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# Effects of riparian zone buffer widths on vegetation diversity in southern Appalachian headwater catchments



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## ABSTRACT

In mountainous areas such as the southern Appalachians USA, riparian zones are difficult to define. Vegetation is a commonly used riparian indicator and plays a key role in protecting water resources, but adequate knowledge of floristic responses to riparian disturbances is lacking. Our objective was to quantify changes in stand-level floristic diversity of riparian plant communities before (2004) and two, three, and seven years after shelterwood harvest using highlead cable-yarding and with differing no-cut buffer widths of 0 m, 10 m, and 30 m distance from the stream edge. An unharvested reference stand was also studied for comparison. We examined: (1) differences among treatment sites using a mixed linear model with repeated measures; (2) multivariate relationships between ground-layer species composition and environmental variables (soil water content, light transmittance, tree basal area, shrub density, and distance from stream) using nonmetric multidimensional scaling; and (3) changes in species composition over time using a multi-response permutation procedure. We hypothesized that vegetation responses (i.e., changes in density, species composition, and diversity across the hillslope) will be greatest on harvest sites with an intermediate buffer width (10-m buffer) compared to more extreme (0-m buffer) and less extreme (30-m buffer and no-harvest reference) disturbance intensities. Harvesting initially reduced overstory density and basal area by 83% and 65%, respectively, in the 0-m buffer site; reduced by 50% and 74% in the 10-m buffer site; and reduced by 45% and 29% in the 30-m buffer site. Both the 0-m and 10-m buffer sites showed increased incident light variability across the hillslope after harvesting; whereas, there was no change in the 30-m and reference sites over time. We found significant changes in midstory and ground-layer vegetation in response to harvesting with the greatest responses on the 10-m buffer site, supporting our hypotheses that responses will be greatest on sites with intermediate disturbance. Ground-layer species composition differed significantly over time in the 0-m buffer and 10-m buffer sites (both  $P < 0.0001$ ), but did not change in the 30-m buffer and reference sites (both  $P > 0.100$ ). Average compositional dissimilarity increased after seven years, indicating greater within-stand heterogeneity (species diversity) after harvesting. These vegetation recovery patterns provide useful information for evaluating management options in riparian zones in the southern Appalachians.

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## 1. Introduction

Riparian communities are critical components of forest ecosystems (Naiman and Decamps, 1997; Verry et al., 2004), serving as the interface between terrestrial and aquatic communities (Kominoski et al., 2013; Kuglerová et al., 2014). Studies suggest that the effectiveness of a riparian zone in promoting stream and ecosystem health is strongly related to the diversity and richness of a riparian community's vegetation (Sweeney et al., 2004;

Hagan et al., 2006). More recent studies have investigated plant functional attributes (e.g., Mouillot et al., 2013), while others concluded that a diverse flora stabilizes ecosystem processes (e.g., Garnier et al., 2016); and some have linked biodiversity to ecosystem services (e.g., Durance et al., 2016). Changes to riparian plant community composition could lead to altered diversity and redundancy of plant functional trait distributions as a result of species declines (see review, Kominoski et al., 2013). In many regions, the native flora contribute to fulfill numerous stream ecosystem functions such as water quality enhancement, flood and erosion control, bank stability, wildlife uses, and in-stream root habitat (Sweeney et al., 2004; Boggs et al., 2016; Witt et al., 2016). As a result, there has been a strong push to protect riparian ecosystems

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from disturbances such as harvesting or development, through the use of buffers (Pielech et al., 2015; Cristan et al., 2016; Schilling, 2016). However, the boundaries of riparian areas are often hard to define and it can be difficult to determine acceptable buffer widths (Holmes and Goebel, 2011; Kuglerová et al., 2014), particularly for headwater streams (Alexander et al., 2007; Clinton et al., 2010).

Headwater (first- and second-order) perennial streams comprise about 50% of the total stream network length in most forest watersheds (Wipfli et al., 2007); and between 74% and 80% in the U.S. (Hill et al., 2014). Higher order stream systems may experience repeated flooding and develop terracing and alluvial deposits that can be linked directly to subsurface hydrology, geomorphology, and flood-plain development; characteristics that can be useful in delineating riparian zones (Verry et al., 2004). Characteristics of lower order streams can vary among geo-physiographic regions, and headwaters range from steep, swift, and cold montane streams to warm, low gradient streams (Meyer et al., 2007). For example, first-order streams in the U.S. Lake States can have a valley floor (from 37 to 87 m), narrow floodplains (4–16 m wide), and/or alluvial benches (Palik et al., 2012); features that easily distinguish riparian zones from the upland forest (Holmes and Goebel, 2011). In contrast, small perennial streams in montane headwater catchments often lack alluvial benches, have steeper sideslopes, and have a closed canopy cover relative to larger or low gradient streams; features that may diminish the distinction between riparian zones and the surrounding forest (Goebel et al., 2003; Dieterich et al., 2006; Hagan et al., 2006; Clinton et al., 2010). In addition, small southern Appalachian streams may not have riparian obligate vegetation communities, or riparian indicator plant species, such as seen in other regions, particularly obligate wetland species or those associated with larger tributaries (Zenner et al., 2012; De Steven et al., 2015). With the increasing emphasis on managing headwater riparian zones (Sanders and McBroom, 2013; MacDonald et al., 2014) and the differences among headwater catchments (Meyer et al., 2007; Hill et al., 2014), setting a standard sized buffer width across geo-physiographic regions becomes problematic.

In previous work on the Appalachian watersheds used in this study, Clinton (2011) concluded that a 10 m buffer width was adequate to protect water resources after upslope forest harvest; however, wider riparian buffers can potentially provide additional benefits such as wildlife corridors (Sweeney and Newbold, 2014) and unique habitat for flora and fauna (Richardson and Béraud, 2014). Riparian buffers may also influence vegetation responses in harvested watersheds outside of the buffer area by providing propagules and modifying micro-environmental changes (Dovčiak and Brown, 2014; MacDonald et al., 2014). Therefore, a better understanding of floristic responses to different riparian buffer widths can provide important information for management planning and protection of ecosystem services (Sweeney et al., 2004; Kuglerová et al., 2014; Hill et al., 2014; Sweeney and Newbold, 2014). To address this, we quantified changes in floristic composition on harvested areas that implemented three riparian buffer widths: 0 m (i.e., no riparian buffer), 10 m, and 30 m distance away from the stream edge, as well as an unharvested reference site. We hypothesized that stand-level vegetation responses (i.e., changes in density, species composition, and diversity across the hillslope) will be greatest on harvest sites with an intermediate buffer width (10-m buffer) compared to more extreme (0-m buffer) and less extreme (30-m buffer and no-harvest reference) disturbance intensities, as suggested by the intermediate disturbance hypothesis (*sensu* Connell, 1978; Biswas and Mallik, 2010). Our hypothesis is based on the premise that an intermediate-width buffer will create more heterogeneous post-harvest micro-environmental conditions that will facilitate a

greater vegetation response as measured by changes in density, species composition, and diversity.

## 2. Methods

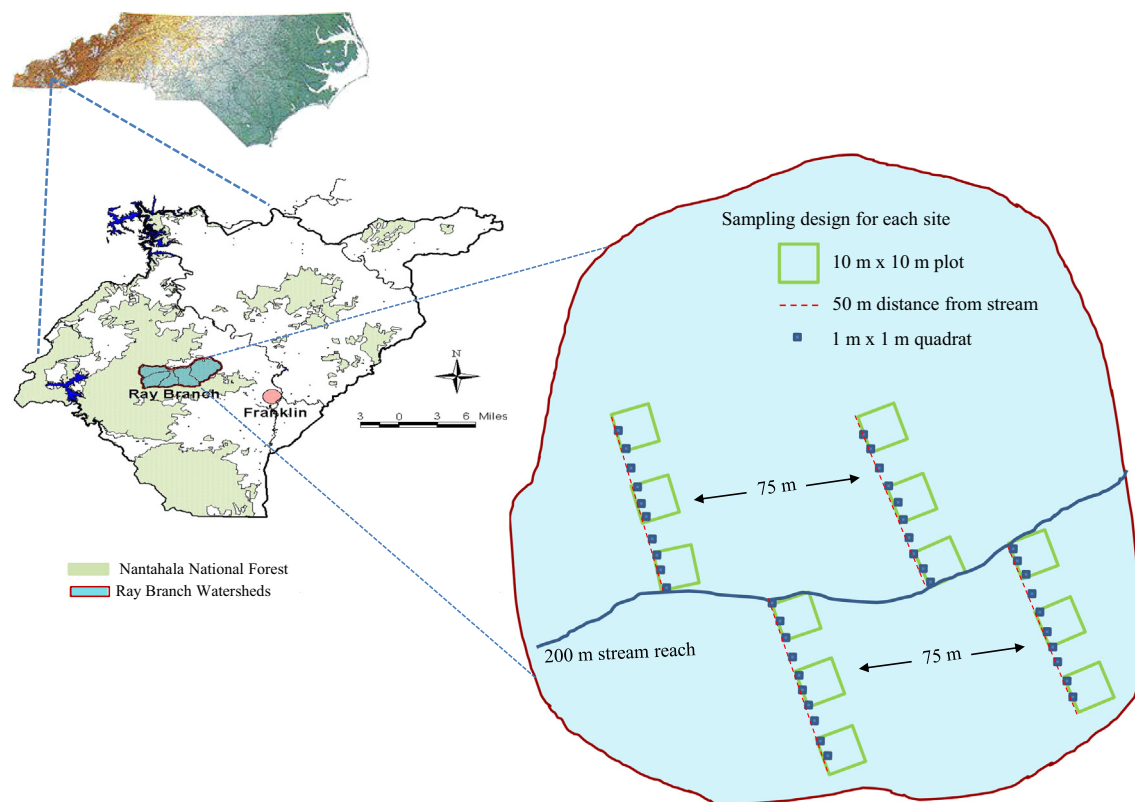
### 2.1. Site descriptions

Study sites were located in the Ray Branch watershed in the Nantahala National Forest of the Southern Appalachian Mountains in western North Carolina (35°15'N, 83°35'W). The area has abundant rainfall (mean, 1800 mm yr<sup>-1</sup>) distributed evenly throughout the year. Less than 5 percent of total annual precipitation falls as snow or ice. Mean annual air temperature is 12.6 °C ranging from 3.3 °C to 21.6 °C in January and July, respectively (Laseter et al., 2012).

