

RESEARCH ARTICLE

Legacy of thinning on woody species composition and structure in southern Appalachian Mountain hardwood forests: restoration implications

Tara L. Keyser^{1,2} , Jason A. Rodrigue³

In the Appalachian Mountains, *Liriodendron tulipifera* monocultures are widespread, with these forests lacking both species and structural diversity. In this study, we developed models that described the effects of thinning treatments, conducted almost 60 years ago, on the density, composition, and functional identity of the woody understory in *L. tulipifera* forests. The woody understory of these thinned *L. tulipifera* forests was diverse, with the small seedling (<1.4 m), large seedling (≥1.4 m and <2.54 cm dbh), and sapling (≥2.54 and <12.7 cm) layers possessing 38, 32, and 23 species, respectively. Although model performance was low to moderate ($r^2 = 0.05\text{--}0.40$), we found that legacy effects, alone or in combination with environmental variables, explained, in part, the variability associated with the density, composition, and functional identity of the small seedling, large seedling, and sapling size classes, with the relative influence of legacy versus environmental effects varying by metric and size class. Post-thinning basal area and/or percent of basal area removed were not the primary legacy effects influencing the woody understory. Instead, legacy effects associated with species composition of the overstory before and/or after thinning along with average stem diameter post-thinning, variation in stem diameter post-thinning, and age at the time of thinning were more influential than density or thinning intensity. This study provides evidence that conserving species diversity during forest management activities can have positive long-term effects on composition and function of the woody understory and increase restoration potential.

Key words: forest thinning, *Liriodendron tulipifera*, regeneration potential, restoration, temperate deciduous forests, yellow poplar

Implications for Practice

- Restoring complexity to even-aged forests that lack species and structural diversity is an objective in temperate forests worldwide, and quantifying the effects of past forest management on the woody understory is critical to developing effective restoration treatments.
- Land use legacies, including previous forest management, can constrain ecological conditions and restrict restoration opportunities.
- Thinnings conducted approximately 60 years ago still influence the composition and function of the woody understory in *Liriodendron tulipifera* monocultures, although post-thinning overstory diversity promoted large seedlings/sapling diversity, suggesting these monocultures could develop more diverse canopies.
- Legacy effects should be considered when interpreting forest conditions and resultant restoration potential, as where the vegetation response could be confounded by past forest management even after seemingly long periods without disturbance.

Introduction

Restoration of ecological complexity and integrity and associated biodiversity are common goals associated with the active management of temperate forests worldwide (Messier et al. 2013). Silvicultural practices applied to achieve ecological goals and objectives have evolved from the application of traditional silvicultural methods which were developed and implemented to homogenize growing conditions for the efficient production of timber (Puettmann et al. 2009). In many areas,

Author contributions: TLK, JAR conceived of this research; TLK developed the methodology and completed the formal analysis; TLK wrote the original draft; TLK, JAR were responsible for review and editing.

¹United States Department of Agriculture Forest Service, Southern Research Station, Center for Forest Restoration and Management, 200 W.T. Weaver Blvd, Asheville, NC 28804, U.S.A.

²Address correspondence to T. L. Keyser, email tara.keyser@usda.gov

³United States Department of Agriculture Forest Service, Region 8, 160 Zillicoa Street, Suite A, Asheville, NC 28801, U.S.A.

Published 2022. This article is a U.S. Government work and is in the public domain in the USA.

doi: 10.1111/rec.13689

Supporting information at:

<http://onlinelibrary.wiley.com/doi/10.1111/rec.13689/supinfo>

contemporary approaches to forest management are focused on using multifunctional silviculture to restore or maintain key ecosystem functions and processes, increase adaptive capacity to global change pressures, and increase heterogeneity of structure and composition in efforts to sustain ecosystem services across spatial and temporal scales (Palik et al. 2020).

Although silviculture and, more broadly, forest management objectives have changed in recent decades (D'Amato et al. 2018), particularly as related to public land management, the structure, composition, and function of contemporary forests are often influenced by land use history (Flinn & Marks 2007; Dyer 2010). At the landscape-level, legacy effects associated with past management regimes are manifested in present-day landscape patterns of forest ages, structures, and compositions (Wulder et al. 2009). At the stand-level, where management activities are planned and implemented, legacy effects are more nuanced and depend on disturbance intensity and interactions with abiotic and biotic conditions during and after disturbance (Brown et al. 2015; Mitchell et al. 2017).

Legacy effects associated with past forest management practices may persist for decades and can affect structure, composition, and function of ecological attributes, including understory vegetation (Perring et al. 2018), tree regeneration (Canuel et al. 2019), growth and productivity (Devine & Harrington 2009), dead and downed wood (Muurinen et al. 2019), and soil properties (James et al. 2018). These legacy effects, in turn, influence how forests respond to disturbance (Mausolf et al. 2018), including restoration activities, and could possibly constrain future ecological processes and conditions (Royo & Carson 2006; Garbarino & Weisberg 2020).

In the southern Appalachian Mountains, an area of the southeastern US with inherently high levels of ecological complexity and biodiversity (Jenkins et al. 2015), land use practices in the late nineteenth and early twentieth centuries coupled with the loss of a keystone species, *Castanea dentata* (Ellison et al. 2005), have, due to weakened environmental-species relationships, homogenized forest conditions (Vellend et al. 2007) and, in some instances, created novel species compositions relative to those that were present prior to European colonization (Elliott & Swank 2008; Elliott & Vose 2011). In productive areas of the Appalachians, forests that experienced land clearing for agriculture and/or heavy cutting are often dominated by *Liriodendron tulipifera*, which, due to its ability to outcompete other native tree species via regeneration from seed rain, seed bank (Keyser et al. 2012), and stump sprouting (Keyser & Loftis 2015), often form even-aged monocultures that lack species and structural diversity (Kalisz 1986; Keyser 2012). Although considered an early seral species due to its shade intolerance, *L. tulipifera* is long-lived and a component of remnant old-growth forests (Buckner & McCracken 1978).

Prior to European colonization, *L. tulipifera* was restricted to mesic and topographically sheltered portions of the landscape (e.g. coves, concave toeslopes, north and east-facing toeslopes) (Ayres & Ashe 1905) where it was a component of complex and highly diverse forests (Whitaker 1956; Della-Bianca 1983). However, past land use and lack of disturbance following colonization have created conditions favorable to the expansion

and/or perpetuation of *L. tulipifera* following heavy canopy reduction via natural or silvicultural disturbances across landscape positions and associated productivity gradients (Elliott & Swank 2008; Swaim et al. 2018). Ecological restoration efforts in *L. tulipifera* monocultures are focused on promoting structural complexity and restoring species diversity (Keyser & Brown 2014; Kremer & Bauhus 2020) in efforts to increase heterogeneity of forest conditions at sub-stand, stand, and landscape levels. It is important to understand these restoration efforts are focused, not on recreating a past condition, but recovering or restoring ecological attributes, including those associated with compositional and structural diversity, that confer resilience and adaptive capacity to global change (Gann et al. 2019; D'Amato & Palik 2020).

There are approximately 1.5 million hectares of pure *L. tulipifera* forests exist throughout the eastern US, 90% of which are 80 years and younger, with an additional approximately 244,000 ha converted to pure *L. tulipifera* forest annually through natural processes (e.g. mortality of species other than *L. tulipifera* leading to dominance and change in forest type to *L. tulipifera*) or forest management activities (USDA Forest Service, Forest Inventory and Analysis Program 2021). In *L. tulipifera* stands that regenerated during the early part of the twentieth century, thinning treatments were often implemented to increase growth and decrease rotation age of this valuable timber species (Franklin et al. 1990). Although silviculture and objectives associated with forest management have changed in recent decades, there remains a need to understand how previously applied, classical silvicultural treatments focused on timber production affect present-day forest structure and function in efforts to inform restoration treatments. Without the disturbances associated with European colonization, forests in areas of the landscape where *L. tulipifera* now dominates (e.g. cove forests; Simon et al. 2005) would have been characterized by uneven-aged forests comprised of shade-intolerant (e.g. *L. tulipifera*, *Juglans nigra*), mid-tolerant (e.g. *Magnolia acuminata*, *Quercus rubra*), and tolerant (e.g. *Fagus grandifolia*, *Acer saccharum*) (Della-Bianca 1983; Busing 1998) species. Understanding stand dynamics in these previously managed *L. tulipifera* monocultures is critical to developing effective and efficient treatments that restore diversity and function to what were historically highly diverse and complex ecosystems.

