Effects of fire and its severity on occupancy of bats in mixed pine-oak forests

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ABSTRACT

Prescribed burning has become more common for the management of eastern forests in North America, so understanding if and how foraging bats respond to structural changes generated by fire is of increasing importance. Our objective was to investigate the effects of post-fire landscape conditions on the occurrence of foraging bats in mixed forests of the Cumberland Plateau physiographic region. We deployed Anabat II bat detectors in 164 paired burned and unburned forest sites for ≥ 2 nights from mid-May through August 2014 and 2015 to monitor bat foraging and commuting habitat use. We conducted vegetation surveys to quantify site-specific structural characteristics, which indicated that measures of structure were significantly lower in burned sites than unburned sites. We used Program Presence to test a priori hypotheses of species-specific probability of detection and site occupancy related to weather, burn history (i.e., site burned within the past 10 years or unburned), and site and landscape characteristics. Bats were detected at 94% of burned sites and 83% of unburned sites. Probability of detection was affected by weather conditions, vegetative structure, and burn history for most species. Occupancy for all species/species groups examined was positively associated with burning and generally associated with lower vegetative structure. Although burn severity did not affect most species groups, occupancy of *Myotis* species and tri-colored bats (*Perimyotis subflavus*) was lower in sites that received moderate severity burns than in sites that received low severity burns. Therefore, while prescribed fire may provide vegetative structure conducive to efficient foraging for all bats of the Cumberland Plateau, our results demonstrate that retaining some unburned forests while creating mosaics of lower and higher severity burns across the landscape will result in favorable foraging conditions for all resident bat species.

1. Introduction

Many southeastern pine (*Pinus*) and oak (*Quercus*) forests in the United States are fire dependent and must be maintained with frequent burning (Flatley et al., 2013, 2015). Suppression of natural fire periodicity in these forests has significantly altered the structural dynamics of local plant communities, resulting in hazardous wildfires, a decline in native vegetation and wildlife, propagation of invasive species, and disease (Wade et al., 1989). With prescribed burning, land managers seek to reduce fuel accumulation and restore forest ecosystems in areas where wildland fires have been habitually suppressed (Swift et al., 1993; Vose et al., 1994; Brose et al., 2001). In general, recurrent prescribed burning influences forest structure by decreasing mid- and understory tree density and basal area, thereby reducing fuel loads and opening the canopy (Anderson and Brown, 1986; Peterson and Reich, 2001). However, the effects of prescribed fire are often heterogeneous across the landscape due to the complexity of forest ecosystems (differing vegetative composition and structure, topography, and climate) and variation among fire regimes, including season, intensity, severity, and frequency of burns (Waldrop et al., 1992).

In the United States, southeastern pine and oak forests serve as primary roosting and foraging habitat for many temperate bat species experiencing unprecedented population declines, principally due to mortality associated with wind energy development and the emerging infectious disease, white-nose syndrome (WNS; Arnett et al., 2008; Blehert et al., 2009; Frick et al., 2010; Hayes, 2013). Understanding if, and how, bats respond to prescribed fire and its effects is therefore of growing importance. While bats can be adversely affected by heat, smoke, or displacement if roost structures or foraging resources are consumed or degraded during burning (Dickinson et al., 2010; Perry, 2012), observed increases in foraging and commuting activity following fire has primarily been attributed to favorable changes in forest structure that likely increase foraging efficiency (Loeb and Waldrop, 2008; Smith and Gehrt, 2010; Armitage and Ober, 2012; Silvis et al., 2016).

Although wing morphology and echolocation call structure (i.e., ecomorphology) of smaller species make them adept at maneuvering in cluttered (i.e., densely vegetated) habitats, compared to larger bats more adapted for fast, unrestricted flight (Aldridge and Rautenbach, 1987; Sleep and Brigham, 2003), all bats may benefit from reduced structural complexity after fire. Inconsistent findings, however, suggest smaller species may be less responsive than larger "clutter intolerant" bats (e.g., Lacki et al., 2009; Cox et al., 2016; Silvis et al., 2016) warranting further investigation.

Acoustic detectors record echolocation calls allowing researchers to non-invasively survey sites for bats in a broader range of areas than capture alone (Britzke et al., 2013). Because the probability of recording bats with acoustic detectors fluctuates with a number of factors including environmental conditions and the characteristics of species' echolocation calls (Lacki et al., 2007), analysis methods that account for detection probability are required (Duchamp et al., 2006; Rodhouse et al., 2011). Incorporating detection probability into models of habitat use yields more robust models and allows for stronger comparisons among treatments (Duchamp et al., 2006; MacKenzie et al., 2006; Gorreson et al., 2008; Weller, 2008).

Our objective was to investigate the effects of post-fire landscape conditions on the occurrence of commuting and foraging bats in the Cumberland Plateau physiographic region by comparing bat presence in burned and unburned sites while accounting for differences in probability of detection. Specifically, we tested the effects of burn history (i.e., burned or unburned), vegetation structure, weather, sampling date, survey period, and year, on the probability of detection for individual species and species groups, and the effects of burn history, vegetation structure, forest type, topographic characteristics (elevation and aspect), and year on bat occupancy for individual species and species groups. We hypothesized that site occupancy would be best explained as a function of forest structure. Therefore, we predicted occupancy would be influenced most by the factors that affected measures of forest structure such as burn history, forest type, elevation, and aspect. We expected occupancy would vary by species due to echolocation characteristics and wing morphology. We predicted occupancy of larger species, such as the hoary bat (*Lasiurus cinereus*), big brown bat (*Eptesicus fuscus*), silver-haired bat (*Lasionycteris noctivagans*), eastern red bat (*L. borealis*), and evening bat (*Nycticeius humeralis*) would be positively related to burning, and negatively related to structural complexity, whereas occupancy of smaller bats like the Indiana bat (*Myotis sodalis*), eastern small-footed bat (*M. leibii*), little brown bat (*M. lucifugus*), northern long-eared bat (*M. septentrionalis*), and tri-colored bat (*Perimyotis subflavus*) would be less associated with burning and vegetative structure.

To better understand the effects of burn characteristics on bat occupancy, we examined the effects of burn severity, burn frequency (i.e., repeated burn entries), and burn recency (i.e., time since the site was last burned) on occupancy within burned sites. We hypothesized that burn parameters would affect site occupancy through their effect on structural complexity with sites subjected to more severe, frequent, and recent fire having higher occupancy for all bats, but especially the larger-bodied and less maneuverable species. Because fires burn differently depending on a site's previous burn history, forest type, elevation, and aspect position, we predicted bat occupancy would vary as a result of additive combinations and interactions among these factors.

2. Methods

2.1. Study area

The study was conducted in Big South Fork National River and Recreation Area (BISO), which is located in Fentress, Scott, Pickett, and Morgan counties in northeastern Tennessee, and McCreary County in southeastern Kentucky, within the Cumberland Plateau physiographic region (Fig. 1). At the time of the study, WNS had been confirmed in

Fentress and Pickett counties, and the entire region surrounding the park was considered within the endemic WNS zone by the U.S. Fish and Wildlife (United States Fish and Wildlife Service, 2016). Encompassing over 50,000 ha, the majority of BISO is forested and predominately comprised of mixed oak and pine forests, with mixed mesophytic forest and grassland interspersed (Worsham et al., 2013). Active forest management activities consist primarily of fire management, such as prescribed fire, fire suppression, and mechanical fuel removal. Managers at BISO aim to reduce hazardous fuels, maintain historic landscapes, restore or enhance habitat, and control exotic species through their prescribed fire program (National Park Service, 2004). In the 10 years prior to this study, 10 forested treatment units throughout the park were established and successfully burned. All burns occurred in late winter or early spring. To meet logistical needs and management objectives, burn unit size ranged from ~10 to 1150 ha. Prescribed fires were typically low-intensity, understory burns, though some stands required higher intensity or repeated fires to achieve and maintain management objectives (Southern Appalachian/Piedmont Fire Effects Monitoring Team, 2012). Therefore, burned units varied by area, time since last burn (1–10 years), burn frequency (1-4x), and burn severity (low-moderate-high). No logging or thinning activities were conducted within the units prior to or following prescribed fire treatments.