Four catchments (treatment sites) with 1st order perennial streams, similar topography, soils and vegetation were selected from the Ray Branch area (Fig. 1). Catchments were east-facing, approximately 10 ha in size and had stream gradients ranging from 7 to 23%. Soils are Evard-Cowee-Saunook, mostly Saunook predominating along riparian areas, and Evard in the uplands. Saunook are fine-loamy, mixed, mesic Humic Hapludults; and Evard are loamy, oxidic, mesic Typic Hapludults (Thomas, 1996). Elevation ranges from 1000 to 1200 m. Forest composition in each of the four sites had a dense canopy with mesophytic trees including *Acer rubrum* L., *Betula lenta* L., *Carya* spp., *Liriodendron tulipifera* L., *Quercus rubra* L., and *Tsuga canadensis* (L.) Carr. (see Supplementary Table A1) with a lush and diverse herbaceous layer (see Supplementary Table A2). Midstory vegetation consisted primarily of advanced *Quercus* spp. regeneration, with scattered *Pinus strobus* L. and *Tsuga canadensis*. Although often abundant in southern Appalachian riparian areas (Vandermast and Van Lear, 2002), very few evergreen shrubs (*Rhododendron maximum* L. and *Kalmia latifolia* L.) were present on the study sites (see Clinton et al., 2010 for detailed description of pretreatment conditions).

### 2.2. Experimental treatments and measurements

Our experimental treatments were part of a commercial harvest and could not be replicated. Hence, we used a Before-After/Control-Impact experimental design (BACI) to address the concern of pseudoreplication (Stewart-Oaten et al., 1986; van Mantgem et al., 2001). Each site was assigned to one of the following uncut buffer-width treatments: 0 m (no buffer, i.e., harvesting to the stream edge), 10 m distance from the stream edge, 30 m distance from the stream edge, and an unharvested reference site that spanned a distance of 60–80 m from stream edge to ridge. Pretreatment vegetation measurements (see below) occurred in June–July 2004. The three harvest sites were designated by the Nantahala National Forest to receive a two-age shelterwood prescription using primarily cable-yarding due to steep slopes. Cable-yarding also minimizes forest floor disturbance because logs are suspended above the ground during removal (Miller and Sirois, 1986). Leave-trees at each treatment site were marked, and all remaining unmarked standing timber was felled outside the designated buffer zone. Harvesting began in October, 2005. The goal of the prescription was to leave 5 m<sup>2</sup> ha<sup>-1</sup> residual basal area; however, the resulting residual basal area across the hillslope was generally lower (Table 1). No trees were felled within the buffer zones and no losses were observed due to windthrow, ice or insects during our study period. The size of the harvested area was comparable among all treated catchments; 9.7 ha for the 0-m buffer site, 6.0 ha for the 10-m buffer site and 8.5 ha for the 30-m buffer site (Joan Brown, Nantahala Ranger District Silviculturist; personal communication).



**Fig. 1.** Study catchments were located in western North Carolina, USA, in the Ray Branch area of the Nantahala National Forest. Each catchment (site) received a different buffer-width treatment. Each site had four 50-m length transects arranged perpendicular to the stream channel, and approximately 75 m apart. Three 10-m  $\times$  10-m plots were placed along each transect from stream edge to upper slope with 10 m distance between plots, and ten 1 m  $\times$  1 m quadrats were placed at 5 m intervals from stream edge. This sampling design yielded a total of 48 plots and 160 quadrats.

**Table 1**

Overstory (trees  $\geq 2.5$  cm dbh) mean density and basal area (BA) for each treatment site before (2004) and after (2007, 2008, and 2012) treatment. Treatments sites were three harvest buffer-widths from stream: 0-m, 10-m, and 30-m buffers, and an uncut reference site. Plots within sites were classed by distances from the stream edge (near-stream, mid-slope, and upper-slope). Standard errors are in parentheses.

| Treatment                    | Density (stems ha <sup>-1</sup> ) |            |            |            | BA (m <sup>2</sup> ha <sup>-1</sup> ) |              |              |              |
|------------------------------|-----------------------------------|------------|------------|------------|---------------------------------------|--------------|--------------|--------------|
|                              | 2004                              | 2007       | 2008       | 2012       | 2004                                  | 2007         | 2008         | 2012         |
| <i>Near-stream (0–10 m)</i>  |                                   |            |            |            |                                       |              |              |              |
| 0-m buffer                   | 675 (103)                         | 350 (104)  | 575 (111)  | 1475 (175) | 26.87 (8.90)                          | 14.42 (3.52) | 14.93 (3.54) | 18.47 (4.24) |
| 10-m buffer                  | 575 (48)                          | 625 (48)   | 625 (85)   | 1050 (87)  | 12.73 (3.58)                          | 13.08 (3.58) | 13.21 (3.52) | 15.27 (3.47) |
| 30-m buffer                  | 1050 (96)                         | 850 (96)   | 775 (85)   | 625 (75)   | 32.48 (13.3)                          | 32.17 (13.6) | 32.41 (14.1) | 30.44 (13.8) |
| Reference                    | 1375 (205)                        | 1275 (262) | 1325 (250) | 1400 (311) | 49.65 (16.9)                          | 48.93 (17.4) | 46.56 (18.6) | 47.10 (19.8) |
| <i>Mid-slope (20–30 m)</i>   |                                   |            |            |            |                                       |              |              |              |
| 0-m buffer                   | 975 (250)                         | 50 (29)    | 850 (272)  | 2600 (579) | 26.28 (1.68)                          | 6.64 (3.95)  | 7.42 (4.06)  | 11.35 (4.37) |
| 10-m buffer                  | 475 (75)                          | 50 (50)    | 250 (126)  | 1500 (258) | 22.51 (10.9)                          | 0.04 (0.04)  | 0.21 (0.12)  | 1.72 (0.35)  |
| 30-m buffer                  | 1075 (180)                        | 850 (64)   | 900 (71)   | 925 (95)   | 27.93 (4.48)                          | 25.59 (4.25) | 27.57 (2.71) | 27.74 (3.84) |
| Reference                    | 1025 (138)                        | 1275 (131) | 1325 (155) | 1375 (180) | 40.12 (19.0)                          | 42.54 (20.2) | 43.38 (20.3) | 45.45 (21.6) |
| <i>Upper-slope (40–50 m)</i> |                                   |            |            |            |                                       |              |              |              |
| 0-m buffer                   | 850 (96)                          | 25 (25)    | 575 (265)  | 2850 (751) | 38.11 (13.2)                          | 11.04 (11.0) | 11.75 (11.5) | 14.82 (11.4) |
| 10-m buffer                  | 500 (71)                          | 100 (41)   | 350 (87)   | 2050 (340) | 39.61 (5.25)                          | 6.57 (3.91)  | 6.86 (3.94)  | 10.22 (4.52) |
| 30-m buffer                  | 1025 (246)                        | 25 (25)    | 300 (147)  | 2600 (406) | 20.86 (5.41)                          | 0.92 (0.92)  | 0.18 (0.08)  | 2.80 (0.64)  |
| Reference                    | 1475 (328)                        | 1675 (298) | 1700 (319) | 1675 (315) | 24.50 (7.47)                          | 26.57 (7.89) | 26.89 (8.11) | 28.91 (8.81) |

Vegetation was sampled before harvest (2004) and in the second, third, and seventh growing seasons after harvest (2007, 2008, and 2012). We placed four transects per site and three 10-m  $\times$  10-m plots along each transect at 0 m, 20 m, and 40 m distances from the stream edge (hereafter, distance from stream) to inventory vegetation (Fig. 1). Vegetation was measured in layers: the overstory layer included all woody stems  $\geq 2.5$ -cm diameter at breast height (DBH, 1.37 m above ground); the midstory layer included all woody stems  $< 2.5$ -cm DBH and  $\geq 0.5$  m height; and the ground-layer included woody stems  $< 0.5$ -m height and

all herbaceous species. We measured overstory and midstory in the 10-m  $\times$  10-m plots. DBH of all overstory trees was measured to the nearest 0.1 cm and recorded by species. For the midstory, all woody stems (shrubs, vines and trees) were counted and recorded by species. All tree seedlings  $< 0.5$  m height were also counted in each 10-m  $\times$  10-m plot. We did not separate seed germinates from stump sprouts, and we did not separate the tree seedling ( $< 0.5$  m height) size class and the midstory tree sapling ( $< 2.5$  cm dbh,  $> 0.5$  m height) size class in the plot scale counts.

For the ground-layer sampling, we placed ten 1.0-m<sup>2</sup> quadrats at 5 m intervals along each 50 m transect (Fig. 1). In each quadrat, percent cover of ground flora species was estimated visually and recorded by species. Percent cover was estimated using a scale that emphasizes intermediate accuracy (Gauch, 1982): 1% intervals from 1% to 5%, 5% intervals from 5% to 20%, and in 10% intervals above 20%. Nomenclature for tree species follows Kirkman et al. (2007) and for all other species follows Gleason and Cronquist (1991). The above sampling design resulted in 12 plots for overstory, midstory and tree seedlings, and 40 ground-layer quadrats per site; a total of 48 plots and 160 quadrats.

To characterize microenvironmental responses to treatments along the hillslope gradient from near stream to upland forest, we measured light and soil moisture content in each ground-layer quadrat ( $n = 40$  per site) throughout the growing season (May–Sept) of each year. Incident light, photosynthetic active photon flux density ( $Q_i$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), was measured with a portable light meter (Sunfleck Ceptometer, Decagon Devices, Pullman, WA) 1.0 m above each quadrat. 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. Soil moisture content (SMC) was measured by time domain reflectometry (Hydrosense II soil moisture probes, Campbell Scientific Inc., Logan, UT) using 30-cm stainless steel rods.

### 2.3. Data analysis

To analyze the BACI experimental design, we used a mixed linear model with repeated measures (PROC MIXED, SAS 9.4, 2002–2012) to identify significant treatment-to-treatment differences in vegetation and microenvironment. Separate analyses were performed for each vegetative layer, i.e., overstory, midstory shrubs and vines, tree regeneration (seedlings plus saplings), and ground-layer. Distance was near-stream (0-m distance from stream edge), mid-slope (20-m distance from stream edge), and upper-slope (40-m distance from stream edge). For the ground-layer data, quadrats were assigned as near-stream (0, 5, and 10 m), mid-slope (15, 20, 25, and 30 m), and upper-slope (35, 40, and 45 m) depending on distance from stream; then, quadrat values for ground-layer cover and richness were averaged to the nearest plot ( $n = 48$  plots) as assigned above before applying subsequent analyses. In the repeated statement, for all vegetative layers, the experimental unit ('subject') was the plot within each site. Treatment (0-m buffer, 10-m buffer, 30-m buffer, and reference) and distance were analyzed as between-subject effects, and year as the 'within-subject' repeated measure. We used the unstructured covariance option in the repeated statement because it produced the largest value for the Akaike's Information Criterion (AIC) and Schwarz' Bayesian Criterion (SBC) (Littell et al., 1996). We evaluated the main effects of treatment, year, distance and their interactions. If overall F-tests were significant ( $p \leq 0.05$ ) then least squares means tests (LS-means, Tukey-Kramer adjusted  $T$ -statistic) were used to evaluate pairwise differences among year, treatment, and distance interactions.

