Check for updates

Received: 30 January 2020 | Revised: 6 July 2020 | Accepted: 4 October 2020

DOI: 10.1111/avsc.12538

RESEARCH ARTICLE

Applied Vegetation Science IAVS

Response of taxonomic and functional diversity to disturbance severity in temperate hardwood forests

Tara L. Keyser[1] | Beverly S. Collins[2] | Cathryn H. Greenberg[1]

[1]U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC, USA

[2]Department of Biology, Western Carolina University, Cullowhee, NC, USA

Correspondence
Tara L. Keyser, USDA Forest Service, Southern Research Station, 1577 Brevard Road, Asheville, NC 28806, USA.
Email: tara.keyser@usda.gov

Funding information
This study was funded by the USDA Forest Service, Southern Research Station — Upland Hardwood Ecology and Management Research Work Unit.

Co-ordinating Editor: José Paruelo

Abstract

Aims: Quantify changes in taxonomic and functional diversity (FD) and identity to determine if responses to a disturbance severity gradient follow a "colonization/competition" hypothesis: diversity will (a) increase with disturbance severity as more open conditions favor species with traits linked to colonization; and (b) become more similar between regeneration and overstorey layers as environmental filtering favors species with traits linked to increasing competition for light.

Location: North Carolina, USA.

Methods: Taxonomic (richness [S], evenness [E], and Shannon diversity [H']) and functional diversity (richness [F_{Ric}], evenness [F_{Eve}], and dispersion [F_{Dis}]) and identities were calculated for regeneration and overstorey before and after restoration treatments: control (CONT); "undesirable" subcanopy stems removed via herbicide (HERB); repeated burning (RRXF); and timber harvest followed by burning (HARV).

Results: In the overstorey, HARV affected taxonomic and FD. In HARV, S and H' were lower than in other treatments. At high levels of species richness, F_{Eve} was lower in HARV than in HERB and RRXF. Similarly, at high levels of species richness, F_{Dis} was greater in HARV than other treatments. In the regeneration layer, taxonomic and FD did not differ across treatments during any of the post-treatment years. In the regeneration stratum, HARV increased the means of traits associated with rapid post-disturbance establishment, carbon capture, and maximum height. Greater dissimilarity in composition between the overstorey and regeneration suggests stronger treatment effects on regeneration in HARV than less severe treatments.

Conclusion: Patterns do not support the hypothesis that taxonomic diversity increases with disturbance severity or decreases with time after disturbance in the regeneration layer. Of the restoration treatments tested in this study, only HARV affected aspects of functional identity of the regeneration stratum; even so, FD remained unchanged. In mixed *Quercus* forests, functional identity rather than taxonomic or FD may provide insight into nuanced effects of restoration treatments on ecosystem function.

© 2020 International Association for Vegetation Science.
This article has been contributed to by US Government employees and their work is in the public domain in the USA.

KEYWORDS
disturbance, environmental filtering, fire, persistence niche, plant functional traits, Quercus–Carya forest, restoration

1 | INTRODUCTION

Functional diversity has been used to quantify effects of disturbance and disturbance severity on vegetation diversity, observed patterns of community assembly, and ecosystem processes in natural and managed boreal, temperate, and tropical forests (Decocq *et al*., 2004; Schamp & Aarseen, 2009; Hollingsworth *et al*., 2013; Mouillot *et al*., 2013; Sabatini *et al*., 2014). As it incorporates potential redundancy in traits among species (Ruiz-Jaen & Potvin, 2011) and is a mechanistic description of a species' niche or function (Cadotte *et al*., 2011), functional diversity complements taxonomic diversity and can bridge the gap that links biological diversity with ecological processes such as disturbance (McGill *et al*., 2006). The use of complementary taxonomic and functional diversity metrics to analyze and quantify effects of natural disturbance and forest management activities on diversity, including over gradients of disturbance severities and environmental conditions, is becoming more prevalent (Decocq *et al*., 2004; Biswas & Mallik, 2010; Baraloto *et al*., 2012; Bell *et al*., 2014; Kern *et al*., 2014; Sabatini *et al*., 2014; Curzon *et al*., 2017).

Both taxonomic and functional diversity vary over environmental gradients and through forest succession after disturbance. In general, species and traits associated with post-disturbance "colonization" or fast growth and low tolerance for competition (e.g., low shade tolerance, seed mass, wood density, and greater maximum height) increase with disturbance severity, while species and traits associated with "competition" or slower growth and higher tolerance (e.g., greater shade tolerance, seed mass, and wood density) are favored with less disturbance and over time in undisturbed forest (Curzon *et al*., 2017; Wilfahrt, 2018). For example, the degree of post-disturbance decreases in shade tolerance, seed mass, and wood density, and increases in maximum height and drought tolerance, were related to disturbance severity in forests of eastern North America (Wilfahrt, 2018). As forest succession advances, competition and increased strength of environmental filtering on traits associated with light and nutrient acquisition can lead to convergence toward a subset of species (Craven *et al*., 2018), and thus lower trait and taxonomic diversity.

In the eastern United States, *Quercus–Carya* forests cover mesic to sub-xeric sites over a range of elevations. These forests originated after widespread clearcut-logging and high-grading, often followed by burning, around the turn of the 20th century, and are now "mid-successional." A gradual decline in successful regeneration and recruitment of foundation *Quercus* species (Hanberry & Nowacki, 2016) and other associated species that are mid-tolerant of shade (e.g., *Carya*) has led to forest restoration activities, including timber harvesting and burning, designed to promote establishment and recruitment of *Quercus* species across its geographic range (Rodríguez-Trejo & Myers, 2010; Dey, 2014). Although studies have quantified the effects of these restoration activities on the absolute and relative abundance of target species (Hutchinson *et al*., 2005; Brose, 2010; Keyser *et al*., 2017) and taxonomic diversity (Elliott *et al*., 1999; Schweitzer & Dey, 2011), little information exists regarding impacts on complementary metrics that describe taxonomic and functional diversity in combination with functional identity of the tree community. This limits the ability to extrapolate the effects of these restoration practices on biological diversity to ecological function (Scharenbroch *et al*., 2012).

We quantified changes in taxonomic and functional diversity, as well as the individual species and trait responses (taxonomic and functional identity) that account for diversity changes, between regeneration and overstorey strata to determine if responses to a gradient of disturbance severity created by three different *Quercus* restoration practices vary in relation to position within the forest canopy (Bell *et al*., 2014). Although the primary goal of these restoration practices is to promote regeneration and recruitment of *Quercus* and *Carya* species over time, secondary goals include conserving the suite of traits that contribute to ecosystem functioning, including continued production of fleshy fruit and hard mast, creating more open canopy conditions, and reducing the abundance of later-successional species that have been found to dramatically change nutrient cycling, water quantity, and forest floor flammability (Greenberg *et al*., 2007; Alexander & Arthur, 2010; Alexander & Arthur, 2014; Caldwell *et al*., 2016; Kreye *et al*., 2018).

Building on recent research (Sabatini *et al*., 2014; Curzon *et al*., 2017; Craven *et al*., 2018; Wilfahrt, 2018), we hypothesized that taxonomic and functional diversity follow the "colonization/competition" hypothesis. That is, diversity of regeneration and dissimilarity between canopy and regeneration strata will: (a) increase with disturbance severity as more open conditions (i.e., reduced canopy cover) favor early-successional species with traits linked to colonization (low seed mass and wood density, greater maximum height) (e.g., *Liriodendron tulipifera*); and (b) decrease in the regeneration layer with time after disturbance as environmental filtering favors later-successional species with traits linked to increasing competition for light (high seed mass and wood density) (e.g., *Quercus* and *Carya* species). We further hypothesize that dominant traits, assessed by community-weighted means (i.e., functional identity), of the regeneration layer will shift towards those associated with early-successional communities as disturbance severity increases. To address the restoration objective of increasing *Quercus* regeneration in these forests, we also investigated whether mid-tolerant traits and species increased with the restoration treatments.

2 | METHODS

2.1 | Study site description

The research was conducted on the North Carolina Wildlife Resource Commission's 1,333 ha Cold Mountain Game Lands (CMGL) in Haywood County, North Carolina (35.40° N, 82.93° W), within the Blue Ridge physiographic province of the southern Appalachian Mountains. Elevation ranges from 900 m to 1,500 m and slope ranges from 35% to 55%. Climate is characterized by short, mild winters, with daily temperatures averaging 3°C in January to 24°C in July. Annual precipitation is approximately 1,300 mm, evenly distributed throughout the year. Forest cover is predominantly montane *Quercus–Carya*, which has a canopy dominated by a mixture of *Quercus alba* L., *Quercus rubra* L., *Quercus velutina* Lam., *Carya* species (*Carya glabra* (Mill.) Sweet,*Carya tomentosa* (Lam.) Nutt., *Carya cordiformis* (Wangenh.) K. Koch),*Liriodendron tulipifera* L., and *Betula lenta* L., and subcanopy dominated by shade-tolerant species, including *Acer rubrum* L., *Acer pensylvanicum L.* L., *Oxydendrum arboretum* (L.) DC., *Halesia tetraptera Ellis*, *Cornus florida* L., and *Nyssa sylvatica* Marsh.

