

Herbaceous-layer diversity and tree seedling recruitment are enhanced following *Rhododendron maximum* shrub removal

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ABSTRACT

Forest ecosystems dominated by *Tsuga canadensis* are undergoing fundamental changes in function and composition from infestations by hemlock woolly adelgid (*Adelges tsugae*). We proposed that the first step to restoring southern Appalachian riparian forests following *T. canadensis* mortality would be eliminating the evergreen shrub, *Rhododendron maximum*. We hypothesized that removing *R. maximum* would increase light transmittance, soil moisture and temperature; and subsequently, enhance herbaceous-layer diversity and promote tree seedling recruitment and survival. We tested these hypotheses at two locations, CWT, Coweeta Hydrologic Laboratory; WOC, White Oak Creek) in the Nantahala Mountain Range of western North Carolina, both with heavy *T. canadensis* mortality and a dense *R. maximum* subcanopy. The treatments were designed to remove only soil O-horizon (FF), remove only *R. maximum* (CR), remove *R. maximum* and soil O-horizon (CFFR), and untreated, reference (REF). We installed permanent plots across treatments and locations and measured light transmittance (Q_i/Q_o), soil water content (θ), herbaceous-layer cover and diversity (Shannon's index (H'_{cover}) and species richness), and tree seedling recruitment.

As expected, cutting the *R. maximum* subcanopy (CR and CFFR) immediately increased Q_i/Q_o in the spring months across locations, and it was sustained through the first growing season. θ was generally high across plots, averaging 26% during the growing season, and didn't vary over time. By the second growing season (2017) after treatments, herbaceous-layer cover and diversity increased on CR and CFFR. Herbaceous-layer cover was significantly related to Q_i/Q_o ($r^2 = 0.22$, $p < 0.001$) and θ ($r^2 = 0.13$, $p = 0.009$), while diversity was only related to Q_i/Q_o (H'_{cover} , $r^2 = 0.14$, $p < 0.001$; species richness, $r^2 = 0.21$, $p < 0.001$). Tree seedling density was related to Q_i/Q_o ($r^2 = 0.10$, $p = 0.001$) and θ ($r^2 = 0.26$, $p < 0.001$). Tree seedling density was low before treatment (1.4 ± 0.3 seedlings m^{-2}) and increased by 10-fold in CR and CFFR two growing seasons after treatment. In CR, species with the highest density ranked *Betula* spp. > *Acer rubrum* > *Quercus coccinea* > *Liriodendron tulipifera* > *Q. rubra*. In CFFR, tree seedling recruitment ranked *Betula* spp. > *A. rubrum* > *L. tulipifera*. These vegetation responses have important implications for potential recovery of riparian forests following *T. canadensis* mortality.

1. Introduction

Forest ecosystems dominated by *Tsuga canadensis* (L.) Carrière are undergoing fundamental changes in function and composition from infestations by hemlock woolly adelgid (HWA, *Adelges tsugae* Annand) (Ellison et al., 2005; Lovett et al., 2016). HWA is an invasive insect native to Japan, first documented in the eastern U.S. in the 1950s, that is attacking *T. canadensis* trees of all ages and sizes (Elliott and Vose, 2011), throughout much of the tree's range (Evans et al., 2012; Orwig et al., 2012; Foster et al., 2014; Morin and Liebhold, 2015; Case et al., 2017). In southern Appalachian forests, complete mortality of *T.*

canadensis from HWA infestation typically occurs after six years (Elliott and Vose, 2011; Ford et al., 2012), and *T. canadensis* and *Rhododendron maximum* L. often co-occur (Elliott and Swank, 2008; Narayanaraj et al., 2010; Webster et al., 2012).

Rhododendron maximum is an evergreen, ericaceous shrub that is largely self-replacing due to its clonal reproduction strategy (Elliott and Vose, 2012). It occurs primarily in riparian or cove forests, it is highly shade tolerant, forms a dense subcanopy layer that strongly attenuates light incident on the forest floor (Clinton, 2003), and reduces soil moisture and temperature (Cofer et al., 2018). As a result, it has little to no herbaceous or woody cover (henceforth, herbaceous-layer) below its

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canopy (Clinton, 1995; Beckage et al., 2000), and it strongly reduces tree seedling recruitment (Hille Ris Lambers and Clark, 2003; Beier et al., 2005). Over time, a thick recalcitrant organic soil layer accumulates under these shrubs (Monk et al., 1985), soil zinc concentrations can be high (Nilsen et al., 2001), and soil nitrogen availability to non-ericaceous species decreases (Wurzburger and Hendrick, 2007, 2009). Recent evidence suggests that this shrub expands considerably following canopy disturbances, such as the *Castanea dentata* (Marsh.) Borkh. mortality in the mid-1930s due to the chestnut blight (Elliott and Vose, 2012), and *T. canadensis* mortality more recently (Ford et al., 2012; Pfennigwerth et al., 2018a,b). While tree seedling recruitment has also responded positively to these canopy disturbances (Ford et al., 2012), over the long-term *R. maximum* has limited recruitment of these trees into the canopy. Thus, in the southern extent of the HWA infestation range, forest dynamics following *T. canadensis* mortality may become increasingly dominated by *R. maximum* (Ford and Vose, 2007; Kincaid and Parker, 2008; Roberts et al., 2009; Ford et al., 2012), likely leading to permanently altered forest structure.

Active and adaptive management strategies will be required to transform degraded riparian forests into more diverse future forests (Folke et al., 2004, 2010; Vose et al., 2013; Messier et al., 2015; Kern et al., 2017; Webster et al., 2018). Science-based restoration methods to aid land-managers in the recovery of forest structure, function, and diversity are needed. Responding to this need, we conducted a *R. maximum* and organic soil (soil O-horizon) removal experiment in riparian corridors once dominated by *T. canadensis*. We hypothesized that the removal of *R. maximum* would: (1) increase incident light on the herbaceous-layer, and soil temperature and moisture; (2) increase understory plant diversity, with a more rapid response in sites with removal of both the shrub layer and the soil O-horizon; and (3) increase tree seedling and herbaceous species recruitment due to greater light and soil moisture. We explored these hypotheses using two approaches: one, a replicated experimental plot-level test; and the other, an operational implementation trial at the stream reach scale (3 ha).

2. Methods

2.1. Site descriptions

We conducted our study at two locations, representing two different spatial and sampling scales, Coweeta Hydrologic Laboratory (replicated plots) and White Oak Creek watershed (300-m stream reaches). Both lie in the Nantahala Mountain Range of western North Carolina, USA, within the Blue Ridge Physiographic Province, near the southern end of the Appalachian Mountain chain (Fig. 1). Soils are deep sandy loams and are underlain by folded schist and gneiss. Two soil orders are found within both locations, immature Inceptisols and older developed Ultisols. Soil types include the Cullasaja-Tuckasegee complex along the stream channel and the Edneyville-Chestnut complex and Plot fine sandy loams on the uplands (Thomas, 1996). Both locations had similar characteristics in terms of high density of *R. maximum* < 3 m height and dead *T. canadensis* (Table 1); all *T. canadensis* trees were dead at the time of this study. The remaining live overstory included deciduous trees of *Acer rubrum* L., *Liriodendron tulipifera* L., *Betula lenta* L., *Quercus montana* Willd., *Quercus rubra* L., and *Carya* spp.

For the replicated plot-scale experiment, we selected areas within the Coweeta Hydrologic Laboratory (CWT, latitude 35°03'N, longitude 83°25'W). Prior to mortality, *T. canadensis* comprised 52% of the overstory basal area (Table 1). Plots were located in mesic, riparian areas with low-to-moderate slopes (< 30%) and across an elevation range from 760 to 1060 m (Fig. 1a, inset). Mean annual temperature is 12.6 °C; and seasonally ranges 3.3–21.6 °C, with abundant rainfall (ca. 1800 mm annual mean) (Laseter et al., 2012).

For the operational stream reach-scale, we selected three perennial 2nd order streams within the White Oak Creek watershed (WOC, 35°20'N latitude, 83°58'W longitude), approximately 21 km north-west

of CWT (Fig. 1). For each stream reach, sampled areas were along a 300 m reach. For these stream reaches, dead *T. canadensis* comprised 40% of the overstory basal area and the *R. maximum* subcanopy was dense (Table 1, Fig. 2a). The three stream reaches were located on Holloway Branch, Split Whiteoak Branch, and Kit Springs. Across reaches, slopes are moderate (30–60%) and elevation ranges from 1160 to 1390 m. The climate at WOC is similar to CWT, but cooler and with more precipitation (ca. 1900 mm annual rainfall, mean annual temperature is 10.8 °C).

2.2. Experimental design

We used a Before–After/Control–Impact experimental design (BACI) (van Mantgem et al., 2001) with four treatments implemented at the replicated plot-scale at CWT and three treatments implemented at the stream reach-scale at WOC. Only three treatments were implemented at WOC because of adverse weather conditions. The four treatments were designed to (1) remove only the soil O-horizon (i.e., forest floor, hereafter, FF), (2) remove only the *R. maximum* subcanopy (hereafter, CR), (3) remove *R. maximum* subcanopy and soil O-horizon (hereafter, CFFR), and (4) untreated, no removal (reference, hereafter, REF). The CR and CFFR treatments included cutting *R. maximum* followed by immediate application of herbicide on cut stumps (Romancier, 1971; Esen and Zedaker, 2004; Harrell, 2006). The herbicide was a triclopyr amine (Garlon 3A®, DOW AgroSciences, Indianapolis, IN) formulation (44.4% Triclopyr Triethylamine Salt) with an aquatic label mixed to a ratio of 50% herbicide/50% water. *Rhododendron maximum* cutting (CR, CFFR) occurred in spring (March–May) 2015 (Fig. 2b), and the prescribed fires (FF, CFFR) were implemented in spring (March) 2016 (Fig. 2c). Prescribed fires were hand lit across plots at CWT and across the entire delineated stream reach (3 ha) at WOC (see below). The fire technique included backfires along the upper ridge and ignitions at 10–25 m intervals depending on slope steepness during weather conditions specified in the USDA Forest Service, Nantahala National Forest, Prescribed Burning Plan (USFS, 2011).

For the CWT location, we established sixteen 20 m × 20 m plots across the 2185 ha Coweeta Basin (Fig. 1a, inset). Six of the 16 plots have been monitored for vegetation dynamics, carbon and nutrient pools and fluxes, and soil solution chemistry since 2004 (Nuckolls et al., 2009; Knoepp et al., 2011; Ford et al., 2012). We established 10 additional plots with similar characteristics, and then, randomly selected among the 16 plots to apply the treatments resulting in four replicates of each treatment.