In this study, we quantified the density, composition (i.e. species richness), and functional identity of the woody regeneration layer in previously thinned second-growth *L. tulipifera* forests to identify whether legacy effects of forest management, conducted almost 60 years ago, are still evident and influencing current structure, composition, and function and resultant restoration potential. Of the legacy effects tested (Table 1), we hypothesized that, due to its effects on understory light availability (Tsai et al. 2018), density immediately post-thinning (residual basal area [m^2/ha] of the overstory), and/or thinning intensity (the percent of basal area removed), would have a significant influence on the density, composition, and function of the woody understory. Although hypotheses related to the relationship between the woody understory and other legacy effects, including species richness of the overstory pre- and

Table 1. Legacy and environmental variables utilized in model development.

Abbreviation	Definition
Legacy effects	
PostBA	Basal area (m ² /ha) of overstory stems (stems >12.7 cm dbh) post-thinning
BARED	Percent of pre-thinning basal area removed during thinning
PostQMD	Quadratic mean diameter (cm) of overstory trees post-thinning
PostCVDBH	Coefficient of variation of the stem diameter of overstory trees post-thinning
PrePBAOT	Percent of overstory basal area of species other than yellow-poplar pre-thinning
PostPBAOT	Percent of overstory basal area of species other than yellow-poplar post-thinning
PreS	Species richness of the overstory pre-thinning
PostS	Species richness of the overstory post-thinning
AGE	Stand age at the time of thinning
Environmental effects	
SI	Site index (m, base-age 50) of <i>L. tulipifera</i>
SLP	Slope (%)
TASP	Transformed aspect (Beers et al. 1966); varied between 0 (225°) and 2.0 (45°)
ELEV	Elevation (m)

post-thinning, average tree size, and variation of average tree size, along with traditional environmental variables (e.g. slope, aspect, elevation) were developed (Table S1), we expected those attributes to exert relatively less control over the woody understory than post-thinning density and thinning intensity.

Methods

Study Area, Experimental Design, and Data Collection

This study was conducted in the Blue Ridge Mountains section of the Central Appalachian Broadleaf Forest—Coniferous Forest—Meadow Province (Cleland et al. 2007). Study sites were located throughout western North Carolina on the Pisgah and Nantahala National Forests. Climate is temperate and is characterized by cool summers and mild winters. Between 1960 and 1963, 141, 0.1 ha plots were established in *L. tulipifera* stands to examine growth and yield of thinned yellow-poplar stands as a function of site quality, stand age, and density as quantified by basal area (m²/ha) throughout the southern Appalachian Mountains, from northern Georgia to central Virginia (Knoebel et al. 1986). Plots were in even-aged, naturally regenerated stands in which *L. tulipifera* dominated the overstory (stems ≥11.4 cm dbh) basal area.

At the time of plot establishment in the original study, all live overstory trees within each plot were tagged. For all tagged trees, species, dbh (cm), and total height (m) were recorded. Slope (%), aspect (degrees), elevation (m), and site-index (m) (Beck 1962) were also recorded during the initial inventory. Site index is an indirect measure of site productivity and corresponds to the expected height of *L. tulipifera* at 50 years of age. Following the initial inventory, plots, plus a 20 m buffer,

were commercially thinned to a randomly assigned basal area via a low thinning. Stems <11.4 cm were mechanically removed after thinning. Trees that were too poor for merchantable products but needed to be removed to achieve the assigned post-thinning basal area were treated with herbicide to deaden the stem. The herbicide application would have eliminated the potential of these individuals to regenerate via stump sprouts. It is unclear how many trees received this herbicide treatment or whether additional trees, beyond those needed to achieve assigned residual basal area, received chemical application.

In 2018, we revisited 67 of the original 141 plots located in western North Carolina. Post-thinning basal area of these plots ranged from 8.7 to 35.4 m²/ha, with between 7 and 50% of the basal area removed from 63% of the plots and between 50 and 74% removed from 37% of the plots. The woody reproduction layer (stems <12.7 cm dbh) was inventoried using three, 0.002 ha (2.5 m radius) subplots located 8 m from plot center at 0, 120, and 240°. In each subplot, we enumerated stems by species into three size classes: small seedlings (stems <1.4 m); large seedlings (stems ≥1.4 m and <2.54 cm dbh), and saplings (stems ≥2.54 and <12.7 cm dbh).

In each subplot, the tallest stem between 0.5 and 12.7 cm dbh was destructively sampled to determine age structure of the regeneration layer. Only species characteristics of cove hardwood forests were destructively sampled (Table 2). In total, we destructively sampled 97 stems for the age structure analysis. Trees were felled in a manner that left an approximately 5 cm stump. A 3–5 cm cross-section was obtained from the stump of the destructively sampled tree. The samples were taken back to the lab, mounted, and sanded until annual growth rings were visible. Annual rings were counted under a dissecting microscope to estimate year of establishment in one of six time periods (1965 [1960–1969], 1975 [1970–1979], 1985 [1980–1989], 1995 [1990–1999], 2005 [2000–2009], and 2015 [2010–2018]). We did not cross-date the age data, as we were interested in the general trends of the establishment dates of cove hardwood species relative to when the thinning occurred to identify if the thinning resulted in a pulse of recruitment of these more desirable species. Consequently, there is a possibility that missing rings could have produced slight deviations in true establishment age of some of the species sampled (Lorimer et al. 1999).

Data Analysis

Plot-level density (stems/ha), species richness, and functional identity of the advance reproduction layer, by size class, were calculated as the average of the three subplots. Functional identity, defined as the community weighted mean, of each size class was calculated using four traits obtained from the literature and chosen to represent different life history, mechanical, and physiological strategies: shade tolerance (CWMst), wood-specific gravity (CWMwsg; g/cm³) (Miles & Smith 2009), dry seed mass (CWMdsm; log 10 mg) (USDA Plants Database 2011), and maximum height at maturity (CWMhgt; m) (USDA Plants Database 2011). Shade tolerance values were continuous variables between 1 and 5, with lower values signifying a lower shade tolerance (Niinemets & Valladarest 2006).

We examined the effects of legacy (i.e. variables that describe overstory structure and composition immediately

Table 2. Stems/ha \pm standard deviation of species in the small (stems <1.4 m), large (stems \geq 1.4 m and <2.54 cm dbh), and sapling (stems \geq 2.54 and <12.7 cm dbh) size classes. Percent of plots that each species was observed included in parentheses. ^aIndicates species utilized in the destructive sampling for the age structure analysis; ^bIndicates species that typically occupy the canopy in cove hardwood forests.

