious) mesophytic traits. Similarly, yellow-poplar and sweet birch are closely associated with mesic sites – and therefore mesophytic – but are also shade-intolerant, and thus unlikely to increase in the shaded understories of mature hardwood forests. In fact, our results - indicating that red maple (a generalist species) will gradually replace oak, but also yellow-poplar (a mesophytic species), in the overstory of mature cove hardwood forests (CHM) - suggest that this forest type will, in fact, become *less* mesophytic over time. Similarly, our results indicating that red maple, as well as blackgum and sourwood – species associated with subxeric upland sites – will eventually replace oak in the overstory of mature upland hardwood forests suggests that this forest type will, in fact, become more “*xerophytic*” over time. Our study corroborates many others indicating that oak regeneration failure in mature, undisturbed hardwood forests will gradually lead to reduced dominance by oak and increased dominance by red maple and other shade-tolerant species. Further, our results suggest that “mesophication” does not accurately describe the likely successional trajectory within undisturbed mature cove- and upland hardwood forests as they transition toward a more generalist, less mesophytic (in CHM) or even xerophytic (in UHM) overstory species composition.

5. Conclusions

Our study illustrates strikingly different pathways, rates, and outcomes for shifting species dominance from oak- to non-oak species among undisturbed mature and post-harvest stands on mesic and subxeric sites. In undisturbed mature forests this slow successional trajectory is not necessarily contingent on *actively* increasing shade-tolerant species in the regeneration strata that (e.g., Nowacki and Abrams, 2008) but can also occur through a *passive* process whereby shade-tolerant species gradually replace overstory oaks simply because they are present in the regeneration strata, whereas oaks are not. Regardless, a paucity of oak- and an abundance of red maple saplings in mature cove- and upland hardwood forest understories will likely ensure that red maple will gradually replace oaks as an overstory dominant as mature oak trees senesce and die, regardless of site quality. However, differences in species composition of the regeneration- and overstory strata between undisturbed mature cove- versus upland hardwood forest types additionally suggest that their successional trajectories may differ. In mesic cove hardwood forests, oak and yellow-poplar dominated overstories will eventually become less “mesophytic” and more “generalist” as both species are replaced largely by red maple, whereas oak dominated overstories in subxeric upland hardwood forests will become more “xerophytic-generalist” as mature oak trees are gradually replaced largely by red maple, blackgum, and sourwood in the natural process of forest turnover. Interestingly, increased dominance by red maple, whose historic abundance was likely limited by frequent, human-ignited fire (Nowacki and Abrams, 1998; Arthur et al., 2021), is likely to occur in both cove hardwood forests - where fire was historically uncommon - and in upland hardwood forests, where fire return intervals were short (Lafon et al., 2017; Arthur et al., 2021).

In stark contrast to the slow pace and (likely) successional outcomes in undisturbed mature forests, shelterwood harvests with heavy overstory removal promoted rapid shifts in species dominance with strikingly different patterns of species dominance. Following shelterwood harvests, both shade-intolerant mesophytic species (e.g., yellow-poplar and sweet birch) and shade-tolerant generalist species (e.g., red maple) rapidly responded to increased light. Oak regeneration was scant, likely a combination of few *in situ* pre-harvest saplings (as in both M treatments) and preferential onsite retention of mature oak trees, resulting in relatively few oak stumps and thereby the potential for stump sprouting. Although interspecific competition may further alter successional trajectories as SW stands continue to develop, our results indicate that yellow-poplar, sweet birch, and red maple will replace oak as the dominant canopy species (compared mature forest type controls), and shift species dominance toward a "mesophytic-generalist" composition on both mesic and subxeric post-harvest sites. Our study indicates that successional trajectories differ among post-harvest and mature cove and upland hardwood forests and suggests that changes do not always imply increases in mesophytic species, or "mesophication".

Author contributions

Cathryn H. Greenberg designed and directed the study, conducted data analyses, created some figures, and wrote the majority of the manuscript. M. Woodbridge conducted multivariate analyses, created some figures, reviewed, and wrote portions of the manuscript.

CRediT authorship contribution statement

C.H.Greenberg: Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **M.Woodbridge**: Writing – review & editing, Writing – original draft, Visualization, Formal analysis.

Declaration of Competing Interest

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.