2.2. Study design

To investigate the relationship between burn history and bat presence, we selected 11 burn units (10 prescribed fire units, 1 wildfire unit) that had been burned at least once in the last 10 years, and 11 adjacent unburned units (Fig. 1). Slopes within the burned and unburned units were 0.2–27% and elevation was approximately 340–510 m above sea level. Based on the National Park Service Vegetation Inventory data (National Park Service, 2008) we identified three forest categories: (1) Hemlock-Hardwood Cove forests (HHC) which were generally low elevation, mesic sites dominated by hemlock and mesic-hardwood species, (2) Mixed Oak-Hardwood forests (MOH) which were on mid-slopes and were generally open hardwood-dominated stands with some pines interspersed, and (3) Appalachian Pine-Oak forests (APO) which were generally higher elevation stands dominated by Virginia pine (*P. virginiana*), shortleaf pine (*P. echinata*), and pitch pine (*P. rigida*) with some xeric oak/hardwood species interspersed. With ArcGIS v. 10.1 (ESRI, Redlands, CA), we selected paired survey sites of the same forest type in adjacent burned and unburned units using randomly generated points based on accessibility and constrained by distance from road (≥50 m), distance to standing bodies of water or perennial streams/creeks (≥100 m). Because Anabat detectors only detect bats within 15–30 m of the microphone (Adams et al., 2012), all detectors used on the same night were ≥100 m from each other to avoid simultaneous detection of a bat in two sites (mean distance between paired burned and unburned sites was 1545 m and ranged from 110 m to 7021 m). If the area within 10 m of a selected point was not suitable for acoustic monitoring (e.g., substantial obstructions around the detector) we surveyed another point in the same forest type at a similar elevation in its place. Sampling was proportional to burn unit area and time since last burn.

2.3. Vegetation surveys

At each site, we characterized vegetation structure and composition within a 0.1 ha circular plot. We counted and measured all live and dead stems ≥1.4 m tall and ≥3 cm diameter at breast height (DBH) to estimate sapling and sawlog/polewood density and stand basal area (SBA). We established a 1 m-wide × 34 m-long transect at a randomly chosen compass direction across each plot and counted all woody stems ≥1.4 m tall and < 3 cm DBH to estimate seedling density and assess amount of understory clutter. We took hemispherical photos using a fish-eye lens positioned 1.5 m above the ground and 1 m in front of the
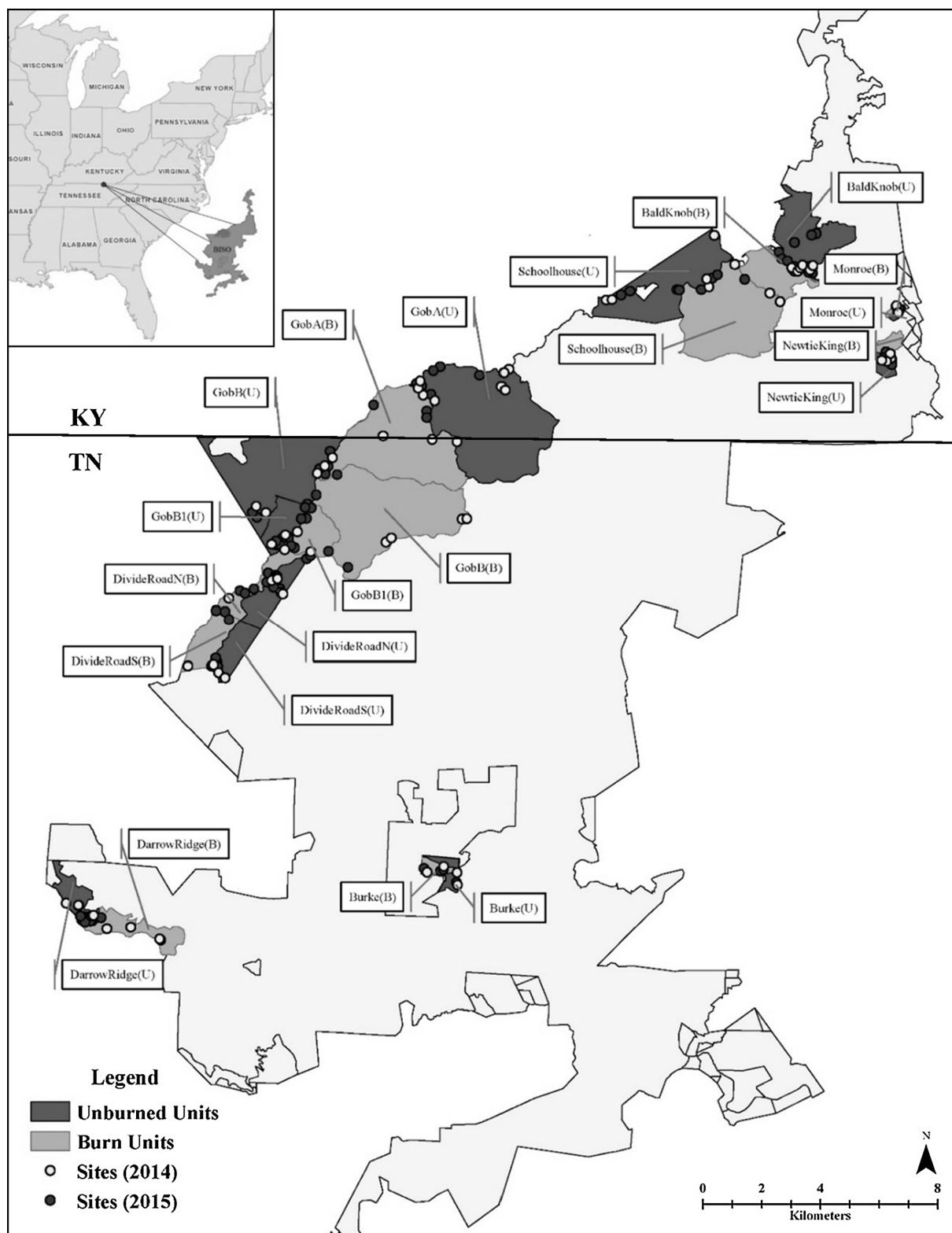
Fig. 1. Map of the Big South Fork National River and Recreation Area, TN/KY, USA. Dots indicate the location of sites sampled in burned and unburned units within the park.

deployed detector to quantify canopy closure at each site. We converted each photo to a binary image using ImageJ v. 1.46 software (U.S. National Institutes of Health, Bethesda, Maryland), and then analyzed the ratio of black to white pixels (i.e., canopy versus sky) to estimate percent canopy closure (Korhonen et al., 2006).

We obtained characteristics of past burns (burn year, frequency,

severity) from park records. We calculated severity of the most recent burn from the delta normalized burn ratio (dNBR) and reclassified to three categories of severity (low, moderate, and high; Key and Benson, 2006). Due to lack of access to high severity sites, we only sampled low and moderate severity burn sites. Elevation and aspect were calculated using ArcGIS 10.1 (ESRI, Redlands, CA).