Species	Small Seedlings	Large Seedlings	Saplings
<i>Acer pennsylvanicum</i> ^a	82.1 \pm 387.7 (13%)	19.8 \pm 131.6 (3%)	11.9 \pm 70.0 (3%)
<i>A. rubrum</i> ^a	5,694.9 \pm 5,558.4 (87%)	209.0 \pm 496.7 (31%)	50.6 \pm 105.0 (19%)
<i>A. saccharum</i> ^{a,b}	66.7 \pm 363.0 (4%)	28.3 \pm 128.2 (6%)	3.0 \pm 22.3 (1%)
<i>Aesculus flava</i> ^b	51.3 \pm 212.3 (10%)	11.3 \pm 60.8 (3%)	32.7 \pm 112.0 (7%)
<i>Albizia julibrissin</i>	2.6 \pm 20.7 (1%)	0.0 \pm 0.0 (0%)	0.0 \pm 0.0 (0%)
<i>Amelanchier arborea</i>	230.8 \pm 492.7 (40%)	11.3 \pm 52.4 (4%)	0.0 \pm 0.0 (0%)
<i>Betula lenta</i> ^{a,b}	210.3 \pm 974.2 (24%)	33.9 \pm 114.9 (10%)	98.2 \pm 158.2 (31%)
<i>Carpinus caroliniana</i> ^a	97.4 \pm 648.1 (4%)	8.5 \pm 48.2 (3%)	17.9 \pm 93.6 (3%)
<i>Carya species</i> ^{a,b}	1,302.6 \pm 1,200.7 (94%)	121.5 \pm 235.4 (25%)	29.8 \pm 84.7 (12%)
<i>Castanea dentata</i>	7.7 \pm 35.2 (4%)	5.7 \pm 43.4 (1%)	0.0 \pm 0.0 (0%)
<i>C. pumilla</i>	2.6 \pm 20.7 (1%)	0.0 \pm 0.0 (0%)	0.0 \pm 0.0 (0%)
<i>Cladrastis kentukea</i> ^b	28.2 \pm 112.5 (7%)	5.7 \pm 30.4 (3%)	8.9 \pm 49.4 (3%)
<i>Cornus alternifolia</i>	15.4 \pm 105.1 (3%)	0.0 \pm 0.0 (0%)	0.0 \pm 0.0 (0%)
<i>C. florida</i> ^a	110.3 \pm 407.5 (24%)	2.8 \pm 21.7 (1%)	62.5 \pm 184.1 (15%)
<i>Diospyros virginiana</i>	0.0 \pm 0.0 (0%)	2.8 \pm 21.7 (1%)	0.0 \pm 0.0 (0%)
<i>Fagus grandifolia</i> ^b	2.6 \pm 20.7 (1%)	0.0 \pm 0.0 (0%)	0.0 \pm 0.0 (0%)
<i>Fraxinus americana</i> ^{a,b}	1,089.7 \pm 1,626.1 (66%)	76.3 \pm 173.2 (24%)	26.8 \pm 82.7 (10%)
<i>Helasia tetraptera</i> ^{a,b}	143.6 \pm 447.7 (12%)	96.1 \pm 292.3 (12%)	107.1 \pm 302.2 (12%)
<i>Ilex ambigua</i>	5.1 \pm 29.0 (3%)	0.0 \pm 0.0 (0%)	0.0 \pm 0.0 (0%)
<i>I. monatana</i>	10.3 \pm 65.1 (3%)	2.8 \pm 21.7 (1%)	0.0 \pm 0.0 (0%)
<i>I. opaca</i>	66.7 \pm 358.2 (10%)	36.7 \pm 161.0 (6%)	11.9 \pm 53.7 (4%)
<i>Juglans nigra</i> ^{a,b}	15.4 \pm 70.5 (6%)	0.0 \pm 0.0 (0%)	0.0 \pm 0.0 (0%)
<i>Liriodendron tulipifera</i> ^{a,b}	520.5 \pm 1,070.6 (60%)	11.3 \pm 52.4 (4%)	11.9 \pm 53.7 (4%)
<i>Magnolia acuminata</i> ^{a,b}	28.2 \pm 86.2 (10%)	2.8 \pm 21.7 (1%)	6.0 \pm 31.2 (3%)
<i>M. fraseri</i> ^{a,b}	38.5 \pm 143.6 (10%)	5.7 \pm 30.4 (3%)	11.9 \pm 43.3 (6%)
<i>Nyssa sylvatica</i>	46.2 \pm 119.7 (16%)	8.5 \pm 48.2 (3%)	0.0 \pm 0.0 (0%)
<i>Oxydendrum arboreum</i>	35.9 \pm 192.1 (7%)	14.1 \pm 56.1 (6%)	17.9 \pm 68.7 (6%)
<i>Pinus strobus</i> ^a	261.5 \pm 1,135.7 (12%)	39.6 \pm 136.1 (10%)	20.8 \pm 78.3 (6%)
<i>Prunus serotina</i> ^b	371.8 \pm 653.4 (45%)	17.0 \pm 67.1 (6%)	0.0 \pm 0.0 (0%)
<i>Quercus alba</i> ^{a,b}	702.6 \pm 1,574.9 (51%)	19.8 \pm 62.6 (9%)	0.0 \pm 0.0 (0%)
<i>Q. coccinea</i> ^a	159.0 \pm 498.6 (28%)	2.8 \pm 21.7 (1%)	0.0 \pm 0.0 (0%)
<i>Q. falcata</i>	35.9 \pm 194.3 (4%)	0.0 \pm 0.0 (0%)	0.0 \pm 0.0 (0%)
<i>Q. montana</i> ^a	189.7 \pm 1,038.7 (21%)	11.3 \pm 68.3 (3%)	6.0 \pm 44.5 (1%)
<i>Q. rubra</i> ^{a,b}	1,294.9 \pm 1,141.8 (85%)	59.3 \pm 171.7 (19%)	8.9 \pm 49.4 (3%)
<i>Q. velutina</i> ^a	400.0 \pm 661.3 (51%)	14.1 \pm 71.2 (4%)	0.0 \pm 0.0 (0%)
<i>Robinia pseudoacacia</i> ^{a,b}	92.3 \pm 226.4 (22%)	14.1 \pm 56.1 (6%)	11.9 \pm 53.7 (4%)
<i>Sassafras albidum</i>	830.8 \pm 2,085.5 (33%)	79.1 \pm 238.4 (15%)	14.9 \pm 48.0 (7%)
<i>Tilia heterophylla</i> ^{a,b}	59.0 \pm 279.9 (7%)	19.8 \pm 93.3 (6%)	11.9 \pm 62.4 (3%)
<i>Tsuga canadensis</i> ^{a,b}	66.7 \pm 212.1 (15%)	36.7 \pm 138.6 (7%)	71.4 \pm 252.0 (10%)
Total	14,369 \pm 9,383	1,028 \pm 844	655 \pm 377

pre- and post-thinning) and environmental variables (Tables 1 & 3) on the structure (i.e. density), composition, and functional identity of the advance reproduction layer using multiple linear regression. We employ the term “legacy effect” to denote the long-term response, which in this study was approximately 60 years, to the thinning treatment. Pre-thinning legacy effects examined were limited to those associated with pre-thinning composition, including richness of the overstory prior to thinning (PreS) and the percent of the overstory basal area represented by species other than *L. tulipifera* (PrePBAOT), and were used as a surrogate for possible propagule sources in undisturbed forest surrounding the 0.1 ha (plus buffer) plots. We used the least absolute shrinking and selection operator (LASSO) (Tibshirani 1996) to select possible explanatory variables (Proc GLMSELECT, SAS 9.4). In GLMSELECT, both dependent

and independent variables are automatically standardized to their Z-score. LASSO differs from traditional variable selection methods in that all variables are included in the model and then a penalty factor is applied to the coefficients. This penalization places a restriction on the magnitude of the coefficients. Variables that do not contribute to response variables are shrunk more than important variables, with those contributing minimally or not at all removed from the model. A 10-fold-cross-validation determined the optimal LASSO penalization parameter, with 80% of the data used for model fitting and 20% for model testing. The LASSO method has the additional benefit of tolerating multicollinearity better than traditional selection methods (Dormann et al. 2013).

Following variable selection via LASSO, we fitted general linear models (GLMs) with the selected variables. Variables in

Table 3. Explanatory variable for the 67 study plots. Variables defined in Table 1.

Variable	Minimum	Mean	Maximum	Standard Deviation
Legacy effects				
PostBA	8.7	19.0	35.4	7.3
BARED	7.0	37.2	74.2	18.2
PostQMD	16.0	33.3	51.4	8.6
PostCVDBH	9.9	19.5	36.9	6.1
PrePBAOT	0.0	15.1	44.4	10.0
PostPBAOT	0.0	4.1	28.4	7.6
AGE	18	47	76	15
PreS	1.0	5.2	10.0	2.0
PostS	1.0	1.7	6.0	1.2
Environmental effects				
SI	22.9	32.1	39.0	3.5
SLP	1.0	30.7	61.0	14.1
TASP	0.00	1.56	2.0	0.49
ELEV	631	874	1,141	124

the fitted equations were considered informative if the 85% confidence interval of their parameter estimate excluded zero (Arnold 2010). Similar to the LASSO procedures, GLMs were fitted using Z-scores of all variables, as this allowed us to determine the relative importance of each predictor variable (Hu et al. 2018). Assumptions of normality and homogenous variance were assessed visually, with density of both the small and large seedling layers square-root transformed. Model performance of GLMs was measured in terms of r^2 . A priori hypotheses related to the influence of legacy and environmental variables on characteristics of the woody understory are presented in Table S1.

Results

Across all plots, 38, 31, and 23 species were observed in the small seedling, large seedling, and sapling layers, respectively (Table 2). In the small seedling layer, the most frequently observed species was *Carya* (94% of all plots) followed by *Acer rubrum* (87%) and *Quercus rubra* (85%), with 3% of plots lacking small seedlings. In the large seedling layer, 12% of plots lacked seedlings, and *A. rubrum* (31%) was the most frequently observed species followed by *Carya* and *Fraxinus americana* (both 24%) and *Q. rubra* (19%). A total of 16% of plots lacked saplings. In plots with saplings *Betula lenta* was the most frequently documented species (31%) followed by *A. rubrum* (19%) and *Cornus florida* (15%). Across size classes and plots, species typical of old-growth cove forests were relatively sparse, including *Acer saccharum*, *Aesculus flava*, and *Fagus grandifolia*.