For each of the stream reaches at the WOC location, we delineated a 300 m length, 50 m width on each side of the stream as the treated area (3 ha, Fig. 1b, inset). Each stream reach received one of three treatments: Holloway (CR), Split Whiteoak (CFFR), and Kit Springs (REF). WOC did not have a FF treatment. Within each stream reach, we established six transects (three on each side of the stream) extending from stream edge to the 50 m boundary. Transects were arrayed perpendicular to, and on each side of, the stream; and at least 50 m apart. We placed two 20 m × 20 m plots along (or near) each transect line with 10 m distance between plots, for a total of 12 plots per stream reach. A fourth stream reach was selected for this study to receive a prescribed fire (Rocky Bald, FF); however, the fire was not implemented due to adverse weather conditions.

2.3. Microenvironment measurements

To characterize microenvironmental responses to treatments, we measured incident light, i.e., photosynthetically active photon flux density (Q_p , $\mu\text{mol m}^{-2} \text{s}^{-1}$) and soil water content (θ , %) in each plot in the growing season months (June–August) of each year. At CWT, automated sub-hourly θ and soil temperature (T_{soil} , °C) measurements were taken and averages were recorded hourly (CS655, Campbell Scientific Inc., Logan, UT). Probes were placed in the soil to span

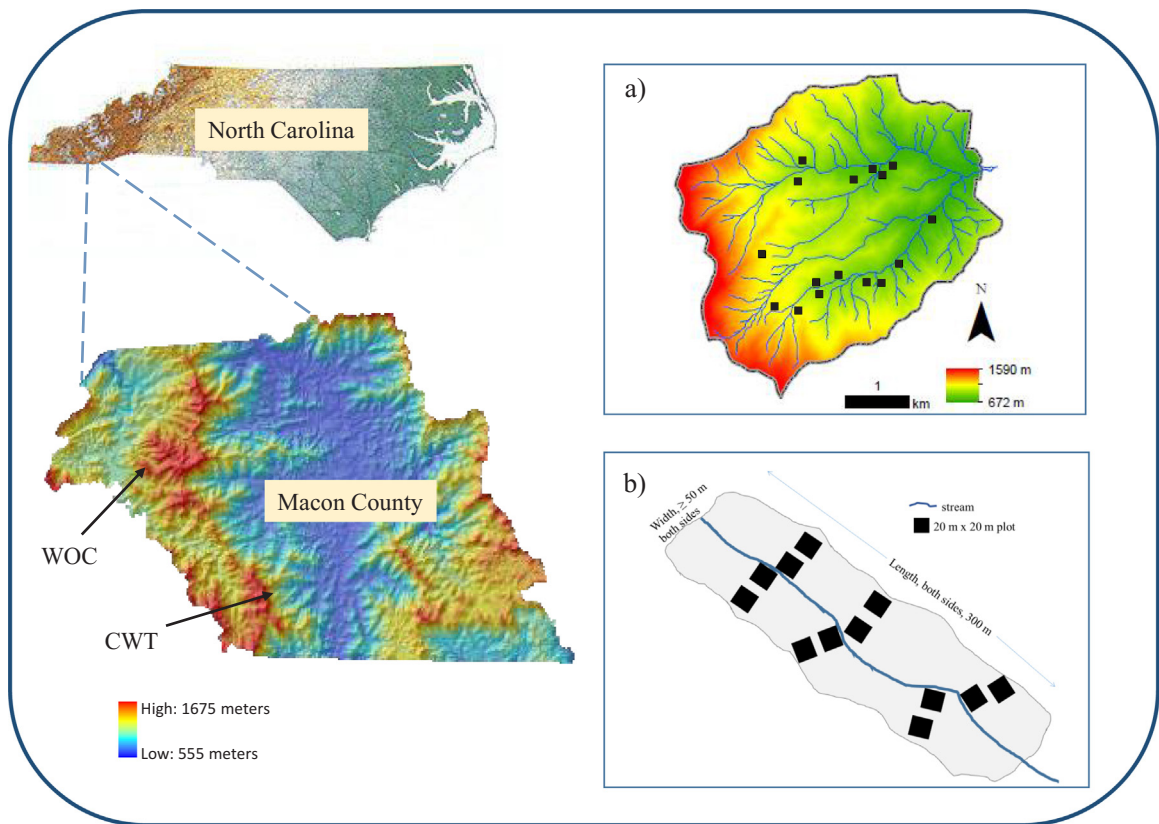


Fig. 1. Locations of Coweeta Hydrologic Laboratory (CWT) and the White Oak Creek (WOC) watershed in Macon County, western North Carolina, the southern end of the Appalachian Mountain chain. Macon County is color coded by elevation derived from a Digital Elevation Model (deq.nc.gov). Insets show plot placements for: a) CWT, plot locations (black squares) across the Coweeta Basin (20 m × 20 plots are shown for visibility, size is not to map scale); and b) WOC, stream reach design, a 3-ha treatment area including the 20 m × 20 m plot layout for all stream reaches.

Table 1
Mean (± se) density (stems ha⁻¹) and basal area (m² ha⁻¹) of dead *Tsuga canadensis*, live *Rhododendron maximum*, and live deciduous trees before (2014) the treatments were implemented at both locations (CWT, Coweeta; WOC, White Oak Creek).

	CWT		WOC	
	Density	Basal area	Density	Basal area
<i>Tsuga canadensis</i> (dead)	458 (76)	23.21 (1.85)	378 (33)	16.67 (1.49)
<i>Rhododendron maximum</i>				
Stems ≥ 2.5 cm dbh	2255 (155)	6.96 (0.68)	3125 (171)	5.29 (0.30)
Stems < 2.5 cm dbh	5070 (656)	0.40 (0.05)	10,473 (824)	0.82 (0.06)
Total live deciduous overstory [§] (trees ≥ 2.5 cm dbh)	494 (67)	21.01 (1.81)	860 (72)	25.24 (1.28)

[§] Dominant deciduous trees included *Acer rubrum*, *Liriodendron tulipifera*, *Betula lenta*, *Quercus montana*, *Quercus rubra*, and *Carya* spp.

7.5–20.5 cm mineral soil depth. All lead wires were connected to data loggers with a multiplexer peripheral (AM25T, Campbell Scientific Inc., Logan, UT). Q_i was measured using GaAsP photodiodes calibrated annually against a commercial quantum sensor (described in [Ford et al., 2012](#)). Probes and photodiodes were arrayed in an alternating grid pattern throughout each plot; photodiodes were placed at 1 m above ground level. Sensors were queried every 60 s and 15 min averages were logged. To characterize the change in incident light over time, we calculated light transmittance (Q_i/Q_o), where Q_o ($\mu\text{mol m}^{-2} \text{s}^{-1}$) was measured at an open-field climate station located approximately 2 km

from the plots. To compare light transmittance across locations, we extracted Q_i and Q_o values between 1100 and 1400 EST for the growing season months. We also provide the continuous measurements for all months in Supplementary Fig. A1.

At WOC, we measured Q_i and θ at four equidistant points along a diagonal transect within each plot. Q_i ($\mu\text{mol m}^{-2} \text{s}^{-1}$) was measured with a portable light meter (Sunfleck Ceptometer, Decagon Devices, Pullman, WA). We calculated light transmittance as fractional Q_i/Q_o , where Q_o ($\mu\text{mol m}^{-2} \text{s}^{-1}$) was measured every 30 min in a nearby open field also with a Sunfleck Ceptometer. Q_i and Q_o measurements were taken between 1100 and 1400 EST. θ (%) was measured by time domain reflectometry (Hydrosense II, Campbell Scientific Inc., Logan UT) integrated across 0–30 cm soil depth. Microenvironment measurements were taken over the growing season months and monthly values were averaged as a growing season estimate per plot.

2.4. Vegetation sampling

All vascular plants were measured pre-treatment during plot establishment (2014), and in the first and second growing seasons after treatments were complete, July 2016 and 2017. The herbaceous-layer included a percent cover estimate for woody stems < 0.5 m height and all herbaceous species in 1.0 m² quadrats with 4 per plot at CWT and 2 per plot at WOC. Quadrats were located within the plot at 2-m from the plot boundary. Percent cover of herbaceous-layer species was visually estimated using a scale that emphasizes intermediate accuracy ([Gauch, 1982](#)): 1% intervals from 1 to 5%, 5% intervals from 5 to 20%, and 10% intervals above 20%. In addition, tree seedlings (≤ 0.5 m height) and saplings (< 2.5 cm diameter at breast height (dbh), 1.37 m above ground), > 5 m height) were counted in a 1-m × 20-m transect nested within each plot at both locations. All tree seedlings were assumed to be

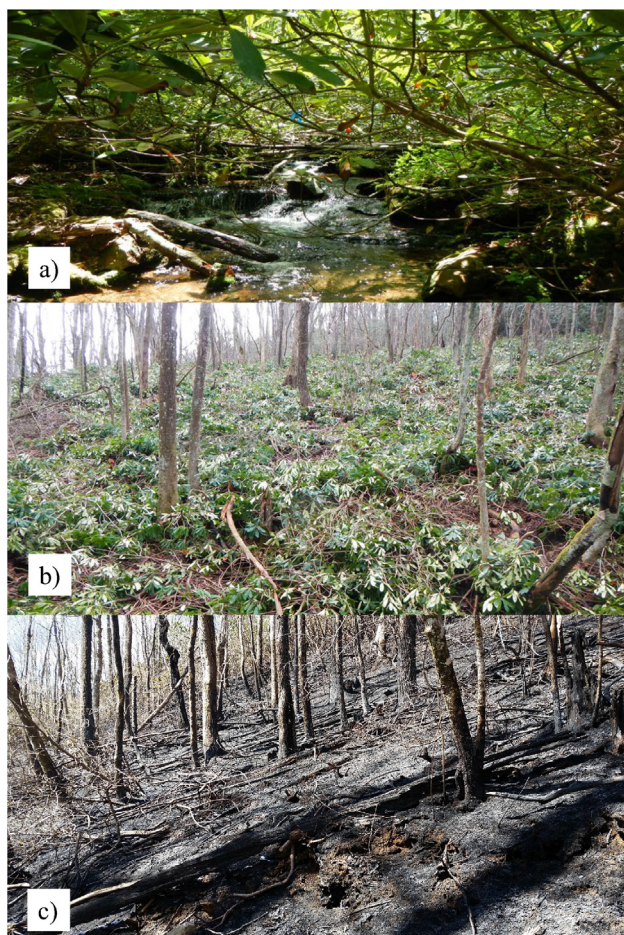


Fig. 2. The CFFR treatment site at White Oak Creek operational trial: a) before treatment, dense *Rhododendron maximum* covered the entire stream reach site (September 2014), b) after *R. maximum* was cut (March 2015), and c) after the prescribed fire (April 2016). Photos taken by Joel Scott.

seed origin because no tree species were cut (i.e., no stump sprouts), *Robinia pseudoacacia* is the only tree species that could root sprout. Nomenclature for tree species follows Kirkman et al. (2007) and for all other species follows Gleason and Cronquist (1991). In each plot and treatment, herbaceous-layer species diversity (alpha diversity) was evaluated using species richness as a measure of diversity and Shannon-Wiener's diversity index (H'), which incorporates both richness and evenness (Magurran, 2004). H' was calculated based on percent cover (H'_{cover}). Species richness and H'_{cover} were calculated for each plot per treatment.

