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Effects of shelterwood harvest and prescribed fire in upland Appalachian hardwood forests on bat activity

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ABSTRACT

Little is known about the effects that oak forest regeneration treatments consisting of a combination of shelterwood harvesting and prescribed fire have on bats, despite increasing use of these treatments. We quantified changes in bat activity levels in relation to oak forest regeneration treatments consisting of harvesting at 50% and 70% retention levels and prescribed fire in two upland Appalachian hardwood forests in Ohio. We monitored bat activity immediately post-harvest, three growing seasons post-harvest, and after application of prescribed fire to harvested stands before the fourth growing season. Total bat activity levels were higher in thinned and thinned and burned treatments than in unthinned controls in all years, but did not differ between harvest treatment levels immediately post-harvest, three growing seasons post-harvest, or between harvest treatment levels within years. Total bat activity post-prescribed fire changed only in the 50% retention harvest treatment blocks, wherein activity decreased. Activity levels of big brown (*Eptesicus fuscus*) bats were greater in harvested treatment blocks than controls in all years. Activity levels of eastern red (*Lasiurus borealis*), and *Myotis* spp. and tri-colored (*Perimyotis subflavus*) collectively did not differ among treatment blocks post-fire, but were greater in harvested treatment blocks than controls three growing seasons post-harvest. Community composition was strongly related to vegetation volume, with eastern red bats and *Myotis* and tri-colored bats displaying positive relationships with clutter in low height strata, and big brown bats displaying a negative relationship with clutter in all height strata. The positive relationship between eastern red and *Myotis* and tri-colored bats and clutter in low height strata may explain why activity levels of these species decreased post-prescribed fire. Our study suggests that the harvesting component of oak forest regeneration treatments may benefit bats for several years, and that while bat activity levels may decline post-prescribed fire, overall activity levels are nonetheless greater than in unthinned areas.

1. Introduction

Oak (*Quercus* spp.) forests account for a substantial proportion of forested habitats in the eastern United States (Smith et al., 2004). In recent decades however, reduced or little oak regeneration in this region has become common (Brooks, 2003; Nowacki and Abrams, 2008; Pierce et al., 2006). These decreases are attributed to changes in natural disturbance patterns, particularly wildfire, that have allowed oak competitors to establish successional pathways (Abrams, 1992; Brooks, 2003; Nowacki and Abrams, 2008; Spetich and He, 2008). Because oaks are valuable to both wildlife (McShea et al., 2007) and humans (Marschall et al., 2014; Ward, 2002), forest management techniques designed to promote oak regeneration have been developed and are being implemented in managed forests across the eastern United States. These treatments generally utilize a combination of timber harvesting and prescribed fire to remove mid and understory competitors such as red maple (*Acer rubrum*) and to increase solar exposure for more shade-intolerant oak seedlings and saplings (Albrecht and McCarthy, 2006; Brose et al., 1999; Hutchinson et al., 2005; Iverson et al., 2008). Although these techniques have demonstrated effectiveness for improving oak recruitment (Brose et al., 2013), little currently is known about how the combination of thinning and prescribed fire affect bats.

Relative to many other aspects of bat ecology, the impacts of forest thinning on bats are well understood. Vegetation density, and understory structural volume of woody vegetation in general, can significantly impede maneuverability and foraging efficiency of bats (Siemers and Schnitzler, 2004). Because of this, it is expected

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that bat activity should be greatest in areas of reduced vegetation structure, and indeed, studies on bat activity in managed forest landscapes generally have found that decreases in canopy volume following forest harvest increase bat activity levels (Loeb and Waldrop, 2008; Menzel et al., 2002; Titchenell et al., 2011). Even within unthinned forest stands, bat activity levels are positively related to canopy openness and presence of canopy gaps (Ford et al., 2005; Fukui et al., 2011; Menzel et al., 2005). It is apparent, then, that the vegetative characteristics of forests are an important factor in determining bat community composition and activity levels (Adams et al., 2009; Hodgkison et al., 2004; Menzel et al., 2005; Smith and Gehrt, 2010) and that differences in bat activity between harvested and unharvested forests, or among treatment levels, are due in large part to structural differences in forest condition (Adams et al., 2009; Owen et al., 2004). Relatedly, changes in vegetation structure as a result of forest management also impact bat prey, which also have been found to be related to bat activity (Dodd et al., 2012). Low activity levels of bats within clearcuts, and the higher levels of bat activity in clumps of retained trees within clearcuts, however, suggest that some level of vertical structure is important for bats (Hogberg et al., 2002).