To examine the multivariate relationships among ground-layer species composition and environmental variables, we used separate nonmetric multidimensional scaling (NMS) (Kruskal, 1964; McCune and Mefford, 1999) ordination analyses for sample years (2004, 2007, 2008 and 2012). We used percent cover of ground-layer species as the measure of abundance in the NMS analyses to explore the vegetation-environment relationships across all sites. We excluded uncommon species (i.e., <3% frequency), from the analyses to reduce noise and influence of extreme values. Variation among plots was analyzed using the Sorensen distance measure with 60 runs of real data, 50 runs of randomized data, and a

maximum of 250 iterations for each run. A three-dimensional solution was identified as optimal, with the best solution used as the starting point for the final ordination run. We report the final stress of the ordination and coefficients of determination ( $R^2$ ) for each ordination axis calculated as a proportion of the variation explained in the reduced matrix relative to that in the original matrix. Reliable solutions for ecological community data sets often have final stress values between 10 and 20 (McCune and Grace, 2002).

A secondary matrix of site environmental variables (light transmittance (fractional  $Q_i/Q_o$ ), soil moisture content, tree basal area, shrub density, and distance from stream) was used to help interpret the ordination results. In the resulting ordination biplot, labeled points indicate species or plots and line-vectors indicate environmental variables. The length of each line-vector represents the rate of change in the weighted average as inferred from the biplot, showing how much the species distributions and sites differ along that environmental variable. The most important variables are those with the longest line-vector. Monte Carlo permutations were applied to NMS analyses to determine if the strength of species sorting along the environmental variable was greater than would be expected by chance ( $P < 0.020$ ) (Crowley, 1992). We chose to graph only the environmental variables with an  $R^2 \geq 0.10$ . We used the "proportion of max" feature in PC-ORD version 5 (McCune and Mefford, 1999) in the secondary matrix to create better uniformity among the NMS graphical displays of the three years (2004, 2007, 2012).

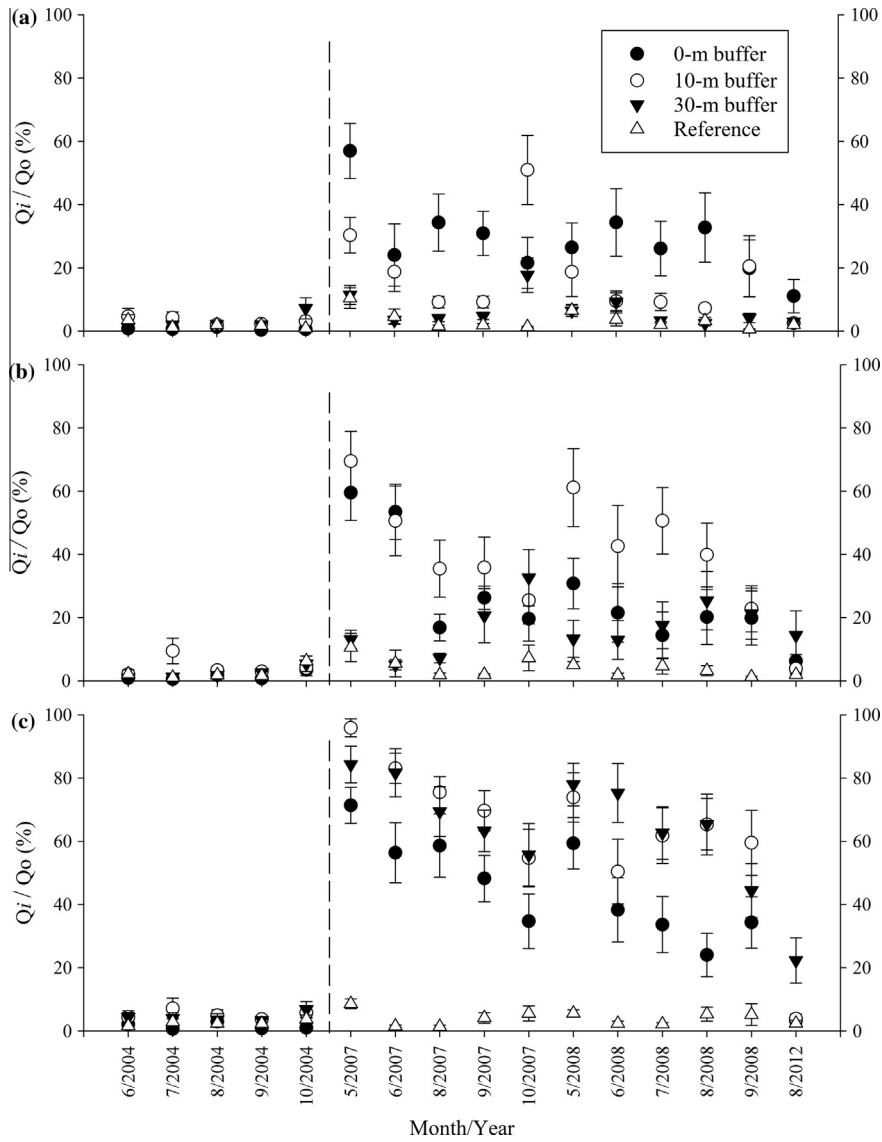
To compare species composition among all sample years (2004, 2007, 2008, 2012), we used a multiresponse permutation procedure (MRPP) (Mielke, 1979; McCune and Mefford, 1999). MRPP is a non-parametric multivariate test of differences between a priori groups, which provides a  $T$ -test statistic and a  $P$ -value. A stronger separation between groups is reflected by a more negative  $T$  statistic. We compared Sørensen distance and Euclidean distance (with and without ranking). Since these distances showed similar results and Sørensen distances are less prone to exaggerate the influence of outliers (McCune and Grace, 2002), we are reporting on Sørensen distance without ranking. When comparisons across sample years were significant, we applied multiple pair-wise comparisons using Sørensen distance. We used a conservative approach by applying a Bonferroni adjustment (McCune and Grace, 2002); i.e., with six multiple comparisons  $P = 0.05/6 = 0.008$ . We used PC-ORD version 5 (McCune and Mefford, 1999) for the MRPP group separation tests.

## 3. Results

### 3.1. Microenvironment changes

Before the treatments (2004), light transmittance ( $Q_i/Q_o$ ) was low and averaged from 1.5 to 4.2% across the hillslope, with no difference across the 50-m transect from near stream to upland zones (Fig. 2a–c). After the treatments in 2007, light transmittance significantly increased in all harvested sites, averaging from 35.6 to 42.2% across the hillslope. There were significantly treatment \* distance interactions (Table 2). On the 0-m buffer site, light transmittance was significantly higher after harvest for all slope positions ( $t = 6.76$ , near-stream;  $t = 6.97$ , mid-slope; and  $t = 12.44$ ; upper-slope, all  $P < 0.001$ ). On the 10-m buffer site, light transmittance increased in the near-stream position ( $t = 4.20$ ,  $P < 0.024$ ) as well as in the harvested mid- and upper-slopes ( $t = 8.03$  and  $t = 16.77$ , respectively, both  $P < 0.001$ ). On the 30-m buffer site, light transmittance increased significantly only in the harvested upper-slope ( $t = 15.79$ ,  $P < 0.001$ ). By 2012, light transmittance declined to levels similar to the pre-harvest year ( $t = 1.72$ , 0.26, and 3.03





**Fig. 2.** Mean ( $\pm$ se bars) light transmittance ( $Q_i/Q_0$ ) over time for the four treatment sites: 0-m buffer, 10-m buffer, 30-m buffer, and reference: (a) near-stream, (b) mid-slope and (c) upper-slope positions. Dashed line separates pre-harvest and post-harvest samples.

for the 0-m, 10-m, and 30-m buffer sites, respectively; all  $P > 0.10$ , not significant) (Fig. 2a–c).

For soil moisture content (SMC), significant effects were related to distance and treatment \* year interactions (Table 2). Across years (before and after treatment) and sites, soil moisture content was higher overall in the near-stream zone, averaging 28% versus 21–22% at distances of 10 m or more from the stream (Fig. 3a–c). After harvest treatments, the 10-m buffer site had significantly greater soil moisture content than the 0-m buffer ( $t = 5.68$ ,  $P < 0.001$ ), 30-m buffer ( $t = 4.00$ ,  $P = 0.007$ ), and reference ( $t = 5.40$ ,  $P < 0.001$ ) sites; by 2012, soil moisture content across the hillslope averaged  $33.7\% \pm 3.4$  for the 10-m buffer site,  $25.5\% \pm 0.5$  for the 0-m buffer site,  $27.9\% \pm 4.2$  for the 30-m buffer site, and  $25.9\% \pm 2.0$  for the reference site.

### 3.2. Overstory

As measured initially in summer 2007, harvest reduced overstory density and basal area, respectively, by 83% and 65% in the 0-m buffer site, by 50% and 74% for the 10-m buffer site; and by 45% and 29% in the 30-m buffer site (Table 1). By 2012, both the

0-m and 10-m buffer sites had nearly three times greater density than before the harvest treatments, whereas density in the 30-m buffer site was similar to its pretreatment condition. Basal area remained significantly lower over time on all harvested sites compared to the reference (Tables 1 and 2). Density and basal area did not change significantly over time in the reference forest.

### 3.3. Midstory responses

Because distance and treatment \* distance interaction were not significant in our repeated measures model for midstory density of shrubs and vines (Table 2), we show only treatment and year effects in Fig. 4. After the harvest treatments, midstory density of shrubs and vines significantly increased across the hillslope on all harvested sites (Table 2, Fig. 4), with a significant year \* treatment interaction. Density increased in the second year after harvest in the 0-m and 10-m buffer sites, whereas the response was delayed in the 30-m buffer site. Between 2004 and 2012, density increased by 146%, 556%, and 141%, respectively for the 0-m, 10-m and 30-m buffer sites (Fig. 4).

**Table 2**  
Mixed-model repeated-measures analysis for light transmittance (fractional Qi/Qo) and soil moisture content (SMC); and the vegetation variables of overstory density and basal area, midstory density of shrubs and vines, and tree regeneration (density of seedlings plus saplings < 2.5 cm dbh), and ground-layer cover and species richness by herbaceous or woody plants. Model parameters were year (n = 4), harvest treatment (n = 4), and distance from stream (n = 3). The parameters that were significant are highlighted in bold; at the  $\alpha \leq 0.05$  level for main effects and at  $P \leq 0.003$  for interaction terms with a Bonferroni adjustment.