2.5. Statistical analyses

To test for treatment differences in herbaceous-layer vegetation and microenvironment, we used a mixed linear model with repeated measures (PROC MIXED, SAS 9.4, 2002–2012) for each parameter (θ , T_{soil} and Q_i/Q_o , herbaceous-layer cover, H'_{cover} , and richness, and tree seedlings). Plot was the subject, treatment was analyzed as between-subject effects, and year as the repeated factor. We used the compound symmetric covariance option in the repeated statement because it produced the smallest value for the Akaike's Information Criterion (AIC) and Schwarz' Bayesian Criterion (SBC) (Littell et al., 2004). Degrees of freedom were approximated using Satterthwaite's formula (Littell et al., 2004). If overall F -tests were significant then least squares means tests (LS-means, Tukey-Kramer adjusted t -statistic) were used to evaluate pairwise differences. Because our hypotheses were directional, we used one-tailed hypothesis tests and considered parameters with p -

Table 2

Repeated measures mixed model analyses for subcanopy microclimate (light transmittance (Q_i/Q_o), soil water content (θ), and soil temperature (T_{soil}), and herbaceous-layer cover, Shannon's diversity (H'_{cover}), species richness, and tree seedling (stems ≤ 0.5 m height) density. Models included three years (pre-treatment (2014) and the first (2016) and second (2017) growing seasons post-treatment), and four treatments (FF, forest floor (soil O-horizon) removal; CR, *Rhododendron maximum* removal; CFFR, *R. maximum* and forest floor (soil O-horizon) removal; and REF, reference). Separate models are provided for the replicated plot-scale experiment at Coweeta (CWT) and the operational stream reach-scale at White Oak Creek (WOC). Values are degrees of freedom for the numerator and denominator (ndf , ddf), F -statistic and probability (P).

Parameters	CWT			WOC [§]		
	ndf , ddf	F	P	ndf , ddf	F	P
Q_i/Q_o						
Year	2, 24	15.16	< 0.0001	2, 66	21.38	< 0.0001
Treatment	3, 12	1.42	0.1425	2, 33	17.32	< 0.0001
Year * treatment	6, 24	1.29	0.1489	4, 66	9.27	< 0.0001
θ						
Year	2, 24	5.71	0.0047	2, 64.6	1.95	0.0755
Treatment	3, 12	1.57	0.1245	2, 33.2	0.93	0.2021
Year * treatment	6, 24	0.77	0.3012	4, 64.6	1.55	0.0985
$T_{\text{soil}}^{\dagger}$						
Year	2, 24	17.19	< 0.0001			
Treatment	3, 12	0.19	0.4512			
Year * treatment	6, 24	2.9	0.0144			
Herbaceous-layer cover						
Year	2, 24	1.66	0.1058	2, 66	27.53	< 0.0001
Treatment	3, 12	0.86	0.2442	2, 33	0.85	0.2175
Year * treatment	6, 24	2.44	0.0276	4, 66	7.02	< 0.0001
H'_{cover}						
Year	2, 24	5.83	0.0043	2, 66	12.21	< 0.0001
Treatment	3, 12	2.37	0.0611	2, 33	0.29	0.3762
Year * treatment	6, 24	0.80	0.2910	4, 66	3.24	0.0087
Species richness						
Year	2, 24	16.58	< 0.0001	2, 66	49.05	< 0.0001
Treatment	3, 12	2.54	0.0526	2, 33	1.34	0.1375
Year * treatment	6, 24	1.93	0.0582	4, 66	4.15	0.0024
Tree seedlings						
Year	2, 24	5.31	0.0061	2, 66	33.11	< 0.0001
Treatment	3, 12	1.51	0.1308	2, 33	8.93	0.0004
Year * treatment	6, 24	1.50	0.1106	4, 66	6.56	0.0001

[§] The FF, forest floor (soil O-horizon) removal treatment could only be tested within the CWT location, WOC did not have a FF treatment.

[†] T_{soil} could only be tested within the CWT location, T_{soil} was not measured at WOC.

values ≤ 0.05 statistically significant. We provided separate models for each location because they had different spatial sampling scales.

3. Results

3.1. Replicate plot-level experiment at Coweeta (CWT)

3.1.1. Microclimate

At CWT, light transmittance (Q_i/Q_o) was similar across plots prior to treatment (Table 2, $p > 0.05$, Fig. 3a); and increased with *R. maximum* removal, confirming the first part of our first hypothesis. Prior to treatment, Q_i/Q_o was low under the evergreen shrub canopies, averaging less than 3% of open conditions at mid-day during the growing season (Fig. 3a). After treatment, Q_i/Q_o was significantly higher ($> 40\%$, $p < 0.05$) in the dormant season and spring months for CR and CFFR (Fig. A1).

While we expected both soil moisture and temperature to increase with *R. maximum* removal, only soil temperature significantly increased over time, partially confirming the second part of our first hypothesis. Soil water content (θ) was generally high across plots, averaging 26%

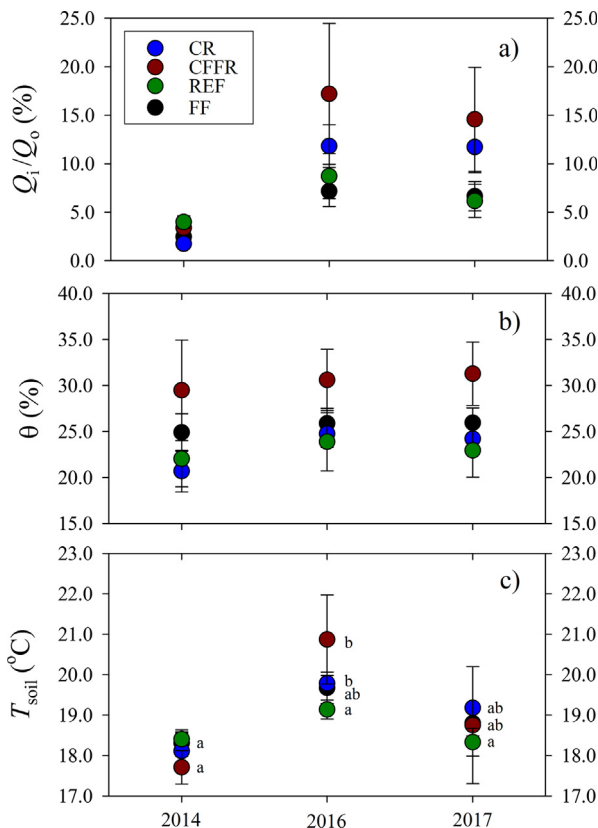


Fig. 3. Coweeta (CWT) subcanopy microclimate: (a) mean ($\pm$ se) light transmittance (Q_i/Q_o), (b) mean ($\pm$ se) soil water content, and (c) mean ($\pm$ se) soil temperature (T_{soil}). Years were pre-treatment (2014) and post-treatment (2016, 2017) for the data collected midday (between 1100 and 1400 h, EST) in growing season months (June–August). Four treatments were FF, forest floor (soil O-horizon) removal; CR, *Rhododendron maximum* removal; CFFR, *R. maximum* and soil O-horizon removal; and REF, reference. Different letters denote significant ($P < 0.05$) differences among treatments and years.

during the growing season, didn't vary over time, and treatment had no significant effect on θ (Fig. 3b, $p > 0.05$). Prior to treatment, T_{soil} in the growing season months was similar across all plots, averaging 18 ± 0.2 °C (Fig. 3c). After treatment, T_{soil} increased by 1 °C in CR and 2 °C CFFR (2014 vs. 2016, CR, $t_{23.5} = 3.44$, $p = 0.036$; CFFR, $t_{23.5} = 6.51$, $p < 0.001$), until the second growing season (2016 vs. 2017, CR, $t_{23.5} = -1.25$, $p = 0.489$; CFFR, $t_{23.5} = -4.37$, $p = 0.004$) when T_{soil} declined.

3.1.2. Herbaceous-layer responses

At CWT, herbaceous-layer cover was similar among all plots prior to treatment (2014) and during the first growing season after (2016) treatments were implemented ($p > 0.05$, Tables 2, 3). By the second growing season (2017), herbaceous-layer cover increased with *R. maximum* removal. Between 2014 and 2017, cover was significantly greater in CR ($t_{24} = 3.28$, $p = 0.049$); while CFFR ($t_{24} = 0.10$, $p = 0.500$), FF ($t_{24} = 0.07$, $p = 0.500$) and REF ($t_{24} = 0.16$, $p = 0.500$) did not change over time (Table 4). H'_{cover} was similar among treatments before and after treatment ($p > 0.05$, Tables 2, 3). In contrast, species richness increased for CR (2014 vs. 2016, $t_{24} = 4.27$, $p = 0.006$; 2014 vs. 2017, $t_{24} = 3.99$, $p = 0.011$) (Table 3). Burning the plots to remove only the soil O-horizon (FF) did not increase herbaceous-layer cover, H'_{cover} , or species richness (for all comparisons $p > 0.05$, Table 3). Cover of herbaceous plants (i.e., forbs + ferns + grasses) was low ($2.1 \pm 1.0\%$) before treatment, and did not increase ($p > 0.05$) after treatment (Table A1).