Conversely, the effects of fire on bats have been poorly studied, but theoretical impacts have been discussed relative to changes in forest structure and bat foraging efficiency, roosting behavior, and prey availability (Carter et al., 2002; Perry, 2012; Johnson et al., 2012). To date, the majority of studies on the effects of fire on bat activity have focused on pine-dominated landscapes (Armitage and Ober, 2012; Buchalski et al., 2013; Loeb and Waldrop, 2008). Differences in forest type are known to play significant roles in patterns of bat activity (Kalcounis et al., 1999; Tibbels and Kurta, 2003), and there is reason to believe that effects of fire may vary across regions based on its roles within different forest and ecosystem types (Brown and Smith, 2000). It also is unclear how the reintroduction of fire to eastern hardwood forest ecosystems after a century of fire suppression will alter current ecosystem processes.

Prescribed fire is capable of having significant impacts on forest structure through reductions in understory volume and creation of canopy gaps; even moderate intensity fires can top-kill mature trees and remove saplings from the understory (Hutchinson et al., 2008; Signell et al., 2005). Fire also may alter insect prey abundance and distribution (Campbell et al., 2007; McCullough et al., 1998; Swengel, 2001). Decreases in canopy volume and understory vegetation resulting from prescribed fire may increase bat activity similar to patterns seen in studies of forest harvest (Perry, 2012). Indeed, some studies have observed greater levels of activity in burned areas in relation to decreased vegetation structure (Armitage and Ober, 2012; Buchalski et al., 2013; Smith and Gehrt, 2010), but this has not been observed in all studies (Loeb and Waldrop, 2008). As suggested by Fisher and Wilkinson (2005) in their review of fire impacts on mammals in the boreal forest, differences in responses to prescribed fire may be related to the heterogeneous nature of fire intensity across space.

Mid- and overstory trees killed by prescribed fire (Bagne et al., 2008; Signell et al., 2005) may create roosts for cavity-dwelling forest species as fire-killed trees senesce and decay, or conversely, may weaken and remove existing snags and roosts (Boyles and Aubrey, 2006). In studies on the northern long-eared bat (*Myotis septentrionalis*), Johnson et al. (2009) and Lacki et al. (2009) both documented preferential roosting in burned forest stands, with bats apparently benefitting from increased solar radiation provided by canopy openings. Similarly, Perry et al. (2007) found that 5 of the 6 bat species preferred to roost in or near stands that had undergone partial harvest, midstory removal, and burning. The relationship between roosting area use and activity has been relatively unexamined, but preferential use of recently burned stands with abundant roosts may result in non-additive changes in bat activity levels within burned areas as some bat species exhibit specific patterns of activity around roosts (Johnson et al., 2011).

Our objectives in this study were to (1) determine whether total bat activity changed as a result of oak forest regeneration treatments consisting of overstory retention harvest and prescribed fire, (2) determine whether presence and relative activity of individual bat species changed as a result of oak forest regeneration treatments, and (3) assess the specific relationship between interspecific levels of bat activity relative to vegetation volume. We predicted *a priori* that bat activity would be negatively related to vegetation volume, with activity levels greater immediately post-harvest than 3 years post-harvest, and would increase following prescribed fire as a result of decreased vegetation volume. Relative to individual species patterns, we predicted that activity of big brown (*Eptesicus fuscus*) and eastern red (*Lasiurus borealis*) bats would be negatively related to vegetation volume, whereas *Myotis* spp. and tri-colored bats (*Perimyotis subflavus*) activity would be relatively insensitive to vegetation volume.

2. Methods

2.1. Study area and design

This study was conducted in Richland Furnace (82°36′W longitude, 39°10′N latitude) and Zaleski (82°23′W longitude, 39°15′N latitude) State Forests, Ohio; both forests lie in the unglaciated Allegheny Plateau region, where topography is characterized by numerous hills and drainages (Kerr, 1985). Within the study area, slopes ranged from 10% to 24%, and elevation ranged from approximately 213 to 304 m above sea level. Within each forest we selected six 10-ha study blocks. We designated four study blocks within each forest as harvest treatments and two as controls. Within each forest, two of the harvest treatment blocks were reduced to 50% of full stocking and two to 70% of full stocking. We used a systematic sampling design to establish 8 sampling points with at least 60 m spacing within each treatment block for use in bat activity and vegetation monitoring. Harvest treatment blocks were commercially thinned between June 2005 and March 2006, and subsequently were burned by the Ohio Department of Natural Resources Division of Forestry in either fall 2009 or spring 2010. To meet logistical needs and management objectives, burn unit size ranged from ~10 to 30 ha. Backing and strip fires were used to control fire intensity; despite this, burn intensity was highly variable, with temperatures ranging from ~426 to 537 °C (R. Williams, unpublished data). Fifty and 70% overstory retention harvests combined with prescribed fire 3–5 years post-harvest are consistent with recommendations for promoting regeneration and recruitment of oak species (Brose et al., 1999; Iverson et al., 2008).