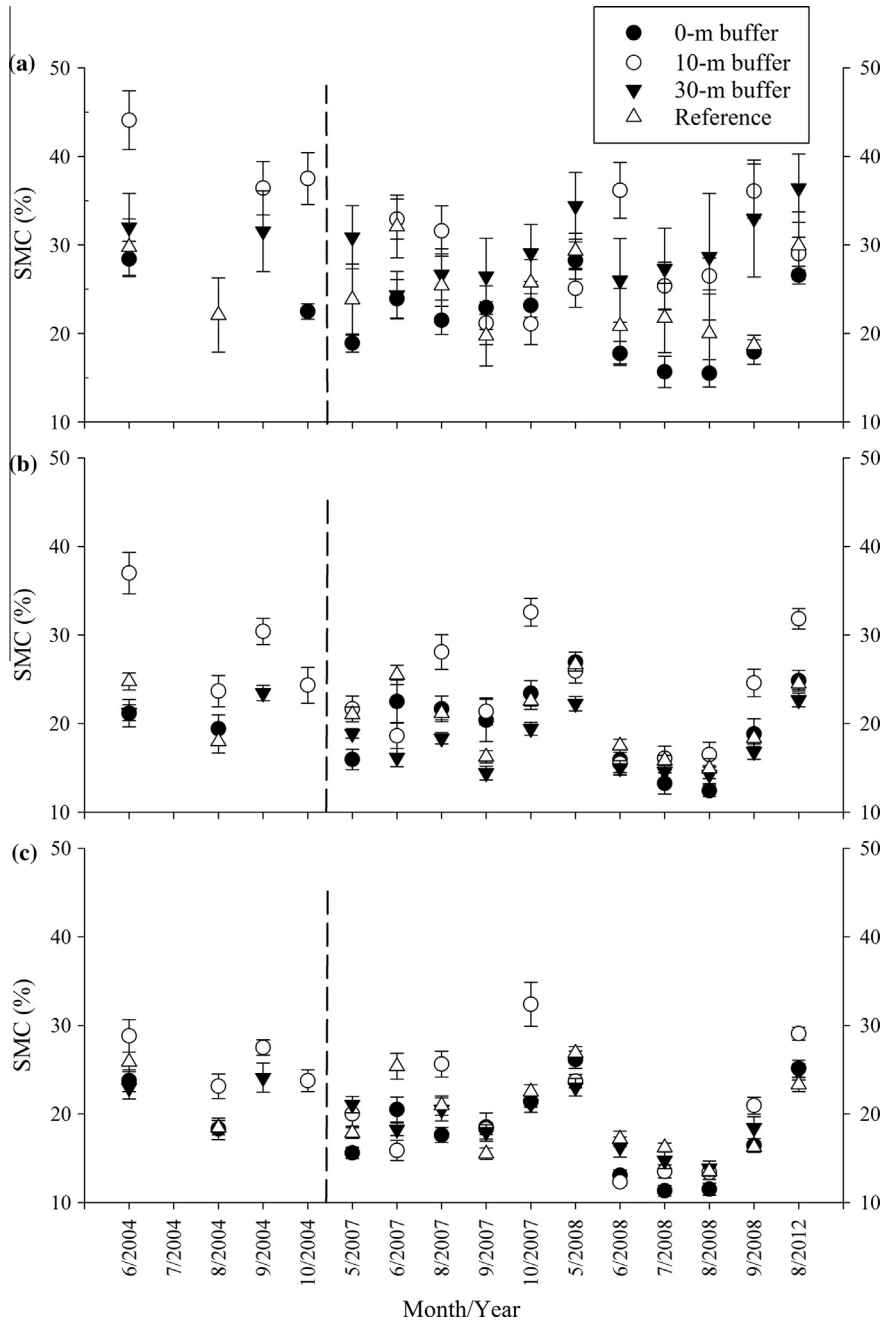
| Parameters                  | DF <sub>Num/Den</sub> | F     | P                 | DF <sub>Num/Den</sub> | F      | P                 |
|-----------------------------|-----------------------|-------|-------------------|-----------------------|--------|-------------------|
| <b>Microenvironment</b>     |                       |       |                   |                       |        |                   |
|                             | Qi/Qo                 |       |                   | SMC                   |        |                   |
| Year                        | 3/458                 | 83.81 | <b>&lt;0.0001</b> | 3/437                 | 386.77 | <b>&lt;0.0001</b> |
| Treatment                   | 3/251                 | 24.20 | <b>&lt;0.0001</b> | 3/154                 | 9.36   | <b>&lt;0.0001</b> |
| Distance                    | 2/251                 | 44.66 | <b>&lt;0.0001</b> | 2/154                 | 22.60  | <b>&lt;0.0001</b> |
| Year * treatment            | 9/458                 | 11.82 | <b>&lt;0.0001</b> | 9/437                 | 17.77  | <b>&lt;0.0001</b> |
| Year * distance             | 6/458                 | 22.04 | <b>&lt;0.0001</b> | 6/437                 | 1.41   | 0.2079            |
| Treatment * distance        | 6/251                 | 12.11 | <b>&lt;0.0001</b> | 6/154                 | 1.87   | 0.0901            |
| Year * treatment * distance | 18/458                | 5.34  | <b>&lt;0.0001</b> | 18/437                | 2.19   | <b>0.0034</b>     |
| <b>Overstory</b>            |                       |       |                   |                       |        |                   |
|                             | Density               |       |                   | Basal area            |        |                   |
| Year                        | 3/91.6                | 93.95 | <b>&lt;0.0001</b> | 3/108                 | 58.71  | <b>&lt;0.0001</b> |
| Treatment                   | 3/30.9                | 8.12  | <b>0.0004</b>     | 3/36.4                | 4.003  | <b>0.0147</b>     |
| Distance                    | 2/30.9                | 0.45  | 0.6389            | 2/36.4                | 1.19   | 0.3144            |
| Year * treatment            | 9/91.6                | 16.28 | <b>&lt;0.0001</b> | 9/108                 | 11.23  | <b>&lt;0.0001</b> |
| Year * distance             | 6/91.6                | 13.36 | <b>&lt;0.0001</b> | 6/108                 | 10.16  | <b>&lt;0.0001</b> |
| Treatment * distance        | 6/30.9                | 0.63  | 0.7063            | 6/36.4                | 0.70   | 0.6519            |
| Year * treatment * distance | 18/91.6               | 3.64  | <b>&lt;0.0001</b> | 18/108                | 2.60   | <b>0.0014</b>     |
| <b>Midstory density</b>     |                       |       |                   |                       |        |                   |
|                             | Shrubs & vines        |       |                   | Tree regeneration     |        |                   |
| Year                        | 3/104                 | 29.78 | <b>&lt;0.0001</b> | 3/104                 | 48.55  | <b>&lt;0.0001</b> |
| Treatment                   | 3/37.3                | 14.46 | <b>&lt;0.0001</b> | 3/37.3                | 28.51  | <b>&lt;0.0001</b> |
| Distance                    | 2/37.3                | 1.44  | 0.2491            | 2/37.3                | 21.73  | <b>&lt;0.0001</b> |
| Year * treatment            | 9/104                 | 6.92  | <b>&lt;0.0001</b> | 9/104                 | 16.94  | <b>&lt;0.0001</b> |
| Year * distance             | 6/104                 | 1.73  | 0.1208            | 6/104                 | 7.98   | <b>&lt;0.0001</b> |
| Treatment * distance        | 6/37.3                | 1.76  | 0.1334            | 6/37.3                | 4.31   | <b>0.0015</b>     |
| Year * treatment * distance | 18/104                | 1.20  | 0.2763            | 18/104                | 2.97   | <b>0.0002</b>     |
| <b>Ground-layer</b>         |                       |       |                   |                       |        |                   |
|                             | Herbaceous cover      |       |                   | Herbaceous richness   |        |                   |
| Year                        | 3/112                 | 4.38  | <b>0.0059</b>     | 3/121                 | 1.02   | 0.3883            |
| Treatment                   | 3/29.4                | 14.72 | <b>&lt;0.0001</b> | 3/41.7                | 28.99  | <b>&lt;0.0001</b> |
| Distance                    | 2/111                 | 2.98  | <b>0.0547</b>     | 2/131                 | 3.18   | <b>0.0449</b>     |
| Year * treatment            | 9/113                 | 3.05  | <b>0.0027</b>     | 9/121                 | 0.86   | 0.5654            |
| Year * distance             | 6/87.7                | 0.75  | 0.6128            | 6/103                 | 0.55   | 0.7656            |
| Treatment * distance        | 6/111                 | 14.25 | <b>&lt;0.0001</b> | 6/132                 | 12.83  | <b>&lt;0.0001</b> |
| Year * treatment * distance | 18/87.7               | 0.86  | 0.6224            | 18/103                | 0.19   | 0.9999            |
| <b>Ground-layer</b>         |                       |       |                   |                       |        |                   |
|                             | Woody cover           |       |                   | Woody richness        |        |                   |
| Year                        | 3/440                 | 20.30 | <b>&lt;0.0001</b> | 3/423                 | 11.78  | <b>&lt;0.0001</b> |
| Treatment                   | 3/194                 | 5.90  | <b>0.0007</b>     | 3/175                 | 5.05   | <b>0.0022</b>     |
| Distance                    | 2/194                 | 6.29  | <b>0.0022</b>     | 2/175                 | 2.77   | 0.0655            |
| Year * treatment            | 9/439                 | 11.99 | <b>&lt;0.0001</b> | 9/423                 | 7.96   | <b>&lt;0.0001</b> |
| Year * distance             | 6/440                 | 4.08  | <b>0.0005</b>     | 6/423                 | 1.83   | 0.0921            |
| Treatment * distance        | 6/194                 | 0.90  | 0.4971            | 6/175                 | 0.52   | 0.7905            |
| Year * treatment * distance | 18/439                | 1.82  | 0.0213            | 18/423                | 0.82   | 0.6791            |