Density

Across plots, average tree regeneration density and associated variability of the woody understory decreased as size class increased (Fig. 1). The number and influence of legacy effects included in final models describing density increased from the

small seedling to sapling layer. In the seedling layer, density decreased as SLP increased, whereas the relationship between density and PreS was positive (Table S2). In the sapling layer, a combination of legacy and environmental factors described 20% of the variability in density (Table S4). SLP was the most influential of the variables selected and had a negative relationship with sapling density. Informative legacy effects included PostQMD and PostPBAOT. As PostPBAOT increased, sapling density increased, while the relationship with PostQMD was negative. Although legacy effects were included in the final models for large seedling density, model performance was low ($r^2 \leq 0.05$; Table S3).

Richness

Species richness of the woody understory and associated variability decreased as size class increased, averaging 9.0, 3.2, and 2.4 in the small seedling, large seedling, and sapling layers, respectively (Fig. 1). Across size classes, legacy effects alone or in combination with environmental variables were selected in the models describing species richness, with variability described by models ranging from 13% in the sapling layer to 19% in the small and large seedling layers (Tables S2–S4). For small seedlings, richness was best described by the negative effect of TASP and positive effect of PrePBAOT (Table S2). Similarly, PrePBAOT exerted a positive influence on richness of the large seedling layer, while richness decreased as PostQMD increased (Table S3). In the sapling layer, legacy effects of PreS and PostQMD exhibited a positive and negative relationship with richness, respectively (Table S4).

Functional Identity

Shade tolerance (CWMst) of the woody understory increased as size class increased (Fig. 1). Across size classes, legacy effects alone or in combination with environmental factors described CWMst of the woody understory. Model performance for all size classes was relatively high ($r^2 \geq 0.25$). For small seedlings, the most parsimonious model contained only legacy effects, with PostQMD having a negative influence on CWMst, while the influence of PreS was positive (Table S2). CWMst of the large seedling layer decreased as both SLP and PostQMD increased (Table S3). In the sapling layer, the most parsimonious model demonstrated that SLP was, by far, the most important variable affecting CWMst. Legacy effects, however, were also included, with CWMst inversely related to AGE and positively related to PrePBAOT (Table S4).

Across all plots, average CWMwsg was greater in the small seedling than large seedling and sapling layers (Fig. 1). Although legacy effects alone or in combination with environmental factors were included in the final models describing CWMwsg of the small and large seedling layers, model performance was low ($r^2 \leq 0.08$) (Tables S2 & S3). For saplings, 19% of variability in CWMwsg was explained by AGE and SLP, both of which positively affected CWMwsg (Table S4).

Average CWMdsm was negatively related with size class, while the variability in CWMdsm increased from the small

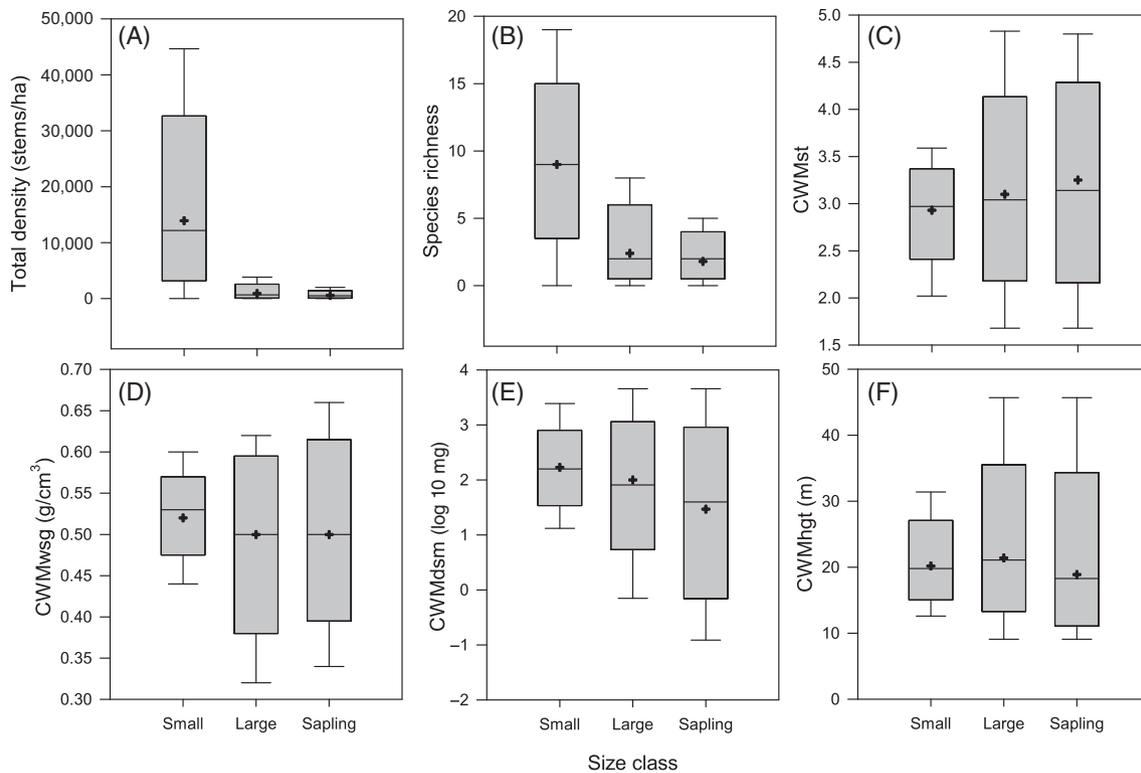


Figure 1. Box plots displaying range of characteristics of the small seedling (stems <1.4 m), large seedling (stems ≥ 1.4 and <2.54 cm dbh), and sapling (stems ≥ 2.54 and <12.7 cm dbh), including density (stems/ha, panel A), species richness (panel B), and community weighted mean shade tolerance (CWMst, panel C), wood specific gravity (CWMwsg [g/cm^3], panel D), dry seed mass (CWMdsm [log 10 mg], panel E), and height at maturity (CWMhgt (m), panel F). Values represent the minimum, lower quartile, median, upper quartile, and maximum. Mean values denoted by +.

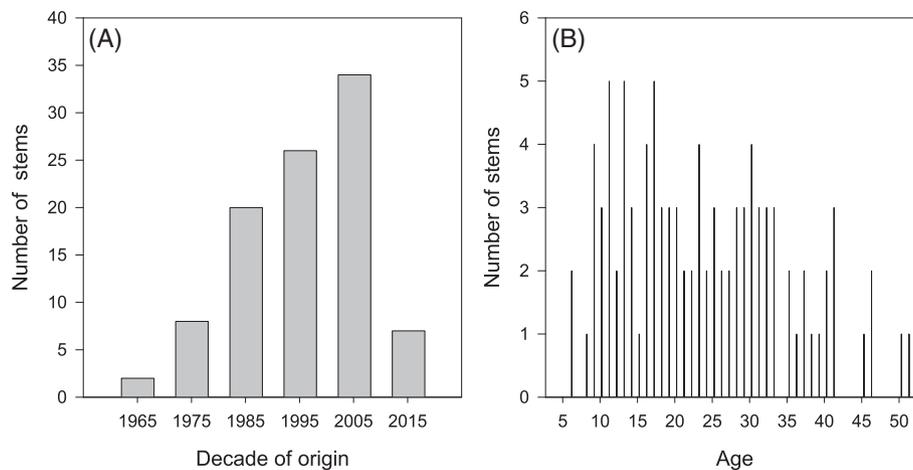


Figure 2. Number of destructively sampled stems by establishment date (years on x-axis represent mid-point year) (A) and age (B).

seedling to sapling layers (Fig. 1). Neither environmental nor legacy effects were included in the models describing CWMdsm of the small seedling layer (Table S2). Although model performance was low ($r^2 = 0.10$), TASP and PostQMD were included as informative parameters in the final model describing CWMdsm of the large seedling layer (Table S3). Model performance for CWMdsm in the sapling layer was highest

($r^2 = 0.20$), with CWMdsm best explained by a combination of SI and AGE, which were positively and negatively related to CWMdsm, respectively (Table S4).

Height at maturity (CWMhgt) averaged 20.3, 21.4, and 18.9 m in the small seedling, large seedling, and sapling layers, respectively (Fig. 1). The most parsimonious model describing CWMhgt of the small seedling layer ($r^2 = 0.26$) contained only

legacy effects (Table S2), while final models for the large seedling ($r^2 = 0.23$) and sapling ($r^2 = 0.28$) layers contained both legacy and environmental effects (Tables S3 & S4). For small seedlings, CWMhgt decreased as PreS, PostCVDBH, and AGE increased. For large seedlings and saplings, the most parsimonious model demonstrated that ELEV, which was inversely related to CWMhgt, was, by far, the most influential of the variables examined. Legacy effects considered informative included PrePBAOT in the large seedling layer, which was positively related to CWMhgt, and PreS in the sapling layer, which was positively related to CWMhgt of the sapling layer.