2.2. Bat activity

We sampled bat activity using Anabat II broadband ultrasonic bat detectors (Titley Electronics, Ballina New South Wales, Australia) connected to voice activated micro-cassette recorders in May–August 2006 and June–September in 2009 and 2010. Because we used micro-cassette recorders with limited storage capacity, we monitored for three hours nightly beginning one half-hour before sunset. We monitored activity at all sampling sites in two treatment blocks simultaneously on nights when monitoring occurred. Sampling order was random without replacement, but due to logistical constraints, we monitored treatment blocks within the same forest. We hung detectors 1.5 m above ground level oriented upward at a 45° angle and facing away from nearby vegetation to maximize bat detection (Weller and Zabel, 2002) and did not sample during rain.

We transferred recorded passes from micro-cassette to computer using a Zero-Crossing Analysis Interface module and Anabat version 6.3 g (Titley Electronics, Ballina New South Wales, Australia). Similar to the method used by Owen et al. (2004), we identified species in AnaLook version 4.9j (Titley Electronics, Ballina New South Wales, Australia) using a combination of quantitative and qualitative characteristics. We retained for analysis only those bat passes that contained 2 or more calls separated by >1 s for analysis, and identified to species only those that were of high quality. Because recording quality of tapes is lower than that of computers (Johnson et al., 2002; White and Gehrt, 2001), we grouped Myotine (*Myotis* spp.) to minimize classification errors (Titchenell et al., 2011; Yates and Muzika, 2006). At our study sites, Myotine bat species that could be present could include *M. septentrionalis*, *M. leibii*, *M. lucifugus*, and *M. sodalis*, but previous netting has documented only *M. septentrionalis* and *M. lucifugus* (74% and 26% of Myotine captures, respectively) (Titchenell et al., 2011). Furthermore, we included tri-colored bats into the Myotine group (MYPE) to reflect similarities in habitat preferences. We identified the calls of big brown bats, eastern red bats, and hoary bats (*Lasiurus cinereus*) individually.

2.3. Vegetation structure

We recorded vegetation measurements for all woody stems at the same randomly selected 29 sampling sites (6 control, 10 50% retention, 13 70% retention) in each year of our study. Each plot was stratified into 0.08 ha overstory (trees $\geqslant$10 cm diameter at breast height (dbh)), 0.04 ha sapling (trees $\geqslant$1.4 m in height and $\leqslant$10 cm dbh), and 0.02 ha large seedling (trees $\geqslant$1.4 m in height and $\leqslant$10 cm dbh) circular sub-plots circumscribed around site center. For each measured stem, we recorded dbh, total height, height to base of live crown, and crown diameter (determined by two measurements: maximum crown diameter and crown diameter at a right angle to the axis of the maximum crown diameter). Using the algorithm of Avina et al. (2007), we estimated tree vegetation volume (m^3/ha) in five predetermined height strata (0–3 (TRI), 3–6 (SIX), 6–9 (NINE), 9–12 (TWLV), and 12+ m (TWLVP)) (Smith and Gehrt, 2010).

2.4. Statistical analysis

We averaged the total number of nightly and species-group specific bat passes per sampling site to obtain a relative measure of bat activity (Gehrt and Chelsvig, 2003). We used a repeated measures two-way mixed-effects analysis of variance (ANOVA) with treatment and year as fixed effects and forest and site as random effects to determine if the mean total number of passes differed among treatment blocks and years; inclusion of forest and site as random effects allowed us to account for the repeated measures of these factors. We used planned generalized linear hypothesis tests with Tukey's adjustment for multiple comparisons to determine which treatment means differed within years. We used a $\log(x + 0.8)$ transformation to meet assumptions of normality.

Because activity levels for individual species and species-groups were non-normally distributed and could not be normalized with a transformation, we used a permutational ANOVA (perANOVA) to determine whether species and species-group activity levels differed among treatments within years; we did not assess differences among years because call identification rates varied between years. Because there currently are no post hoc tests for perANOVAs, we used a pairwise approach with Wilcoxon tests and a Bonferroni correction for multiple comparisons to determine which treatment block means differed.

We obtained treatment area mean vegetation volume estimates per height strata by averaging across sites within treatment blocks, and used a repeated measures multiple analysis of variance (MANOVA) to determine whether harvest treatments impacted crown volume within strata. Use of a repeated measures MANOVA rather than separate ANOVAs for each height strata allowed us to account for the correlated nature of canopy volume across strata as well as the correlated nature of our repeated measures. We used redundancy analysis (RDA) with Hellinger transformed species data to assess interspecific variation in activity relative to prescribed fire and vegetation volume within our measurement strata. The use of the Hellinger transformation is appropriate for Euclidean distance based ordination techniques (Legendre and Gallagher, 2001). To control for repeated measurements on individual plots within treatment blocks, we conditioned our analysis by plot identifier. We performed a Monte Carlo test with 999 permutations to determine whether our ordination results were statistically significant.