To assess tree regeneration we combined tree seedling (<0.5 m height) and midstory sapling (<2.5 cm dbh, >0.5 m height) counts (Fig. 5a–c, Supplementary Table A3); both were counted at the plot scale. Between 2004 and 2007, density of tree regeneration increased significantly (Table 2); by 269% on the 0-m buffer site and 350% on the 10-m buffer site; and increases were the greatest at mid- and upper-slope positions on the 10-m buffer site (Fig. 5b and c). At the near-stream position, density of tree regeneration increased significantly after harvest on the 0-m buffer site (2004 vs. 2007,  $t = 4.23$ ,  $P = 0.002$ ; 2004 vs. 2008,  $t = 4.23$ ,  $P = 0.002$ ; 2004 vs. 2012,  $t = 4.23$ ,  $P = 0.002$ ) and the 10-m buffer site (2004 vs. 2007,  $t = 4.90$ ,  $P < 0.001$ ; 2004 vs. 2008,  $t = 4.76$ ,  $P < 0.001$ ; 2004 vs. 2012,  $t = 0.68$ ,  $P = 1.000$ ). At the mid-slope position, tree regeneration increased significantly on the 0-m buffer site (2004 vs. 2007,  $t = 5.20$ ,  $P = 0.001$ ; 2004 vs. 2008,  $t = 3.31$ ,  $P = 0.114$ ; 2004 vs. 2012,  $t = 1.90$ ,  $P = 0.858$ ) and the 10-m buffer site (2004 vs. 2007,  $t = 8.17$ ,  $P < 0.001$ ; 2004 vs. 2008,  $t = 10.45$ ,  $P < 0.001$ ; 2004 vs. 2012,  $t = 8.92$ ,  $P < 0.001$ ). At the upper-slope position, tree regeneration increased significantly on the 0-m buffer site (2004 vs. 2007,  $t = 4.65$ ,  $P = 0.004$ ; 2004 vs. 2008,  $t = 3.75$ ,  $P = 0.041$ ; 2004 vs. 2012,  $t = 2.75$ ,  $P = 0.339$ ) and the 10-m buffer site (2004 vs. 2007,  $t = 6.22$ ,  $P < 0.001$ ; 2004 vs. 2008,  $t = 9.08$ ,

$P < 0.001$ ; 2004 vs. 2012,  $t = 8.87$ ,  $P < 0.001$ ). Tree regeneration did not change significantly on the 30-m buffer site until 2012 and only on the upper-slope position ( $t = 3.81$ ,  $P = 0.036$ ), and the reference site did not change over time (Fig. 5a–c). Most tree species increased seedling and sapling density after harvest, but those with the largest increases were *A. rubrum* (460%), *Robinia pseudoacacia* (1509%), and *Quercus* (219%) on the 0-m buffer site; and *A. rubrum* (369%), *L. tulipifera* (1688%), *Quercus* (1315%), and *Sassafras albidum* (983%) on the 10-m buffer site (Supplementary Table A3). By 2012, *L. tulipifera* seedlings became even more abundant than in the second year after harvest (2007), increasing from 1492 stems ha<sup>-1</sup> to 2533 stems ha<sup>-1</sup> on the 0-m buffer site and from 2092 stems ha<sup>-1</sup> to 6667 stems ha<sup>-1</sup> on the 10-m buffer site. On the 30-m buffer site, seedlings that increased in density were *A. rubrum*, *Q. rubra*, *Hamamelis virginiana*, and *Quercus* (Supplementary Table A3).

### 3.4. Ground-layer responses

In the ground-layer, we sampled a total of 175 species across the four catchments overtime, 123 of these occurred on more than 3% of the sampled quadrats, and only 51 of the total species had



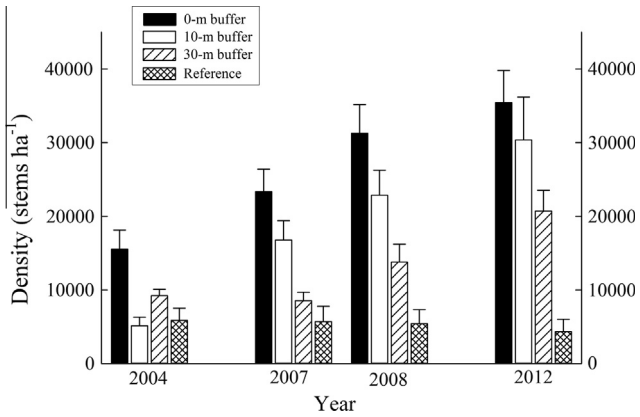
**Fig. 3.** Mean ( $\pm$ se bars) soil moisture content (SMC) over time for the four treatment sites: 0-m buffer, 10-m buffer, 30-m buffer, and reference: (a) near-stream, (b) mid-slope, and (c) upper-slope positions. Dashed line separates pre-harvest and post-harvest samples.

$\geq 1.5\%$  average cover (35 herbaceous, 16 woody). More than half of the species were perennial forbs (52.2%), and the remaining species were tree seedlings (20.3%), woody shrubs (10.1%), woody vines (4.3%), ferns (8.0%), graminoids (3.6%), or annual forbs (1.4%) (Supplementary Table A2). We did not observe any introduced or invasive species (viewed <http://plants.usda.gov> on 03/05/2016 for listed species) in the ground-layer; however, one *Rosa multiflora* plant, an introduced species, was observed in the midstory on the 10-m buffer site in 2012. We did not detect any significant differences in species richness or cover in the ground-layer with distance from stream before the treatment. After treatment, all harvested sites had significantly greater ground-layer cover than before the harvest (Table 2, Fig. 6a–f), but only the 10-m buffer site had higher richness on the mid-slope and upper-slope positions

(Fig. 7c–f). Similar to findings for the tree regeneration, some individual species in the ground-layer had higher cover and frequency after the harvest treatments than before (Supplementary Table A2). Numerous species increased in cover on the 0-m and 10-m buffers after harvest, including *Aster divaricatus*, *Aster* sp., *Astilbe biternata*, *Collinsonia canadensis*, *Dennstaedtia punctilobula*, *Desmodium nudiflorum*, *Disporum lanuginosum*, and *Solidago curtisii*. In addition, some species such as *Laportia canadensis*, *A. biternata*, *Viola rotundifolia*, and *Tiarella cordifolia* were clearly more abundant near the stream ( $\leq 10$  m).

The NMS ordination for the 2004 data (Fig. 8a) converged on three axes for the final solution. The final stress for the three-dimensional solution was 16.18. The proportion of variance explained was 12% for Axis 1, 48% for Axis 2, and 15% for Axis 3