2.2 | Experimental design

In a completely randomized design, four replications (i.e., stands) of four restoration treatments were assigned to sixteen undisturbed, mature (>80 year) stands located throughout CMGL and comprised primarily of *Quercus–Carya* forest cover types. Treatments comprised a disturbance severity gradient as measured by proportional reduction in total stems per hectare of the forest canopy (stems ≥ 5.0 cm dbh) caused by the treatments: untreated control (CONT), herbicide (HERB), repeated low-severity prescribed burning (RRXF), and partial timber harvest followed by low-severity prescribed fire (HARV). Nine years after treatment, stems per hectare were reduced by an average 19%, 54%, 32%, and 80% in CONT, HERB, RRXF, and HARV, respectively (Table 1). Average quadratic mean diameter of live trees between YR0 and YR9 increased by 2.4 cm, 9.8 cm, 4.7 cm, and 9.1 cm in the CONT, HERB, RRXF, and HARV treatments, respectively. Although CONT received no active management treatment, the small change in average diameter of live trees suggests the decrease in density was the result of background density-dependent mortality of primarily small, suppressed trees that occurs in fully to overstocked forest stand (Zeide, 1987).

TABLE 1 Mean stems per hectare ≥5 cm dbh in YR0 (pre-treatment) and YR9 along with proportional reduction in stems per hectare between YR0 and YR9 in control (CONT), herbicide (HERB), repeated prescribed fire (RRXF), and timber harvest and burn (HARV) treatments

	CONT	HERB	RRXF[a]	HARV[b]
YR0	752 (69)	687 (88)	750 (41)	493 (107)
YR9	603 (45)	312 (27)	510 (38)	85 (9.2)
% Change	−19%[A]	−54%[B]	−32%[C]	−80%[D]

Note: Uppercase letters denote significant differences in proportional reduction in stems per hectare (α = 0.10).

[a]YR9 is nine growing seasons from the initial prescribed fire; four growing seasons following the second prescribed fire.

[b]YR9 is nine growing seasons after the timber harvest; three (two HARV units) or four (two HARV units) growing seasons following the prescribed fire.

The HERB treatment removed subcanopy stems other than *Quercus* and *Carya* < 25.0 cm dbh via herbicide (Garlon® 3A, active ingredient triclopyr, Dow Chemical Company, Indianapolis, IN, USA) in an effort to reduce stem density in the subcanopy, increase light levels in the forest understorey, and promote growth and development of species mid-tolerant of shade, primarily *Quercus* and *Carya*, in the tree seedling layer (Loftis, 1990). Herbicide was applied using the stem injection method (Kochenderfer *et al*., 2012) in September 2008, prior to leaf fall and after pre-treatment data collection.

For the RRXF treatment, low-severity prescribed burns were conducted in an effort to decrease stem density in the subcanopy, increase understorey light levels, and promote development of species mid-tolerant of shade in the tree regeneration layer. Due to the lack of favorable fire weather (high humidity, frequent rain, and/or atmospheric conditions unsuitable for smoke dispersal), all four replicates could not be treated during the same year. Two stands were burned 25 February 2009 and again on 2 April 2014. The remaining two replicates were burned 1 April 2010 and again on 18 March 2015. Burns were conducted in the dormant season prior to bud swell.

In the HARV treatment, a commercial timber harvest was conducted. Trees were marked to leave between 9.2 and 11.5 m^2/ha residual basal area of dominant, co-dominant, or strong intermediate stems (Oliver & Larson, 1996), with the goal of the harvest to reduce basal area to levels associated with an open *Quercus* woodland (Hanberry & Abrams, 2018) and release all seedlings in the forest understorey. A low-severity dormant season prescribed burn was conducted four to six years post-harvest (exact timing was dependent on favorable burning conditions), to kill pyrophobic species (e.g., *Acer rubrum*, *Nyssa sylvatica*) and favor pyrophilic species (e.g., *Quercus* and *Carya*) in the tree regeneration layer (Brose, 2010). Due to the lack of favorable logging weather, characterized by extremely saturated soils, all four replicates could not be harvested during the same year. Logging operations were completed in two HARV stands before the beginning of the 2010 growing season, with the prescribed burn conducted on 18 March 2016. Harvest operations in the remaining two replicates were completed before the start of the 2011 growing season, with the prescribed burn conducted on 18 March 2015.

2.3 | Data collection

Prior to treatment (spring/summer 2008), three 0.05 ha plots were systematically located in a grid to sample vegetation characteristics in each of the sixteen 5-ha (~225 m × ~ 225 m) stands (treatment

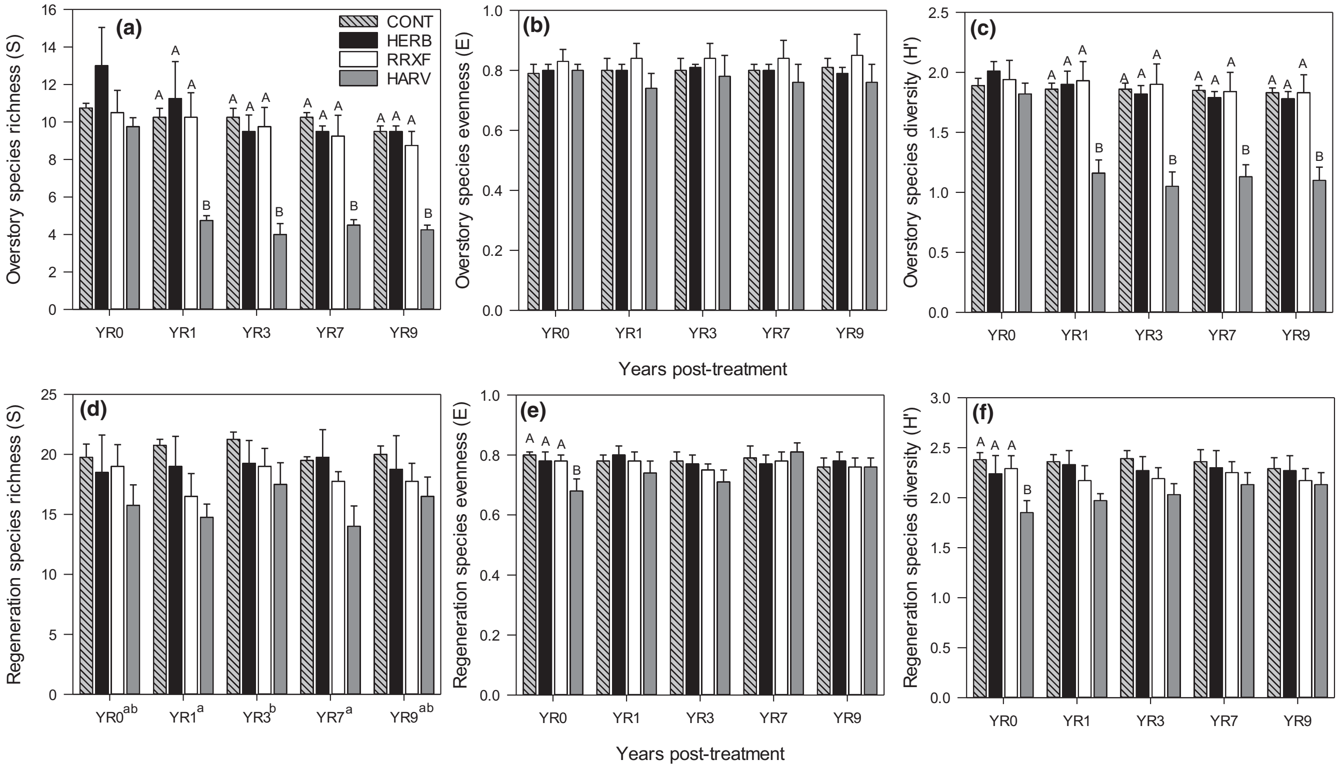

FIGURE 1 Taxonomic diversity (richness, evenness, diversity) in the overstorey (stems ≥5 cm dbh) (panels a, b, c) and regeneration (stems <5 cm dbh) (panels d, e, f) layers in treatments representing a gradient of disturbance severity. Values represent the mean ± one standard error. Within a given year, means with the same letter do not differ significantly among treatments. Lowercase letters that do not differ indicate no significant differences averaged across treatments

areas). Species and stem diameter at 1.4 m above groundline (i.e., diameter at breast height [dbh]) of all canopy trees (stems ≥ 25.0 cm dbh) were recorded and individuals were tagged in the 0.05-ha plot. Species and dbh of subcanopy trees (stems ≥ 5.0 cm and < 25.0 cm dbh) were inventoried and individuals tagged within a 0.01-ha subplot concentrically nested within the larger, 0.05-ha plot. Together, canopy and subcanopy stems represent the overstorey stratum. Woody regeneration (stems < 5.0 cm dbh) was tallied, by species, in two 0.004-ha circular regeneration subplots originating 8 m from the center of the 0.05-ha plot and concentrically nested 0.01-ha plot center at bearings of 45° and 225°. *Carya* individuals were identified to only the genus level.