We performed all analyses using the R statistical program version 2.14 (R. Development Core Team, 2014) with statistical significance for all tests accepted at $\alpha \leqslant 0.05$. We fit mixed effects models using the *lme4* library (Bates et al., 2014, p. 4) and the RDA using the *vegan* library (Oksanen et al., 2015).

3. Results

3.1. Vegetation structure

Vegetation volume differed within strata and harvest treatment levels among years (MANOVA: $F = 2.15$, $P < 0.03$), and approached difference among harvest treatments (MANOVA: $F = 1.89$, $P = 0.07$). Vegetation volume was higher in control blocks than in harvest treatment blocks in all but the 0–3 and 12+ m height strata (Fig. 1). Vegetation volume increased in all except the 12+ m height

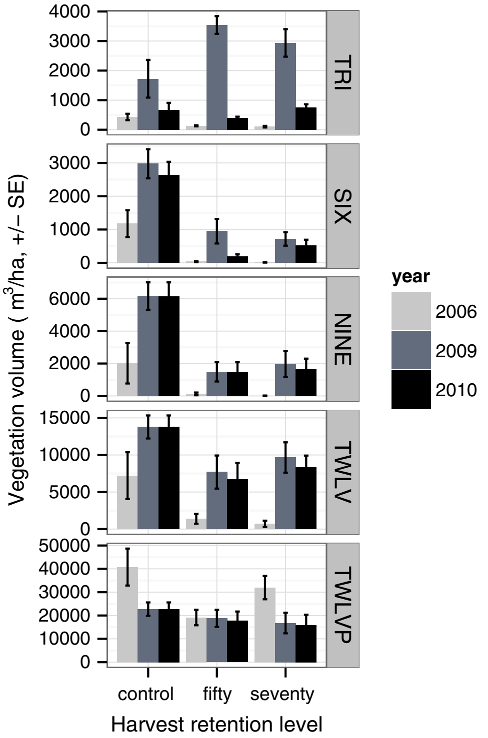

Fig. 1. Mean vegetation volume (±SE) by height strata (0–3 (TRI), 3–6 (SIX), 6–9 (NINE), 9–12 (TWLV), and 12+ m (TWLVP)) in harvested and control sites in Richland Furnace and Zaleski state forests in southeastern Ohio immediately post-harvest (2006), three growing seasons post-harvest (2009), and post-prescribed fire (2010).

strata between the first and third growing seasons post-harvest, with the greatest level of relative increase observed in the 0–3 and 3–6 m height strata. Prescribed fire reduced vegetation volume in all height strata, but large effects were limited to the 0–3 and 3–6 m height strata, where vegetation volume decreased by over 50% in some cases.

3.2. Bat activity

We monitored bat activity 38 nights in 2006, for a total of 609 detector nights (at least 6 nights per treatment block), with 11,581 total bat passes recorded. Of the passes identified by species in 2006, 326 were red bats, 336 were big brown bats, and 113 were MYPE bats. In 2009, we monitored bat activity on 36 nights, for a total of 576 detector nights (6 nights per treatment block), with a total of 9190 total bat passes were recorded. Of the passes identified to species in 2009, 1544 were red bats, 1653 were big brown bats, 846 were MYPE bats, and 171 were hoary bats. We monitored bat activity on 42 nights in 2010, for a total of 672 detector nights (7 nights per treatment block) and recorded 8035 bat passes; 303 passes were red bats, 1841 were big brown bats, 385 were MYPE, and 36 were hoary bats.

Total mean nightly bat activity differed among treatment blocks (ANOVA: $F = 73.96$, $P < 0.001$), years (ANOVA: $F = 16.86$, $P < 0.001$), and the interaction of treatment and year (ANOVA: $F = 3.22$, $P = 0.01$; Fig. 2). Total activity was lower in control treatment blocks than in harvest treatment blocks in all years (Fig. 3), but did not differ among control treatment blocks across years or between harvest treatment levels within a year. Pre-post fire activity differed only in the 50% retention treatments (Fig. 4).

Big brown bat mean nightly activity differed among treatment blocks in all years (perANOVA: $F = 4.93$, $P = 0.006$; $F = 9.87$, $P = 0.001$; $F = 9.49$, $P = 0.001$, in 2006, 2009, and 2010, respectively; Fig. 5), with higher activity levels in harvest treatment blocks than controls in all years. Mean nightly big brown bat activity did not differ between harvest treatment levels ($P > 0.05$) in any year.