2.4. Acoustic surveys

From mid-May through mid-August 2014 and 2015 we concurrently monitored bat presence and activity in our paired burned and unburned sites for ≥2 nights using Anabat II detectors (Titley Scientific, Columbia, MO) coupled with compact flash zero-crossing interface modules (ZCAIM). Anabat II detectors and ZCAIMs were housed together in metal ammunition cans with the microphone nested at the base of a 45° PVC tube to keep it dry (Britzke et al., 2010). Containers were set on tripods approximately 1.3–1.5 m high, with microphones oriented away from structural clutter (Weller and Zabel, 2002). Detectors were programmed to record from 15 min prior to sunset until 15 min after sunrise. To minimize equipment bias, we calibrated all detectors prior to field sampling (Larson and Hayes, 2000) and randomly assigned detectors to survey sites (Britzke, 2004). While acoustic sampling order was distributed throughout the park to avoid geographical bias, all paired sites monitored in a single night were located in similar areas of the park due to logistical constraints. We recorded temperature at each site every 30 mins with an iButton data logger (Embedded Data Systems, Lawrenceburg, KY) placed below the detector housing. Precipitation, relative humidity, and wind speed were obtained from the Remote Automated Weather Station (RAWS) located in the park, and daily barometric pressure was obtained from the closest (approximately 52 km northwest) Automated Weather Observing Station (AWOS) to the park (Weather Underground, 2015). Sampling on nights with moderate to heavy rain was avoided when possible. If moderate to heavy rain occurred and lasted > 30 min while sampling, detectors remained deployed for an additional 1–2 nights.

2.5. Statistical analyses

We conducted a 2-way Analysis of Variance (ANOVA) to test the main effects of burn history (burned, unburned), forest type (HHC, MOH, APO), and their interaction on stand basal area (SBA), % canopy closure, stem density < 3 cm DBH (seedling class), stem density 3–9.9 cm DBH (sapling class), and stem density ≥10 cm DBH (polewood/sawlog class). The majority of stems classified as polewood/sawlogs (80%) were 10–29 cm DBH, although stem size ranged as high as 234 cm DBH. We calculated least squares means and conducted post hoc analysis with Tukey's procedure to evaluate differences among means. Analyses were conducted using JMP Pro 12.0.1 (SAS Institute, Cary, NC), with a significance level of α = 0.05 for all statistical tests. We report least squares means ± 1 standard error.

We used a customized noise filter created in AnalookW v. 3.9f software (Titley Scientific, Columbia, MO) for cluttered environments to remove files containing only noise, retaining any file with discernable bat call pulses (Britzke and Murray, 2000). Remaining files were visually examined in AnaLookW to verify they contained ≥1 echolocation pulse and were used as an index of overall bat activity. We classified these files to species using Wildlife Acoustics Kaleidoscope Pro v. 3.1.5 bat call analysis software (Wildlife Acoustics, Maynard, MA). Based on past surveys and historic observations (National Park Service, 2004), we classified calls to 12 species that potentially occurred in the park: big brown bats, eastern red bats, evening bats, hoary bats, Rafinesque's big-eared bats (*Corynorhinus rafinesquii*), silver-haired bats, tri-colored bats, eastern small-footed bats, gray bats (*M. grisescens*), Indiana bats, little brown bats, and northern long-eared bats using the Bats of North America 3.1 classifier with the default settings and a minimum of three pulses. The output was manually vetted for accuracy. We grouped *Myotis* spp. (MYSP), eastern red bat and evening bat (LABO/NYHU), and big brown bat and silver-haired bat passes (EPFU/LANO) due to the similarity of their echolocation characteristics (O'Farrell et al., 1999; Robbins and Britzke 1999). When multiple species were detected in a single pass they were counted separately.

We constructed a comprehensive detection history of 0's (no-detection) and 1's (detection) for all surveys (MacKenzie et al., 2006). We

treated each night a detector was deployed at a site as one visit, and a site was considered occupied if at least one pass of a species or species group was identified during a single night of sampling. Although we use the terms "site occupancy" and "occurrence" our models should be interpreted as use, as foraging bats do not constantly occupy a site. For foraging bats this is a valid relaxation of the closure assumption of occupancy models (MacKenzie, 2005).

We used single-season occupancy models (Mackenzie et al., 2006) in PRESENCE v. 10.5 software (Proteus Research and Consulting, Dunedin, New Zealand) to evaluate probability of detection and site occupancy for each species or species-group present. Analyses were conducted in a stepwise fashion. We first assessed detection probability for each species while holding occupancy constant and then incorporated the significant detection covariates into subsequent occupancy models (MacKenzie et al., 2002). To investigate the influence of burn parameters on detection probabilities and site usage within burned sites, we ran additional analyses using burned sites only (82 total sites and 288 detector nights). We generated candidate models based on hypotheses concerning factors that may influence detection and site occupancy and included additive combinations of models and interactions between factors based on our hypotheses (Table 1). We standardized continuous covariates using z-score unless another standardization was deemed more appropriate. To avoid problems associated with multicollinearity, correlation coefficients were calculated and only uncorrelated predictor variables (Pearson's $|r|$ < 0.70) were used (Moore and McCabe, 1993).

We used Akaike's Information Criterion adjusted for small sample size (AICc; Hurvich and Tsai, 1989), the difference between the model with the lowest AICc and all other models (ΔAICc), and Akaike model weights (ω_i) to evaluate the relative strengths of candidate models (Burnham and Anderson, 2002). Models that did not converge or produced nonsensical parameter estimates (e.g., extremely large or negative standard errors) were eliminated (Long et al., 2011). We had a relatively large sample size compared to the number of parameters in our models (largest K = 38, n = 164 or 86 sites) suggesting that lack of convergence was not due to overparameterization. Instead we believe lack of convergence occurred when species were either almost ubiquitous or very rare. We assessed goodness-of-fit with our global models using the parametric bootstrap method described by MacKenzie and Bailey (2004) to produce a Pearson chi-square statistic (X^2) and p-value, and an overdispersion parameter estimation ($\hat{c}$). Because there was no evidence of lack-of-fit (i.e., the observed statistic was not unusually large compared to the expected, $\hat{c} \leq 1$) for any of our models, we proceeded to model selection using AICc. When the global model did not converge, we used the next most parametrized model to assess fit (MacKenzie and Bailey, 2004). Models that accounted for ≥90% of cumulative AIC weights were considered competing, and established as the confidence set (Royall, 1997; Hein et al., 2009). We created a composite model to incorporate model selection uncertainty by model-averaging parameter estimates and standard errors for each covariate across all models in the confidence set in which the covariate appeared (Burnham and Anderson, 2002). Covariates were considered significant if their resulting 85% confidence interval excluded zero (Arnold, 2010).
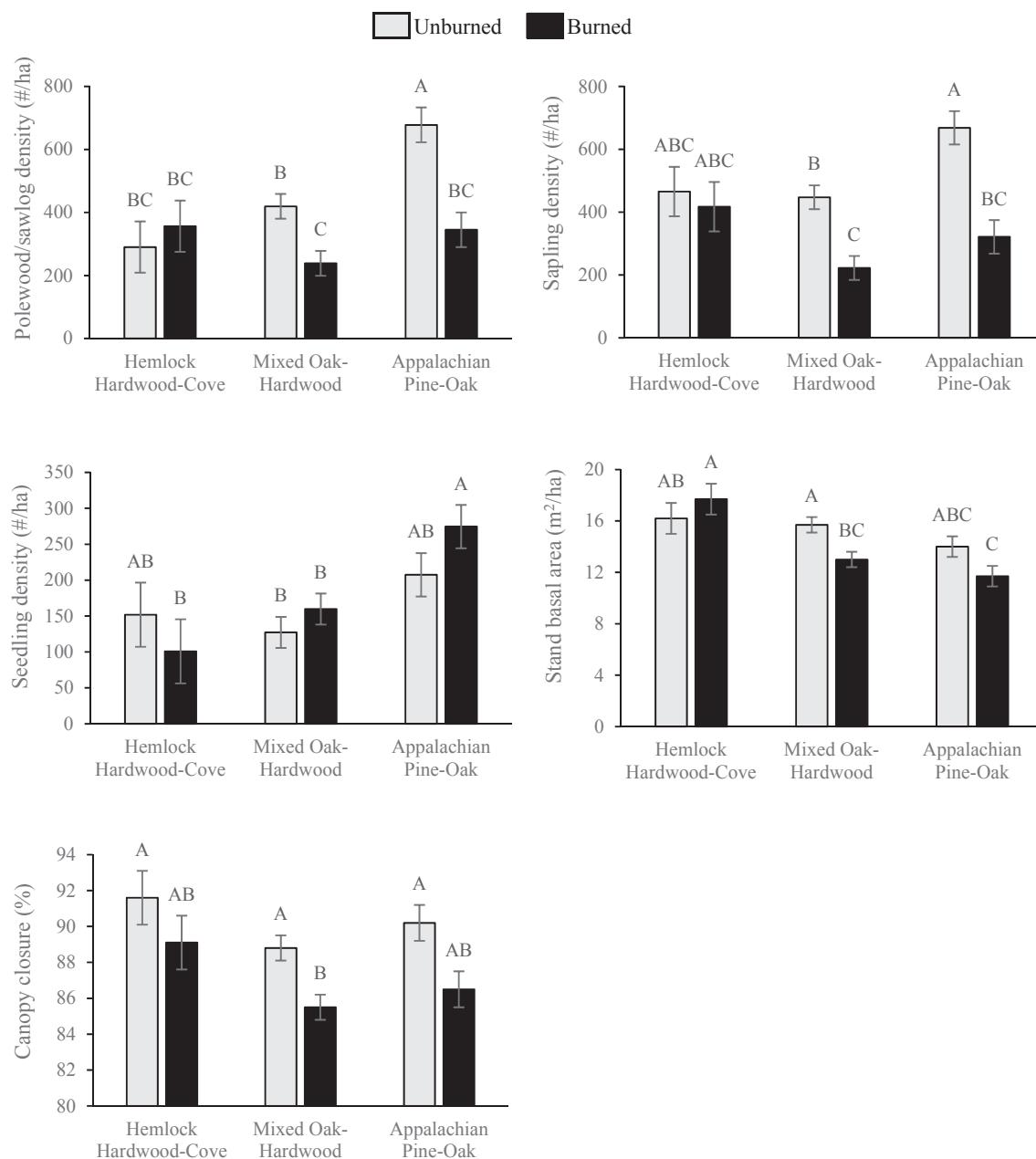
3. Results