Age Structure

Across all subplots, approximately 50% of all destructively sampled individuals were 22 years old or younger (Fig. 2). The two most recently established stems were *L. tulipifera* and *Magnolia fraseri*, both 6 years old. The oldest individual was a *F. americana* that was 51 years. Only eight species were older than 30 years of age, including *A. pensylvanicum*, *Aesculus flava*, *B. lenta*, *Carya*, *F. americana*, *Helasia tetraptera*, *Robinia pseudoacacia*, and *Tsuga canadensis*. The most frequently observed species in the greater than or equal to 30-year age class were *F. americana* (six individuals) and *Carya* species (eight individuals).

Discussion

To identify potential restoration treatments that could increase species diversity in previously managed *L. tulipifera* monocultures, we quantified how both legacy and environmental variables affect the current structure, composition, and function of the woody regeneration layer. We found the woody understory of these second-growth and previously thinned *L. tulipifera* forests was well-developed and diverse, with 39 tree species observed throughout the understory, with the small seedling layer most diverse (38 species) followed by the large seedling (32 species) and sapling (23 species) layers. The total number of species present in the woody understory (stems <12.7 cm dbh) second-growth pure *L. tulipifera* cove forests, which was comprised of species from across the shade tolerance spectrum, exceeded that in old-growth cove forests (Busing 1994). In the large seedling and sapling layers, which represent the individuals most likely to recruit following canopy disturbance (Loftis 1990a), however, density and richness of species that typically characterize cove forests (e.g. *A. saccharum*, *A. flava*, *F. grandifolia*, *Tilia heterophylla*) was substantially lower than in old-growth cove forests (Busing 1998).

Although information is sparse, in second-growth *L. tulipifera* forests that lack a history of management, understories are dominated by shade-tolerant species, such as *H. tetraptera*, *A. rubum*, *T. canadensis*, and *A. saccharum*, all of which were present in the large seedling and sapling layers in the thinned *L. tulipifera* stands used in this study (Lafon 2004). Interestingly, the large seedling and sapling *B. lenta* and *Carya* that we documented, which are species mid-tolerant of shade, are either less abundant or absent from

comparable unmanaged second-growth *L. tulipifera* forests (Clebsch & Busing 1989; Lafon 2004). Establishment and recruitment of *B. lenta* responds positively to canopy disturbance, with studies showing that once established, *B. lenta* can survive long periods of suppression (Yanai et al. 1998; Royo et al. 2019). Similarly, the limited amount of data available specific to *Carya* suggests seedling and sapling-sized *Carya* positively respond to thinning and can persist in the understory >40 years (Lefland et al. 2018).

Modeling characteristics of the woody understory in deciduous broadleaved forests have proven difficult given myriad factors that influence seedling establishment and recruitment, including seed production and dispersal coupled with seedbed conditions (Willis et al. 2016), seed predation (Royo & Carson 2008), herbivory (Boerner & Brinkman 1996), climate (Fisichelli et al. 2014), topographic and edaphic conditions (Frey et al. 2007), and competition (Knight et al. 2008). Although herbivory has long-lasting effects on composition and structure of developing vegetation (Royo & Carson 2022), *Odocoileus virginianus* density across our study area averages <10 individuals/km² (North Carolina Wildlife Resources Commission 2020), suggesting that at least currently, browse pressure has is negligible. Model performance varied from a low of $r^2 = 0.05$ to $r^2 = 0.40$, suggesting for many of the understory metrics we examined, the limited number of legacy effects and environmental variables we examined were not the primary drivers of the woody understory structure, diversity, and function. Despite the variability in model performance, we found support for our hypothesis that past forest management activities, which in the case of this study were thinning treatments that removed between 7 and 74% of the pre-thinning basal area, still influence the woody understory decades after the cessation of management in *L. tulipifera* forests of the southeastern United States. Contemporary structure and composition of these *L. tulipifera* stands are related to the past thinning treatments, with heavily thinned stands maintaining lower basal area than less heavily thinned stands (Keyser 2010, 2012). For 14 of the 18 models developed, legacy effects were considered informative and described the density, composition, and functional identity of the small seedling, large seedling, and sapling size classes, with the relative influence of legacy versus environmental effects varying by metric and size class.

Contrary to our expectation, post-thinning basal area (RBA) and/or percent of basal area removed during thinning (BARED) were not the primary legacy effects influencing the woody understory. Instead, legacy effects associated with species composition of the overstory before and/or after thinning (PreS, PostS, PrePBAOT, PostPBAOT) along with metrics that describe average stem diameter after thinning (PostQMD), age at the time of thinning (AGE), and variation in stem diameter after thinning (PostCVDBH) were more influential than metrics associated with RBA or BARED. Although surprising, absolute measures of density often have limited influence on attributes of the advance reproduction layer (Eerikäinen et al. 2007). For example, in mixed *Pinus-Quercus* forests in Spain, the composition and density of the seedling layer was independent of overstory density, with variability best described by the percent of the overstory basal area represented by *Pinus* species (López-Marcos et al. 2020). In

contrast, although 11 years post-thinning Dodson et al. (2014) documented no differences in seedling (stems <1.4 m tall) density among *Pseudotsuga menziesii* stands thinned to different densities, sapling (stems ≥ 1.4 m and <5 cm dbh) density in unthinned stands was lower than in stands thinned to moderate (200 stems/ha) and low densities (100 stems/ha). Larsen et al. (2007) demonstrated that although density and size distribution of advance reproduction decreased with increasing overstory density in *Quercus* forests of the eastern United States, the magnitude of this trend varied, suggesting modeled relationships do not reflect the range of density-size-species combinations possible.

For some of the attributes, including density, richness, and CWMwsg of the small seedling layer, CWMseed and CWMhgt of the large seedling layer, and density, CWMst, and CWMhgt of the sapling layer, environmental variables were more influential than legacy effects. The influence of environmental variables on the characteristics of the woody understory was generally as expected. For example, as SLP increased, density of the small seedling layer and CWMst of the large seedling layer decreased. Similarly, ELEV, while only an informative parameter for a few understory attributes, had an overall negative effect on variables such as richness of the large seedling layer and CWMhgt of both the large seedling and sapling layers. In mountainous areas, slope, elevation, and aspect interact to influence various microclimate variables, including light intensity, soil moisture, air temperature, and evapotranspiration, all of which have been shown to influence and exert control over structure and composition, including in the forest understory (Small & McCarthy 2005).

The age structure of the regeneration layer suggests establishment of sampled cove species occurred on a relatively continual basis since the thinning. Of the 97 stems sampled, over 60% established after 1990. Although we expected to see a pulse of recruitment from the regeneration layer during the immediate years following thinning due to the increase in growing space and resources (e.g. light) that accompanies thinning, it is possible that the sampling method employed was insufficient at capturing the establishment patterns immediately post-thinning, as stems that established in the immediate years post-thinning could have recruited into size classes beyond those sampled in the regeneration layer (>12.7 cm dbh). The presence of older, (≥ 30 year), mid-tolerant species, including *Carya* and *F. americana*, suggests the understory light environment in these monocultures that lack structural diversity could be sufficient to facilitate the recruitment of cove hardwood species that range from mid-tolerant to tolerant of shade.

From a restoration perspective, the characteristics of the large seedling and sapling layers are most relevant, as they represent the individuals likely to recruit into progressively higher canopy positions following partial or complete overstory disturbance unless management is conducted that reduces their abundance. As species richness of the overstory increased, richness of the sapling layer increased. This finding is consistent with studies that demonstrate a positive relationship between overstory and understory diversity and underscore the importance of local seed source availability for enhancing diversity in the woody understory of monoculture forests (Willis et al. 2016; Kremer & Bauhus 2020).

For example, as the proportion of deciduous broadleaved species increased in *Picea* plantations, the diversity of the lower canopy stratum almost doubled (Jobidon et al. 2004). Similarly, Willis et al. (2016) found interspecific differences in shade tolerance was a poor predictor of seedling density in northern US broadleaved forests. Instead, the authors reported that proximity to seed source was an important and significant predictor of presence and abundance for both shade-tolerant (e.g. *T. canadensis*) and shade intolerant species (e.g. *Prunus serotina*).