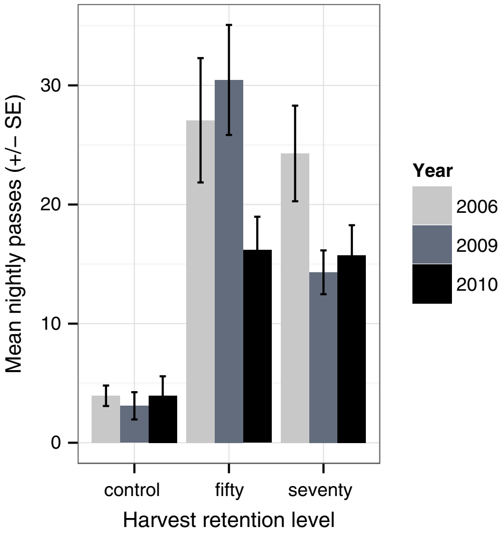

Fig. 2. Total mean nightly passes (±SE) in harvested and control sites in Richland Furnace and Zaleski state forests in southeastern Ohio immediately post-harvest (2006), three growing seasons post-harvest (2009), and post-prescribed fire (2010).

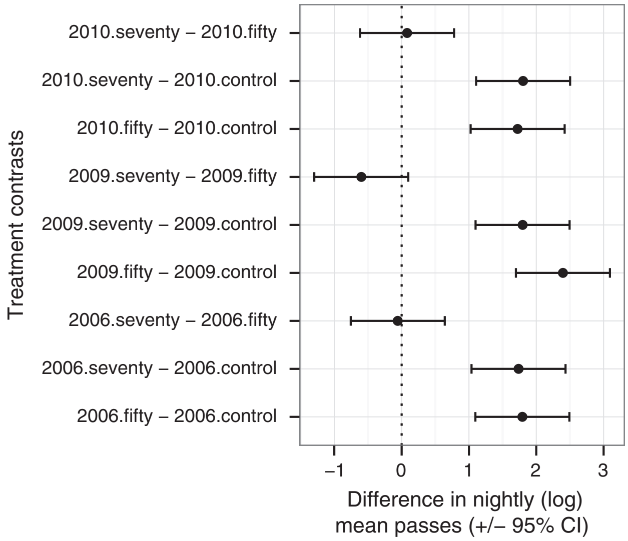

Fig. 3. Estimated differences in total bat activity between treatment and control blocks within years in Richland Furnace and Zaleski state forests in southeastern Ohio immediately post-harvest (2006), three growing seasons post-harvest (2009), and post-prescribed fire (2010). Contrasts with 95% confidence interval crossing 0 (dashed line) were not statistically significant. Estimates >0 show that activity is greater in the first listed treatment block for any given contrast.

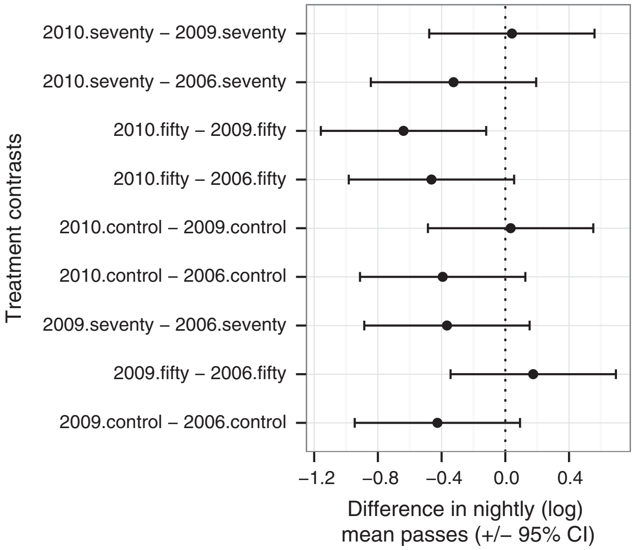

Fig. 4. Estimated differences in total bat activity between years within treatment and control blocks in Richland Furnace and Zaleski state forests in southeastern Ohio immediately post-harvest (2006), three growing seasons post-harvest (2009), and post-prescribed fire (2010). Contrasts with 95% confidence intervals crossing 0 (dashed line) were not statistically significant. Estimates >0 show that activity is greater in the first listed treatment block for any given contrast.

Mean eastern red bat nightly activity differed among treatment blocks immediately post-harvest and three growing seasons post-harvest, but not after prescribed fire (perANOVA: $F = 2.39$, $P = 0.037$; $F = 10.63$, $P = 0.001$; $F = 0.13$, $P = 0.945$, in 2006, 2009, and 2010, respectively; Fig. 5). Eastern red bat mean nightly activity was greater in harvest treatment blocks than in control blocks immediately post-harvest and three growing seasons post-harvest ($P < 0.001$), but did not differ between harvest treatment levels in either case.

Mean nightly MYPE activity differed among treatment blocks three growing seasons post-harvest, but not immediately post-harvest or after prescribed fire (perANOVA: $F = 2.57$, $P = 0.065$; $F = 4.25$, $P = 0.006$; $F = 0.48$, $P = 0.627$, in 2006, 2009, and 2010, respectively; Fig. 5). Mean MYPE nightly activity was greater in harvested treatment blocks than control blocks three growing seasons post-harvest ($P < 0.001$), but did not differ between harvest treatment blocks.