3.1. Vegetation structure

We surveyed 164 sites (2014n = 62, 2015n = 102) and found significant differences in measures of structure between burned and unburned sites and among forest types. Stem densities of polewood/sawlogs and saplings, and canopy closure varied significantly with burn history (F (1,158) = 8.90, P = 0.003; F (1,158) = 18.32, P < 0.001; and F (1,158) = 11.35, P = 0.0009, respectively) and forest type (F (2,158) = 7.84, P = 0.0006; F (2,158) = 6.35, P = 0.002, and F (2,158) = 3.72, P = 0.03), whereas stand basal area and seedling density only varied significantly with forest type (F (2,158) = 8.07,

Table 1

Candidate model sets (not including null and global models), covariates, and their predicted influence (positive or negative effect) on detection probabilities (p) and/or occupancy (Ψ) of bats in Big South Fork National River and Recreation Area, May-August 2014 and 2015. Models were run using all sites or burn sites only. Occupancy (Ψ) was held constant in all detection models. Covariates and their predictive influence for additive models are not repeated (see corresponding single models).

Model (p/Ψ)	Covariates (Expected Influence)	Dataset
Weather (p)	mean nightly temperature ($+$)	All sites/Burn sites
	mean daily barometric pressure ($+$)	
	mean nightly relative humidity ($-$)	
	total nightly precipitation ($-$)	
	mean nightly wind speed ($-$)	
Julian Date (p)	Julian date ($+$)	All sites/Burn sites
Survey (p)	survey specific	All sites/Burn sites
Year (p/Ψ)	year	All sites/Burn sites
Burn History (p/Ψ)	burn history ($+$)	All sites
Structure (p/Ψ)	polewood/sawlog density ($-$)	All sites/Burn sites
	sapling density ($-$)	
	seedling density ($-$)	
	stand basal area ($-$)	
	canopy closure ($-$)	
Forest Type (Ψ)	Hemlock-Hardwood Cove (HHC) ($-$)	All sites/Burn sites
	Mixed Oak-Hardwood (MOH) ($+$)	
	Appalachian Pine-Oak (APO) ($+$)	
Topography (Ψ)	elevation ($+$)	All sites/Burn sites
	northern aspect ($-$)	
	eastern aspect ($-$)	
Burn Severity (Ψ)	low severity ($+$)	Burn sites
	moderate severity ($+$)	
Burn Frequency (Ψ)	burn frequency ($+$)	Burn sites
Time Since Last Burn (Ψ)	time since last burn (TSLB) ($-$)	Burn sites
Time Since Last Burn^2 (Ψ)	TSLB^2 ($-/+$)	Burn sites
Weather + Structure (p)		All sites/Burn sites
Weather + Burn History (p)		All sites
Structure + Burn History (p/Ψ)		All sites
Weather + Structure + Burn History (p)		All sites
Weather + Julian Date (p)		All sites/Burn sites
Forest Type + Burn History (Ψ)		All sites
Topography + Burn History (Ψ)		All sites
Structure * Burn History (Ψ)	polewood/sawlog density * burn history	All Sites
	sapling density * burn history	
	seedling density * burn history	
	stand basal area * burn history	
	canopy closure * burn history	
Forest Type * Burn History (Ψ)	HHC * burn history	All Sites
	MOH * burn history	
	APO * burn history	
Topography * Burn History (Ψ)	elevation * burn history	All Sites
	northern aspect * burn history	
	eastern aspect * burn history	
Structure + Burn Severity (Ψ)		Burn Sites
Forest Type + Burn Severity (Ψ)		Burn Sites
Forest Type * Burn Severity (Ψ)	HHC * burn severity	Burn Sites
	MOH * burn severity	
	APO * burn severity	
Topography + Burn Severity (Ψ)		Burn Sites
Topography * Burn Severity (Ψ)	elevation * burn severity	Burn Sites
	northern aspect * burn severity	
	eastern aspect * burn severity	
Structure + Burn Frequency (Ψ)		Burn Sites
Forest Type + Burn Frequency (Ψ)		Burn Sites
Forest Type * Burn Frequency (Ψ)	HHC * burn frequency	Burn Sites
	MOH * burn frequency	
	APO * burn frequency	
Topography + Burn Frequency (Ψ)		Burn Sites
Topography * Burn Frequency (Ψ)	elevation * burn frequency	
	northern aspect * burn frequency	
	eastern aspect * burn frequency	
Structure + Time Since Last Burn (Ψ)		Burn Sites
Forest Type + Time Since Last Burn (Ψ)		Burn Sites
Forest Type * Time Since Last Burn (Ψ)	HHC * TSLB	Burn Sites
	MOH * TSLB	
	APO * TSLB	
Topography + Time Since Last Burn (Ψ)		Burn Sites
Topography + Time Since Last Burn (Ψ)	elevation * TSLB	Burn Sites
	northern aspect * TSLB	
	eastern aspect * TSLB	

Fig. 2. Least squares means and standard errors of structural characteristics in unburned and burned sites for three forest types in Big South Fork National River and Recreation Area May-August 2014 and 2015. Bars with different letters are significantly different (P ≥ 0.05).