2.4 | Data analysis

Taxonomic diversity of the regeneration and overstorey layers was quantified as species richness (*S*), Pielou's Evenness (*E*) (Pielou, 1966), and Shannon diversity (H′) (Shannon & Weaver, 1949). Functional diversity indices of the regeneration and overstorey layers were calculated using five functional traits gleaned from the literature and chosen to represent different life history, mechanical, and physiological strategies (Appendix S1): wood specific gravity (WSG), specific leaf area (SLA), leaf nitrogen concentration (LEAFN), maximum height at maturity (HGT), and dry seed mass (DSM). With the exception of DSM, all trait variables were normally distributed (Shapiro–Wilk test, $p > 0.05$). Dry seed mass, however, was log10-transformed to meet assumptions of normality and reduce skewness of DSM values within the community (Májeková *et al*., 2016).

We calculated functional richness (F_{Ric}), which provides the unweighted range of trait values in the plot (Boersma *et al*., 2016); functional evenness (F_{Eve}), which provides information on how evenly or regularly the trait space is occupied; and functional dispersion (F_{Dis}), which describes the mean distance of each species from the abundance-weighted centroid of all species separately for the selected traits. Both F_{Eve} and F_{Dis} incorporate abundance, whereas F_{Ric} is calculated without regard to abundance. Although there are a variety of functional diversity metrics available (Clark *et al*., 2012), F_{Ric}, F_{Eve} and F_{Dis} were selected due to their complementarity and relationship to community assembly rules (e.g., niche/environmental filtering, random assembly, etc.) (Mouchet *et al*., 2010). Functional diversity indices are often correlated and redundant; however, F_{Eve} and F_{Dis}, in particular, provide distinctive information related to the community and are not related to species richness (Laliberté & Legendre, 2010; Clark, *et al*., 2012; Spasojevic & Suding, 2012; Cooke *et al*., 2019). In addition to multitrait indices, functional identity, which represents the community-weighted mean of each unstandardized trait value, was calculated for the regeneration and overstorey layers. Abundance (stems/ha per species) was used to calculate taxonomic and functional diversity indices (F_{Eve} and F_{Dis}) as well as functional identity for the regeneration layer while basal area (m^2/ha per species) was used as the weighting factor for the overstorey layer. Functional traits were standardized prior to calculating F_{Ric}, F_{Eve}, and F_{Dis} (Villéger *et al.*, 2008). Functional diversity indices and functional identity were calculated using the package "FD" (Laliberté & Legendre, 2010) for the R statistical package (R Development Core Team, 2012).

A repeated-measures linear mixed-effects ANOVA was used to quantify the effects of treatment (CONT, RRXF, HERB, HARV) and time (pre-treatment, one, three, seven, nine years post-treatment) on taxonomic diversity and functional identity. Because of the relationship between species richness and various functional diversity metrics (Schleuter *et al.*, 2010; Biswas & Mallik, 2011; Karadimou *et al.*, 2016), we used a repeated-measures linear mixed-effects ANCOVA as per Biswas and Mallik (2011), with species richness of the respective layer at each sampling period as a covariate, to analyze the effects of treatment and time on F_{Ric}, F_{Eve}, and F_{Dis}. When species richness was significant in the overstorey layer, we analyzed treatment differences at species richness values equal to 6.1, 9, and 11.9 (mean minus one standard deviation, mean, and mean plus one standard deviation). When species richness was a significant covariate in the regeneration layer, we analyzed treatment differences at species richness values of 14.7, 18.3, and 21.9.

All analyses were conducted using the MIXED procedure in SAS v. 9.4 (SAS Institute INC., Cary, NC, USA). A spatial power covariance structure was used to account for repeated measures of unequal intervals on experimental units. Treatment and time were considered fixed effects while unit (treatment) was a random effect. The Kenward– Roger approximation was used to calculate denominator degrees of freedom. When necessary, transformations were used to approximate normality and achieve homogeneous variance; specifically, we used a power transformation for overstorey H' and a square-root transformation for overstorey F_{Ric}, F_{Dis}, community-weighted mean values of SLA and HGT (CWM_{SLA} and CWM_{HGT}). Treatment effects, when part of a significant interaction (treatment × year), were examined using the SLICE option. Post-hoc comparisons were adjusted using a False Discovery Rate (Benjamini & Hockberg, 1995).

We used PERMANOVA in PcORD v7 (MJM software, Corvallis, USA) to determine whether differences in composition between the overstorey and regeneration layers were evident nine years post-treatment and if so, whether the differences increase with the disturbance severity gradient. Dissimilarity was based on the Lance–Williams measure. Also, within treatments, we used PERMANOVA to determine whether differences between overstorey and regeneration decrease over time. Because of the large variability in treatment effects across the relatively large experimental units (e.g., variability in fire effects and efficacy of herbicide treatment), all analyses were considered significant when $p < 0.10$.

2.5 | Nomenclature

Nomenclature follows the USDA Plants Database (http://plants.usda.gov/java/; accessed on 5 March 2018).

3 | RESULTS

3.1 | Taxonomic diversity

In the overstorey layer, we observed a significant interaction between treatment and year on *S* (Appendix S2). In the overstorey, *S* was significantly affected by treatment in YR1 ($p < 0.0001$), YR3 ($p < 0.0001$), YR7 ($p < 0.0001$), and YR9 ($p < 0.0001$). In YR1, *S* was significantly reduced from an average 10.6 in CONT, HERB, and RRXF to 4.8 in HARV (Figure 1). Significant differences in *S* among HARV and other treatments remained through YR9. Evenness was not affected by treatment or year, and averaged (standard error) 0.80 (0.01) throughout the study. We documented a significant interaction between treatment and year on overstorey H', with differences among treatments observed in YR1 ($p = 0.0006$), YR3 ($p = 0.0004$), YR7 ($p = 0.0013$), and YR9 ($p = 0.0012$). Overall, H' was lower in HARV relative to CONT, HERB, and RRXF through YR9.

In the woody regeneration layer, *S* was affected by year, with no significant effects of treatment detected (Appendix S3; Figure 1).

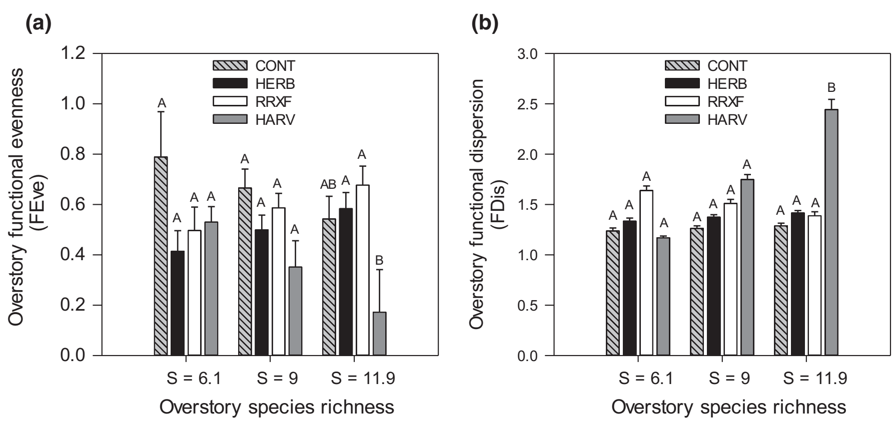

FIGURE 2 Functional evenness (F_{Eve}) (panel a) and dispersion (F_{Dis}) (panel b) of the overstorey layer (stems ≥5 cm dbh) at overstorey species richness values of $S = 6.1$, $S = 9$, and $S = 11.9$. Values represent the lsmean, averaged across years, ± one standard error. Within a given year, lsmeans with the same uppercase letters do not differ significantly among treatments

There was a significant interaction between treatment and year on *E*, with significant differences restricted to YR0 ($p = 0.0376$). In YR0, *E* was significantly lower in HARV than in the CONT and other management treatments. The interaction between treatment and year significantly affected H', with significant differences detected in YR0 ($p = 0.0442$). In YR0, H' in HARV was significantly lower than in CONT and other management treatments.

3.2 | Functional diversity

In the overstorey layer, year, species richness, and the interaction between species richness and year significantly affected F_{Ric} (Appendix S2). Although the positive effect of species richness on F_{Ric} was lower in the years following treatment, richness always exerted a positive influence on F_{Ric}. Treatment along with the interaction between species richness and treatment significantly influenced F_{Eve}. Only at high levels of species richness did F_{Eve} differ among treatments, with HARV possessing significantly lower F_{Eve} than the other management treatments (Figure 2). F_{Dis} was significantly influenced by treatment, year, species richness, and the interaction between species richness and treatment. Similar to F_{Eve}, significant differences among treatments were restricted to high levels of species richness. For example, at species richness values of 6 and 9, no significant differences in F_{Dis} were detected, whereas at a species richness value of 11.9, F_{Dis} in HARV was significantly greater than CONT and other management treatments (Figure 2).