Acknowledgments

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 a separate companion study of native fleshy fruit production at the Savanna River Site, Georgia. Special thanks to J. Adams for excellent project management and fieldwork. 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. Three anonymous reviewers helped to improve this manuscript. Any opinions, findings, conclusions, or recommendations expressed in the material are the authors and do not necessarily reflect the views of the USDA.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123091.

Data availability

Data will be made available on request.

References

Abrams, M.D., 1992. Fire and the development of oak forests. BioScience 42 (5), 346–353.

Abrams, M.D., 1998. The red maple paradox. BioScience 48 (5), 355–364.

Alexander, H.D., Siegert, C., Brewer, J.S., Kreye, J., Lashley, M.A., McDaniel, J.K., Paulson, A.K., Renninger, H.J., Varner, J.M., 2021. Mesophication of oak landscapes: evidence, knowledge gaps, and future research. BioScience 71 (5), 531–542.

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

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

Anderson, M.J., 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. https://doi.org/10.1890/12-2010.1.

Arthur, M.A., Varner, J.M., Lafon, C.W., Alexander, H.D., Dey, D.C., Harper, C.A., Horn, S.P., Hutchinson, T.F., Keyser, T.L., Lashley, M.A., Moorman, C.E., 2021. Fire ecology and management in eastern broadleaf and Appalachian forests. In: Greenberg, C.H., Collins, B.S. (Eds.), Fire Ecology and Management: Past, Present, and Future of US Forested Ecosystems. Springer, New York, pp. 105–147.

Beasley, C., Carter, D.R., Coates, T.A., Keyser, T.L., Greenberg, C.H., 2022. Impacts of oak-focused silvicultural treatments on the regeneration layer nine years posttreatment in a production mixed-oak Southern Appalachian forest. J. Torr. Bot. Soc. 149, 166–180. https://doi.org/10.3159/TORREY-D-21-0003.

Brooke, J.M., Basinger, P.S., Birckhead, J.L., Lashley, M.A., McCord, J.M., Nanney, J.S., Harper, C.A., 2019. Effects of fertilization and crown release on White oak (*quercus alba*) masting and acorn quality. For. Ecol. Manag. 433, 305–312.

Burns, R.M., Honkala, B.H., 1990. Silvics of North America. USDA For. Serv. Agric. Handb. 654.

Chapman, J.I., McEwan, R.W., 2016. Thirty years of compositional change in an old-growth temperate forest: the role of topographic gradients in oak-maple dynamics. PloS One 11 (7), e0160238.

Cook, J.E., Sharik, T.L., Smith, D.W., 1998. Oak regeneration in the Southern appalachians: potential, problems, and possible solutions. S. J. Appl. For. 22 (1), 11–18.

Dyer, J.M., Hutchinson, T.F., 2019. Topography and soils-based mapping reveals fine-scale compositional shifts over two centuries within a central Appalachian landscape. For. Ecol. Manage. 433, 33–42.

Elliott, K.J., Miniat, C.F., Pederson, N., Laseter, S.H., 2015. Forest tree growth response to hydroclimate variability in the Southern appalachians. Glob. Change Biol. 21 (12), 4627–4641.

Elliott, K.J., 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.

Faison, E.K., Foster, D.R., 2014. Did American chestnut really dominate the eastern forest. Arnoldia 72 (2), 18–32.

Fei, S., Kong, N., Steiner, K.C., Moser, W.K., Steiner, E.B., 2011. Change in oak abundance in the eastern United States from 1980 to 2008. For. Ecol. Manag. 262 (8), 1370–1377.

Fei, S., Steiner, K.C., 2008. Relationships between advance oak regeneration and biotic and abiotic factors. Tree Physiol. 28, 1111–1119. PMID: 18450575.

Gottschalk, K.W., 1994. Shade, leaf growth and crown development of *quercus rubra*, *quercus velutina*, *prunus serotina* and *acer rubrum* seedlings. Tree Physiol. 14 (7-8-9), 735–749.

Greenberg, C.H., Collins, B.S., Goodrick, S., Stambaugh, M.C., Wein, G.R., 2021. Introduction to fire ecology across USA forested ecosystems: past, present, and future. In: Greenberg, C.H., Collins, B.S. (Eds.), New York, Fire ecology and management: Past, present, and future of US forested ecosystems. Springer, pp. 1–30.