$P = 0.0005$, and $F (2,158) = 7.99$, $P = 0.0005$). Burned sites contained significantly lower densities of polewood/sawlogs (313 ± 35 stems/ha vs. 462 ± 35 stems/ha) and saplings (320 ± 34 stems/ha vs. 527 ± 34 stems/ha), and a lower percentage of canopy closure ($87\% \pm 0.7$) than unburned sites ($90\% \pm 0.7$). Although the effect of burn history on polewood/sawlog and sapling density, stand basal area, and canopy closure appeared to depend on forest type (Fig. 2), the interaction between burn history and forest type was only significant for polewood/sawlog density ($F (2,158) = 4.17$, $P = 0.02$). Polewood/sawlog density was significantly lower in burned than unburned APO and MOH forest types, whereas mean stem density of polewoods/sawlogs was higher in burned than unburned sites in the HHC forest type (Fig. 2).

3.2. Acoustic activity

We surveyed 224 detector nights in 2014 and 352 detector nights in

2015. While total bat activity was higher in 2014 (5276 bat passes; 23.6 passes/detector night) than in 2015 (3933 bat passes; 11.2 passes/detector night), bats were detected at less sites (84% of sites) in 2014 than in 2015 (91% of sites). Over both years, we detected bats at 88% (n = 145) of all surveyed sites, with bats detected at more burned (94%) than unburned sites (83%). We identified six species/species groups; EPFU/LANO, LABO/NYHU, MYSP, tri-colored bats (PESU), hoary bats (LACI), and Rafinesque's big-eared bats. Because Rafinesque's big-eared bats were only detected at three sites (< 2%) we excluded them from further analyses. EPFU/LANO were detected at the greatest number of sites of any species/species group (58% of sites; 64 burned sites, 31 unburned sites), followed by LABO/NYHU (51% of sites; 58 burned sites, 26 unburned sites). While rarer, MYSP, PESU, and LACI were also detected at more burned than unburned sites (MYSP: 35% of sites; 39 burned sites, 18 unburned sites, PESU: 34% of sites; 38 burned sites, 18 unburned sites, LACI: 21% of sites; 25 burned sites, 10 unburned sites). Within burned sites, EPFU/LANO were the most

detected species group (78% of burned sites), followed by LABO/NYHU (70% of burned sites), MYSP (48% of burned sites), PESU (46% of burned sites), and LACI (26% of burned sites).

3.3. Probability of detection

The confidence sets for probability of detection for all species groups included candidate models that contained "BurnHistory," and "Structure" covariates (Supplemental Table 1). Composite models with 85% confidence intervals that did not include zero indicated that detection for each species group was positively related to burning, with detection for EPFU/LANO and LABO/NYHU also influenced by structural covariates (Supplemental Table 2). When we considered burned sites only, all confidence sets for probability of detection included candidate models containing "Structure" covariates (Supplemental Table 3), with composite models indicating that detection within burned sites was also influenced by structural covariates for each species group observed (Supplemental Table 4).

3.4. Occupancy

Across all sites, four models predicting occurrence of EPFU/LANO were included in the 90% cumulatively weighted confidence set (Table 2). The highest ranked model, "BurnHistory" accounted for 54% of the total model weight and all four models included the "BurnHistory" covariate. EPFU/LANO occurrence was positively related to burning, polewood/sawlog density, and canopy closure (Table 3).

Table 2
Model, number of parameters in the model (K), Akaike's Criterion adjusted for small samples (AIC$_c$), difference between a model AIC$_c$ and the model with the lowest AIC$_c$ (ΔAIC$_c$), and model weights (ω$_i$) for the confidence sets of models used to predict occupancy (Ψ) of five bat species/species in Big South Fork National River and Recreation Area May-August 2014 and 2015. Detection covariates included in the models were temperature (T), barometric pressure (BP), burn history (BH), polewood/sawlog density (Pole), sapling density (Sap), seedling density (Seed), stand basal area (SBA), canopy closure (CC), Julian day (JD), and year (YR). If all structural parameters were used as detection covariates in the models they are denoted as "Structure".

Model	K	AIC$_c$	ΔAIC$_c$	ω$_i$
EPFU/LANO				
Ψ(BurnHistory), p(BH + T + BP + Structure)	11	568.72	0	0.5367
Ψ(BurnHistory + Forest Type), p(BH + T + BP + Structure)	13	570.71	1.99	0.1984
Ψ(BurnHistory * Forest Type), p(BH + T + BP + Structure)	15	572.15	3.43	0.0966
Ψ(BurnHistory * Structure), p(BH + T + BP + Structure)	21	572.16	3.44	0.0961
LABO/NYHU				
Ψ(BurnHistory * Structure), p(BH + T + BP + Sap + Seed + CC)	19	510.48	0	0.9257
MYSP				
Ψ(.), p(Pole + Sap + SBA)	5	441.11	0	0.2657
Ψ(Year), p(Pole + Sap + SBA)	6	441.65	0.54	0.2028
Ψ(BurnHistory), p(Pole + Sap + SBA)	6	441.77	0.66	0.1910
Ψ(Topography), p(Pole + Sap + SBA)	8	443.47	2.36	0.0816
Ψ(ForestType), p(Pole + Sap + SBA)	7	444.22	3.11	0.0561
Ψ(Structure), p(Pole + Sap + SBA)	10	444.28	3.17	0.0544
Ψ(BurnHistory + Topography), p(Pole + Sap + SBA)	9	444.39	3.28	0.0515
PESU				
Ψ(BurnHistory + Topography), p(T + Sap + Seed)	9	460.80	0	0.9047
LACI				
Ψ(BurnHistory), p(Seed + CC)	5	306.26	0	0.3267
Ψ(BurnHistory * Topography), p(Seed + CC)	11	306.69	0.43	0.2635
Ψ(Structure), p(Seed + CC)	9	308.09	1.83	0.1309
Ψ(BurnHistory + Topography), p(Seed + CC)	8	308.91	2.65	0.0868
Ψ(BurnHistory + Structure), p(Seed + CC)	10	309.31	3.05	0.0711
Ψ(Topography), p(Seed + CC)	7	309.69	3.43	0.0588

Table 3
Model-averaged parameter estimates and standard errors (SE), and lower and upper 85% confidence intervals (CI) on parameter estimates included in the confidence set of models used to predict occupancy (Ψ) of five species/species groups in Big South Fork National River and Recreation Area May-August 2014 and 2015.