In the regeneration layer, species richness was significantly and positively related to F_{Ric}. After controlling for the effects of richness, we found treatment and year interacted to significantly influence F_{Ric} (Appendix S3); however, no significant differences among treatments were detected within any given year. Functional evenness was unaffected by species richness, year, or treatment, and averaged 0.49 (0.01) over the course of the study. Functional dispersion was positively related to species richness, and was significantly affected by the interaction between treatment and year. Treatment effects on F_{Dis} were restricted to YR0 ($p = 0.0688$), with F_{Dis} in HARV (1.07) significantly lower than in CONT (1.35), HERB (1.39), and RRXF (1.43).

3.3 | Functional identity

In the overstorey layer, although there were significant effects of the interaction between treatment and year on CWM_{SLA}, and $CWM_{DSM,}$ no significant treatment differences were detected (Appendix S2; Table 2). Neither treatment nor year significant affected CWM_{WSG}, CWM_{LEAFN}, and CWM_{HGT}.

In the regeneration layer, the interaction between treatment and year significantly affected CWM_{WSG}, but no significant differences among treatments within any given year were observed

TABLE 2 Functional identity of the overstorey layer (stems ≥ 5 cm dbh), defined by community-weighted mean values of wood specific gravity (WSG; g/cm^3), specific leaf area (SLA; cm^2/g), leaf nitrogen concentration (LEAFN; %), maximum height at maturity (HGT; m), and dry seed mass (log) (DSM; mg) for pre- (YR0), one (YR1), three (YR3), seven (YR7), and nine (YR9) years post-treatment

WSG	CONT	HERB	RRXF	HARV
YR0 (pre)	0.57 (0.01)	0.53 (0.02)	0.54 (0.01)	0.53 (0.01)
YR1	0.56 (0.01)	0.53 (0.02)	0.54 (0.01)	0.55 (0.01)
YR3	0.56 (0.01)	0.53 (0.02)	0.54 (0.01)	0.55 (0.01)
YR7	0.56 (0.01)	0.53 (0.03)	0.54 (0.02)	0.54 (0.01)
YR9	0.56 (0.01)	0.53 (0.03)	0.54 (0.02)	0.54 (0.01)
AVG	0.56 (0.00)	0.53 (0.01)	0.54 (0.01)	0.54 (0.00)
SLA				
YR0 (pre)	148.5 (2.2)	155.5 (6.2)	157.0 (8.5)	160.1 (6.1)
YR1	148.3 (2.2)	154.1 (6.3)	156.9 (8.5)	140.2 (1.4)
YR3	148.3 (2.2)	153.1 (6.6)	157.0 (8.8)	138.3 (3.4)
YR7	148.5 (2.2)	154.0 (7.0)	155.5 (9.6)	143.3 (3.1)
YR9	148.1 (1.9)	154.0 (7.0)	155.6 (9.6)	142.9 (3.2)
AVG	148.4 (0.8)	154.2 (2.6)	156.4 (3.6)	145.0 (2.3)
LEAFN				
YR0 (pre)	1.87 (0.04)	1.96 (0.08)	1.98 (0.06)	2.14 (0.03)
YR1	1.86 (0.04)	1.96 (0.08)	1.97 (0.07)	2.06 (0.11)
YR3	1.86 (0.03)	1.95 (0.09)	1.98 (0.06)	2.07 (0.12)
YR7	1.88 (0.01)	1.96 (0.08)	1.96 (0.06)	2.08 (0.11)
YR9	1.87 (0.01)	1.96 (0.08)	1.95 (0.06)	2.08 (0.11)
AVG	1.86 (0.01)	1.96 (0.03)	1.97 (0.02)	2.08 (0.04)
HGT				
YR0 (pre)	23.4 (0.5)	26.1 (1.9)	24.0 (0.4)	25.7 (1.1)
YR1	23.6 (0.5)	26.6 (2.0)	23.9 (0.4)	24.2 (0.5)
YR3	23.6 (0.5)	26.8 (2.0)	24.0 (0.4)	24.3 (0.4)
YR7	23.6 (0.5)	26.9 (1.9)	24.2 (0.4)	24.3 (0.2)
YR9	23.6 (0.5)	27.0 (1.9)	24.3 (0.4)	24.3 (0.2)
AVG	23.6 (0.2)	26.7 (0.8)	24.1 (0.2)	24.6 (0.3)
DSM				
YR0 (pre)	2.84 (0.14)	2.48 (0.22)	2.57 (0.17)	2.37 (0.15)
YR1	2.85 (0.14)	2.51 (0.22)	2.58 (0.17)	2.98 (0.21)
YR3	2.85 (0.14)	2.61 (0.26)	2.58 (0.17)	3.02 (0.25)
YR7	2.86 (0.12)	2.61 (0.27)	2.64 (0.18)	2.99 (0.19)
YR9	2.87 (0.12)	2.62 (0.27)	2.64 (0.19)	3.02 (0.19)
AVG	2.86 (0.05)	2.57 (0.10)	2.60 (0.07)	2.87 (0.10)

Note: Values represent mean (standard error). AVG, average; CONT, untreated control; HERB, herbicide; RRXF, repeated prescribed fire; HARV, timber harvest and burn.

(Appendix S3). Neither treatment nor year significantly affected $CWM_{SLA,}$ which averaged 162.7 cm^2/g over the course of the study. The main effect of treatment and year significantly influenced CWM_{LEAFN}, which was greater in HARV than in CONT and other management treatments (Table 3). CWM_{HGT} of the regeneration layer was significantly affected by the interaction between treatment and year, with a significant difference among treatments observed in YR0 (p = 0.0959), in YR3 (p = 0.0010), YR7 (p = 0.0060), and YR9 (p = 0.0058). By YR9, CWM_{HGT} of the regeneration layer was, on average, 3.3 m greater in HARV than in CONT, HERB, and RRXF, while CWM_{HGT} in RRXF was, on average, 1.9 m shorter than in CONT and HERB. Year and treatment significantly influenced $CWM_{DSM,}$ which was lower in HARV than CONT (averaged across all years).

3.4 | Similarity

In YR9, abundance-weighted dissimilarity between the overstorey and regeneration layers of plots differed among treatments (p = 0.0018). Dissimilarity increased from CONT (median = 0.468) through RRXF (0.50) and HERB (0.51) to significantly higher overstorey/understorey dissimilarity in HARV (0.62). However, a similar trend was seen in the pre-treatment year (median dissimilarity = 0.51 [CONT], 0.46 [HERB], 0.55 [RRXF], 0.62 [HARV]), suggesting that site differences were a stronger influence than management treatments on species composition differences between the overstorey and understorey. In support of this argument, overstorey/understorey dissimilarity within treatments did not differ over time (Appendix S4). There was no pattern of decreasing or increasing dissimilarity over time that might indicate convergence or divergence of species composition of the regeneration layer in any treatment (Figure 3). However, dissimilarity was significantly higher in HARV in YR9, and a non-significant trend of increasing (through YR3) then declining dissimilarity in this treatment suggests an initial influx of "new" species that did not persist (Figure 3). Specifically, six taxa recorded in previous years were not present in YR9: *Acer* species, *Betula alleghaniensis* Britton, *Carpinus caroliniana* Walter, *Ostrya virginiana* (Mill) K. Koch, *Oxydendrum arboretum* (L.) DC., and *Pinus strobus* L. All of these taxa have light, wind-dispersed seeds, and tend to establish after disturbance.