3.1.3. Tree seedling responses

Tree seedling density was low, and similar among all plots prior to treatment (1.4 ± 0.3 seedlings m^{-2} , $p > 0.05$, Tables 2, 3). At CWT, there was no significant differences among treatments in the first or second growing seasons after treatment ($p > 0.05$, Table 3).

3.2. Operational trial at the stream reach-scale (WOC)

3.2.1. Microclimate

At WOC, light transmittance (Q_i/Q_o) was less than 3% of open condition and similar across plots prior to treatment ($p > 0.05$, Fig. 4a). After treatment, Q_i/Q_o increased in the CFFR site averaging more than 25% (2014 vs. 2016, $t_{66} = 7.16$, $p < 0.001$; 2014 vs. 2017, $t_{66} = 7.79$, $p < 0.001$) (Fig. 4a), but not in the CR site (2014 vs. 2016, $t_{66} = 1.14$, $p = 0.482$; 2014 vs. 2017, $t_{66} = 2.00$, $p = 0.276$). In 2017, the CFFR site had significantly higher Q_i/Q_o than the CR ($t_{80.7} = 5.01$, $p < 0.001$) and REF ($t_{80.7} = 6.33$, $p < 0.001$) sites. Soil water content (θ) averaged 35% across the WOC sites during the growing season, and didn't vary over time. Soils were consistently wetter at the WOC sites than CWT across all years (Figs. 3b, 4b).

3.2.2. Herbaceous-layer responses

At WOC, herbaceous-layer cover was similar among all plots prior to treatment (2014) and during the first growing season after (2016) treatments were implemented ($p > 0.05$, Tables 2, 3). By the second growing season (2017), herbaceous-layer cover increased with *R. maximum* removal. Between 2014 and 2017, cover was significantly greater in CR ($t_{66} = 3.36$, $p = 0.017$) and CFFR ($t_{66} = 6.92$, $p < 0.001$), while REF ($t_{24} = 0.16$, $p = 0.500$) did not change over time (Table 4). H'_{cover} and species richness were similar prior to treatment ($p > 0.05$, Tables 2, 3); and increased with *R. maximum* removal, confirming our second hypothesis. H'_{cover} increased in both post-treatment years for CR (2014 vs. 2016, $t_{66} = 3.91$, $p = 0.003$; 2014 vs. 2017, $t_{66} = 4.57$, $p < 0.001$) and not until the second growing season for CFFR (2014 vs. 2017, $t_{90} = 3.27$, $p = 0.021$) (Table 3). In contrast, species richness increased in both years for both CR (2014 vs. 2016, $t_{66} = 6.00$, $p < 0.001$; 2014 vs. 2017, $t_{66} = 6.88$, $p < 0.001$) and CFFR (2014 vs. 2016, $t_{66} = 4.68$, $p < 0.001$; 2014 vs. 2017, $t_{66} = 7.03$, $p < 0.001$) (Table 3). The pattern of a more rapid increase in H'_{cover} in plots with only the *R. maximum* subcanopy removed (CR) compared to both the *R. maximum* subcanopy and soil O-horizon removed (CFFR), and similar temporal patterns in cover and richness for both CR and CFFR was contradictory to our expectations. Across locations, herbaceous-layer cover increased with increasing Q_i/Q_o ($r^2 = 0.224$, $p < 0.001$, Fig. 5a) and θ ($r^2 = 0.128$, $p < 0.001$, Fig. 6a). H'_{cover} ($r^2 = 0.136$, $p < 0.001$) and species richness ($r^2 = 0.213$, $p < 0.001$) were related to Q_i/Q_o (Fig. 5b, c). Neither H'_{cover} nor species richness were related to θ in any year (Fig. 6b, c). Herbaceous species that recruited into these removal plots included *Amphicarpaea bracteata*, *Dichanthelium* spp., *Carex* spp., *Erechtites hieracifolia*, and *Lysimachia quadrifolia*, and those that increased by more than 1.0% cover were *Medeola virginiana*, *Dennstaedtia punctilobla*, and two woody species *Gaylussacia ursina* and *Rubus* sp. (Table A1).

3.2.3. Tree seedling responses

At WOC, tree seedling density was low, and similar before treatment across sites (1.9 ± 0.3 seedlings m^{-2} , $p > 0.05$), increased more than 10-fold in the CR and CFFR sites after treatment, and increases were sustained over time (Tables 2, 3). In 2017, tree seedling density was greater at the CR ($t_{76.6} = 5.36$, $p < 0.001$) and CFFR ($t_{76.6} = 4.65$, $p < 0.001$) treatment sites than the REF site (Table 3). Combining all plots across locations, increases in tree seedling density were related to the increased Q_i/Q_o ($r^2 = 0.102$, $p < 0.001$, Fig. 5d) created by *R. maximum* removal, with greater increases in plots with the highest θ ($r^2 = 0.256$, $p < 0.001$, Fig. 6d). Overall, tree seedling density increased with increasing Q_i/Q_o resulting from *R. maximum* removal,

Table 3

Mean ($\pm$ se) for the herbaceous-layer cover (%), Shannon's diversity (H'_{Cover}), species richness (number of species per plot), and tree seedling (stems ≤ 0.5 m height) density (stems m^{-2}); four treatments (FF, forest floor (soil O-horizon) removal; CR, *Rhododendron maximum* removal; CFFR, *R. maximum* and forest floor removal; and REF, reference); and three years (pre-treatment (2014) and the first (2016) and second (2017) growing seasons post-treatment). Separate values are provided for the replicated plot-scale experiment at Coweeta (CWT) and the operational stream reach-scale at White Oak Creek (WOC).

	CWT ($n = 4$ reps per treatment)				WOC ($n = 12$ plots per treatment site)		
	FF	CR	CFFR	REF	CR	CFFR	REF
Cover							
2014	6.38 a (1.76)	7.70 a (4.26)	8.39 a (3.11)	7.45 a (2.44)	12.01 a (1.97)	15.38 a (4.22)	21.63 a (5.73)
2016	4.08 a (1.80)	14.52 ab (4.79)	4.46 a (1.82)	11.26 a (5.29)	10.60 a (2.11)	14.78 a (4.41)	23.93 a (5.55)
2017	6.58 a (3.08)	16.72 b (6.43)	8.66 a (4.21)	7.95 a (2.10)	24.64 b (4.57)	41.43 b (9.54)	24.97 a (6.59)
H'_{Cover}							
2014	0.458 a (0.309)	1.138 a (0.325)	0.964 a (0.141)	1.268 a (0.206)	0.718 a (0.138)	1.060 a (0.210)	1.090 a (0.150)
2016	0.786 a (0.241)	1.497 a (0.222)	1.190 a (0.077)	1.438 a (0.138)	1.214 ab (0.097)	1.128 a (0.151)	1.095 a (0.156)
2017	0.752 a (0.275)	1.483 a (0.335)	0.980 a (0.081)	1.212 a (0.179)	1.297 b (0.137)	1.474 b (0.187)	1.180 a (0.150)
Richness							
2014	4.8 a (1.1)	9.0 a (2.3)	6.5 a (1.2)	8.2 a (1.0)	4.6 a (0.8)	6.4 a (1.0)	5.9 a (0.9)
2016	7.2 a (1.2)	12.8 b (2.0)	8.2 a (1.4)	9.8 a (0.8)	8.0 b (0.8)	9.1 b (0.9)	7.3 a (0.9)
2017	7.5 a (1.2)	12.5 b (1.7)	8.2 a (1.0)	8.0 a (1.1)	8.5 b (0.9)	10.4 b (1.2)	7.2 a (0.7)
Tree seedlings							
2014	0.31 a (0.12)	0.81 a (0.48)	2.69 a (0.79)	1.75 a (0.53)	1.79 a (0.55)	2.67 a (0.64)	1.38 a (0.39)
2016	1.87 a (1.07)	12.38 a (9.32)	6.45 a (2.00)	1.84 a (0.62)	16.61 b (4.20)	16.40 b (2.88)	1.92 a (0.67)
2017	2.62 a (1.15)	15.10 a (8.71)	13.93 a (5.58)	1.96 a (0.64)	27.67 b (7.12)	24.47 b (3.63)	3.50 a (0.75)

Letters denote significant ($P \leq 0.05$) pair-wise differences among years and treatments within locations.

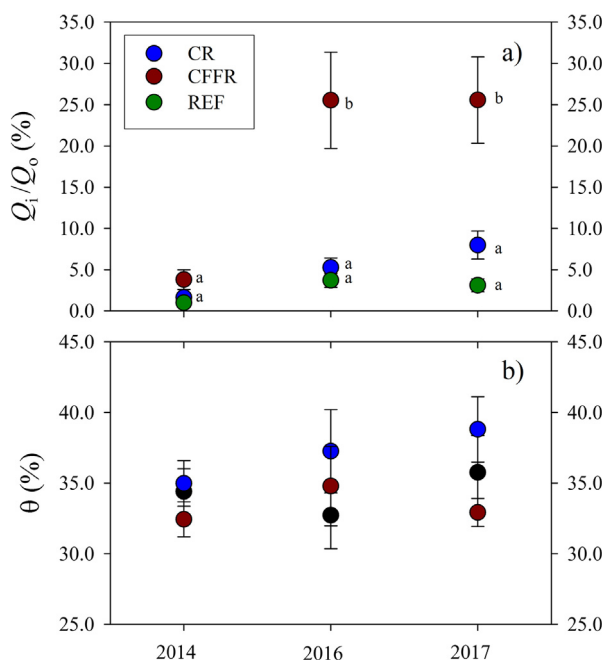


Fig. 4. White Oak Creek (WOC) subcanopy microclimate: a) mean ($\pm$ se) light transmittance (Q_i/Q_o), and b) mean ($\pm$ se) soil water content. Years were pre-treatment (2014) and (post-treatment (2016, 2017) for the data collected midday (between 1100 and 1400 h, EST) in growing season months (June–August). Three treatments were CR, *Rhododendron maximum* removal; CFFR, *R. maximum* and forest floor (soil O-horizon) removal; and REF, reference. Different letters denote significant ($P < 0.05$) differences among treatments and years.

confirming our third hypothesis (Fig. 5d).

Two growing seasons after treatment, in CR, species with the highest density ranked *Betula* spp. > *Acer rubrum* > *Quercus coccinea* > *Liriodendron tulipifera* > *Q. rubra*. In CFFR, tree seedling recruitment ranked *Betula* spp. > *A. rubrum* > *L. tulipifera*, however, *Q. coccinea* and *Q. rubra* were not abundant. Tree seedling density of any other species was low (< 0.6 seedlings m^{-2}) (see Table A2 in Supplementary material for full list).