Parameter	Estimate ± SE	Lower 85% CI	Upper 85% CI
EPFU/LANO			
Ψ (intercept)	−0.35 ± 0.48	−1.04	0.34
Burn History	2.02 ± 0.72	0.98	3.05
Polewood/Sawlog Density	0.47 ± 0.30	0.04	0.90
Sapling Density	−0.19 ± 0.31	−0.63	0.25
Seedling Density	0.05 ± 0.45	−0.59	0.69
Stand Basal Area	0.41 ± 0.38	−0.14	0.95
Canopy Closure	0.75 ± 0.42	0.15	1.36
Burn History * Polewood/Sawlog Density	−1.09 ± 0.64	−2.01	−0.16
Burn History * Sapling Density	−0.79 ± 0.85	−2.01	0.44
Burn History * Seedling Density	0.51 ± 0.75	−0.58	1.59
Burn History * Stand Basal Area	−0.77 ± 0.69	−1.77	0.23
Burn History * Canopy Closure	−1.20 ± 0.64	−2.12	−0.29
Mixed Oak-Hardwood forest type	0.25 ± 0.82	−0.93	1.43
Appalachian Pine-Oak forest type	0.94 ± 0.86	−0.29	2.18
Burn History * Mixed Oak-Hardwood forest type	2.57 ± 1.64	0.21	4.92
Burn History * Appalachian Pine-Oak forest type	1.33 ± 1.45	−0.75	3.42
LABO/NYHU			
Ψ (intercept)	−0.70 ± 0.39	−1.26	−0.14
Burn History	2.87 ± 1.11	1.27	4.47
Polewood/Sawlog Density	0.14 ± 0.25	−0.22	0.50
Sapling Density	−0.55 ± 0.40	−1.12	0.02
Seedling Density	0.59 ± 0.46	−0.08	1.26
Stand Basal Area	0.60 ± 0.40	0.03	1.18
Canopy Closure	1.00 ± 0.47	0.32	1.68
Burn History * Polewood/Sawlog Density	−1.96 ± 0.87	−3.21	−0.71
Burn History * Sapling Density	−0.24 ± 1.04	−1.73	1.26
Burn History * Seedling Density	2.75 ± 1.55	0.52	4.99
Burn History * Stand Basal Area	−0.95 ± 0.69	−1.95	0.04
Burn History * Canopy Closure	−0.79 ± 0.68	−1.77	0.19
MYSP			
Ψ (intercept)	0.60 ± 0.69	−0.39	1.59
Burn History	0.71 ± 0.44	0.08	1.34
Polewood/Sawlog Density	−0.85 ± 0.46	−1.51	−0.20
Sapling Density	−0.68 ± 0.57	−1.51	0.15
Seedling Density	0.75 ± 0.54	−0.03	1.53
Stand Basal Area	0.10 ± 0.36	−0.42	0.61
Canopy Closure	0.15 ± 0.27	−0.24	0.54
Elevation	0.53 ± 0.16	0.30	0.77
Northern aspect	0.20 ± 0.37	−0.33	0.73
Eastern aspect	0.03 ± 0.40	−0.54	0.60
Mixed Oak-Hardwood forest type	0.29 ± 0.81	−0.87	1.46
Appalachian Pine-Oak forest type	−0.30 ± 0.91	−1.61	1.00
Year	−0.93 ± 0.89	−2.21	0.34
PESU			
Ψ (intercept)	−1.07 ± 0.36	−1.59	−0.55
Burn History	1.36 ± 0.46	0.69	2.03
Elevation	0.88 ± 0.25	0.53	1.24
Northern aspect	0.38 ± 0.31	−0.06	0.81
Eastern aspect	−0.07 ± 0.32	−0.53	0.40
LACI			
Ψ (intercept)	−0.72 ± 0.57	−1.53	0.09
Burn History	1.38 ± 0.77	0.27	2.50
Polewood/Sawlog Density	0.42 ± 0.28	0.02	0.82
Sapling Density	−0.95 ± 0.44	−1.58	−0.32
Seedling Density	0.51 ± 0.13	0.32	0.69
Stand Basal Area	−0.18 ± 0.37	−0.72	0.35
Canopy Closure	−0.16 ± 0.32	−0.62	0.30
Elevation	0.19 ± 0.53	−0.58	0.96
Northern aspect	0.02 ± 0.54	−0.76	0.80
Eastern aspect	−0.19 ± 0.64	−1.11	0.73
Burn History * Elevation	1.89 ± 0.76	0.80	2.98
Burn History * Northern aspect	0.35 ± 0.93	−0.99	1.69
Burn History * Eastern aspect	−1.68 ± 1.04	−3.17	−0.19
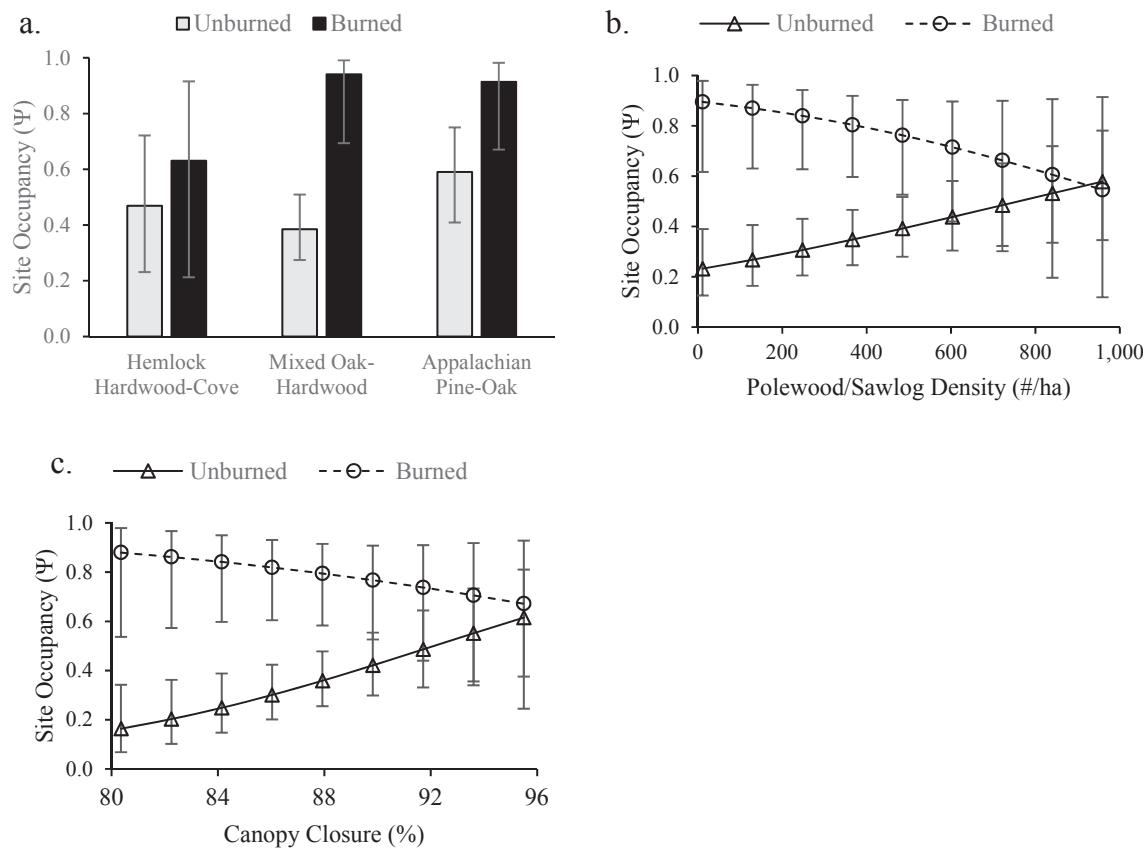
Fig. 3. Site occupancy of EPFU/LANO as a function of interactions between burn history and (a) forest type, (b) polewood/sawlog density, and (c) canopy closure in Big South Fork National River and Recreation Area May-August 2014 and 2015.

Further, while occupancy was higher in burned sites in all forest types, occupancy only differed significantly between burned and unburned sites in MOH forest types (Fig. 3a). Occupancy decreased as polewood/sawlog density and canopy closure increased in burned sites, but increased with polewood/sawlog density and canopy closure in unburned sites (Fig. 3b, 3c).

A total of 22 of the 23 models predicting occurrence of EPFU/LANO within burned sites did not converge or produced nonsensical parameter estimates. Thus, we eliminated the EPFU/LANO burn site model set. EPFU/LANO was very common in our area and, after we adjusted for probability of detection, was essentially ubiquitous within burned sites.

A single model containing "BurnHistory," "Structure," and the interaction between "BurnHistory" and "Structure" comprised the occupancy confidence set for LABO/NYHU across all sites (Table 2). This model accounted for 93% of cumulative AICc weight. Occupancy of LABO/NYHU was positively related to burn, stand basal area, and canopy closure (Table 3). However, stem density affected LABO/NYHU occupancy differently depending on burn history. LABO/NYHU occurrence decreased as polewood/sawlog density increased in burned sites but increased slightly as polewood/sawlog density increased in unburned sites. LABO/NYHU occurrence was positively associated with increasing seedling density in both burned and unburned sites, although this relationship was most apparent in burned sites.