Maintaining species diversity in the overstory after thinning translated into increases in CWMhgt as well as CWMst in the large seedling and/or sapling layers. In mixed-*Quercus* forests, which are juxtaposed to *L. tulipifera* cove forests, canopies are a mix of shade-intolerant and mid-tolerant species (Evans et al. 2019). Frequent disturbances in mixed-*Quercus* forests, including fire, historically limited the establishment and recruitment of shade-tolerant species into canopy positions and maintained the mid-tolerant species composition (Nowacki & Abrams 2008). In comparison, in old-growth cove forests, shade-tolerant species are a primary component of the overstory (Barden 1980), as fire was not a significant factor controlling species composition and stand dynamics in cove forests (Flatley et al. 2015). Maintaining species diversity in the overstory of these *L. tulipifera* stands likely conserved seed sources for light-to-heavy-seeded tree species, which, according to the age structure of the advance reproduction pool, established continuously in the understory of these thinned *L. tulipifera* stands, thereby contributing to the composition and function of the woody understory.

It is apparent from this study that conserving species diversity and associated ecological memory as a key component of forest management activities can have positive long-term effects on composition and function of the woody understory and increase restoration potential. Whether diversity of these thinned *L. tulipifera* cove forests can be restored through future forest management activities or whether these *L. tulipifera* monocultures, due to past use, represent an ecosystem state that is an alternative to the diverse and complex reference cove condition is unknown (Webster et al. 2018). However, the diverse woody understory (large seedling and sapling layers, in particular) suggests restoration of diversity through future commercial and non-commercial forest management activities (e.g. variable density thinning release treatments) or via natural stand processes (e.g. gap-phase mortality) may be possible, as regeneration in temperate deciduous broadleaved forests is largely dependent on advance reproduction present prior to reductions in overstory density (Vickers et al. 2019). If species currently in the large seedling and sapling layers survive and develop further, they will be poised to continue recruitment into canopy positions following perturbation to the *L. tulipifera* canopy, thereby restoring species and structural diversity, although restoring all the desirable cove species appears unlikely given their distribution across plots. From a silvicultural standpoint, activities that promote the further development of desirable cove species may be enhanced through activities that free growing space around existing large seedlings and saplings. These activities could include targeted mechanical or chemical cleanings,

crop-tree release, or the removal of subcanopy stems to increase light availability in the forest understory (Loftis 1990b), all of which are non-commercial treatments that confer an added cost but may accelerate restoration of these monocultures.

In contrast, *L. tulipifera* stands without a sufficient density of desirable cove species in the large seedling or sapling layers may continue to exist as a monoculture (an alternate state), as future gaps caused by natural processes or exogenous disturbance may be quickly colonized by seed-origin *L. tulipifera* (Lafon 2004). In this scenario, the stand would remain dominated by *L. tulipifera*, however, the resultant structure could be more complex and, over time, possibly develop into a multi-aged forest where *L. tulipifera* occupies substantial growing space across age cohorts (Buckner & McCracken 1978). Although increasing species diversity in *L. tulipifera* forests with a depauperate understory may be unattainable, these stands could be managed for structural diversity, including conducting forest management activities, such as thinning, that are focused on accelerating the development of old-growth structural characteristics and increasing resilience to drought (Palik et al. 2020).

The design of this study falls short of the most robust and statistically rigorous before-after-control-impact experimental design. Instead, this study is observational, as we did not have quantitative information that described the advance reproduction pool before the thinning or throughout the time when the understory would have been experiencing rapid changes in response to the thinning. Consequently, the data we present represent a snap-shot in time and do not address temporal changes in understory structure and composition that occurs regardless of thinning or other treatments (Busing 1993). We also lack data from adjacent unmanaged *L. tulipifera* stands of similar age and site quality. As such, we are unable to assess or make conclusions beyond the response of the woody understory to the range of conditions created during the thinning treatments tested in these particular study sites. These shortcomings in our design confound the effects we attribute to thinning with temporal variation in the woody understory. Extrapolation of results beyond the study site and limited study design is not recommended. Despite these limitations, our results may be used to develop hypotheses related to restoring diversity to these as well as other even-aged monocultures that can subsequently be tested using a rigorous experimental design capable of making more definitive conclusions and recommendations. The large sample size ($n = 67$) and range of conditions incorporated into the study suggest results are likely robust, even if just point-in-time descriptions, and provide information that is absent from the literature regarding the long-term influence that past management has on contemporary structure, composition, and function and resultant restoration potential of these *L. tulipifera* forests. Despite almost 60 years of recovery, forest stands used in this study appear to continue to be impacted by previous management activities. Research conducted in previously managed forests should consider the need to account for the role that legacy effects may have on results, especially from manipulative studies, where the vegetation response could be confounded by past management and land use even after a seemingly long period without disturbance.

Acknowledgments

This study was funded by the USDA, Forest Service, Southern Research Station. The authors extend their gratitude to J. Adams, E. Watson, B. Benz, O. Reed, R. Dickson, T. Roof, M. Wood, and D. Stone for assisting with data collection. The authors thank M. Castle for providing a comprehensive statistical review. Three anonymous reviewers provided comments that improved the content and clarity of the manuscript. This paper was written and prepared by a U.S. Government employee on official time; and therefore, it is in the public domain and not subject to copyright. This research was supported the USDA Forest Service. The findings and conclusions in this publication are those of the author(s) and should not be construed to represent an official USDA, Forest Service, or U.S. Government determination or policy.

LITERATURE CITED

- Arnold TW (2010) Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74: 1175–1178. <https://doi.org/10.1111/j.1937-2817.2010.tb01236.x>
- Ayres HB, Ashe WW (1905) The southern Appalachian forests. US Geological Survey. Professional Paper No. 37. Series H. Forestry, 12
- Barden LS (1980) Tree replacement in a cove hardwood forest of the southern Appalachians. *Oikos* 35:16–19. <https://doi.org/10.2307/3544722>
- Beck DW (1962) Yellow-poplar site index curves. USDA for. Serv. Res. Note SE-180. Southeastern Forest Experiment Station, Asheville, North Carolina
- Beers TW, Dress PE, Wensel LD (1966) Notes and observations: aspect transformation in site productivity research. *Journal of Forestry* 64:691–692. <https://doi.org/10.1093/jof/64.10.691>
- Boerner REJ, Brinkman JA (1996) Ten years of tree seedling establishment and mortality in an Ohio deciduous forest complex. *Bulletin of the Torrey Botanical Club* 123:309–317. <https://doi.org/10.2307/2996780>
- Brown CD, Liu J, Yan G, Johnstone JF (2015) Disentangling legacy effects from environmental filters of postfire assembly of boreal tree assemblages. *Ecology* 96:3023–3032. <https://doi.org/10.1890/14-2302.1>
- Buckner E, McCracken W (1978) Yellow-poplar: a component of climax forests. *Journal of Forestry* 76:421–423. <https://doi.org/10.1093/jof/76.7.421>
- Busing RT (1993) Three decades of change at Albright cove, Tennessee. *Castanea* 58:231–242. [https://doi.org/10.2179/0008-7475\(2005\)070\[0115:TDOOAS\]2.0.CO;2](https://doi.org/10.2179/0008-7475(2005)070[0115:TDOOAS]2.0.CO;2)
- Busing RT (1994) Canopy cover and tree regeneration in old-growth cove forests of the Appalachian Mountains. *Vegetatio* 115:19–27. <https://doi.org/10.1007/BF00119383>
- Busing RT (1998) Composition, structure and diversity of cove forest stands in the Great Smoky Mountains: a patch dynamics perspective. *Journal of Vegetation Science* 9:881–890. <https://doi.org/10.2307/3237053>
- Canuel CM, Thiffault N, Hoepfing MK, Farrell JCG (2019) Legacy effects of pre-commercial thinning on the natural regeneration of next rotation balsam fir stands in eastern Canada. *Silva Fennica* 53:10209. <https://doi.org/10.14214/sf.10209>
- Clebsch EEC, Busing RT (1989) Secondary succession, gap dynamics, and community structure in a southern Appalachian cove forest. *Ecology* 70: 728–735. <https://doi.org/10.2307/1940223>
- Cleland DT, Freeouf JA, Keys JE, Nowacki GJ, Carpenter CA, McNab WH (2007) Ecological subregions: sections and subsections for the conterminous United States. General Technical Report WO-76D [Map on CD-ROM] (A.M. Sloan, cartographer). U.S. Department of Agriculture, Forest Service, presentation scale 1:3,500,000; colored, Washington D.C.
- D'Amato AW, Jokela EJ, O'Hara KL, Long JN (2018) Silviculture in the United States: an amazing period of change over the past 30 years. *Journal of Forestry* 116:55–67. <https://doi.org/10.5849/JOF-2016-035>