Greenberg, C.H., Collins, B.S., McNab, W.H., Miller, D.K., 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: Greenberg, C.H., Collins, B.S. (Eds.), Natural Disturbances and Historic Range of Variation: Type, Frequency, Severity, and Post-disturbance Structure in Central Hardwood Forests USA. Springer, New York, pp. 1–32.

Greenberg, C.H., Weeks, K., Warburton, G.S., 2016. The historic role of humans and other keystone species in shaping central hardwood forests for disturbance-dependent wildlife. In: Greenberg, C.H., Collins, B.S. (Eds.), Natural Disturbances and Historic Range of Variation: Type, Frequency, Severity, and Post-disturbance Structure in Central Hardwood Forests USA. Springer, New York, pp. 1319–1353.

Grissino-Mayer, H.D., 2016. Fire as a Once-Dominant disturbance process in the yellow pine and mixed Pine-Hardwood forests of the Appalachian mountains. In: Greenberg, C.H., Collins, B.S. (Eds.), Natural Disturbances and Historic Range of Variation: Type, Frequency, Severity, and Post-disturbance Structure in Central Hardwood Forests USA. Springer, New York, pp. 123–146.

Hilt, D.E., 1985. Where has all my yellow-poplar gone? N. J. Appl. For. 2 (3), 67–69.

Hutchinson, T.F., Sutherland, E.K., Yaussy, D.A., 2005. Effects of repeated prescribed fires on the structure, composition, and regeneration of mixed-oak forests in ohio. For. Ecol. Manag. 218 (1-3), 210–228.

Iverson, L.R., Thompson, I.I.I., F.R., Matthews, S., Peters, M., Prasad, A., Dijak, W.D., Fraser, J., Wang, W.J., Hanberry, B., He, H., Janowiak, M., 2017. Multi-model comparison on the effects of climate change on tree species in the eastern US: results from an enhanced niche model and process-based ecosystem and landscape models. Landsc. Ecol. 32 (7), 1327–1346.

Johnson, J.E., Miller, G.W., Baumgras, J.E., West, C.D., 1998. Assessment of residual stand quality and regeneration following shelterwood cutting in central Appalachian hardwoods. N. J. Appl. For. 15 (4), 203–210.

Johnson, P.S., Shifley, S.R., Roberts, R., 2009. The Ecology And Silviculture Of Oaks. CABI, London.

Kabrick, J.M., Villwock, J.L., Dey, D.C., Keyser, T.L., Larsen, D.R., 2014. Modeling and mapping oak advance reproduction density using soil and site variables. For. Sci. 60, 1107–1117.

Keyser, T.L., Roof, T., Adams, J.L., Simon, D., Warburton, G., 2012. Effects of prescribed fire on the buried seed bank in mixed-hardwood forests of the Southern Appalachian mountains. Southeast. Nat. 11, 669–688. https://doi.org/10.1656/058.011.0407.

Keyser, T.L., Zarnoch, S.J., 2014. Stump sprout dynamics in response to reductions in stand density for nine upland hardwood species in the Southern Appalachian mountains. For. Ecol. Manag. 319, 29–35.

Knott, J.A., Desprez, J.M., Oswalt, C.M., Fei, S., 2019. Shifts in forest composition in the eastern United States. For. Ecol. Manag. 433, 176–183.

Lafon, C.W., Naito, A.T., Grissino-Mayer, H.D., Horn, S.P., Waldrop, T.A., 2017. Fire history of the Appalachian region: a review and synthesis. USDA For. Serv. Gen. Tech. Rep. SRS-219.

Loftis, D.L., Schweitzer, C.J., Keyser, T.L., 2011. Structure and species composition of upland hardwood communities after regeneration treatments across environmental gradients. In: Greenberg, C.H., Collins, B.S., Thompson, III, F.R. (Eds.), Sustaining Young Forest Communities: Ecology and Management of Early Successional Habitats in the Central Hardwood Region, USA. Springer, New York, pp. 59–71.

Lorimer, C.G., 1984. Development of the red maple understory in northeastern oak forests. For. Sci. 30 (1), 3–22.

Lorimer, C.G., 1993. Causes of the oak regeneration problem. In: Loftis, D., McGee, G.E. (Eds.), Oak Regeneration: Serious Problems, Practical Solutions. USDA For. Serv. Gen. Tech. Rep. SE-GTR-84.