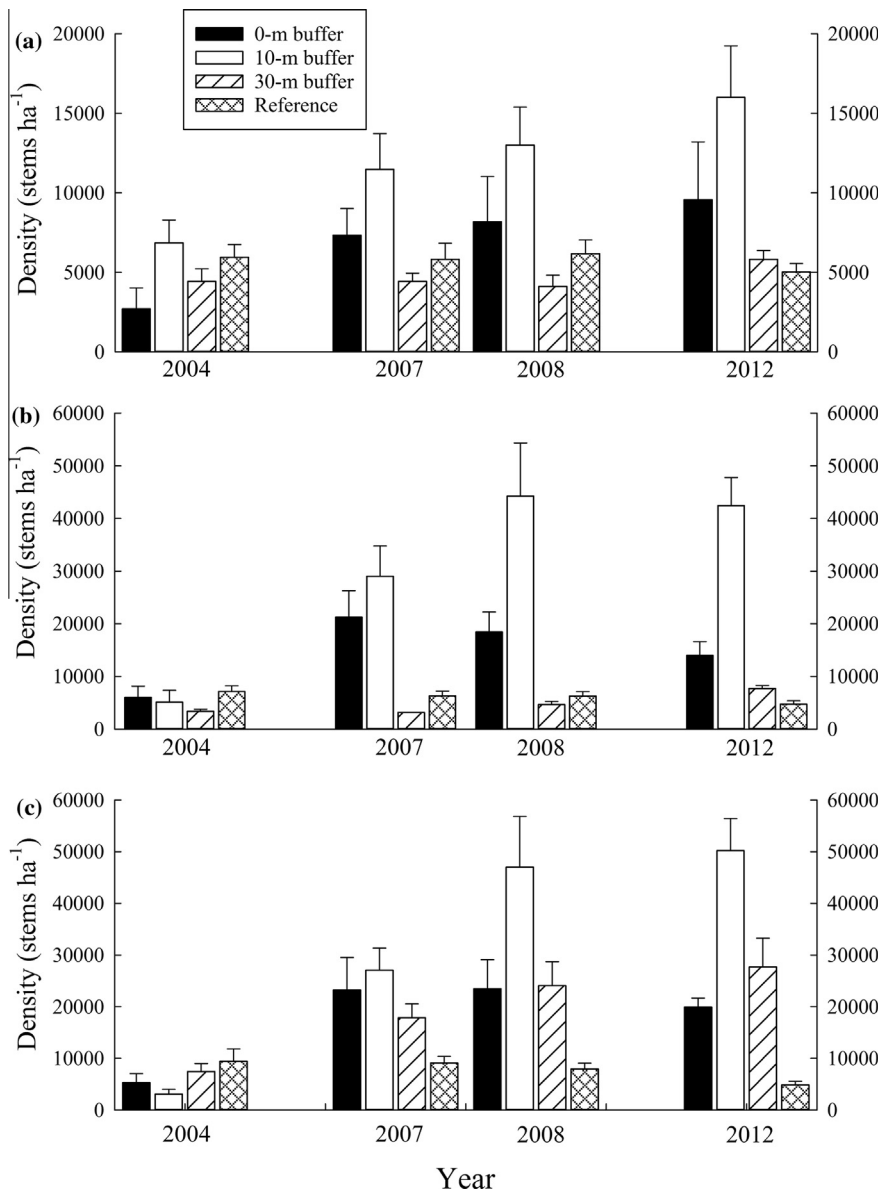




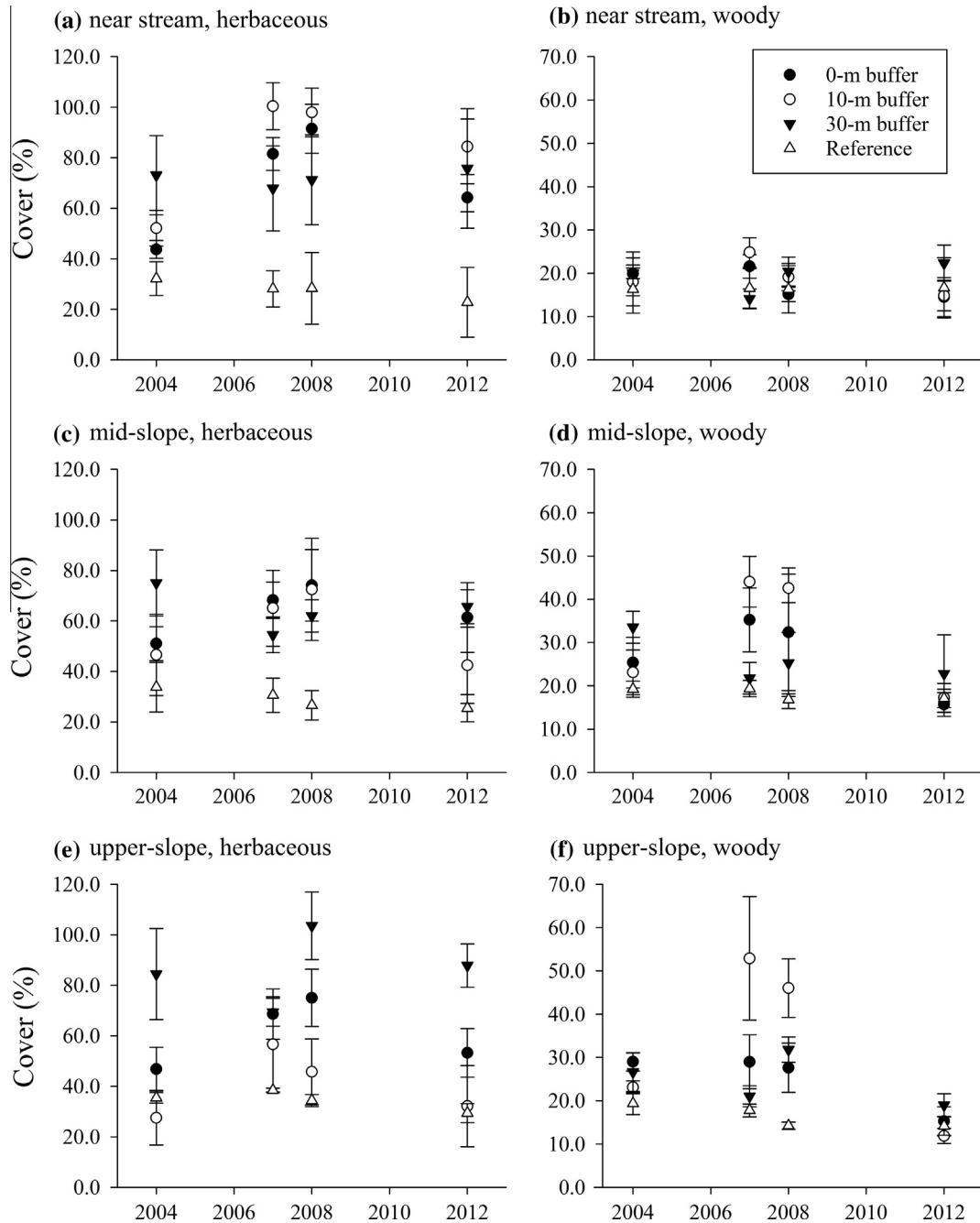
**Fig. 4.** Density of shrubs and vines before (2004) and after harvest (2007, 2008, and 2012) for the four treatment sites: 0-m buffer, 10-m buffer, 30-m buffer, and reference.

(Table 3). When the secondary matrix of site environmental variables was examined, Axis 1 was positively correlated ( $R \geq 0.30$ ) with distance from stream and shrub density and negatively correlated with soil moisture content (SMC); and Axis 2 was negatively correlated with light transmittance (Table 3, Supplementary Fig. A1a). Treatment plots were dispersed across the ordination axis, but near stream plots were concentrated in the upper, left quadrant regardless of treatment (Fig. 8a). Species that were most highly related ( $R \geq 0.50$ ) to one of the first three axes were *Amphicarpaea bracteata*, *D. nudiflorum*, *Polystichum acrostichoides*, *Smilax glauca*, *Thelypteris noveboracensis*, *T. cordifolia*, and *V. rotundifolia* (Supplementary Table A2, Fig. A1a). Four species that occurred before the harvest, but not in post-harvest years were *Campanula divaricata*, *Cardamine diphylla*, *Cimicifuga racemosa*, *Pycnanthemum montanum*.

The NMS ordination for the 2007 data (Fig. 8b) converged on three axes for the final solution and the final stress for the three-dimensional solution was 16.37. The proportion of variance explained was 16% for Axis 1, 42% for Axis 2, and 16% for Axis 3



**Fig. 5.** Mean ( $\pm$ se bars) density of tree regeneration (tree seedlings plus saplings < 2.5 cm dbh) before (2004) and after harvest (2007, 2008, and 2012) for the four treatment sites: 0-m buffer, 10-m buffer, 30-m buffer, and reference; (a) near-stream, (b) mid-slope, and (c) upper-slope.

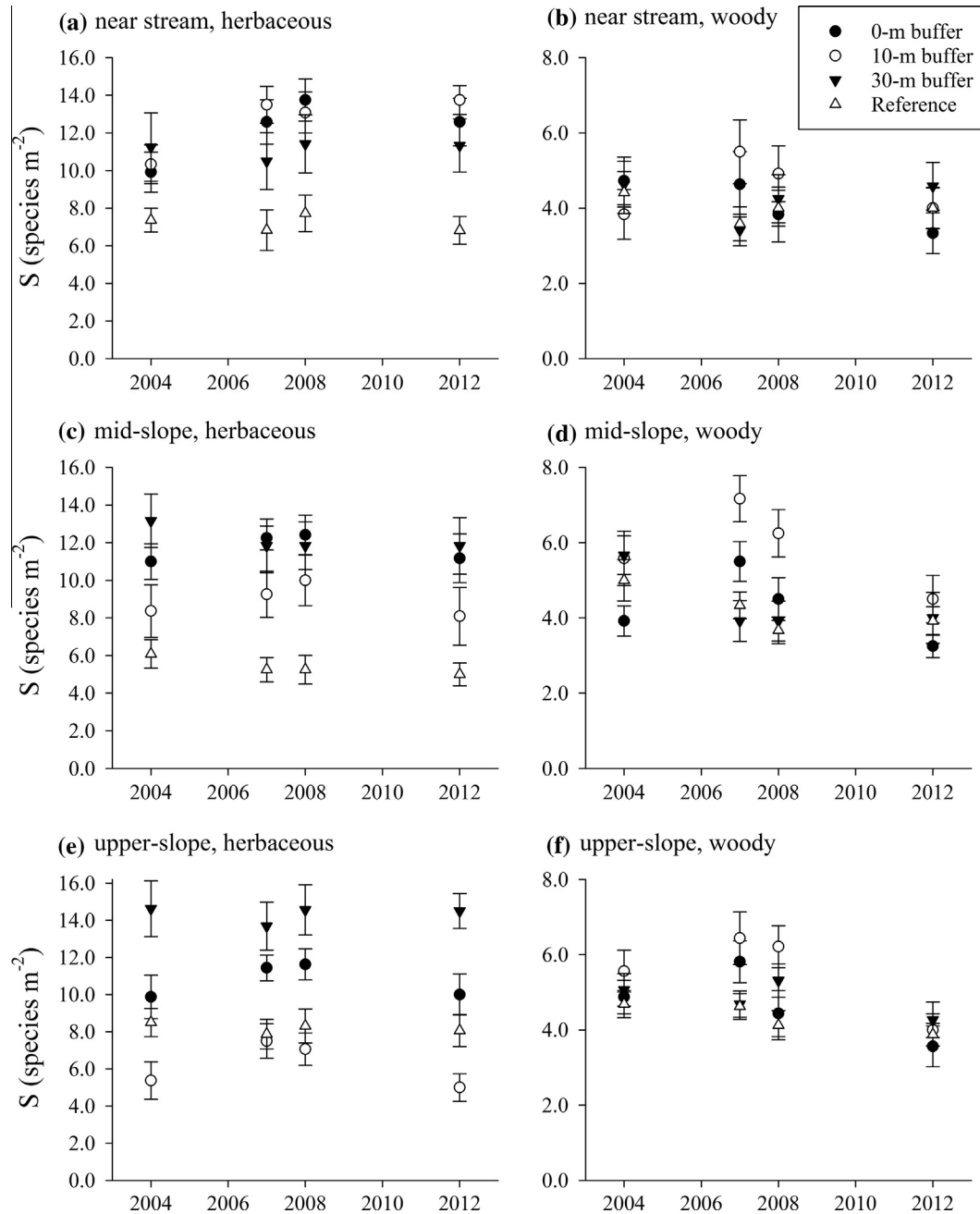


**Fig. 6.** Mean ( $\pm$ se bars) cover for herbaceous and wood species in the ground-layer (<0.5 m height) before (2004) and after harvest (2007, 2008, and 2012) for the four treatment sites: 0-m buffer, 10-m buffer, 30-m buffer, and reference. Near-stream (a) herbaceous and (b) woody cover; mid-slope (c) herbaceous and (d) woody cover; and upper-slope (e) herbaceous and (f) woody cover.

(Table 3). Axis 1 was positively correlated with tree basal area; Axis 2 was positively correlated with distance from stream, light transmittance, and shrub density and negatively correlated with tree basal area; and Axis 3 was negatively correlated with distance from stream (Table 3). After the harvest, treatment effects can be discerned in the 2007 ordination, where the 0-m and 10-m plots were separated in the ordination space from the 30-m and reference plots (Fig. 8b). More species were highly related ( $R \geq 0.50$ ) to one of the first three axes in the 2007 ordination than before the harvests (2004); these included *A. bracteata*, *A. divaricatus*, *Aster* sp., *D. nudiflorum*, *Dichantheium* sp., *D. lanuginosum*, *Eupatorium rugosum*, *Laportea canadensis*, *L. tulipifera*, *Lysimachia quadrifolia*, *Prunella vulgaris*, *Quercus velutina*, *S. glauca*, *T. noveboracensis*,

*V. rotundifolia*, and *Vitis aestivalis* (Supplementary Table A2, Fig. A1b). In 2008, the proportion of variance explained was 18% for Axis 1, 36% for Axis 2, and 23% for Axis 3; and all five environmental variables, including tree basal area, were correlated ( $R \geq 0.30$ ) with at least one of the three axes (Table 3). We do not display the ordination graphs (plots and species) for 2008 because treatment separation and species composition were similar to the 2007 graphs (Fig. 8b, Supplementary Fig. A1b).