4. Discussion

We proposed that the first step to restoring southern Appalachian riparian forests following *Tsuga canadensis* mortality would be to eliminate the evergreen shrub, *Rhododendron maximum*. In our study, we removed the dense *R. maximum* subcanopy from these deciduous forests to improve microenvironmental conditions, with and without soil O-horizon removal to increase nutrient availability and conditions that would promote regeneration of herbaceous flora and tree seedlings. The operational trial at the stream reach-scale (WOC location) showed similar responses to *R. maximum* removal as the replicated plot-scale experiment (CWT location), except that we found even greater increases in light transmittance (Fig. 4a), herbaceous-layer cover and tree seedling recruitment at the stream reach-scale treatments (Table 3). Thus, we propose that removing *R. maximum* at a larger spatial scale is even more beneficial to vegetation recovery than the plot-scale experiment suggests.

As expected, cutting the *R. maximum* subcanopy (CR and CFFR) immediately increased light transmittance in the spring months, it was reduced once the deciduous canopy leafed out, yet remained higher than areas where the subcanopy remained (FF and REF). Similarly, soil temperature increased in the growing season, but soil moisture did not. Not only did the CFFR treatment have higher light, a parallel study showed that it also had higher soil nitrogen availability (inorganic NO_3 and NH_4) than all other treatments (Osburn et al., in preparation). Direct conversion of organic nitrogen to inorganic nitrogen by fire has been found in numerous studies (e.g., Knoepp et al., 2004; Certini, 2005). However, we did not find differences between CR and CFFR in vegetation responses. While NO_3 and NH_4 increased initially following the CFFR treatment, this, in turn, resulted in an increase in soil microbial biomass and production of microbial extracellular enzymes (Osburn et al., in preparation). The net result could be that inorganic nitrogen was not yet available to herbaceous plants and tree seedlings since it was quickly immobilized by the microbial community. Longer-term, however, we would expect that nitrogen availability to plants to increase if the evergreen shrub layer is absent.

While we expected a greater response in the treatments that removed both the *R. maximum* canopy and soil O-horizon compared to the *R. maximum* removal only (CFFR vs. CR), we saw similar responses in the herbaceous-layer and tree seedling recruitment. This suggests

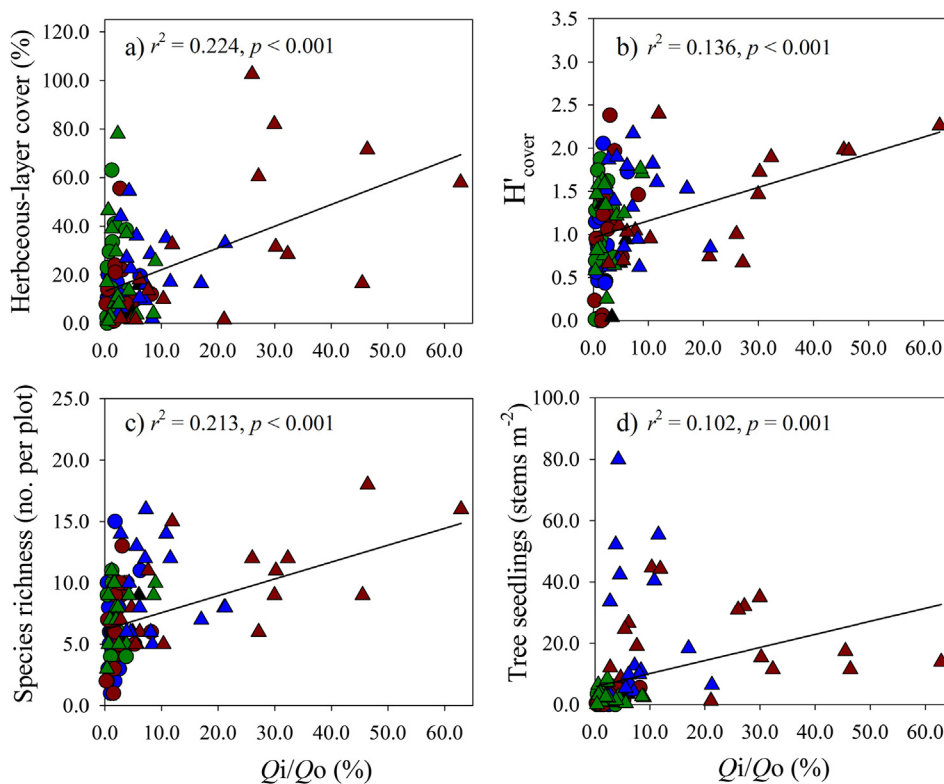


Fig. 5. Relationships between vegetation parameters (herbaceous-layer cover [a], diversity (H'_{cover}) [b]), species richness [c], and tree seedling density [d]) and light transmittance (Q_i/Q_o) across locations. Two locations were Coweeta and White Oak Creek. Four treatments were FF, forest floor (soil O-horizon) removal; CR, *Rhododendron maximum* removal; CFFR, *R. maximum* and soil O-horizon removal; and REF, reference. Symbol colors denote treatments: FF (black), CR (blue), CFFR (red), and REF (green). Symbol shapes denote years: pre-treatment (2014, circles) and two growing seasons post-treatment (2017, triangles). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

that partially removing the recalcitrant O-horizon layer did not impede recruitment or restoration in these degraded stands, that opening up the shrub subcanopy to increase light incident on the forest floor and soil temperature was more important. Equally interesting was the lack of any response in the fire treatment that was intended to only remove the soil O-horizon (FF) but left the *R. maximum* canopy in-tact. However, the prescribed fires (FF and CFFR) consumed only the soil Oi layer

during the burn (personal observation) and it was replaced by leaf fall the next year, and the soil Oe + Oa was not consumed (Table A3). In addition, Osburn et al. (in preparation) did not find an increase in available soil nitrogen (NO_3 , NH_4) following fire in the FF treatment. This suggests that managers cannot expect a single fire application to restore these forests as quickly, or at all, as removing the *R. maximum* subcanopy with a combination of cutting and herbicide application.

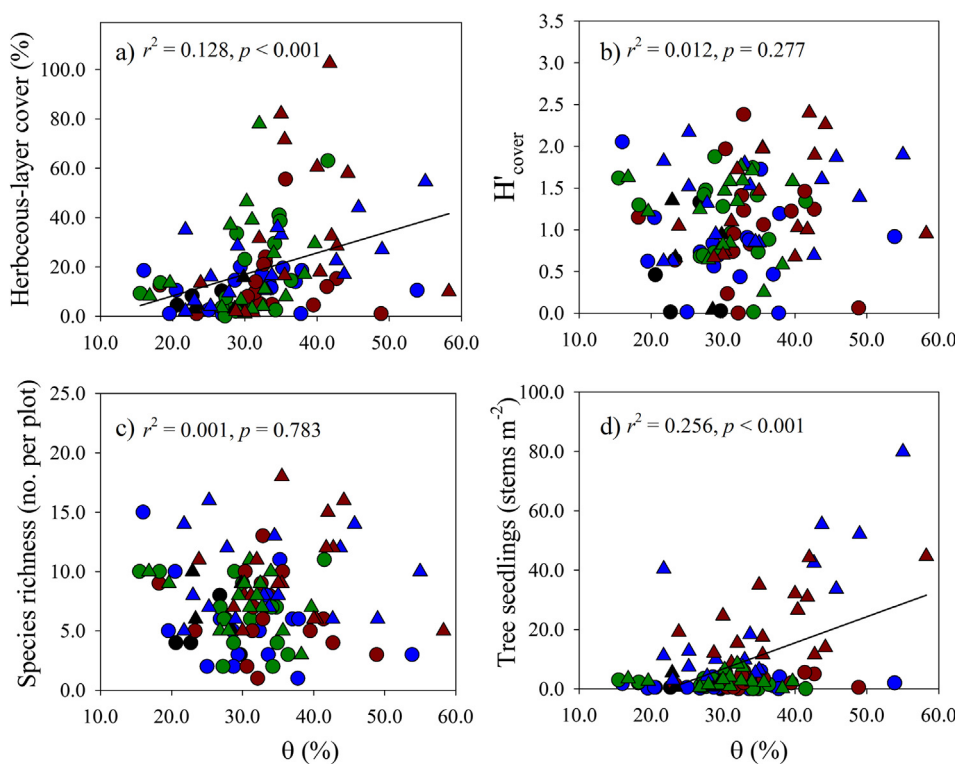


Fig. 6. Relationships between vegetation parameters (herbaceous-layer cover [a], diversity (H'_{cover}) [b], species richness [c], and tree seedling density [d]) and soil water content (θ) across locations. Two locations were Coweeta and White Oak Creek. Four treatments were FF, forest floor (soil O-horizon) removal; CR, *Rhododendron maximum* removal; CFFR, *R. maximum* and soil O-horizon removal; and REF, reference. Symbol colors denote treatments: FF (black), CR (blue), CFFR (red), and REF (green). Symbol shapes denote years: pre-treatment (2014, circles) and two growing seasons post-treatment (2017, triangles). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Few studies have attempted the removal of evergreen *R. maximum* in the eastern US (Hooper, 1969; Romancier, 1971; Yeakley et al., 2003; Harrell, 2006), or similar species in Europe (*Rhododendron ponticum*, Esen and Zedaker, 2004; Dehnen-Schmutz et al., 2004; Tyler et al., 2006; Maclean et al., 2018a, b; Manzoor et al., 2018). Only two of these studies report composition of the post-treatment vegetation (Maclean et al., 2018a; Beckage et al., 2008). Similar to our study, Beckage et al. (2008) reported seedling recruitment of *Betula lenta* and *Liriodendron tulipifera* in their treatment plot where they manually removed *R. maximum*. Their findings are limited in scope, however, as their study design only utilized one 10-m × 30-m plot with no replication, and a severe hurricane disturbance resulted in numerous pits and mounds created by windthrow (Clinton and Baker, 2000; Elliott et al., 2002) that made attributing the seedling response to *R. maximum* removal alone difficult. In our study, we found increased herbaceous-layer diversity and greater numbers of tree seedlings following the removal of the *R. maximum* subcanopy even though the deciduous overstory remained intact. While *Galussacia ursina* (6.8%) and *Rubus* sp. (4.6%) increased in cover following *R. maximum* removal (Table A1), these deciduous species are functionally different than *R. maximum* and are not as likely to preclude other species from recruiting.