4 | DISCUSSION

4.1 | Taxonomic and functional responses to disturbance severity in the overstorey layer

Nine years following restoration treatments that reduced canopy stem density between 32% and 80% compared to the natural successional reduction in CONT, nearly all measures of taxonomic and functional diversity of the overstorey were indistinguishable. Although the disturbances tested in this study represented a severity gradient, all treatments were only partial disturbances. As such,

TABLE 3 Functional identity of the regeneration layer (stems <5 cm dbh), defined by community-weighted mean values of wood specific gravity (WSG; g/cm), specific leaf area (SLA; cm^2/g), leaf nitrogen concentration (LEAFN; %), maximum height at maturity (HGT; m), and dry seed mass (log) (DSM; mg) for pre- (YR0), one (YR1), three (YR3), seven (YR7), and nine (YR9) years post-treatment

WSG	CONT	HERB	RRXF	HARV
YR0 (pre)	0.52 (0.00)	0.53 (0.01)	0.52 (0.01)	0.53 (0.01)
YR1	0.52 (0.00)	0.53 (0.01)	0.51 (0.01)	0.52 (0.01)
YR3	0.52 (0.00)	0.53 (0.01)	0.52 (0.02)	0.50 (0.01)
YR7	0.53 (0.01)	0.53 (0.01)	0.52 (0.02)	0.52 (0.00)
YR9	0.52 (0.01)	0.53 (0.01)	0.53 (0.01)	0.51 (0.01)
AVG	0.52 (0.00)	0.53 (0.00)	0.52 (0.01)	0.52 (0.00)
SLA				
YR0 (pre)	152.8 (4.6)	164.9 (7.4)	168.2 (9.4)	163.6 (2.1)
YR1	154.7 (3.6)	163.2 (6.5)	170.3 (7.6)	165.7 (4.0)
YR3	154.6 (3.2)	163.9 (7.5)	168.3 (7.9)	172.6 (8.1)
YR7	152.0 (5.7)	161.9 (5.7)	167.0 (11.0)	164.6 (6.4)
YR9	153.2 (5.0)	164.1 (8.7)	167.0 (9.5)	162.3 (5.4)
AVG	153.5 (1.8)	163.6 (2.9)	168.2 (3.7)	165.8 (2.4)
LEAFN				
$YR0^{a}$ (pre)	1.89 (0.03)	1.97 (0.03)	2.00 (0.03)	2.08 (0.02)
$YR1^{b}$	1.93 (0.02)	1.99 (0.03)	2.08 (0.05)	2.20 (0.06)
$YR3^{bc}$	1.93 (0.03)	2.00 (0.03)	2.04 (0.06)	2.14 (0.02)
$YR7^{ac}$	1.93 (0.03)	1.98 (0.03)	1.99 (0.06)	2.14 (0.02)
$YR9^{a}$	1.92 (0.02)	1.96 (0.03)	1.97 (0.03)	2.12 (0.01)
AVG	1.92 $(0.01)^{A}$	1.98 $(0.01)^{AB}$	2.02 $(0.02)^{B}$	2.14 $(0.02)^{C}$
HGT				
YR0 (pre)	23.5 $(0.2)^{A}$	23.2 $(0.5)^{AB}$	21.9 $(0.8)^{B}$	24.8 $(0.3)^{A}$
YR1	23.6 (0.4)	23.5 (0.5)	22.7 (1.2)	24.7 (0.8)
YR3	23.4 $(0.2)^{A}$	23.7 $(0.7)^{A}$	21.7 $(0.6)^{B}$	27.3 $(0.8)^{C}$
YR7	23.9 $(0.4)^{A}$	23.5 $(0.7)^{A}$	21.8 $(1.0)^{B}$	26.3 $(0.6)^{C}$
YR9	23.5 $(0.3)^{A}$	23.5 $(0.8)^{A}$	21.6 $(0.8)^{B}$	26.2 $(0.7)^{C}$
AVG	23.6 (0.1)	23.5 (0.3)	22.0 (0.4)	25.9 (0.3)
DSM				
$YR0^{ac}$ (pre)	2.54 (0.13)	2.31 (0.16)	2.26 (0.16)	1.92 (0.07)
$YR1^{b}$	2.42 (0.11)	2.20 (0.18)	2.14 (0.11)	1.89 (0.08)
$YR3^{b}$	2.39 (0.06)	2.21 (0.19)	2.18 (0.12)	1.85 (0.14)
$YR7^{c}$	2.56 (0.14)	2.29 (0.13)	2.39 (0.18)	1.99 (0.16)
$YR9^{c}$	2.45 (0.11)	2.26 (0.19)	2.39 (0.08)	2.09 (0.13)
AVG	2.47 $(0.05)^{A}$	2.26 $(0.07)^{AB}$	2.27 $(0.06)^{AB}$	1.95 $(0.05)^{B}$

Note: Values represent mean (standard error). Uppercase letters denote significant differences (α = 0.10) among treatments within a given year. Lowercase letters indicate significant differences among years, averaged across treatments. AVG, average; LEAFN, leaf nitrogen concentration; HGT, maximum height at maturity; DSM, dry seed mass; CONT, untreated control; HERB, herbicide; RRXF, repeated prescribed fire; HARV, timber harvest and burn.

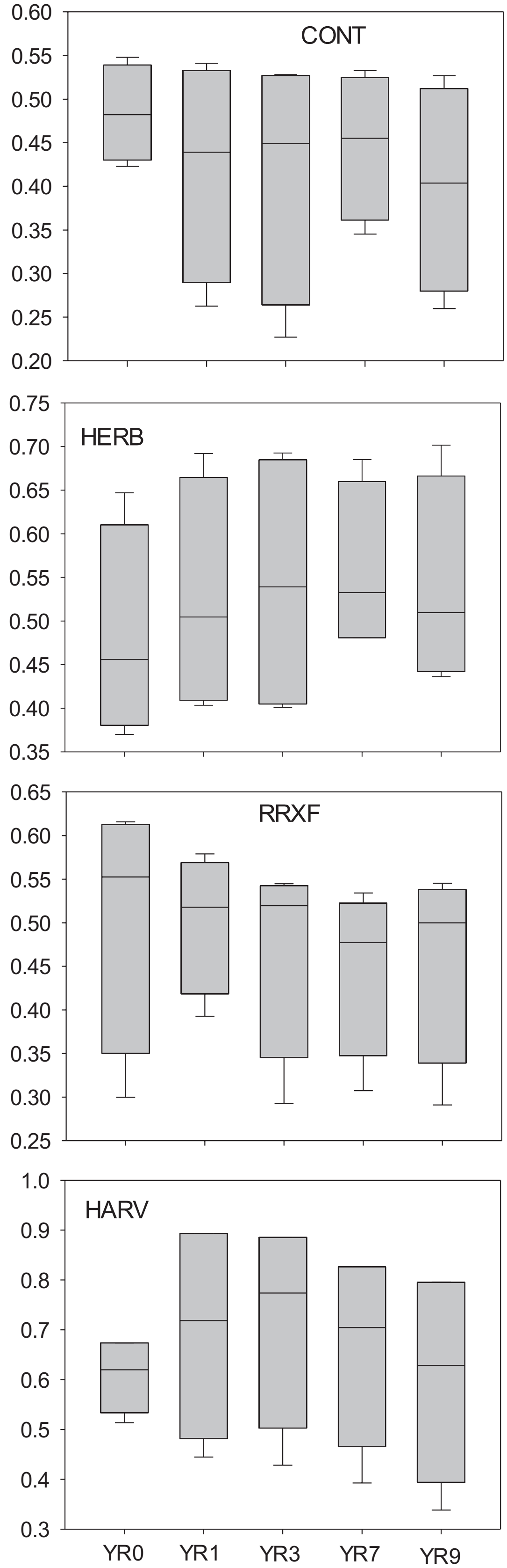

FIGURE 3 Box-plots of median, minimum, maximum, 25th, and 75th quartiles of abundance-weighted (Lance–Williams) dissimilarity between overstorey and regeneration species composition before (YR0) and each sampling year after (YR1, YR3, YR7, YR9) management treatments

the species and functional diversity present prior to disturbance were mostly conserved post-treatment. Even when treatments, such as HERB and RRXF, attempted to reduce the abundance of species with specific traits (e.g., low wood specific gravity, high specific leaf area, etc.), low efficacy of the treatments combined with ingrowth of understorey stems into the overstorey stratum during the nine years post-treatment likely ameliorated any potential effects on both functional and taxonomic diversity.

Our results agree with previous research that suggest that in mature forests, functional and taxonomic diversity are relatively stable over time when disturbances are low-severity or absent (Verburg & van Eijk-Bos, 2003; Schweitzer & Dey, 2011; Curzon *et al.*, 2017; Fang *et al.*, 2019). The limited literature from temperate forests suggests that partial silvicultural disturbances do little to alter overstorey taxonomic and functional diversity metrics relative to unmanaged forests. For example, Curzon *et al.*, (2017) found partial cutting treatments had no significant effect on two measures of functional diversity, functional dispersion and divergence, compared to uncut stands across three sites in the northern US. In comparison with partial cutting techniques, intensive clear-cutting was found to reduce aspects of functional diversity of the overstorey in both cool and warm temperate forests of Japan, an effect that persisted throughout stand development (Kusumoto *et al.*, 2015). Resilience of functional diversity to lower severity, partial disturbances in eastern North America concurs with findings from diverse tropical systems, where low to moderate-severity logging has been shown to have limited effects on taxonomic diversity, F_{Ric}, and functional divergence, although reductions in F_{Eve} and changes in functional identity have been observed (Baraloto *et al.*, 2012; Carreño-Rocabado *et al.*, 2012).