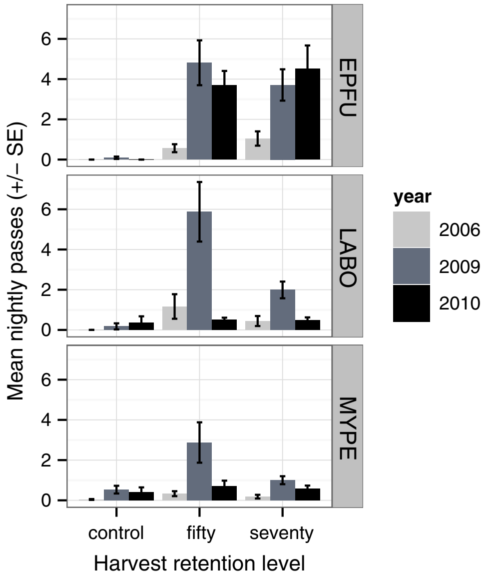

Fig. 5. Mean nightly passes (±SE) of big brown bats (*Eptesicus fuscus*; EPFU), eastern red bats (*Lasiurus borealis*; LABO), and *Myotis* spp. and tri-colored bats (*Perimyotis subflavus*; MYPE) in harvested and control sites in Richland Furnace and Zaleski state forests in southeastern Ohio immediately post-harvest (2006), three growing seasons post-harvest (2009), and post-prescribed fire (2010).

Interspecific variation in bat activity was related to vegetation volume and prescribed fire (pseudo-$F = 2.91$, $P = 0.001$; Fig. 6). While our habitat variables explained 12.1% of the total observed variance in our constrained ordination, site identity accounted for 51.9% of the observed variance. Axis 1 of our RDA explained 53.1% of the constrained variance, and was most strongly related to burn status and vegetation volume in the 3–6 and 6–9 m height strata (Table 1). Axis 2 of our RDA explained an additional 40.4% of the constrained and conditioned variance, and was most strongly related to vegetation volume in the 0–3 m height stratum.

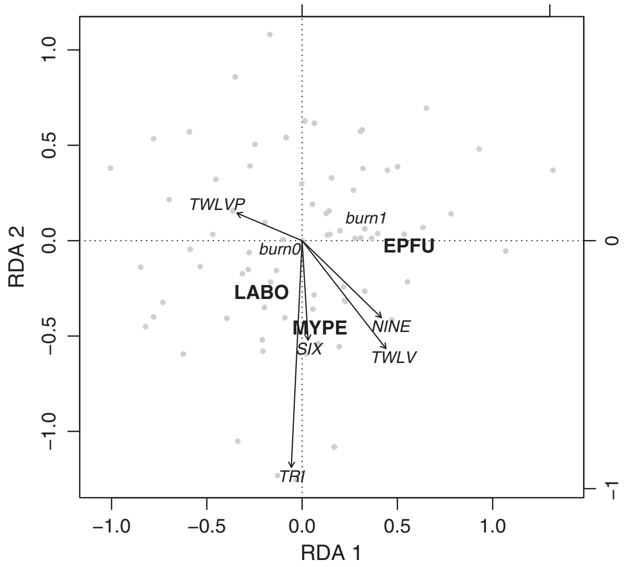

Fig. 6. Redundancy analysis of big brown (*Eptesicus fuscus*; EPFU), eastern red (*Lasiurus borealis*; LABO) and *Myotis* spp. and tri-colored bats (*Perimyotis subflavus*; MYPE) across three years of oak forest regeneration treatments in Richland Furnace and Zaleski state forests in southeastern Ohio. Environmental variables used to constrain the ordination are burned or unburned plot status (burn0 and burn1, respectively), and vegetation volume in 0–3 (TRI), 3–6 (SIX), 6–9 (NINE), 9–12 (TWLV), and 12+ m (TWLVP) height strata. Plot position in species space is shown in gray; the analysis was conditioned on plot identity to account for repeated measurements across years.

Table 1
Standardized linear constraints for the axes of a redundancy analysis of big brown (*Eptesicus fuscus*), eastern red (*Lasiurus borealis*) and *Myotis* spp. and tri-colored bats (*Perimyotis subflavus*) activity across three years of oak forest regeneration treatments in Richland Furnace and Zaleski state forests in southeastern Ohio. Variables used to constrain the ordination are burned or unburned status, and vegetation volume in 0–3 (TRI), 3–6 (SIX), 6–9 (NINE), 9–12 (TWLV), and 12+ m (TWLVP) height strata; the analysis was conditioned on site identity to account for repeated measurements across years.