By 2012, the proportion of variance explained was 17% for Axis 1, 13% for Axis 2, and 46% for Axis 3 (Table 3). Axis 1 was positively correlated ( $R \geq 0.30$ ) with light transmittance; Axis 2 was positively correlated with SMC and shrub density; and Axis 3 was negatively correlated with distance from stream and shrub density

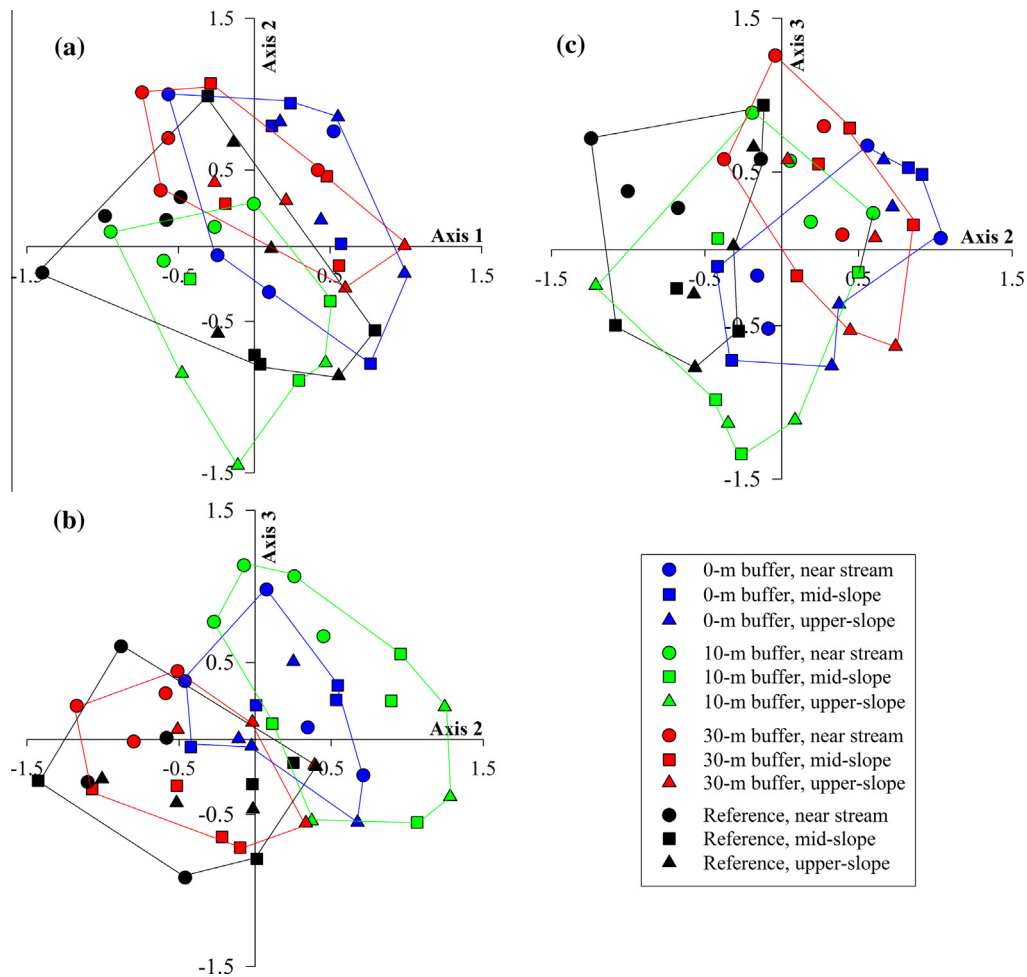


**Fig. 7.** Mean ( $\pm$ se bars) species richness ( $S$ ) for herbaceous and woody species in the ground-layer (<0.5 m height) before (2004) and after harvest (2007, 2008, and 2012) for the four treatment sites: 0-m buffer, 10-m buffer, 30-m buffer, and reference. Near-stream (a) herbaceous and (b) woody  $S$ ; mid-slope (c) herbaceous and (d) woody  $S$ ; and upper-slope (e) herbaceous and (f) woody  $S$ .

(Table 3). The separation among treatments plots was not as distinct (Fig. 8c) as seen in the 2007 ordination (Fig. 8b). In 2012, twenty species were highly related ( $R \geq 0.50$ ) to one of the first three axes, more than in 2004 or 2007, thirteen of these were herbaceous species (Supplementary Table A2, Fig. A1c). Transient species, those that recruited after the harvest in 2007 and were not present in 2012, included *Aralia spinosa*, *Clematis virginiana*, *Danthonia* sp., *Erechtites hieraciifolia*, *Erigeron annuus*, *Gentian* sp., *Lobelia* sp., *Phlox carolina*, *Phytolacca americana*, *Rhus copina*, *Rhus glabra*, *Rubus odora*, and *Rudbeckia hirta* (Supplementary Table A2).

Ground-layer species composition differed significantly over time in the 0-m buffer (MRPP;  $T = -5.71$ ,  $P < 0.001$ ) and 10-m buf-

fer ( $T = -5.72$ ,  $P < 0.001$ ) sites, but did not change after harvest on the 30-m buffer ( $T = -1.02$ ,  $P = 0.151$ ) or reference ( $T = 1.24$ ,  $P = 0.914$ ) sites. Average compositional dissimilarity (Sorensen within-group distance) increased from 2004 to the 2012, indicating greater spatial heterogeneity through time, but only on the 0-m and 10-m buffer sites (i.e., a treatment  $\times$  year interaction) (Table 4). Average dissimilarity increased from 0.474 to 0.534 on the 0-m buffer site and from 0.491 to 0.527 on the 10-m buffer site. Multiple pair-wise comparisons showed significant differences between years. On both the 0-m buffer and 10-m buffer sites, species composition was significantly different before harvest (2004) than years after harvest (2007, 2008, and 2012), and 2007 was significantly different than 2012 (Table 4).



**Fig. 8.** Nonmetric multidimensional scaling (NMS) ordination graphs of the ground-layer plots in years (a) 2004, (b) 2007, and (c) 2012. Symbols with different colors represent the four treatments (0-m, 10-m, 30-m buffers and reference) and different shapes represent the locations across the hillslope (near-stream, mid-slope, and upper-slope). Pearson's parametric correlations ( $R$ ) for the five site variables with the first three NMS ordination axes are provided in Table 3.

## 4. Discussion

### 4.1. Changes in environmental variables

Harvest intensity (e.g., clearcut vs. partial cuts) influences changes (magnitude and duration) in environmental variables that can affect the magnitude and duration of changes in species composition and diversity (Elliott et al., 2002; Boring et al., 2014). The silvicultural prescription for the harvested area was to leave ca.  $5.0 \text{ m}^2 \text{ ha}^{-1}$  residual basal area; however, the harvest intensity was greater for two of the harvested sites, where residual basal area in the 10-m and 30-m buffer sites was  $3.0 \pm 2.2 \text{ m}^2 \text{ ha}^{-1}$  and  $0.9 \pm 0.9 \text{ m}^2 \text{ ha}^{-1}$ , respectively. Conversely, within the 0-m buffer, a partial canopy remained after harvest; the near-stream location was not cut as heavily (50% reduction,  $14.4 \text{ m}^2 \text{ ha}^{-1}$  residual) as the mid-slope (75% reduction,  $6.64 \text{ m}^2 \text{ ha}^{-1}$  residual) or upper-slope (71% reduction,  $11.0 \text{ m}^2 \text{ ha}^{-1}$  residual) locations. As would be expected when removing the overstory, harvesting resulted in increased light transmittance ( $Q_i/Q_0$ ) on all sites outside their buffer zones; however, the 10-m and 30-m buffer sites also experienced higher light within their buffer zones, suggesting that light penetration from the edge increased light availability for ground-layer species and tree regeneration. Both the 0-m and 10-m buffer sites showed increased light transmittance variability across the hillslope after harvesting; whereas, there was no change in the 30-m and reference sites over time.

Light transmittance and soil moisture are critical variables regulating vegetation distribution and post-harvest vegetation response and recovery in the southern Appalachians (Dieterich et al., 2006; Goebel et al., 2006; Elliott et al., 2014). While we found that soil moisture helped explain the variation in ground-layer vegetation across the hillslope on all treatments, at the watershed scale, soil moisture only increased on the 10-m buffer treatment after harvest. Reasons for the lack of soil moisture response on the other harvest sites are unclear, as we selected sites with comparable soils, vegetation, aspect, and topography. However, a recent study in the North Carolina Piedmont suggested that harvesting increases the subsurface flow of upslope soil water to the riparian zone, resulting in greater soil water availability in the riparian zone and greater transpiration of riparian vegetation (Boggs et al., 2015). We did not quantify changes in transpiration of residual vegetation, but variation in subsurface flow dynamics and transpiration responses could be causal factors for the variation in soil moisture responses among treatments. Variation in species distributions along hillslope gradients has been described for the southern Appalachians (Braun, 1950; Whittaker, 1956; Day and Monk, 1974; Elliott et al., 1999). Following disturbance the rate of revegetation and changes in species composition can depend on position along a hillslope (Elliott et al., 1997, 2014), partially attributed to a topographic moisture gradient (Dieterich et al., 2006; Goebel et al., 2006; Hwang et al., 2011).

**Table 3**

Nonmetric multidimensional scaling (NMS); Pearson's parametric correlations (*R*) for the five site variables (DISTANCE = distance from stream; LITE = light transmittance (fractional  $Q_i/Q_0$ ); SMC = soil moisture content; TREEBA = tree basal area of stems  $\geq 2.5$  cm dbh; SHRB DEN = density of stems  $< 2.5$  cm dbh) with the first three ordination axes of ground-layer vegetation in years 2004, 2007, 2008 and 2012. Environmental variables with  $R \geq 0.30$  are highlighted in bold.

|  | <i>R</i>      | <i>R</i>      | <i>R</i>      |
|--|---------------|---------------|---------------|
| <b>2004</b>                            |               |               |               |
| DISTANCE                               | <b>0.475</b>  | -0.294        | 0.237         |
| LITE                                   | 0.135         | <b>-0.441</b> | -0.118        |
| SMC                                    | <b>-0.366</b> | 0.116         | -0.294        |
| TREEBA                                 | 0.048         | -0.098        | 0.217         |
| SHRB DEN                               | <b>0.374</b>  | 0.279         | -0.028        |
| Coefficient of determination ( $R^2$ ) | 0.122         | 0.476         | 0.153         |
| Cumulative variance explained          | 12.2%         | 59.8%         | 75.1%         |
| Final stress of 3-dimensional solution | 16.177        |               |               |
| <b>2007</b>                            |               |               |               |
| DISTANCE                               | 0.192         | <b>0.352</b>  | <b>-0.401</b> |
| LITE                                   | -0.241        | <b>0.581</b>  | 0.072         |
| SMC                                    | -0.099        | -0.227        | 0.241         |
| TREEBA                                 | <b>0.372</b>  | <b>-0.423</b> | -0.054        |
| SHRB DEN                               | -0.183        | <b>0.559</b>  | 0.198         |
| Coefficient of determination ( $R^2$ ) | 0.162         | 0.416         | 0.160         |
| Cumulative variance explained          | 16.2%         | 57.8%         | 73.8%         |
| Final stress of 3-dimensional solution | 16.373        |               |               |
| <b>2008</b>                            |               |               |               |
| DISTANCE                               | -0.273        | <b>-0.314</b> | <b>-0.364</b> |
| LITE                                   | <b>0.320</b>  | <b>-0.334</b> | -0.283        |
| SMC                                    | 0.137         | 0.262         | <b>0.315</b>  |
| TREEBA                                 | <b>-0.438</b> | 0.292         | 0.155         |
| SHRB DEN                               | <b>0.317</b>  | <b>-0.505</b> | <b>-0.313</b> |
| Coefficient of determination ( $R^2$ ) | 0.180         | 0.357         | 0.230         |
| Cumulative variance explained          | 18.0%         | 53.7%         | 76.7%         |
| Final stress of 3-dimensional solution | 15.347        |               |               |
| <b>2012</b>                            |               |               |               |
| DISTANCE                               | 0.081         | -0.235        | <b>-0.456</b> |
| LITE                                   | <b>0.409</b>  | 0.147         | 0.130         |
| SMC                                    | -0.069        | <b>0.410</b>  | 0.262         |
| TREEBA                                 | -0.218        | -0.270        | 0.181         |
| SHRB DEN                               | 0.263         | <b>0.430</b>  | <b>-0.327</b> |
| Coefficient of determination ( $R^2$ ) | 0.165         | 0.128         | 0.455         |
| Cumulative variance explained          | 16.5%         | 29.3%         | 74.8%         |
| Final stress of 3-dimensional solution | 15.801        |               |               |

$N = 48$  each year. Monte Carlo Test for stress in real data was  $P < 0.02$  for all axes shown.