As long as the deciduous overstory is intact, as in our study, tree seed dispersal is possible and some tree species maintain a viable seed bank under a *R. maximum* subcanopy for decades (Hille Ris Lambers et al., 2005; Cofer et al., 2018). For example, Cofer et al. (2018) found that the seed bank under *R. maximum* was dominated by trees (*Betula* spp., *Oxydendrum arboreum*, *Liriodendron tulipifera*) and woody shrubs (*Rubus* sp. and *R. maximum*). We found tree seedling density increased after *R. maximum* removal due to recruitment of several trees species, particularly *Betula* spp., *Acer rubrum*, *L. tulipifera*, and *Quercus*. While *Betula*, *Acer*, and *L. tulipifera* have winged, wind dispersed seeds and a persistent (> 1 year) seed bank strategy (Royo and Ristau, 2013; Cofer et al., 2018), *Quercus* does not. Regeneration of *Quercus* species depends on acorn production which is erratic (Greenberg and Parresol, 2002; Greenberg et al., 2014), large, acorn seeds tend to be locally dispersed, and animal predation can be relatively high (e.g., Schnurr et al., 2002; Garcia and Houle, 2005; Greenberg and Zarnoch, 2018). Acorn production varies among *Quercus* species, individual trees, years, locations, and weather conditions (Fearer et al., 2008), and synchronous masting (production of large seed crops by most individuals within a population) occurs at multi-year intervals (Greenberg and Parresol, 2002). In our study, 2015 was a *Quercus* mast year, where copious *Q. rubra* and *Q. coccinea* seedlings were observed across the Coweeta Basin (personal observation), including some treatment plots. Because of this serendipitous mast year, we found recruitment of *Q. rubra* and *Q. coccinea* seedlings in the CR, but not in the other treatments. The prescribed burn, in the spring of 2016, likely eliminated these new recruits from the CFFR treatment, and they could not become established under the dense *R. maximum* subcanopy of the FF and REF treatments.

In contrast to woody species, recruitment of herbaceous species may be limited due to their short distance dispersal and limited seed bank (Cofer et al., 2018). We found that some herbaceous species recruited and those that were present in low abundance before treatment increased in cover after *R. maximum* removal. These results suggest that herbaceous-layer diversity will further increase over time, particularly with continued removal of *R. maximum*. However, in the two growing seasons post-treatment, we found no recruitment of herbaceous species that are indicators of rich mesophytic coves (Elliott et al., 2014), and herbaceous-layer cover and diversity remained lower than deciduous forests without *R. maximum* (Elliott et al., 2014; Cofer et al., 2018). Maclean et al. (2018a) compared sites with *Rhododendron ponticum*, a non-native invasive in Scotland, where their sites covered a gradient in *R. ponticum* density and time since its clearing. They showed that the herbaceous-layer cover declined as *R. ponticum* density increased, and that where *R. ponticum* had been once cleared the native community did not return even after 30 years (Maclean et al., 2018a). In a companion

study, Maclean et al. (2018b) reported that an insufficient seed source was responsible for the failure of native grasses and forbs to recover following the removal of *R. ponticum*. Thus, colonization of some herbaceous plants (forbs and grasses) could take decades, depending on dispersal distance and vector (Bakker et al., 1996; Nathan et al., 2008) or their ability to build a persistent seed bank (Ozinga et al., 2005).

5. Management implications and recommendations

The effects of *Rhododendron maximum* removal on vegetation responses have rarely been studied in the southern Appalachians or elsewhere. Our study indicates that removing *R. maximum* by cutting and applying herbicide to cut stumps will increase light incident on the forest floor and soil temperature, and thereby increase herbaceous-layer diversity and tree seedling recruitment. These responses were most significant at the scale at which managers might conduct restoration treatments: the reach or landscape scale. These vegetation responses have important implications for potential recovery of riparian forests following *Tsuga canadensis* mortality. Further research and longer-term monitoring is needed to determine whether this approach will ultimately allow newly recruited seedlings to recruit into the next size class and the canopy layer.

Cutting followed by prescribed fire did not provide additional benefit in most cases, i.e., few differences between CR and CFFR treatments. While the prescribed fires consumed much of the litter layer (Oi) during the burn, it was replaced by leaf fall the next year, and in some cases, increased small wood from cutting, and thus the Oe + Oa was not consumed. Consequently, a single application of a low severity fire was not sufficient in reducing the thick recalcitrant soil O-horizon typically found under *R. maximum* subcanopies. Follow-up treatments will be necessary for continued removal of *R. maximum*. It is considered a self-replacing evergreen shrub because it reproduces both vegetatively (asexual) and from seed germination (sexual); it is a clonal plant that produces many ramets through branch layering and stem and root sprouting; and it is long-lived, an individual plant (genet) can be very old (> 120 years), whereas ramets (new stems from layering or root sprouting) are younger (Elliott and Vose, 2012). Thus, after an initial *R. maximum* clearing, successive restoration efforts such as prescribed fire, herbicide application, cutting, or a combination of all three may be required for longer-term *R. maximum* removal (Tyler et al., 2006). Continued removal of *R. maximum* would also allow for the potential regeneration of *Quercus* species because favorable mast years occur at multi-year intervals (Greenberg and Parresol, 2002; Greenberg et al., 2014). However, if repeated fire is prescribed, its timing should be coordinated with seed mast years and tree seed germination so that fire does not eliminate new recruits (Arthur et al., 2012, 2015; Frelich et al., 2015).

Soil amendments, such as NPK fertilizer or liming, may accelerate nutrient cycling and improve ecosystem function. Given the acidic soils beneath *R. maximum* shrubs (Knoepp et al., 2011, 2016; Cofer et al., 2018), it may take years to decades before the acidity is neutralized enough for establishment of herb species adapted to higher soil pH and calcium, particularly mesophytic herbs (Elliott et al., 2014). Repeated fire could further reduce the recalcitrant soil O-horizon and accelerate decomposition, subsequently releasing nutrients bound in these organic soil layers (Osburn et al., in press). Removal of the *R. maximum*-dominated subcanopy followed by successive burns may further enhance herbaceous-layer and understory diversity, whereby released nutrients can be utilized by herbaceous flora and tree seedlings, and increased herbaceous flora will create a positive feedback loop (Elliott et al., 2015).

Seed or seedling introductions may be needed to enhance herbaceous-layer diversity and restore former *Tsuga canadensis*-hardwood stands. It may take decades for some forest herbs to recruit into sites formerly occupied by *R. maximum* for the last 80+ years (Elliott and Vose, 2012). Many forest herbs have short distance seed dispersal

(Bakker et al., 1996), limited seed bank (Cofer et al., 2018; Maclean et al., 2018b) or seeds may lack their associated vector (Nathan et al., 2008; Warren et al., 2015).

Introduction of *T. canadensis* or a functional equivalent may be possible in the future (Vose et al., 2013). Once the invasive insect, HWA, has been successfully controlled (Mayfield et al., 2015; Sumpter et al., 2018), it could be possible to re-introduce *T. canadensis* into riparian forests where *R. maximum* has been removed. *Tsuga canadensis* trees have been dead for more than five years in some forest stands and no viable seeds remain because *T. canadensis* soil seed longevity is less than two years (Baskin and Baskin, 1998). However, seed and seedling banking for *T. canadensis* preservation has been ongoing for the last 12 years (Hastings et al., 2017), allowing for a seed source for potential reintroduction and restoration efforts.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.foreco.2018.08.016>.