- D'Amato AW, Palik BJ (2020) Building on the last "new" thing: exploring the compatibility of ecological and adaptation silviculture. *Canadian Journal of Forest Research* 51:172–180. <https://doi.org/10.1139/cjfr-2020-0306>
- Della-Bianca L (1983) Sixty years of stand development in a southern Appalachian cove-hardwood stand. *Forest Ecology and Management* 5:229–241. [https://doi.org/10.1016/0378-1127\(83\)90074-9](https://doi.org/10.1016/0378-1127(83)90074-9)
- Devine WD, Harrington CA (2009) Western redcedar response to precommercial thinning and fertilization through 25 years posttreatment. *Canadian Journal of Forest Research* 39:619–629. <https://doi.org/10.1139/X08-199>
- Dodson EK, Burton JL, Puettmann KJ (2014) Multiscale controls on natural regeneration dynamics after partial overstory removal in Douglas-fir forests in western Oregon, U.S.A. *Forest Science* 60:953–961. <https://doi.org/10.5849/forsci.13-011>
- Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, et al. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36:27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
- Dyer JM (2010) Land-use legacies in a central Appalachian forest: differential response of trees and herbs to historic agricultural practices. *Applied Vegetation Science* 13:195–206. <https://doi.org/10.1111/j.1654-109X.2009.01061.x>
- Eerikäinen K, Miina J, Valkonen D (2007) Models for the regeneration establishment and the development of established seedlings in uneven-aged, Norway spruce dominated forest stands of southern Finland. *Forest Ecology and Management* 242:444–461. <https://doi.org/10.1016/j.foreco.2007.01.078>
- Elliott KJ, Swank WT (2008) Long-term changes in forest composition and diversity following early logging (1919–1923) and the decline of American chestnut (*Castanea dentata*). *Plant Ecology* 197:155–172. <https://doi.org/10.1007/s11258-007-9352-3>
- Elliott KJ, Vose JM (2011) The contribution of the Coweeta hydrologic laboratory to developing an understanding of long-term (1934–2008) changes in managed and unmanaged forests. *Forest Ecology and Management* 261:900–910. <https://doi.org/10.1016/j.foreco.2010.03.010>
- Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, Ford CR, et al. (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3:479–486. [https://doi.org/10.1890/1540-9295\(2005\)003\[0479:LOFSCF\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2)
- Evans JP, Oldfield CA, Reid JL (2019) Differential resistance to tree species loss between two dominant communities in a resilient southeastern landscape. *Natural Areas Journal* 39:182–188. <https://doi.org/10.3375/043.039.0205>
- Fischelli N, Wright A, Rice K, Mau A, Buschena C, Reich PB (2014) First-year seedlings and climate change: species-specific responses of 15 north American tree species. *Oikos* 123:13351–11340. <https://doi.org/10.1111/oik.01349>
- Flatley WT, Lafon CW, Grissino-Mayer HD, LaForest LB (2015) Changing fire regimes and old-growth forest succession along a topographic gradient in the Great Smoky Mountains. *Forest Ecology and Management* 350:96–106. <https://doi.org/10.1016/j.foreco.2015.04.024>
- Flinn KM, Marks PL (2007) Agricultural legacies in forest environments: tree communities, soil properties, and light availability. *Ecological Applications* 17:452–463. <https://doi.org/10.1890/05-1963>
- Franklin C, Hazel DW, Rucker RR, Kronrad GD (1990) Thinning and harvesting regimes for yellow-poplar. *Southern Journal of Applied Forestry* 14:101–103. <https://doi.org/10.1093/sjaf/14.3.101>
- Frey BR, Ashton MS, McKenna JJ, Ellum D, Finkral A (2007) Topographic and temporal patterns in tree seedling establishment, growth, and survival among masting species of southern New England mixed-deciduous forests. *Forest Ecology and Management* 245:54–63. <https://doi.org/10.1016/j.foreco.2007.03.069>
- Gann GD, McDonald T, Walder B, Aronson J, Nelson CR, Jonson J, et al. (2019) International principles and standards for the practice of ecological restoration. Second edition. *Restoration Ecology* 27:S1–S46. <https://doi.org/10.1111/rec.13035>
- Garbarino M, Weisberg PJ (2020) Land-use legacies and forest change. *Landscape Ecology* 35:2641–2644. <https://doi.org/10.1007/s10980-020-01143-0>
- Hu Z, Michaletz ST, Johnson DJ, McDowell NG, Huang Z, Zhou X, Xu C (2018) Traits drive global wood decomposition rates more than climate. *Global Change Biology* 24:5259–5269. <https://doi.org/10.1111/gcb.14357>
- James JA, Kern CC, Miesel JR (2018) Legacy effects of prescribed fire season and frequency on soil properties in a *Pinus resinosa* forest in northern Minnesota. *Forest Ecology and Management* 415-416:47–57. <https://doi.org/10.1016/j.foreco.2018.01.021>
- Jenkins CN, Van Houtan KS, Pimm SL, Sexton JO (2015) US protected lands mismatch biodiversity priorities. *Proceedings of the National Academy of Sciences* 112:5081–5086. <https://doi.org/10.1073/pnas.1418034112>
- Jobidon R, Guillaume C, Thiffault N (2004) Plant species diversity and composition along an experimental gradient of northern hardwood abundance in *Picea mariana* plantations. *Forest Ecology and Management* 198:209–221. <https://doi.org/10.1016/j.foreco.2004.04.020>
- Kalisz PJ (1986) Soil properties of steep Appalachian old fields. *Ecology* 67:1011–1023. <https://doi.org/10.2307/1939824>
- Keyser TL (2010) Thinning and site quality influence aboveground tree carbon stocks in yellow-poplar forests of the southern Appalachians. *Canadian Journal of Forest Research* 40:659–667. <https://doi.org/10.1139/X10-013>
- Keyser TL (2012) Patterns of growth dominance in thinned yellow-poplar stands in the southern Appalachian Mountains, U.S.A. *Canadian Journal of Forest Research* 42:406–412. <https://doi.org/10.1139/x11-196>
- Keyser TL, Brown PM (2014) Long-term response of yellow-poplar to thinning in the southern Appalachian Mountains. *Forest Ecology and Management* 312:148–153. <https://doi.org/10.1016/j.foreco.2013.10.010>
- Keyser TL, Loftis DL (2015) Stump sprouting of 19 upland hardwood species 1 year following initiation of a shelterwood with reserves silvicultural system in the southern Appalachian Mountains, U.S.A. *New Forests* 45:449–464. <https://doi.org/10.1007/s11056-015-9470-z>
- Keyser TL, Roof T, Adams JL, Simon D, Warburton G (2012) Effects of prescribed fire on the buried seed bank in mixed-hardwood forests of the southern Appalachian Mountains. *Southeastern Naturalist* 11:669–688. <https://doi.org/10.1656/058.011.0407>
- Knight KS, Oleskyn J, Jagodzinski AM, Reich PB, Kasprovic M (2008) Overstory tree species regulate colonization by native and exotic plants: a source of positive relationships between understory diversity and invisibility. *Diversity and Distributions* 14:666–675. <https://doi.org/10.1111/j.1472-4642.2008.00468.x>
- Knoebel BR, Burkhardt HE, Beck DE (1986) A growth and yield model for thinned stands of yellow-poplar. *Forest Science Monograph* 27
- Kremer KN, Bauhus J (2020) Drivers of native species regeneration in the process of restoring natural forests from mono-specific, even-aged tree plantations: a quantitative review. *Restoration Ecology* 28:1074–1086. <https://doi.org/10.1111/rec.13247>
- Lafon CW (2004) Stand dynamics of a yellow-poplar (*Liriodendron tulipifera* L.) forest in the Appalachian Mountains, Virginia, U.S.A. *Dendrochronologia* 22:43–52. <https://doi.org/10.1016/j.dendro.2004.09.002>
- Larsen DR, Metzger MA, Johnson PS (2007) Oak regeneration and overstory density in the Missouri Ozarks. *Canadian Journal of Forest Research* 27:868–875. <https://doi.org/10.1139/x97-010>
- Leftland AB, Duguid MC, Morin RS, Ashton MS (2018) The demographics and regeneration dynamic of hickory in second-growth temperate forest. *Forest Ecology and Management* 419-420:187–196. <https://doi.org/10.1016/j.foreco.2018.03.027>
- Loftis DL (1990a) Predicting postharvest performance of advance red oak reproduction in the southern Appalachians. *Forest Science* 36:908–916. <https://doi.org/10.1093/forests/36.4.908>
- Loftis DL (1990b) A shelterwood method for regenerating red oak in the southern Appalachians. *Forest Science* 36:917–929. <https://doi.org/10.1093/forests/36.4.917>
- López-Marcos D, Tirrión MB, Bravo F, Martínez-Ruiz C (2020) Can mixed pine forests conserve understory richness by improving the establishment of understory species typical of native oak forests. *Annals of Forest Science* 77:15. <https://doi.org/10.1007/s13595-020-0919-7>