In an earlier companion study on these sites, Knoepp and Clinton (2009) found increased soil N availability (i.e., extractable soil  $\text{NO}_3$  and  $\text{NH}_4$ , soil solution N, and soil  $\text{NO}_3$  release), but N responses were limited to the harvested slope section, i.e., no changes were detected within the buffer zone. Thus, on our sites, the edge effect resulted in increased light transmittance within the narrow buffer zone (i.e., on the 10-m buffer site), but no detectable edge effects for nutrients (Knoepp and Clinton, 2009) or soil moisture (this study).

**Table 4**

MRPP pairwise comparisons for change in ground-layer species composition within buffer-width treatments between years; pre-harvest (2004), and the 2nd (2007), 3rd (2008), and 7th (2012) growing seasons after harvest. We used a conservative approach to determine significant differences between years by applying a Bonferroni adjustment; with six multiple comparisons  $P = 0.05/6 = 0.008$ . Significant differences are highlighted in bold.

| Comparisons   | 0-m buffer |                  | 10-m buffer |                  | 30-m buffer |                 | Reference |                 |
|---------------|------------|------------------|-------------|------------------|-------------|-----------------|-----------|-----------------|
|               | <i>T</i>   | <i>P</i> -value  | <i>T</i>    | <i>P</i> -value  | <i>T</i>    | <i>P</i> -value | <i>T</i>  | <i>P</i> -value |
| 2004 vs. 2007 | -4.21      | <b>0.001</b>     | -4.37       | <b>0.001</b>     | -0.13       | 0.374           | 0.74      | 0.751           |
| 2004 vs. 2008 | -6.25      | <b>&lt;0.001</b> | -4.00       | <b>0.002</b>     | -0.02       | 0.414           | 0.78      | 0.772           |
| 2004 vs. 2012 | -3.14      | <b>0.007</b>     | -3.56       | <b>0.004</b>     | -1.72       | 0.062           | 0.18      | 0.498           |
| 2007 vs. 2008 | -0.28      | 0.340            | 0.81        | 0.782            | 0.34        | 0.568           | 1.03      | 0.879           |
| 2007 vs. 2012 | -3.54      | <b>0.004</b>     | -5.65       | <b>&lt;0.001</b> | -1.04       | 0.143           | 0.68      | 0.722           |
| 2008 vs. 2012 | -2.23      | 0.029            | -2.28       | 0.027            | -0.98       | 0.153           | 0.86      | 0.806           |

#### 4.2. Vegetation responses

We found significant changes in midstory and ground-layer vegetation in response to harvesting with the greatest responses on the 10-m buffer site, supporting our hypotheses that responses will be greatest on sites with an intermediate buffer width (intermediate disturbance). For example, midstory density increased by 556% on the 10-m buffer, and much less so on the 0-m (146%) and 30-m (141%) buffer sites due to the recruitment and growth of shrubs and vines. Tree regeneration (seedling plus saplings) density and species richness were also higher on the 10-m buffer than the other sites. While *Carya* spp., *Q. rubra* and *Q. velutina* increased substantially in the 10-m buffer; *A. rubrum*, *L. tulipifera* and *R. pseudoacacia* had even higher seedling numbers than the former three species. This response is consistent with other studies that show that the creation of partial canopies and in close proximity to retained forests (i.e., forest edges) facilitate enhanced recruitment (see review Baker et al., 2013). In northern Minnesota, Kastendick et al. (2014) found greater recruitment of early successional hardwoods (*Betula*, *Populus*) following partial harvests in riparian zones, but little recruitment of mid successional (*Fraxinus*, *Quercus*) or late successional (*Acer*, *Tilia*) hardwoods. In our study, we found recruitment of both early (*Liriodendron*, *Robinia*) and mid to late successional (*Quercus*, *Carya*, *Acer*) species.

In the ground-layer of the 10-m buffer, herbaceous species cover and richness increased across the hillslope (within and outside the buffer zone) after the harvest and for all post-harvest years; whereas, woody species cover increased for the first two years then returned to pre-harvest levels by 2012. Woody species that recruited into the ground-layer likely grew into the midstory layer after the first couple of years, as seen in the higher midstory density through 2012 on all harvested sites. While some studies have found that riparian forests are invaded by nonnative species following harvests (e.g., McNeish et al., 2015); our sites had no notable invasions, as we found only one individual of the invasive plant, *R. multiflora*, across all sites and sample years after harvest. However, we do not know if this individual plant emerged from the seedbank or was introduced during the harvest operation. Plant invasions may not be prevalent on our sites because they are forest interiors, headwater catchments, and away from major travel corridors; thus, they have fewer opportunities for invasion than other locations dominated by nonnative plants (Schulz and Gray, 2013).

Our results concur with Biswas and Mallik (2010), who found that the highest species and functional diversity in riparian communities occurred at an intermediate intensity of disturbance. In contrast, MacDonald et al. (2014) found that species richness in riparian boreal forests was greatest at the highest level of disturbance (i.e., clearcut with no buffer). However, they also found differences in understory (measured the same as "ground-layer") vegetation response depending on hillslope position, where



streamside communities maintained a condition similar to uncut forests and upland communities were colonized by early successional species. Their results indicated that streamside understory vegetation was inherently more resistant to stand-replacing disturbance than upland assemblages (MacDonald et al., 2014).

The NMS analyses allowed us to account for variation within and across sites in the ground-layer species composition and associated environmental variables. We found that the magnitude of response in the ground-layer depended on a number of temporally variable factors. Before the harvest, four variables (soil moisture, light transmittance, distance from stream and shrub density) explained a large proportion of the species distribution. After the harvest, overstory residual basal area became important in the second growing season; five years later, residual basal area was no longer related and light was less important. Initial increases in light were due to the reduced overstory basal area; and some species were transient in response to changing environmental conditions over time. For example, when light decreased in the ground-layer as midstory density increased, light demanding or transient species were no longer able to survive. We found that accounting for the variation in harvesting intensity (i.e., residual basal area) across the hillslope was important in understanding species changes over time. Similar to our findings, Zenner et al. (2012) showed that partial harvest treatments created gradients in residual basal area, both among treatments and from stream edges to uplands, which resulted in corresponding gradients in light availability and correlated directly with ground-layer vegetation responses.

Species composition shifted after treatment on the 0-m and 10-m buffers, but no significant changes were observed on the 30-m buffer or the reference sites over time. Some studies have found that partial overstory removal resulted in ground-layer vegetation responses (Elliott and Knoepf, 2005; D'Souza et al., 2012; Palik et al., 2012; Zenner et al., 2012; MacDonald et al., 2014); while others have found little to no response (Mallik et al., 2013, 2014). In a recent meta-analysis, Richardson and Béraud (2014) concluded that the magnitude and direction of responses following riparian forest harvesting were quite variable and that the individual outcomes were partially due to underlying environmental differences among study sites.

#### 4.3. Management implications

The effects of alternate buffer widths on vegetation responses have rarely been studied in headwater catchments of the southern Appalachians; however, our study indicates that in addition to protecting water resources (Clinton, 2011), a 10 m buffer width also increases herbaceous species and tree seedling abundance relative to a 30 m buffer. These vegetation responses may have important implications for wildlife habitat (O'Keefe et al., 2013; Clipp and Anderson, 2014; Maignet et al., 2014; Studinski and Hartman, 2015) and other ecosystem functions such as biogeochemical cycling (Elliott et al., 2015) and ecohydrology (Swank et al., 2014; Bosch et al., 2014; Boggs et al., 2015). Lichens and mosses could also be influenced by partial harvests (Dynesius and Hylander, 2007; Ray et al., 2015), and they may respond differently than vascular plants. These bryophytes can provide ecosystem functions, such as association with nitrogen fixing bacteria, soil moisture retention, and habitat for other organisms (Deluca et al., 2002). It is uncertain how bryophytes would respond to alternate riparian buffer widths. In a Swedish boreal forest, Hylander et al. (2005) found that moss cover and richness were greater within the 10 m buffer compared to the adjacent clearcut area, but they did not examine alternate buffer widths.

It is important to evaluate the results of our study in the context of geomorphology (steep montane vs. low gradient streams),

watershed and stream size (i.e., headwater), land use (i.e., forest), and harvest technique (i.e., cable yarding). For example, larger tributaries and areas adjacent to developed land (residential/commercial and agricultural) may require wider buffers ( $\geq 30$  m) to preserve ecosystem services, such as water quality and wildlife habitat (Weller et al., 2010; Wasser et al., 2014; Cristan et al., 2016). Outside U.S. National Forests, increased agricultural, residential and commercial development has created narrow buffer corridors ( $<30$  m) (Wasser et al., 2014); and, where developed land use types are dominant, stream integrity (e.g., stream bank stability) can be compromised (Rheinhardt et al., 2012). Hence, while the 10 m buffer protected water resources (Clinton, 2011) and resulted in greater herbaceous species and tree seedling abundance in our study, a wider buffer may be required to protect water resources (or other ecosystem services) in other situations. A better understanding of how alternate buffer widths affect a wide range of ecosystem attributes and services will provide critical information to land managers as they plan harvest activities.

In the U.S. and other countries, fixed-width buffers are a common best management practice (BMP) to protect aquatic ecosystems (Blinn and Kilgore, 2001; Cristan et al., 2016); however, variable width buffers using geospatial mapping methods have been suggested in a few studies (Kuglerová et al., 2014; Ågren et al., 2015; Salo et al., 2016; Tiwari et al., 2016). Because they are more difficult to ascertain and apply, variable width buffers have not been widely adopted in U.S. state's BMPs (Schilling, 2016). If variable width buffers become more prominent, particularly along large stream networks, future research should consider the influence of these buffers in protecting and enhancing multiple ecosystem services such as water quality, aquatic organisms, and riparian biodiversity.

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#### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.05.046>.

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