References

- Arthur, M.A., Alexander, H.D., Dey, D.C., Schweitzer, C.J., Loftis, D.L., 2012. Refining the oak-fire hypothesis for management of oak-dominated forests of the eastern United States. *J. Forest.* 110, 257–266. <https://doi.org/10.5849/jof.11-080>.
- Arthur, M.A., Blankenship, B.A., Schorgendorfer, A., Loftis, D.L., Alexander, H.D., 2015. Changes in stand structure and tree vigor with repeated prescribed fire in an Appalachian hardwood forest. *For. Ecol. Manage.* 340, 46–61. <https://doi.org/10.1016/j.foreco.2014.12.025>.
- Bakker, J.P., Poschlod, P., Strykstra, R.J., Bekker, R.M., Thompson, K., 1996. Seed banks and seed dispersal: important topics in restoration ecology. *Acta Bot. Neerl.* 45, 461–490. <http://natuurtijdschriften.nl/record/541067>.
- Baskin, C.C., Baskin, J.M., 1998. In: *Seeds: Ecology, Biogeography and Evolution of Dormancy and Germination*. Academic Press, San Diego, CA, pp. 627.
- Beckage, B., Clark, J.S., Clinton, B.D., Haines, B.L., 2000. A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories. *Can. J. For. Res.* 30, 1617–1631. <https://doi.org/10.1139/x00-075>.
- Beckage, B., Kloeppel, B.D., Yeakley, J.A., Taylor, S.F., Coleman, D.C., 2008. Differential effects of understory and overstory gaps on tree regeneration. *J. Torrey Bot. Soc.* 135, 1–11. <https://doi.org/10.3159/07-RA-034.1>.
- Beier, C.M., Horton, J.L., Walker, J.F., Clinton, B.D., Nilsen, E.T., 2005. Carbon limitation leads to suppression of first year oak seedlings beneath evergreen understory shrubs in southern Appalachian hardwood forests. *Plant Ecol.* 176, 131–142. <https://doi.org/10.1007/s11258-004-0119-9>.
- Case, B.S., Buckley, H.L., Barker-Plotkin, A.A., Orwig, D.A., Ellison, A.M., 2017. When a foundation crumbles: forecasting forest dynamics following the decline of the foundation species *Tsuga canadensis*. *Ecosphere* 8 (7), e01893. <https://doi.org/10.1002/ecs2.1893>.
- Certini, G., 2005. Effects of fire on properties of forest soils: a review. *Oecologia* 143, 1–10. <https://doi.org/10.1007/s00442-004-1788-8>.
- Clinton, B.D., 1995. Temporal variation in photosynthetically active radiation (PAR) in mesic southern Appalachian hardwood forests with and without *Rhododendron* understories. In: Gottschalk, K.W., Fosbroke, S.L.C. (Eds.), *Proceedings 10th Central Hardwood Forest Conference*. USDA Forest Service General Technical Report NE-197, Northeastern Forest Experiment Station, Randor, PA, pp. 534–540.
- Clinton, B.D., 2003. Light, temperature, and soil moisture responses to elevation, evergreen understory, and small canopy gaps in the southern Appalachians. *For. Ecol. Manage.* 186, 243–255. [https://doi.org/10.1016/S0378-1127\(03\)00277-9](https://doi.org/10.1016/S0378-1127(03)00277-9).
- Clinton, B.D., Baker, C.R., 2000. Catastrophic windthrow in the southern Appalachians: characteristic of pits and mounds and initial vegetation responses. *For. Ecol. Manage.* 126, 51–60. [https://doi.org/10.1016/S0378-1127\(99\)00082-1](https://doi.org/10.1016/S0378-1127(99)00082-1).
- Cofer, T.M., Elliott, K.J., Bush, J.K., Miniat, C.F., 2018. *Rhododendron* maximum impedes seed bank dynamics following eastern hemlock loss in riparian forests. *Ecosphere* 9 (4). <https://doi.org/10.1002/ecs2.2204>.
- Dehnen-Schmutz, K., Perrings, C.M., Williamson, M., 2004. Controlling *Rhododendron ponticum* in the British Isles: an economic analysis. *J. Environ. Manage.* 70, 323–332. <https://doi.org/10.1016/j.jenvman.2003.12.009>.
- Elliott, K.J., Hitchcock, S.L., Krueger, L., 2002. Vegetation response to large-scale disturbance: Hurricane Opal and salvage logging in the southern Appalachians. *J. Torrey Bot. Soc.* 129, 48–59. <https://doi.org/10.2307/3088682>.
- Elliott, K.J., Swank, W.T., 2008. Long-term changes in forest composition and diversity following early logging (1919–1923) and the decline of American chestnut (*Castanea dentata*). *Plant Ecol.* 197, 155–172. <https://doi.org/10.1007/s11258-007-9352-3>.
- Elliott, K.J., Vose, J.M., 2011. The contribution of the Coweeta Hydrologic Laboratory to developing an understanding of long-term (1934–2008) changes in managed and unmanaged forests. *For. Ecol. Manage.* 261, 900–910. <https://doi.org/10.1016/j.foreco.2010.03.010>.
- Elliott, K.J., Vose, J.M., 2012. Age and distribution of an evergreen clonal shrub in the Coweeta Basin: *Rhododendron maximum* L. *J. Torrey Bot. Soc.* 139, 149–166. <https://doi.org/10.3159/TORREY-D-11-00076.1>.
- Elliott, K.J., Vose, J.M., Rankin, D., 2014. Herbaceous species composition and richness of mesophytic cove forests in the southern Appalachians: synthesis and knowledge gaps. *J. Torrey Bot. Soc.* 141, 39–71. <https://doi.org/10.3159/TORREY-D-13-00054.1>.
- Elliott, K.J., Vose, J.M., Knoepp, J.D., Clinton, B.D., Kloeppel, B.D., 2015. Functional role of the herbaceous layer in eastern deciduous forests. *Ecosystems* 18, 221–236. <https://doi.org/10.1007/s10021-014-9825-x>.
- Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von, B., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* 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).
- Esen, D., Zedaker, S.M., 2004. Control of *Rhododendron ponticum* and *R. flavum* in the eastern beech (*Fagus orientalis*) forests of Turkey. *New For.* 27, 69–79. <https://doi.org/10.1023/A:1025072105849>.
- Evans, D.M., Dolloff, C.A., Aust, W.M., Villamagna, A.M., 2012. Effects of eastern hemlock decline on large wood loads in streams of the Appalachian Mountains. *J. Am. Water Resour. Assoc.* 48, 266–276. <https://doi.org/10.1111/j.1752-1688.2011.00610.x>.
- Fearer, T.M., Norman, G.W., Pack, J.C., Bittner, S., Healy, W.M., 2008. Influence of physiographic and climatic factors on spatial patterns of acorn production in Maryland and Virginia, USA. *J. Biogeogr.* 35, 2012–2025. <https://doi.org/10.1111/j.1365-2699.2008.01960.x>.
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., Holling, C.S., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annu. Rev. Ecol. Syst.* 35, 557–581. <https://doi.org/10.1146/annurev.ecolsys.35.021103.103711>.
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., Holling, C.S., 2010. Regime shifts, resilience, and biodiversity in ecosystem management. In: Gunderson, L.H., Allen, C.R., Holling, C.S. (Eds.), *Foundations of Ecological Resilience*. Island Press, Washington, DC, pp. 119–150.
- Ford, C.R., Vose, J.M., 2007. *Tsuga canadensis* (L.) Carr. mortality will impact hydrologic processes in southern Appalachian forest ecosystems. *Ecol. Appl.* 17, 1156–1167. <https://doi.org/10.1890/06-0027>.
- Ford, C.R., Elliott, K.J., Clinton, B.D., Kloeppel, B.D., Vose, J.M., 2012. Forest dynamics following eastern hemlock mortality in the southern Appalachians. *Oikos* 121, 523–536. <https://doi.org/10.1111/j.1600-0706.2011.19622.x>.
- Foster, D.R., Baiser, B., D'Amato, A., Ellison, A.M., Orwig, D., Plotkin, A.A., Oswald, W., Thompson, J. (Eds.), 2014. *Hemlock: A Forest Giant on the Edge*. Yale University Press, New Haven, CN, pp. 305.
- Frelich, L.E., Reich, P.B., Peterson, D.W., 2015. Fire in upper Midwestern oak forest ecosystems: an oak forest restoration and management handbook. USDA Forest Service General Technical Report PNW-GTR-914, Pacific Northwest Research Station, Portland, OR, 64 p.
- Garcia, D., Houle, G., 2005. Fine-scale spatial patterns of recruitment in red oak (*Quercus rubra*): what matters most, abiotic or biotic factors? *Écoscience* 12, 223–235. <https://doi.org/10.2980/11195-6860-12-2-223.1>.
- Gauch, H.G., 1982. *Multivariate Analysis in Community Ecology*. Cambridge University Press, New York, NY, pp. 298.
- Gleason, H.A., Cronquist, A., 1991. *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*, second ed. The New York Botanical Garden, Bronx, NY, pp. 910.
- Greenberg, C.H., Parresol, B.R., 2002. Dynamics of acorn production by five species of southern Appalachian oaks. In: McShea, W.J., Healy, W.M. (Eds.), *Oak Forest Ecosystems: Ecology and Management for Wildlife*. Johns Hopkins Press, Baltimore, MD, pp. 140–172.
- Greenberg, C.H., Keyser, C.E., Rathburn, L.C., Rose, A.K., Fearer, T.M., McNab, W.H., 2014. Forecasting long-term acorn production with and without oak decline using forest inventory data. *For. Sci.* 60, 222–230. <https://doi.org/10.5849/forsci.12-106>.
- Greenberg, C., Zarnoch, S.J., 2018. A test of the predator satiation hypothesis, acorn predator size, and acorn preference. *Can. J. For. Res.* 48, 237–245. <https://doi.org/10.1139/cjfr-2017-0381>.
- Harrell, C.W., 2006. Effects of prescribed burning, mechanical and chemical treatments to