	RDA1	RDA2	RDA3
TRI	0.05	−0.09	0.00
SIX	−0.12	−0.02	−0.05
NINE	0.17	−0.03	−0.26
TWLV	−0.06	−0.02	0.22
TWLVP	−0.01	−0.02	−0.08
Burn (indicator)	0.22	0.01	−0.02

4. Discussion

4.1. Effects of shelterwood harvest on bat activity

Consistent with other research (Loeb and Waldrop, 2008; Menzel et al., 2002; Owen et al., 2004), we found that, in all years of our study, total and species specific activity were greater in harvest treatment blocks than control blocks. Proportions of passes identified in this study are low compared to those of other studies, but mean nightly activity was greater than has been reported in other studies in upland forests (Brooks, 2003; Grindal and Brigham, 1998; Owen et al., 2004). It is important to note that our estimates of mean nightly activity are limited by the reduced recording time dictated by the use of cassette recorders. Overstory thinning is believed to allow increased foraging efficiency of bats, and greater levels of bat activity in harvested stands likely is due to the reduced vegetation volume relative to controls. The lack of difference in activity levels between 50% and 70% treatment levels was relatively surprising, given that these two treatment levels should theoretically differ substantially in structure. In practice, shelterwood harvesting often results in a close approximation, rather than exact match, of the desired retention level. In this study, our comparison of vegetation volume across height strata in our different treatments indicated that structural differences between these two treatments were minor. For forest management purposes, differences in structure may be sufficient to promote oak regeneration, but relative to bats, these differences appear to be minor. Higher levels of total and species level activity in treatment blocks than controls suggest that all species we studied benefitted from reduced vegetation volume.

Although bats are sensitive to vegetation structure (Adams et al., 2009; Müller et al., 2013), we found that total bat activity within treatment blocks did not differ between the first and third growing seasons post-harvest, despite the considerable increase in vegetation volume. Greater activity levels in harvested treatment blocks than controls generally was consistent across years, suggesting that forest thinning treatments may benefit bats for several years. Notably, we detected bat activity at vegetation volumes greater than the thresholds levels identified by Titchenell et al. (2011) that resulted in decreased activity and probability of presence of individual species. Bat activity has been found to be vertically stratified in response to vegetation structure (Adams et al., 2009; Hodgkison et al., 2004; Müller et al., 2013; Plank et al., 2012), and it is possible that bats shifted foraging behavior vertically in response to increased vegetation volume, thereby avoiding negative impacts of increases in vegetation volume, particularly in the 0–3 m height stratum, which experienced the greatest relative volume change.

4.2. Effects of prescribed fire on bat activity

Vegetative structure less than 3 m was most variable in response to harvest treatments and time since treatment, as we observed the greatest relative changes in volume in the 0–3 m height stratum between all measurement periods. We found that prescribed fire substantially impacted vegetation in the 0–3 and 3–6 m height strata, reducing volume to levels nearly equivalent to those in the first year post-harvest.

Increased levels of bat activity in burned areas generally have been related to reduced vegetation structure resulting from burning (Armitage and Ober, 2012; Buchalski et al., 2013; Smith and Gehrt, 2010). Although we observed substantial decreases in vegetation volume below 6 m, total bat activity in the 50% retention harvest treatment blocks decreased post-fire. Similarly, prescribed burning apparently decreased activity of eastern red bat and MYPE bat activity, as we found no difference in activity among burned treatment blocks and control blocks post-fire. Decreases in total activity in 50% retention harvest treatment blocks may have been driven by decreased activity of eastern red bats because the greatest decrease in activity of this species was observed in the 50% retention harvest treatment blocks. Decrease in activity and lack of difference among treatment and control blocks, respectively, were unexpected given the results of other studies both in relatively similar (Smith and Gehrt, 2010) and dissimilar (Armitage and Ober, 2012; Buchalski et al., 2013) habitat types. Typically, bat activity increases following reductions in vegetative structure, particularly for large-bodied species like the eastern red bat (Betts, 2009; Erickson and West, 2003; Humes et al., 1999; Menzel et al., 2002; Owen et al., 2004). Given that previous research on relationships of *Myotis* species to forest conditions have found differences in some specific habitat relationships (Brooks and Ford, 2005; Ford et al., 2005), our assessment of the response of the combined *Myotis* species and tri-colored bats should be interpreted cautiously, as pooling may have masked individual species responses. In particular, increased use by more open-tolerant species may have been masked by decreases in activity of vegetation-tolerant species. Consistent with the high levels of bat activity in harvest treatment blocks relative to control blocks three growing seasons post-harvest, greater total activity in 70% retention harvest treatment blocks, and higher activity of big brown bats in burned treatment blocks relative to controls following prescribed burning suggests that pre-fire vegetation volumes were not limiting foraging activity of this species.