4.2 | Taxonomic and functional responses to disturbance severity in the regeneration layer

Over the nine years of this study, post-treatment patterns in regeneration do not support the hypothesis that taxonomic diversity increases with disturbance severity through the most severe treatment, which included timber harvest that removed 80% of standing trees and a dormant season burn. Regeneration patterns also do not support the hypothesis that taxonomic diversity decreases with time after disturbance (i.e., converges). Although E and H' in HARV, which were lower than in CONT prior to treatment, increased to a point where no statistical differences were detected between YR1 and YR9, surprisingly, neither S, E, nor H' of the regeneration stratum differed across treatments during any of the post-treatment years. The effects of disturbance on taxonomic diversity of the tree regeneration layer often vary with the disturbance severity. For example, taxonomic diversity of the regeneration layer following heavy cutting (e.g., group openings, heavy shelterwood harvests, and clear-cutting with reserves) has been shown to significantly increase relative to undisturbed forests (Jenkins & Parker, 1998; Elliott & Knoepp, 2005; Nuttle *et al*., 2013), while only minor changes occur following lighter cutting and other low-severity vegetation management treatments (e.g., light thinning, single-tree selection) (Schweitzer & Dey, 2011; Seiwa *et al*., 2012; Raymond *et al*., 2018).

Results from this study do not strongly support the hypothesis that functional diversity in the regeneration layer increases with disturbance severity or decreases over time, at least regarding the gradient of disturbance and time frame tested in this study. Functional richness, evenness, and dispersion did not differ among treatments, and indices of functional diversity did not differ with the severity of restoration treatment. Literature that describes the effects of silvicultural disturbance on the functional structure and diversity of the regeneration stratum in temperate forests is lacking. In boreal forests of Canada, however, functional richness and functional diversity of the understorey did not differ between undisturbed upland forests and three- to five-year-old forests that originated via clear-cutting (Biswas & Mallik, 2010). Further, in tropical forests of French Guiana, low-intensity selective logging had no effect on aspects of functional diversity of the juvenile tree layer (stems <10 cm dbh), including functional richness and divergence, in gaps, gap edge, or unlogged portions of the forest (Baraloto *et al*., 2012).

Disturbance severity may, however, affect the extent to which species composition of regeneration differs from the overstorey, at least in the first years after treatment. Although a gradient of increasing overstorey/understorey dissimilarity from CONT to HARV in YR9 may reflect pre-existing differences among sites, a non-significant increase in dissimilarity of the overstorey and understorey strata through YR3, followed by a decrease through YR9, reflected "new" species, with wind-blown seeds and representing a suite of functional traits, that established but did not persist in HARV. Heavy reduction of canopy cover in this highest-severity treatment opened sufficient growing space to facilitate the establishment and growth of species along the shade tolerance continuum (Elliott & Knoepp, 2005). However, rapid and prolific response of *Rubus* in HARV (cover estimated to be 21%; unpublished data) reduced light levels (Balandier *et al*., 2005) and likely dampened tree regeneration, thereby reducing any potential response of both taxonomic and functional diversity metrics to this treatment (Donoso & Nyland, 2006; Kern *et al*., 2013).

4.3 | Functional trait responses to management treatments

Although we found very minor effects of treatments on functional and taxonomic diversity metrics, functional identity in the regeneration layer was affected by treatments. Results suggest the most severe restoration treatment, HARV, increased the means of traits in the woody regeneration layer associated with rapid post-disturbance establishment, carbon capture, and maximum height at maturity. CWM_{LEAFN} was greater in HARV than in CONT and HERB treatments in all years, and CWM_{HGT} was greater in HARV than in all treatments in YR3 through YR9. By YR9, CWM_{HGT} was 2.7 m greater in HARV than in CONT and HERB, and 4.6 m greater in HARV than in RRXF. In contrast, CWM_{DSM} was lower in HARV than in the unmanaged CONT. Greater dissimilarity between the overstorey and regeneration strata species composition through YR3 in this treatment also suggests stronger initial treatment effects on regeneration in HARV.

Changes in functional identity without concomitant changes in functional or taxonomic diversity following disturbance have been observed in both tropical and temperate forest systems (e.g., Carreño-Rocabado *et al*., 2012; Curzon *et al*., 2017; Both *et al*., 2018). As the severity of disturbance increases, growing space and associated resources increase. This increase in resource availability often favors species with acquisitive traits (e.g., rapid growth, low seed mass, high maximum height, low wood specific gravity) rather than conservative growth traits (e.g., slow growth, high seed mass, high wood specific gravity). For example, Yguel *et al*. (2019) documented no effect of logging intensity on species richness (woody stems ≥ 10 cm dbh), but higher logging intensity resulted in decreased wood density and seed size and increased heliophily after 27 years. Of the restoration treatments tested in this study, only the highest-severity treatment, HARV, impacted aspects of functional identity in the regeneration layer; even so, functional diversity metrics remained unchanged, as indicated by the lack of effect on F_{Ric}, F_{Eve}, or F_{Dis}.

5 | CONCLUSIONS AND MANAGEMENT APPLICATIONS

The 80+-year-old second-growth hardwood forests examined here exhibit composition and structure typical of mature, eastern US hardwood forests. These forests established after intense logging and wildfires, followed by loss of *Castanea dentata* (Marshall) Borkh. from chestnut blight (*Cryphonectria parasitica* (Murrill) M.E. Barr), occasional fires, and ice and windstorms; these disturbances created a range of environmental conditions conducive to the regeneration of tree species adapted to a variety of light conditions. Our results through nine years post-treatment suggest common management treatments to promote regeneration of canopy *Quercus* and *Carya* species do not increase taxonomic or functional diversity in the regeneration layer. However, the most severe treatment, harvest followed by burning (HARV), led to an initial, although transitory, increase in species not in the canopy; these species were characterized by light, wind-dispersed seeds. Further, HARV increased the means of traits associated with rapid post-disturbance establishment, carbon capture, and maximum height at maturity, and lowered mean dry seed weight. Although these traits suggest the regeneration layer is poised to develop and contribute to future structure and composition, HARV, along with other restoration treatments, failed to cause a change to the regeneration layer that would indicate the restoration of a functioning *Quercus*–*Carya* forest, including lower leaf nitrogen content, an increase in seed mass, and an increase in wood specific gravity.

In mixed *Quercus* forests broadly, burning, like that employed in RRXF and HARV, has been hypothesized to reduce the abundance and competitiveness of species not well-adapted to fire, including many shade-tolerant (e.g., *Acer rubrum*, *Nyssa sylvatica*) and shade-intolerant species (e.g., *Liriodendron tulipifera*), particularly in the regeneration layer (Brose, 2014). Following on this hypothesis, aspects of both taxonomic and functional diversity, including metrics of evenness, diversity, and divergence, would be expected to change, particularly in the regeneration layer, with repeated fire. In our research, RRXF and HARV had no significant impact on the diversity of the tree regeneration layer. Lack of any significant change in diversity metrics in this and other studies throughout eastern North America (e.g., Scherer *et al*., 2018) is likely related to relatively low mortality rates by deciduous broad-leaved species following low-severity fire. Low rates of fire-related mortality of stems >15 cm dbh (Keyser *et al*., 2018) provides for a continued seed source that promotes the continued establishment and development of individuals in the regeneration layer during fire-free periods. In addition, prolific resprouting of woody stems following fire-induced top-kill, leads to "persistent" species that, once established, are difficult to remove (Alexander *et al*., 2008; Fan *et al*., 2012; Keyser, 2019).

Overall, our results suggest the upland, mixed *Quercus* forests of the southern Appalachian Mountains are relatively resilient to changes in diversity in response to the disturbance severity gradient created by restoration treatments tested in this study. It is possible that as stand development progresses, or as the vegetation developed in response to the restoration treatments interacts with natural disturbance events (e.g., drought), taxonomic and functional diversity and identity could change in a manner that differs from the results of this study (Wilfahrt, 2018). The *Quercus* restoration treatments tested in this study did little to affect taxonomic or functional diversity in either the overstorey or regeneration strata. However, treatments did alter functional identity of the regeneration layer. In forest types such as mixed-*Quercus* forests, where species composition following silvicultural disturbance is heavily influenced by pre-disturbance composition and ability of species to persist, functional identity rather than taxonomic or functional diversity metrics may provide insight into more nuanced effects of restoration treatments on ecosystem function.

ACKNOWLEDGEMENTS

This study was internally funded by the USDA Forest Service, Southern Research Stations-Research Work Unit 4157. The authors thank the Gordon Warburton and Dean Simon of the North Carolina Wildlife Resources Commission for providing the study area and implementing the treatments. We extend our gratitude to Kenny Frick, Jacqui Adams, Tracy Roof, Brandy Benz, and numerous other students and technicians for assistance with data collection. We thank the many individuals from NCWRC and Haywood Technical College who assisted with the prescribed burns. This paper was written and prepared, in part, by USA Government employees on official time and, therefore, is in the public domain and not subject to copyright in the USA.

AUTHOR CONTRIBUTIONS

TLK and BSC conducted the statistical analyses and equally contributed to writing the manuscript. TLK and CHG developed the experimental design.