McEwan, R.W., Muller, R.N., McCarthy, B.C., 2005. Vegetation-environment relationships among woody species in four canopy-layers in an old-growth mixed mesophytic forest. Castanea 70, 32–46.

McMinn, J.W., 1992. Diversity of woody species 10 years after four harvesting treatments in the oak-pine type. Can. J. For. Res. 22, 1179–1183.

McNab, W.H., 2011. Subregional variation in upland hardwood forest composition and disturbance regimes of the central hardwood region. In: Greenberg, C.H., Collins, B. S., Thompson, III, F.R. (Eds.), Sustaining Young Forest Communities: Ecology and Management of Early Successional Habitats in the Central Hardwood Region, USA. Springer, New York, pp. 11–26.

Morrissey, R.C., Jacobs, D.F., Seifert, J.R., Fischer, B.C., Kershaw, J.A., 2008. Competitive success of natural oak regeneration in clearcuts during the stem exclusion stage. Can. J. For. Res. 38 (6), 1419–1430.

Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and "mesophication" of forests in the eastern United States. BioScience 58 (2), 123–138.

Nyland, R.D., Bashant, A.L., Bohn, K.K., Verostek, J.M., 2006. Interference to hardwood regeneration in northeastern North America: ecological characteristics of American beech, striped maple, and hobblebush. N. J. Appl. For. 23 (1), 53–61.

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.

Oliver, C.D., Larson, B.C., 1996. Forest Stand Dynamics: Updated Edition. John Wiley and Sons.

Palus, J.D., Goebel, P.C., Hix, D.M., Matthews, S.N., 2018. Structural and compositional shifts in forests undergoing mesophication in the wayne national forest, southeastern ohio. For. Ecol. Manag. 430, 413–420.

Peck, J.E., 2016. Multivariate analysis for ecologists: Step-by-step. In: MjM software design. 2nd ed. Gleneden Beach, OR.

Pittillo, J.D., Hatcher, R.D., Jr, Buol, S.W., 1998. Introduction to the environment and vegetation of the Southern blue ridge province. Castanea 202, 216.

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, 2025. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available from ⟨https://www.R-project.org⟩.

Ryan, S.M., Copenheaver, C.A., Carter, D.R., Lorber, J.H., 2024. Evidence of mesophication following selective cutting and shelterwood in Virginia's eastern deciduous forest, USA. For. Ecol. Manag. 560, 121840.

Schimper, A.F.W., 1903. Plant Geography upon A Physiological Basis (Translated by W. R. Fischer, edited by P. Groom, L.B. Balfour). Clarendon Press, Oxford.

Schweitzer, C.J., Dey, D.C., 2011. Forest structure, composition, and tree diversity response to a gradient of regeneration harvests in the mid-Cumberland plateau escarpment region, USA. For. Ecol. Manag. 262 (9), 1729–1741.

Shannon, C.E., 1948. A mathematical theory of communication. Bell Syst. Tech. J. 27, 379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x.

Shure, D.J., Phillips, D.L., Edward Bostick, P., 2006. Gap size and succession in cutover Southern Appalachian forests: an 18 year study of vegetation dynamics. Plant Ecol. 185, 299–318.

Tift, B.D., Fajvan, M.A., 1999. Red maple dynamics in Appalachian hardwood stands in west virginia. Can. J. For. Res. 29, 157-16.

Trimble, G.R., 1973. The regeneration of central Appalachian hardwoods with emphasis on the effects of site quality and harvesting practice. USDA For. Serv. Res. Pap.

Vickers, L.A., Fox, T., 2015. Species Composition of Developing Central Appalachian Hardwood Stands following Clearcutting. In: Proc. 17th Biennial Southern Silvicultural Research Conference. USDA For. Serv. e–Gen. Tech. Rep. SRS–203, 62-69.

Whittaker, R.H., 1956. Vegetation of the great smoky mountains. Ecol. Monogr. 26 (1), 1–69.

Woodbridge, M., Keyser, T., Oswalt, C., 2022. Stand and environmental conditions drive functional shifts associated with mesophication in eastern US forests. Front. For. Glob. Change 5, 991934.

Wyatt, J.L., Silman, M.R., 2010. Centuries-old logging legacy on spatial and temporal patterns in understory herb communities. For. Ecol. Manag. 260 (1), 116–124.