Decreased eastern red bat activity following prescribed fire was somewhat surprising, as this species is a relatively fast flier and has been associated with open habitat types (Brooks and Ford, 2005; Elmore et al., 2005; Ford et al., 2005). However, a similar pattern of low eastern red bat activity in burned stands also was observed by Loeb and Waldrop (2008) in southern pine stands. As a caveat, slightly lower identification rates at the species level pre-post prescribed fire may suggest a greater difference than actually exists. Eastern red bats widely are considered moth (Lepidoptera) specialists (Clare et al., 2009; Hickey and Fenton, 1990; Whitaker, 2004). Given that lepidopterans appear to be particularly sensitive to prescribed fire in the short term, with decreased abundance in recently and frequently burned stands (Armitage and Ober, 2012; Evans et al., 2013; Scandurra et al., 2014; Schaeffer, 2013; Swengel and Swengel, 2006), it seems possible that decreased prey availability post-fire may have resulted in our observed changes in eastern red bat activity. Additionally, it is noteworthy that eastern red bats are known to hibernate in leaf litter (Mormann and Robbins, 2007), and it is possible that dormant season fires may cause direct mortality of hibernating eastern red bats, thereby reducing local populations and thus activity. Population reduction based changes in activity seem unlikely, however, because eastern red bat home ranges are sufficiently large (Elmore et al., 2005) that bats from adjacent, unburned areas, would still utilize such habitat, potentially at the same level if intraspecific competition was reduced.

4.3. Interspecific variation in bat activity

Similar to Titchenell et al. (2011) and Smith and Gehrt (2010), we found that interspecific variation in activity levels were strongly related to vegetation volume below 6 m. Bats differ substantially in their morphology (Aldridge and Rautenbach, 1987) display different species-specific responses to vegetation volume height strata (Adams et al., 2009; Müller et al., 2013; Titchenell et al., 2011). In general, large-bodied bats, and those with high aspect ratios and low wing loading, tend to avoid habitats with dense vegetation, whereas small-bodied bats and those with low aspect ratios and wing loading often are adapted to dense vegetation (Hodgkison et al., 2004). As expected, we found that big brown bat activity was negatively related to clutter volume, and positively associated with prescribed fire, and that bats in the MYPE group were associated with the more vegetated sites that would be characteristic of the forests conditions with which these species generally are associated (Ford et al., 2005; Menzel et al., 2005; Patriquin and Barclay, 2003). Surprisingly, MYPE activity had little apparent response to prescribed fire, although at least one *Myotis* species (*M. septentrionalis*) has been found to respond favorably to prescribed fire (Johnson et al., 2009; Lacki et al., 2009), and was more positively related to vegetation volume below 6 m than to volume above 6 m. In contrast to other studies (Menzel et al., 2005; Titchenell et al., 2011) and our expectations, we found that activity levels of eastern red bats were positively, rather than negatively, related to vegetation volume below 6 m.

Our RDA provides evidence that prescribed fire has at least some effects on bats that are vegetation volume independent. Relative to our treatments, different responses to vegetation volume support our assertion that patterns of big brown and MYPE bat activity that we observed were caused by changes in forest structure resulting from our treatments. Further, the importance of prescribed fire in determining the structure of our ordination, and the clear negative relationship between eastern red bats and prescribed fire in our RDA, are in agreement with our ANOVA results showing less activity in burned plots. Finally, the large amount of variation explained by our analysis suggests that vegetation structure across height strata is a primary driver in local patterns of bat activity, a result consistent with other studies (Adams et al., 2009; Müller et al., 2013; O'Keefe et al., 2014).

5. Management implications

Oak forest regeneration treatments had marked impacts on bat activity. Harvesting increased bat activity relative to controls, with increased levels of activity persisting 3 years post-harvest. Differences in treatment levels appear to be minimal, suggesting that relative to managing oak forests for foraging bats, forest managers may be flexible in selecting the most appropriate retention harvest level for local site conditions. Despite decreasing vegetation volume, which widely has been found to increase bat activity, prescribed fire had no apparent effect on big brown bat activity levels immediately post-fire, but substantially decreased activity levels of eastern red bats. Because we were unable to assess *Myotis* species' activity levels independently, it is unclear how prescribed fire affected this species group. Decreases in eastern red bat activity possibly are due to changes in prey availability, but this remains to be assessed experimentally. Despite the decreased level of eastern red bat activity, activity levels of all bat species still were greater in burned stands than within unthinned, unburned stands, suggesting that while prescribed fire may not improve habitat quality, burned habitats still are beneficial relative to unthinned, unburned stands. Benefits of fire to bats may not be apparent in the first year post-fire and it is important for forest and wildlife managers to consider all possible effects of prescribed fire on bat ecology when determining whether burning is appropriate for bat habitat management goals. The long-term implications of fire, and of repeated burning, remain to be assessed, but understanding clearly the long-term impacts of fire on bats and their habitat will be important as oak-forest regeneration techniques are applied at operational scales.

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