DATA AVAILABILITY STATEMENT

The data used in this publication are stored on an internal server of the USDA Forest Service. Data supporting the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Tara L. Keyser https://orcid.org/0000-0001-8967-9344

REFERENCES

Alexander, H.D. & Arthur, M.A. (2014) Increasing red maple leaf litter alters decomposition rates and nitrogen cycling in historically oak-dominated forests of the Eastern U.S. *Ecosystems*, 17, 1371–1383. https://doi.org/10.1007/s10021-014-9802-4

Alexander, H.D. & Arthur, M.A. (2010) Implications of a predicted shift from upland oaks to red maple on forest hydrology and nutrient availability. *Canadian Journal of Forest Research*, 40, 716–726. https://doi.org/10.1139/X10-029

Alexander, H.D., Arthur, M.A., Loftis, D.L. & Green, S.R. (2008) Survival and growth of upland oak and co-occurring competitor seedlings following single and repeated prescribed fires. *Forest Ecology and Management*, 256, 1021–1030. https://doi.org/10.1016/j.foreco.2008.06.004

Balandier, P., Collet, C., Miller, J.H., Reynolds, P.E. & Zedaker, S.M. (2005) Designing forest vegetation management strategies based on mechanisms and dynamics of crop tree competition by neighbouring vegetation. *Forestry*, 79, 3–27. https://doi.org/10.1093/forestry/cpi056

Baraloto, C., Hérault, B., Paine, C.E., Massot, H., Blanc, L., Bonal, D. *et al* (2012) Contrasting taxonomic and functional responses of a tropical tree community to selective logging. *Journal of Applied Ecology*, 49, 861–870. https://doi.org/10.1111/j.1365-2664.2012.02164.x

Bell, F.W., Hunt, S., Dacosta, J., Sharma, M., Larocque, G.R., Winters, J.A. & *et al* (2014) Effects of silviculture intensity on plant diversity response patterns in young managed northern temperate and boreal forests. *Ecoscience*, 21, 327–339. https://doi.org/10.2980/21-(3-4)-3710

Benjamini, Y. & Hockberg, Y. (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Bulletin*, 57, 289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Biswas, S.R. & Mallik, A.U. (2011) Species diversity and functional diversity relationship varies with disturbance intensity. *Ecosphere*, 2(4), art52. https://doi.org/10.1890/ES10-00206.1

Biswas, S.R. & Mallik, A.U. (2010) Disturbance effects of species diversity and functional diversity in riparian and upland plant communities. *Ecology*, 91, 28–35. https://doi.org/10.1890/08-0887.1

Boersma, K.S., Dee, L.E., Miller, S.J., Bogan, M.T., Lytle, D.A. & Gitelman, A.I. (2016) Linking multidimensional functional diversity to quantitative methods: a graphical hypothesis-evaluation framework. *Ecology*, 97, 583–593. https://doi.org/10.1890/15-0688.1

Both, S., Riutta, T., Paine, C.E., Elias, D.M.O., Cruz, R.S., Jain, A. *et al* (2018) Logging and soil nutrients independently explain plant trait explain plant trait expression in tropical forests. *New Phytologist*, 221, 1853–1865. https://doi.org/10.1111/nph.15444

Brose, P.H. (2014) Development of prescribed fire as a silvicultural tool for the upland oak forests of the eastern United States. *Journal of Forestry*, 112, 525–533. https://doi.org/10.5849/jof.13-088

Brose, P.H. (2010) Long-term effects of single prescribed fires on hardwood regeneration in oak shelterwood stands. *Forest Ecology and Management*, 260, 1516–1524. https://doi.org/10.1016/j.foreco.2010.07.050

Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, 48, 1079–1087. https://doi.org/10.1111/j.1365-2664.2011.02048.x

Caldwell, P.V., Miniat, C.F., Elliott, K.J., Swank, W.T., Brantley, S.T. & Laseter, S.H. (2016) Declining water yield from forested mountain watersheds in response to climate change and forest mesophication. *Global Change Biology*, 22, 2997–3012. https://doi.org/10.1111/gcb.13309

Carreño-Rocabado, G., Peña-Claros, M., Bongers, F., Alarcón, A., Lincona, J.C. & Poorter, L. (2012) Effects of disturbance intensity on species and functional diversity in a tropical forest. *Journal of Ecology*, 100, 1453–1463. https://doi.org/10.1111/j.1365-2745.2012.02015.x

Clark, C.M., Flynn, D.F., Butterfield, B.J. & Reich, P.B. (2012) Testing the link between functional diversity and ecosystem functioning in a Minnesota grassland experiment. *PLoS One*, 7(12), e52821. https://doi.org/10.1371/journal.pone.0052821

Cooke, R.S.C., Bates, A.E. & Eigenbrod, F. (2019) Global trade-offs of functional redundancy and functional dispersion for birds and mammals. *Global Ecology and Biogeography*, 28, 484–495. https://doi.org/10.1111/geb.12869

Craven, D., Hall, J.S., Berlyn, G.P., Ashton, M.S. & van Breugel, M. (2018) Environmental filtering limits functional diversity during succession in a seasonally wet tropical secondary forest. *Journal of Vegetation Science*, 29, 511–520. https://doi.org/10.1111/jvs.12632

Curzon, M.T., D'Amato, A.W., Fraver, S., Palik, B.J., Bottero, A., Foster, J.R. & *et al* (2017) Harvesting influences functional identity and diversity over time in forests of the northeastern USA. *Forest Ecology and Management*, 400, 93–99. https://doi.org/10.1016/j.foreco.2017.05.056

Decocq, G., Aubert, M., Dupont, F., Alard, D., Saguez, R., Wattez-Franger, A. *et al* (2004) Plant diversity in a managed temperate deciduous forest: understory response to two silvicultural systems. *Journal of Applied Ecology*, 41, 1065–1079. https://doi.org/10.1111/j.0021-8901.2004.00960.x

Dey, D.C. (2014) Sustaining oak forests in eastern North America: regeneration and recruitment, the pillars of sustainability. *Forest Science*, 60, 926–942. https://doi.org/10.5849/forsci.13-114

Donoso, P.J. & Nyland, R.D. (2006) Interference to hardwood regeneration in northeastern North America: the effects of raspberries (*Rubus* spp.) following clearcutting and shelterwood methods. *Northern Journal of Applied Forestry*, 23, 288–296. https://doi.org/10.1093/njaf/23.4.288

Elliott, K.J. & Knoepp, J.D. (2005) The effects of three regeneration harvest methods on plant diversity and soil characteristics in the southern Appalachians. *Forest Ecology and Management*, 211, 296–317. https://doi.org/10.1016/j.foreco.2005.02.064

Elliott, K.J., Hendrick, R.L., Major, A.E., Vose, J.M. & Swank, W.T. (1999) Vegetation dynamics after a prescribed fire in the southern Appalachians. *Forest Ecology and Management*, 114, 199–213. https://doi.org/10.1016/s0378-1127(98)00351-x

Fan, Z.F., Ma, Z.Q., Dey, D.C. & Roberts, S.D. (2012) Response of advance reproduction of oaks and associated species to repeated prescribed fires in upland oak-hickory forests, Missouri. *Forest Ecology and Management*, 266, 160–169. https://doi.org/10.1016/j.foreco.2011.08.034

Fang, S., Munoz, F., Ye, J., Lin, F., Yuan, Z., Kuang, X. *et al* (2019) Deterministic processes drive functional and phylogenetic temporal changes of woody species in temperate forests in Northeast China. *Annals of Forest Science*, 76, 42. https://doi.org/10.1007/s13595-019-0830-2

Greenberg, C.H., Levey, D.J. & Loftis, D.L. (2007) Fruit production in mature and recently regenerated forests of the Appalachians. *Journal of Wildlife Management*, 71, 321–335. https://doi.org/10.2193/2005-747

Hanberry, B.B. & Abrams, M.D. (2018) Recognizing loss of open forest ecosystems by tree densification and land use intensification in the Midwestern USA. *Regional Environmental Change*, 18, 1731–1740. https://doi.org/10.1007/s10113-018-1299-5

Hanberry, B.B. & Nowacki, G.J. (2016) Oaks were the historical foundation genus of the east-central United States. *Quaternary Science Reviews*, 145, 94–103. https://doi.org/10.1016/j.quascirev.2016.05.037

Hollingsworth, T.N., Johnson, J.F., Bernhardt, E.L. & Chapin, F.S. (2013) Fire severity filters regeneration traits to shape community assembly in Alaska's boreal forest. *PLoS One*, 8, e56033. https://doi.org/10.1371/journal.pone.0056033

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. *Forest Ecology and Management*, 218, 210–228. https://doi.org/10.1016/j.foreco.2005.07.011

Jenkins, M.A. & Parker, G.R. (1998) Composition and diversity of woody vegetation in silvicultural openings of southern Indiana forests. *Forest Ecology and Management*, 109, 57–74. https://doi.org/10.1016/s0378-1127(98)00256-4

Karadimou, E.K., Kallimanis, A.S., Tsiripidis, I. & Dimopoulos, P. (2016) Functional diversity exhibits a diverse relationship with area, even a decreasing one. *Scientific Reports*, 6, 1–9. https://doi.org/10.1038/srep35420

Kern, C.C., Montgomery, R.A., Reich, P.B. & Strong, T.F. (2014) Harvest-created canopy gaps increase species and functional trait diversity of the forest ground-layer community. *Forest Science*, 60, 335–344. https://doi.org/10.5849/forsci.13-015