- curtail rhododendron dominance and reduce wildfire fuel loads. MS thesis, Virginia Polytechnic Institute and State University, Blacksburg, VA, 79 p.
- Hastings, J.M., Potter, K.M., Koch, F.H., Megalos, M., Jetton, R.M., 2017. Prioritizing conservation seed banking locations for imperiled hemlock species using multi-attribute frontier mapping. *New For.* 48, 301–316. <https://doi.org/10.1007/s11056-017-9575-7>.
- Hille Ris Lambers, J., Clark, J.S., 2003. Effects of dispersal, shrubs, and density-dependent mortality on seed and seedling distributions in temperate forests. *Can. J. For. Res.* 33, 783–795. <https://doi.org/10.1139/x03-001>.
- Hille Ris Lambers, J., Clark, J.S., Lavine, M., 2005. Implications of seed banking for recruitment of southern Appalachian woody species. *Ecology* 86, 85–95. <https://doi.org/10.1890/03-0685>.
- Hooper, R.M., 1969. Prescribed burning for laurel and rhododendron control in the southern Appalachians. USDA Forest Service Research Note SE-116, Southeastern Forest Experiment Station, Asheville, NC, 6 p.
- Kern, C.C., Burton, J.I., Raymond, P., D'Amato, A.W., Keeton, W.S., Royo, A.A., Walters, M.B., Webster, C.R., Willis, J.L., 2017. Challenges facing gap-based silviculture and possible solutions for mesic northern forests in North America. *Forestry* 90, 4–17. <https://doi.org/10.1093/forestry/cpw024>.
- Kincaid, J.A., Parker, A.J., 2008. Structural characteristics and canopy dynamics of *Tsuga canadensis* in forests of the southern Appalachian Mountains, USA. *Plant Ecol.* 199, 265–280. <https://doi.org/10.1007/s11258-008-9431-0>.
- Kirkman, L.K., Brown, C.L., Leopold, D.J., 2007. *Native Trees of the Southeast*. Timber Press Inc., Portland, OR, pp. 370.
- Knoepp, J.D., Vose, J.M., Swank, W.T., 2004. Long-term soil responses to site preparation burning in the southern Appalachians. *For. Sci.* 50, 540–550. <https://doi.org/10.1093/forestscience/50.4.540>.
- Knoepp, J.D., Vose, J.M., Clinton, B.D., Hunter, M.D., 2011. Hemlock infestation and mortality: impacts on nutrient pools and cycling in Appalachian forests. *Soc. Sci. Am. J.* 75, 1935–1945. <https://doi.org/10.2136/sssaj2010.0409>.
- Knoepp, J.D., Vose, J.M., Jackson, W.A., Elliott, K.J., Zarnoch, S., 2016. High elevation watersheds in the southern Appalachians: indicators of sensitivity to acidic deposition and the potential for restoration through liming. *For. Ecol. Manage.* 377, 101–117. <https://doi.org/10.1016/j.foreco.2016.06.040>.
- Laseter, S.H., Ford, C.R., Vose, J.M., Swift Jr., L.W., 2012. Long-term temperature and precipitation trends at the Coweeta Hydrologic Laboratory, Otto, North Carolina, USA. *Hydrol. Res.* 43, 890–901. <https://doi.org/10.2166/nh.2012.067>.
- Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., 2004. *SAS System for Mixed Models*, sixth ed. SAS Publishing, Cary, NC, pp. 633.
- Lovett, G.M., Weiss, M., Liebhold, A.M., Holmes, T.P., Leung, B., Lambert, K.F., Orwig, D.A., Campbell, F.T., Rosenthal, J., McCullough, D.G., Wildova, R., Ayres, M.P., Canham, C.D., Foster, D.R., LaDeau, S.L., Weldy, T., 2016. Nonnative forest insects and pathogens in the United States: impacts and policy options. *Ecol. Appl.* 26, 1437–1455. <https://doi.org/10.1016/j.foreco.2016.05.1176>.
- Macleane, J.E., Mitchell, R.J., Burslem, D.F.R.P., Genney, D., Hall, J., Pakeman, R.J., 2018a. Understorey plant community composition reflects invasion history decades after invasive rhododendron has been removed. *J. Appl. Ecol.* 55, 874–884. <https://doi.org/10.1111/1365-2664.12973>.
- Macleane, J.E., Mitchell, R.J., Burslem, D.F.R.P., Genney, D., Hall, J., Pakeman, R.J., 2018b. Seed limitation, not soil legacy effects, prevents native understorey from establishing in oak woodlands in Scotland after removal of *Rhododendron ponticum*. *Restor. Ecol.* <https://doi.org/10.1111/rec.12664>.
- Magurran, A.E., 2004. *Measuring Biological Diversity*. Blackwell Publishing, Oxford, UK, pp. 264.
- Manzoor, S.A., Griffiths, G., Lizuka, K., Lukac, M., 2018. Land cover and climate change may limit invasiveness of *Rhododendron ponticum* in Wales. *Front. Plant Sci.* 9, 664. <https://doi.org/10.3389/fpls.2018.00664>.
- Mayfield III, A.E., Reynolds, B.C., Coots, C.I., Havill, N.P., Brownie, C., Tait, A.R., Hanula, J.L., Joseph, S.V., Galloway, A.B., 2015. Establishment, hybridization and impact of *Laricobius* predators on insecticide-treated hemlocks: exploring integrated management of the hemlock woolly adelgid. *For. Ecol. Manage.* 335, 1–10. <https://doi.org/10.1016/j.foreco.2014.09.021>.
- Messier, C., Puettmann, K., Chazdon, R., Andersson, K.P., Angers, V.A., Brotons, L., Filotas, E., Tittler, R., Parrott, L., Levin, S.A., 2015. From management to stewardship: viewing forests as complex adaptive systems in an uncertain world. *Conserv. Lett.* 8, 368–377. <https://doi.org/10.1111/cons.12156>.
- Monk, C.D., McGinty, D.T., Day Jr., F.P., 1985. The ecological importance of *Kalmia latifolia* and *Rhododendron maximum* in the deciduous forest of the southern Appalachians. *Bull. Torrey Bot. Club* 112, 187–193. <http://www.jstor.org/stable/2996415>.
- Morin, R.S., Liebhold, A.M., 2015. Invasions by two non-native insects alter regional forest species composition and successional trajectories. *For. Ecol. Manage.* 341, 67–74. <https://doi.org/10.1016/j.foreco.2014.12.018>.
- Narayanaraj, G., Bolstad, P.V., Elliott, K.J., Vose, J.M., 2010. Terrain and landform influence on *Tsuga canadensis* (L.) Carrière (Eastern hemlock) distribution in the southern Appalachian Mountains. *Castanea* 75, 1–18. <https://doi.org/10.2179/08-049.1>.
- Nathan, R., Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., Tsoar, A., 2008. Mechanisms of long-distance seed dispersal. *Trends Ecol. Evol.* 23, 638–647. <https://doi.org/10.1016/j.tree.2008.08.003>.
- Nilsen, E.T., Clinton, B.D., Lei, T.T., Miller, O.K., Semones, S.W., Walker, J.F., 2001. Does *Rhododendron maximum* L. (Ericaceae) reduce the availability of resources above and belowground for canopy tree seedlings? *Am. Midland Nat.* 145, 325–343. <https://www.jstor.org/stable/3083110>.
- Nuckolls, A., Wurzbarger, N., Ford, C.R., Hendrick, R.L., Vose, J.M., Kloeppel, B.D., 2009. Hemlock declines rapidly with hemlock woolly adelgid infestation: impacts on the carbon cycle of southern Appalachian forests. *Ecosystems* 12, 179–190. <https://doi.org/10.1007/s10021-008-9215-3>.
- Orwig, D.A., Thompson, J.R., Povak, N.A., Manner, M., Niebyl, D., Foster, D.R., 2012. A foundation tree at the precipice: *Tsuga canadensis* health after the arrival of *Adelges tsugae* in central New England. *Ecosphere* 3, 1–16. <https://doi.org/10.1890/ES11-0277.1>.
- Osburn, E.D., Knoepp, J.D., Elliott, K.J., Miniat, C.F., Barrett, J.E. Soil microbial response to Rhododendron understorey removal in southern Appalachian forests: effects on extracellular enzymes. *Soil Biol. Biochem.*, in press.
- Ozinga, W.A., Schaminée, J.H.J., Bekker, R.M., Bonn, S., Poschod, P., Tackenberg, O., Bakker, J., van Groenendael, J.M., 2005. Predictability of plant species composition from environmental conditions is constrained by dispersal limitation. *Oikos* 108, 555–561. <https://doi.org/10.1111/j.0030-1299.2005.13632.x>.
- Pfennigwerth, A.A., Bailey, J.K., Schweitzer, J.A., 2018a. Trait variation along elevation gradients in a dominant woody shrub is population-specific and driven by plasticity. *AoB Plants* 9 (4), plx027. <https://doi.org/10.1093/aobpla/plx027>.
- Pfennigwerth, A.A., Van Nuland, M.E., Bailey, J.K., Schweitzer, J.A., 2018b. Plant-soil feedbacks mediate shrub expansion in declining forests, but only in the right light. *J. Ecol.* 106, 179–194. <https://doi.org/10.1111/1365-2745.12833>.
- Roberts, S.W., Tankersley Jr., R., Orvis, K.H., 2009. Assessing the potential impacts to riparian ecosystems resulting from hemlock mortality in Great Smoky Mountains National Park. *Environ. Manage.* 44, 335–345. <https://doi.org/10.1007/s00267-009-9317-5>.
- Romancier, R.M., 1971. Combining fire and chemicals for the control of rhododendron thickets. USDA Forest Service Research Note SE-149, Southeastern Forest Experiment Station, Asheville, NC, 7 p.
- Royo, A.A., Ristau, T.E., 2013. Stochastic and deterministic processes regulate spatio-temporal variation in seed bank diversity. *J. Veg. Sci.* 24, 724–734. <https://doi.org/10.1111/jvs.12011>.
- SAS Institute Inc., 2002–2012. *SAS/STAT Guide for Personal Computers*, Version 9.4, Cary, NC.
- Schnurr, J.L., Ostfeld, R.S., Canham, C.D., 2002. Direct and indirect effects of masting on rodent population and tree seed survival. *Oikos* 96, 402–410. <https://doi.org/10.1034/j.1600-0706.2002.960302.x>.
- Sumpter, K.L., McAvoy, T.J., Brewster, C.C., Mayfield III, A.E., Salom, S.M., 2018. Assessing an integrated biological and chemical control strategy for managing hemlock woolly adelgid in southern Appalachian forests. *For. Ecol. Manage.* 411, 12–19. <https://doi.org/10.1016/j.foreco.2018.01.018>.
- Tyler, C., Pullin, A.S., Stewart, G.B., 2006. Effectiveness of management interventions to control invasion by *Rhododendron ponticum*. *Environ. Manage.* 37, 513–522. <https://doi.org/10.1007/s00267-005-0127-0>.
- Thomas, D., 1996. *Soil Survey of Macon County, North Carolina*. USDA, Natural Resources Conservation Service, Washington, DC, USA.
- USFS, 2011. Nantahala Pisgah NF Forest Plan Amendments: Prescribed fire amendment 26, < http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5346291.pdf > (accessed January 5, 2018).
- van Mantgem, P., Schwartz, M.W., Keifer, M.B., 2001. Monitoring wildfire effects: coming to terms with pseudoreplication. *Nat. Areas J.* 21, 266–273. <http://pubs.er.usgs.gov/publication/1008230>.
- Vose, J.M., Wear, D.N., Mayfield III, A.E., Nelson, C.D., 2013. Hemlock woolly adelgid in the southern Appalachians: control strategies, ecological impacts, and potential management responses. *For. Ecol. Manage.* 291, 209–219. <https://doi.org/10.1016/j.foreco.2012.11.002>.
- Warren II, R.J., Pearson, S.M., Henry, S., Rossouw, K., Love, J.P., Olejniczak, M.J., Elliott, K.J., Bradford, M.A., 2015. Cryptic indirect effects of exurban edges on a woodland community. *Ecosphere* 6, 1–13. <https://doi.org/10.1890/ES15-00318.1>.
- Webster, C.R., Dickinson, Y.L., Burton, J.I., Frelich, L.E., Jenkins, M.A., Kern, C.C., Raymond, P., Saunders, M.R., Walters, M.B., Willis, J.L., 2018. Promoting and maintaining diversity in contemporary hardwood forests: Confronting contemporary drivers of change and the loss of ecological memory. *For. Ecol. Manage.* 421, 98–108. <https://doi.org/10.1016/j.foreco.2018.01.010>.
- Webster, J.R., Morkeski, K., Wojculewski, C.A., Niederlehner, B.R., Benfield, E.F., Elliott, K.J., 2012. Effects of hemlock mortality on streams in the southern Appalachian Mountains. *Am. Midland Nat.* 168, 112–131. <https://doi.org/10.1674/0003-0031-168.1.112>.
- Wurzbarger, N., Hendrick, R.L., 2007. Rhododendron thickets alter N cycling and soil extracellular enzyme activities in southern Appalachian hardwood forests. *Pedobiologia* 50, 563–576. <https://doi.org/10.1016/j.pedobi.2006.10.001>.
- Wurzbarger, N., Hendrick, R.L., 2009. Plant litter chemistry and mycorrhizal roots promote a nitrogen feedback in a temperate forest. *J. Ecol.* 97, 528–536. <https://doi.org/10.1111/j.1365-2745.2009.01487.x>.
- Yeakley, J.A., Coleman, D.C., Haines, B.L., Kloeppel, B.D., Meyer, J.L., Swank, W.T., Argo, B.W., Deal, J.M., Taylor, S.F., 2003. Hillslope nutrient dynamics following upland riparian vegetation disturbance. *Ecosystems* 6, 154–167. <https://doi.org/10.1007/s10021-002-0116-6>.