- Lorimer CG, Dahir SE, Singer MT (1999) Frequency of partial and missing rings in *Acer saccharum* in relation to canopy position and growth rate. *Plant Ecology* 143:189–202. <https://doi.org/10.1023/A:1009847819158>
- Mausolf K, Wilm P, Härdtle W, Jansen K, Schuldt B, Sturm K, von Oheimb G, Hertel D, Lesuchner C, Fichtner A (2018) Higher drought sensitivity of radial growth of European beech in managed than in unmanaged forests. *Science of the Total Environment* 642:1201–1208. <https://doi.org/10.1016/j.scitotenv.2018.06.065>
- Messier C, Puettmann KJ, Coates KD (2013) Managing forests as complex adaptive systems: building resilience to the challenge of global change. Routledge, New York, NY
- Miles PD, Smith WB (2009) Specific gravity and other properties of wood and bark for 156 tree species found in North America. USDA Forest Service Research Note NRS-3, Newtown Square, Pennsylvania
- Mitchell RM, Bakker JD, Vincent JB, Davies GM (2017) Relative importance of abiotic, biotic, and disturbance drivers of plant community structure in the sagebrush steppe. *Ecological Applications* 27:756–768. <https://doi.org/10.1002/eap.1479>
- Muurinen L, Oksanen J, Vanha-Majamaa I, Virtanen R (2019) Legacy effects of logging on boreal forest understorey vegetation communities in decadal time scales in northern Finland. *Forest Ecology and Management* 436:11–20. <https://doi.org/10.1016/j.foreco.2018.12.048>
- Niinemets U, Valladares F (2006) Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecological Monographs* 76:521–547. [https://doi.org/10.1890/0012-9615\(2006\)076\[0521:TTSDAW\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2)
- North Carolina Wildlife Resources Commission (2020) North Carolina White-tailed deer density. Raleigh, NC. https://www.ncwildlife.org/Portals/0/Hunting/Documents/Deer2020_Deer_Density_Maps.pdf (accessed 27 Feb 2022)
- Nowacki GJ, Abrams MD (2008) The demise of fire and “mesophication” of forests in the eastern United States. *Bioscience* 58:123–138. <https://doi.org/10.1641/B580207>
- Palik BJ, D’Amato AW, Franklin JF, Johnson KN (2020) Ecological silviculture: foundations and applications. Waveland Press, Long Grove, IL
- Perring MP, Bernhardt-Römermann M, Baeten L, Midolo G, Blondell H, Depauw L, et al. (2018) Global environmental change effects on plant community composition trajectories depend upon management legacies. *Global Change Biology* 24:1722–1740. <https://doi.org/10.1111/gcb.14030>
- Puettmann KJ, Coates KD, Messier CC (2009) A critique of Silviculture: managing for complexity. Cambridge University Press, Cambridge, United Kingdom
- Royo AA, Carson WP (2006) On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Canadian Journal of Forest Research* 36:1345–1362. <https://doi.org/10.1139/x06-025>
- Royo AA, Carson WP (2008) Direct and indirect effects of a dense understory on tree seedling recruitment in temperate forests: habitat-mediated predation versus competition. *Canadian Journal of Forest Research* 38:1634–1645. <https://doi.org/10.1139/X07-247>
- Royo AA, Carson WP (2022) Stasis in forest regeneration following deer exclusion and understory gap creation: a ten-year experiment. *Ecological Applications* e2569. <https://doi.org/10.1002/eap.2569>
- Royo AA, Pinchot CC, Stanovick JS, Stout SL (2019) Timing is not everything: assessing the efficacy of pre- versus post-harvest herbicide applications in mitigating the burgeoning birch phenomenon in regenerating hardwood stands. *Forests* 10:324. <https://doi.org/10.3390/f10040324>
- Simon SA, Collins TK, Kauffman GL, McNab WH, Ulrey CJ (2005) Ecological-zones in the southern Appalachians: first approximation. USDA Forest Service Research Paper SRS-41, Asheville, North Carolina
- Small CJ, McCarthy BC (2005) Relationship of understory diversity to soil nitrogen, topographic variation, and stand age in an eastern oak forest, U.S.A. *Forest Ecology and Management* 217:229–243. <https://doi.org/10.1016/j.foreco.2005.06.004>
- Swaim JT, Dey DC, Saunders MR, Weigel DR, Thornton CD, Kabrick JM, Jenkins MA (2018) Overstory species response to clearcut harvest across environmental gradients in hardwood forests. *Forest Ecology and Management* 428:66–80. <https://doi.org/10.1016/j.foreco.2018.06.028>
- Tibshirani R (1996) Regression shrinkage and selection via the lasso. *Journal of the Royal Statistical Society Series B* 58:267–288. <https://doi.org/10.1111/j.2517-6161.1996.tb02080.x>
- Tsai HC, Chiang JM, McEwan RW, Lin TC (2018) Decadal effects of thinning on understory light environments and plant community structure in a subtropical forest. *Ecosphere* 9:e02464. <https://doi.org/10.1002/ecs2.2464>
- USDA Forest Service, Forest Inventory and Analysis Program. 2021. Forest Inventory EVALIDator web-application Version 1.8.0.01. St. Paul, MN: U.S. Department of Agriculture, Forest Service, Northern Research Station <http://apps.fs.usda.gov/Evalidator/evalidator.jsp> (accessed 27 Feb 2022)
- USDA Plants Database. 2011. The PLANTS database. National Plant Data Team <http://plants.usda.gov> (accessed 6 Mar 2018)
- Vellend M, Verheyen K, Flinn KM, Jacquemyn H, Kolb A, van Calster H, et al. (2007) Homogenization of forest communities and weakening of species-environment relationships via agricultural land use. *Journal of Ecology* 95:565–573. <https://doi.org/10.1111/j.1365-2745.2007.01233.x>
- Vickers LA, McWilliams WH, Knapp BO, D’Amato AW, Dey DC, Dickinson YL, et al. (2019) Are current seedling demographics poised to regenerate northern US forests? *Journal of Forestry* 117:592–612. <https://doi.org/10.1093/jofore/fvz046>
- Webster CR, Dickinson YL, Burton JI, Frelich LE, Jenkins MA, Kern CC, Raymond P, Saunders MR, Walters MB, Willis JL (2018) Promoting and maintaining diversity in contemporary hardwood forests: confronting contemporary drivers of change and the loss of ecological memory. *Forest Ecology and Management* 421:98–108. <https://doi.org/10.1016/j.foreco.2018.01.010>
- Whitaker RH (1956) Vegetation of the Great Smoky Mountains. *Ecological Monographs* 26:1–80. <https://doi.org/10.2307/1943577>
- Willis JL, Walters MB, Farinosi E (2016) Local seed source availability limits young seedling populations for some species more than other factors in northern hardwood forests. *Forest Science* 62:440–448. <https://doi.org/10.5849/forsci.15-143>
- Wulder MA, White JC, Andrew ME, Seitz NE, Coops NC (2009) Forest fragmentation, structure, and age characteristics as a legacy of forest management. *Forest Ecology and Management* 258:1938–1949. <https://doi.org/10.1016/j.foreco.2009.07.041>
- Yanai RD, Twery MJ, Stout SL (1998) Woody understory response to changes in overstory density: thinning in Alleghany hardwoods. *Forest Ecology and Management* 102:45–60. [https://doi.org/10.1016/S0378-1127\(97\)00117-5](https://doi.org/10.1016/S0378-1127(97)00117-5)

Supporting Information

The following information may be found in the online version of this article:

Table S1. Hypothesized influence (positive (+), negative (–)) of legacy and environmental variables.

Table S2. Small seedling layer (stems <1.4 m) models.

Table S3. Large seedling layer (stems ≥1.4 and <2.54 cm dbh) models.

Table S4. Sapling layer (stems ≥2.54 and <12.7 cm dbh) models.