Four models predicting occurrence of LABO/NYHU within burned sites were eliminated from the candidate set because they did not converge or produced nonsensical parameter estimates. The null model was the top-ranked model indicating that none of the other a priori models explained LABO/NYHU occupancy within burned sites well (Table 4). Based on the composite model, LABO/NYHU occurrence within burned sites increased with elevation and decreased with easterly aspect, and was significantly higher in 2015 than in 2014 (Table 5).

Seven models predicting occurrence of MYSP across all sites were included in the 90% confidence set (Table 2). The null model was the top-ranked model, indicating that none of the other a priori models explained MYSP occupancy well. Based on the composite model, occupancy of MYSP was positively related to burn and elevation, but negatively related to polewood/sawlog density (Table 3).

The global model was eliminated from the MYSP burn model candidate set because it did not converge. The top model was "BurnSeverity"; however, there were 10 competing models (Table 4). Within burned sites, MYSP occupancy decreased with burn severity, but increased with elevation and canopy closure, and was positively associated with the MOH forest type (Table 5).

The "BurnHistory + Topography," was the top model for PESU across all sites with no closely competing models (Table 2). PESU occurrence was positively associated with burn and increased with elevation (Table 3).

The global model was eliminated from the PESU burn model candidate set because it did not converge. The highest ranked model was "BurnSeverity*Topography" and accounted for 60% of the total model weight although there were seven other models in the confidence set (Table 4). Within burned sites, PESU occupancy was negatively associated with burn severity and positively associated with elevation (Table 5). However, aspect affected PESU occurrence differently depending on burn severity. PESU occupancy in both low and moderate severity burn sites increased as aspect became more northerly, although this effect was more pronounced in burned sites of higher severity. PESU occurrence decreased with an increasing easterly aspect in moderate severity burn sites but increased slightly with a more easterly aspect in low severity burn sites.

Six models predicting occurrence of LACI across all sites were included in the 90% confidence set (Table 2). The "Burn History" covariate was included in four of the seven models, including the highest

Table 4

Model, number of parameters in the model (K), Akaike's Criterion adjusted for small samples (AIC$_c$), difference between a model AIC$_c$ and the model with the lowest AIC$_c$ (ΔAIC$_c$), and model weights (ω$_i$) for the confidence sets of models used to predict occupancy (Ψ) of five species/species groups at burned sites in Big South Fork National River and Recreation Area May-August 2014 and 2015. Detection parameters (p) included in the models were temperature (T), barometric pressure (BP), polewood/sawlog density (Pole), sapling density (Sap), seedling density (Seed), stand basal area (SBA), and canopy closure (CC). If all structural covariates were used in the detection models they are denoted as "Structure". *EPFU/LANO model set was eliminated due to ubiquitous distribution in burned sites.

Model	K	AIC$_c$	ΔAIC$_c$	ω$_i$
LABO/NYHU				
Ψ(.), p(T + Pole + Sap + Seed + CC)	7	270.91	0	0.2733
Ψ(Year), p(T + Pole + Sap + Seed + CC)	8	271.42	0.51	0.2118
Ψ(BurnFrequency), p(T + Pole + Sap + Seed + CC)	8	273.26	2.35	0.0844
Ψ(TimeSinceLastBurn), p(T + Pole + Sap + Seed + CC)	8	273.31	2.40	0.0823
Ψ(BurnSeverity), p(T + Pole + Sap + Seed + CC)	8	273.33	2.42	0.0815
Ψ(Topography), p(T + Pole + Sap + Seed + CC)	10	273.48	2.57	0.0756
Ψ(ForestType), p(T + Pole + Sap + Seed + CC)	9	274.62	3.71	0.0428
Ψ(TimeSinceLastBurn + Topography), p(T + Pole + Sap + Seed + CC)	11	274.83	3.92	0.0385
Ψ(BurnSeverity + Topography), p(T + Pole + Sap + Seed + CC)	11	275.85	4.94	0.0231
MYSP				
Ψ(BurnSeverity), p(Pole + Sap + SBA + CC)	7	285.75	0	0.3716
Ψ(.), p(Pole + Sap + SBA + CC)	6	287.63	1.88	0.1451
Ψ(BurnSeverity + ForestType), p(Pole + Sap + SBA + CC)	9	288.63	2.88	0.0880
Ψ(Year), p(Pole + Sap + SBA + CC)	7	289.06	3.31	0.0710
Ψ(BurnSeverity + Topography), p(Pole + Sap + SBA + CC)	10	289.62	3.87	0.0537
Ψ(TimeSinceLastBurn), p(Pole + Sap + SBA + CC)	7	289.88	4.13	0.0471
Ψ(BurnFrequency), p(Pole + Sap + SBA + CC)	7	289.96	4.21	0.0453
Ψ(ForestType), p(Pole + Sap + SBA + CC)	8	290.62	4.87	0.0325
Ψ(Structure), p(Pole + Sap + SBA + CC)	11	291.59	5.84	0.0200
Ψ(Topography), p(Pole + Sap + SBA + CC)	9	291.66	5.91	0.0194
Ψ(TimeSinceLastBurn^2), p(Pole + Sap + SBA + CC)	8	291.74	5.99	0.0186
PESU				
Ψ(BurnSeverity * Topography), p(Structure)	14	291.38	0	0.6011
Ψ(Topography), p(Structure)	10	295.65	4.27	0.0711
Ψ(BurnSeverity + Topography), p(Structure)	11	295.98	4.60	0.0603
Ψ(.), p(Structure)	7	296.14	4.76	0.0556
Ψ(BurnSeverity), p(Structure)	8	296.30	4.92	0.0514
Ψ(TimeSinceLastBurn + Topography), p(Structure)	11	297.29	5.91	0.0313
Ψ(TimeSinceLastBurn), p(Structure)	8	298.06	6.68	0.0213
Ψ(BurnFrequency + Topography), p(Structure)	11	298.24	6.86	0.0195
LACI				
Ψ(BurnFrequency + Structure), p(Structure)	13	195.91	0	0.2956
Ψ(.), p(Structure)	7	196.66	0.75	0.2032
Ψ(TimeSinceLastBurn + Topography), p(Structure)	11	198.13	2.22	0.0974
Ψ(BurnSeverity), p(Structure)	8	198.49	2.58	0.0814
Ψ(TimeSinceLastBurn), p(Structure)	8	198.50	2.59	0.0810
Ψ(BurnFrequency), p(Structure)	8	198.52	2.61	0.0802
Ψ(TimeSinceLastBurn^2), p(Structure)	9	198.98	3.07	0.0637

Table 5

Model-averaged parameter estimates and standard errors (SE), lower and upper 85% confidence intervals (CI) on parameter estimates included in the confidence set of models used to predict occupancy (Ψ) of five bat species/species groups at burned sites in Big South Fork National River and Recreation Area May-August 2014 and 2015.