Kern, C.C., D'Amato, A.W. & Strong, T.F. (2013) Diversifying the composition and structure of managed, late-successional forests with harvest gaps: what is the optimal gap size? *Forest Ecology and Management*, 304, 110–120. https://doi.org/10.1016/j.foreco.2013.04.029

Keyser, T.L. (2019) Resprouting by seedlings of four North American deciduous broadleaved tree species following experimental burning. *Oecologia*, 190, 207–218. https://doi.org/10.1007/s00442-019-04397-x

Keyser, T.L., McDaniel, V.L., Klein, R.N., Drees, D.G., Burton, J.A. & Forder, M.M. (2018) Short- term stem mortality of ten deciduous broadleaved species following prescribed burning in upland forests of the southern US. *International Journal of Wildland Fire*, 27, 42–51. https://doi.org/10.1071/wf17058

Keyser, T.L., Arthur, M. & Loftis, D.L. (2017) Repeated burning alters the structure and composition of the hardwood regeneration in oak-dominated forests of eastern Kentucky, USA. *Forest Ecology and Management*, 393, 1–11. https://doi.org/10.1016/j.foreco.2017.03.015

Kochenderfer, J.D., Kochenderfer, J.N. & Miller, G.W. (2012) *Manual herbicide application methods for managing vegetation in Appalachian hardwood forests*. USDA For. Serv., Gen. Tech. Rep. NRS 96. Newtown Square, PA. 59 p.

Kreye, J.K., Varner, J.M., Hamby, G.W. & Kane, J.M. (2018) Mesophytic litter dampens flammability in fire-excluded pyrophytic oak-hickory woodlands. *Ecosphere*, 9(1), e02078. https://doi.org/10.1002/ecs2.2078

Kusumoto, B., Shiono, T., Miyoshi, M., Maeshiro, R., Fujii, S., Kuuluvainen, T. & *et al* (2015) Functional response of plant communities to clearcutting: management impacts differ between forest vegetation zones. *Journal of Applied Ecology*, 42, 171–180. https://doi.org/10.1111/1365-2664.12367

Laliberté, E. & Legendre, P. (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91, 299–305. https://doi.org/10.1890/08-2244.1
Loftis, D.L. (1990) A shelterwood method for regenerating red oak in the southern Appalachians. *Forest Science*, 36, 917–929. https://doi.org/10.1093/forestscience/36.4.917
Májeková, M., Paal, T., Plowman, N.S., Bryndova, M., Kasari, L., Norberg, A. *et al* (2016) Evaluating functional diversity: missing trait data and the importance of species abundance structure and data transformation. *PLoS One*, 11(2), e0149270. https://doi.org/10.1371/journal.pone.0149270
McGill, B.J., Enquist, J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21, 178–185. https://doi.org/10.1016/j.tree.2006.02.002
Mouchet, M.A., Villéger, S., Mason, N.W.H. & Mouillot, D. (2010) Functional diversity measures and their ability to discriminate community assembly rules. *Functional Ecology*, 24, 867–876. https://doi.org/10.1111/j.1365-2435.2010.01695x
Mouillot, D., Graham, N.A.J., Villegér, S., Mason, N.W.H. & Bellwood, D.R. (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, 28, 167–177. https://doi.org/10.1016/j.tree.2012.10.004
Nuttle, T., Royo, A.A., Adams, M.B. & Carson, W.P. (2013) Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. *Ecological Monographs*, 83, 3–17. https://doi.org/10.1890/11-2263.1
Oliver, C.D. & Larson, B.C. (1996) *Forest Stand Dynamics: Updated Edition*. New York, NY: John Wiley and Sons.
Pielou, E.C. (1966) The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology*, 13, 131–144. https://doi.org/10.1016/0022-5193(67)90048-3
R Development Core Team (2012) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
Raymond, P., Royo, A.A., Prévost, M. & Dumais, D. (2018) Assessing the single-tree and small group selection cutting system as intermediate disturbance to promote regeneration and diversity in temperate mixedwood stands. *Forest Ecology and Management*, 430, 21–32. https://doi.org/10.1016/j.foreco.2018.07.054
Rodríguez-Trejo, D.A. & Myers, R.L. (2010) Using oak characteristics to guide fire regime restoration in Mexican pine-oak and oak forests. *Ecological Restoration*, 28, 304–323. https://doi.org/10.3368/er.28.3.304
Ruiz-Jaen, M.C. & Potvin, C. (2011) Can we predict carbon stocks in tropical ecosystems from tree diversity? Comparing species and functional diversity in a plantation and a natural forest. *New Phytologist*, 189, 978–987. https://doi.org/10.1111/j.1469-8137.2010.03501.x
Sabatini, F.M., Burton, J.I., Scheller, R.M., Amatangelo, K.L. & Mladenoff, D.J. (2014) Functional diversity of ground-layer plant communities in old-growth and managed northern hardwood forests. *Applied Vegetation Science*, 17, 398–407. https://doi.org/10.1111/avsc.12083
Schamp, B.S. & Aarseen, L.W. (2009) The assembly of forest communities according to maximum species height along resource and disturbance gradients. *Oikos*, 118, 564–572. https://doi.org/10.1111/j.1600-0706.2008.16589.x
Scharenbroch, B.C., Nix, B., Jacobs, K.A. & Bowles, M.L. (2012) Two decades of low-severity prescribed fire increases soil nutrient availability in Midwestern, USA oak (*Quercus*) forest. *Geoderma*, 183–184, 80–91. https://doi.org/10.1016/j.geoderma.2012.03.010
Scherer, S.S., Kern, C.C., D'Amato, A.W., Palik, B.J. & Russell, M.R. (2018) Long-term pine regeneration, shrub layer dynamics, and understory community composition responses to repeated prescribed fire in *Pinus resinoa* forests. *Canadian Journal of Forest Research*, 48, 117–129. https://doi.org/10.1139/cjfr-2017-0345
Schleuter, D., Daufresne, M., Massol, F. & Argillier, C. (2010) A user's guide to functional diversity indices. *Ecological Monographs*, 80, 469–484. https://doi.org/10.1890/08-2225.1
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. *Forest Ecology and Management*, 262, 1729–1741. https://doi.org/10.1016/j.foreco.2011.07.020
Seiwa, K., Etoh, Y., Hisita, M., Masaka, K., Imaji, A., Ueno, N. *et al* (2012) Roles of thinning intensity in hardwood recruitment and diversity in a conifer, *Criptomeria japonica* plantation: a 5-year demographic study. *Forest Ecology and Management*, 269, 177–187. https://doi.org/10.1016/j.foreco.2011.12.014
Shannon, C.E. & Weaver, W. (1949) *The Mathematical Theory of Communication*. Urbana, IL: University of Illinois Press, p. 117.
Spasojevic, M.J. & Suding, K.N. (2012) Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *Journal of Ecology*, 100, 652–661. https://doi.org/10.1111/j.1365-2745-2011.01945.x
Villéger, S., Mason, N.W.H. & Mouillot, D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89, 2290–2301. https://doi.org/10.1890/07-1206.1
Verburg, R., van Eijk-Bos, C. (2003) Effects of selective logging on tree diversity, composition and plant functional type patterns in a Bornean rain forest. *Journal of Vegetation Science*, 14, 99–110. https://doi.org/10.1111/j.1654-1103.2003.tb02132.x
Wilfahrt, P.A. (2018) Functional trait shifts after disturbance reveal broad-scale variability in temperate forest regional recruitment processes. *Journal of Vegetation Science*, 29, 491–500. https://doi.org/10.1111/jvs.12628
Yguel, B., Piponoit, C., Mirabel, A., Dourdain, A., Hérault, B., Gourlet-Fleury, S. *et al* (2019) Beyond species richness and biomass: impact of selective logging and silvicultural treatments on the functional composition of a neotropical forest. *Forest Ecology and Management*, 433, 528–534. https://doi.org/10.1016/j.foreco.2018.11.022
Zeide, B. (1987) Analysis of the 3/2 power law of self-thinning. *Forest Science*, 33, 517–537. https://doi.org/10.1093/forestscience/33.2.517

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Species-specific plant functional trait references

Appendix S2. Statistics associated with the linear mixed-effects model of taxonomic diversity, functional diversity, and functional identity of the overstorey (stems ≥5 cm dbh) layer

Appendix S3. Statistics associated with the linear mixed-effects model of taxonomic diversity, functional diversity, and functional identity of the regeneration (stems <5 cm dbh) layer

Appendix S4. Results of PERMANOVA describing differences in composition between overstorey (stems ≥5 cm dbh) and regeneration (stems <5 cm dbh) layers

How to cite this article: Keyser TL, Collins BS, Greenberg CH. Response of taxonomic and functional diversity to disturbance severity in temperate hardwood forests. *Appl Veg Sci*. 2021;24:e12538. https://doi.org/10.1111/avsc.12538