Parameter	Estimate ± SE	Lower 85% CI	Upper 85% CI
LABO/NYHU			
Ψ (intercept)	2.17 ± 0.92	0.84	3.50
Burn Frequency	0.29 ± 0.92	−1.03	1.61
Time Since Last Burn	0.04 ± 0.56	−0.76	0.85
Burn Severity	−0.31 ± 1.22	−2.07	1.45
Elevation	1.23 ± 0.49	0.52	1.94
Northern aspect	0.14 ± 0.63	−0.77	1.05
Eastern aspect	−1.26 ± 0.78	−2.38	−0.13
Mixed Oak-Hardwood forest type	1.65 ± 1.27	−0.18	3.48
Appalachian Pine-Oak forest type	2.37 ± 1.70	−0.08	4.82
Year	1.67 ± 1.16	0.00	3.34
MYSP			
Ψ (intercept)	1.32 ± 1.13	−0.30	2.94
Burn Frequency	0.09 ± 0.35	−0.41	0.59
Time Since Last Burn	0.07 ± 0.62	−0.82	0.96
Time Since Last Burn^2	−0.78 ± 0.99	−2.21	0.65
Burn Severity	−1.65 ± 0.93	−2.98	−0.31
Polewood/Sawlog Density	1.71 ± 1.89	−1.02	4.43
Sapling Density	0.59 ± 2.07	−2.40	3.57
Seedling Density	−0.69 ± 0.93	−2.04	0.65
Stand Basal Area	0.21 ± 1.13	−1.41	1.84
Canopy Closure	2.02 ± 1.06	0.49	3.54
Elevation	0.73 ± 0.44	0.10	1.36
Northern aspect	0.39 ± 0.59	−0.46	1.24
Eastern aspect	−0.92 ± 0.80	−2.07	0.24
Mixed Oak-Hardwood forest type	1.75 ± 1.13	0.12	3.38
Appalachian Pine-Oak forest type	1.56 ± 1.51	−0.61	3.74
Year	−1.31 ± 2.14	−4.39	1.78
PESU			
Ψ (intercept)	0.63 ± 0.49	−0.08	1.34
Burn Frequency	−0.10 ± 0.35	−0.60	0.40
Time Since Last Burn	0.29 ± 0.34	0.20	0.79
Burn Severity	−1.03 ± 0.71	−2.06	−0.01
Elevation	0.97 ± 0.44	0.34	1.60
Northern aspect	0.35 ± 0.64	−0.58	1.27
Eastern aspect	0.46 ± 0.75	−0.62	1.55
Burn Severity * Elevation	2.33 ± 1.73	−0.17	4.83
Burn Severity * Northern aspect	2.50 ± 1.61	0.18	4.82
Burn Severity * Eastern aspect	−5.29 ± 2.47	−8.85	−1.74
LACI			
Ψ (intercept)	1.81 ± 2.37	−1.60	5.21
Burn Frequency	1.00 ± 1.10	−0.59	2.59
Time Since Last Burn	5.40 ± 8.97	−7.52	18.32
Time Since Last Burn^2	11.23 ± 13.34	−7.98	30.44
Burn Severity	1.29 ± 1.47	−0.83	3.41
Polewood/Sawlog Density	3.45 ± 3.92	−1.35	8.24
Sapling Density	−5.44 ± 3.92	−11.08	0.21
Seedling Density	4.17 ± 2.84	0.09	8.25
Stand Basal Area	−3.56 ± 3.10	−8.02	0.90
Canopy Closure	−5.53 ± 4.44	−11.93	0.87
Elevation	4.75 ± 3.39	−0.13	9.63
Northern aspect	−1.34 ± 1.94	−4.13	1.45
Eastern aspect	−8.31 ± 5.83	−16.70	0.09

ranked model, "BurnHistory". LACI occurrence was positively associated with burn, and polewood/sawlog and seeding density, but was negatively related to sapling density (Table 3). Topography also affected occupancy of LACI, but its effect varied with burn history. LACI occurrence increased with elevation in burned sites but decreased slightly as elevation increased in unburned sites. LACI occurrence was negatively associated with a more easterly aspect in burned sites, while aspect position had little effect on LACI occurrence in unburned sites.

Twelve of the 23 LACI burn occupancy models evaluated did not converge or produced nonsensical parameter estimates and were eliminated. Seven of the 11 remaining models predicting LACI occurrence within burned sites included in the candidate model set (Table 4). The top model included "BurnFrequency" and "Structure" covariates and parameter estimates indicate that within burned sites LACI occupancy was positively associated with seedling density (Table 5).

4. Discussion

Our results indicate that burning may increase the suitability of forested areas for commuting and foraging bats of the Cumberland Plateau. Occupancy of all five species/species groups was positively associated with recent burning (i.e., ≤10 yr), suggesting that regardless of differences in ecomorphology, all species examined responded positively to prescribed fire. Although our data may have been spatially autocorrelated due to the paired nature of our sites, the strong difference we observed in site occupancy between burned and unburned sites suggest the effects of burning overrode any possible effects of spatial autocorrelation that may have existed. Other studies have documented higher use (Starbuck et al., 2015), or increased activity (Lacki et al., 2009; Armitage and Ober, 2012; Cox et al., 2016; Silvis et al., 2016) for some bat species within burned areas, but to our knowledge this is the first study to demonstrate a positive relationship between occupancy and prescribed burning for all species/species groups we recorded.

We predicted that bat occupancy would be positively associated with recent burning due to the structural changes fire produces (Signell et al., 2005; Hutchinson et al., 2008). While it is possible that an indirect or secondary effect of fire on prey abundance contributed to the higher occupancy observed in burned sites (Lacki et al., 2009), multiple studies (Adams et al., 2009; Morris et al., 2010; Armitage and Ober, 2012; Dodd et al., 2012; Cox et al., 2016, Blakey et al., 2016) have identified structure to have primacy over prey availability for determining bat presence and activity whether changes in structure have resulted from prescribed fire or thinning. The results of our analysis of vegetative structure demonstrated the significant impact that prescribed burning had on forest complexity in our study area. Vegetative measures of burned sites differed considerably from unburned sites, with significantly lower canopy closure and densities of polewood/sawlogs and saplings in burned sites.

We found that vegetative structure at the survey site influenced occupancy of all species/species groups except PESU. Sawlog/polewood density was a significant predictor of use for EFPU/LANO, LABO/NYHU, MYSP, and LACI, although the influence on occupancy was not consistent among species groups. Contrary to our predictions that occupancy of larger bat species would be negatively affected by stem density while occupancy of smaller bat species would be unaffected by stem density, we found that EPFU/LANO, LABO/NYHU, and LACI occupancy were positively associated with polewood/sawlog density, and MYSP occupancy was negatively associated with polewood/sawlog density. However, the positive association found between polewood/sawlog density and EPFU/LANO and LABO/NYHU occupancy only occurred in unburned sites, while occupancy decreased with polewood/sawlog density in burned sites for both EPFU/LANO and LABO/NYHU. Although LACI occupancy was positively associated with polewood/sawlog density in both burned and unburned sites, this species forages above the canopy and may have been detected above the vegetation in cluttered habitats (Brigham et al., 1997a). Similarly, the unexpected negative response to polewood/sawlog density we observed for MYSP may have been a result of obscured individual species responses after grouping individual species calls to avoid misclassification (Smith and Gehrt, 2010; Silvis et al., 2016). For example, while *M. septentrionalis* are known to forage in dense habitats where they can glean prey (Faure et al., 1993; Radcliff and Dawson, 2003), other *Myotis* spp. such as *M. sodalis* (Menzel et al., 2005; Carter, 2006) and *M. lucifugus* (Patriquin and Barclay, 2003; Ford et al., 2005) appear to be more plastic in their foraging habitat requirements.

Ford et al. (2006) and Smith and Gehrt (2010) found a negative relationship between canopy closure and occupancy or activity of larger bat species. In contrast, while EPFU/LANO occupancy declined with increased canopy closure within burned sites in our study, their occupancy increased with canopy closure in unburned sites. Likewise, we found a positive association between LABO/NYHU occupancy and canopy closure across burned and unburned sites. Yates and Muzika

(2006) suggested that the positive association between canopy closure and occupancy of LABO they observed could have resulted from an open understory associated with a dense canopy, as LABO occupancy was also negatively related to stand basal area in their study. However, we found a positive relationship between stand basal area and LABO/NYHU occupancy suggesting a positive association with clutter. Though some studies indicate LABO and NYHU are clutter intolerant (Ford et al., 2006; Loeb and O'Keefe, 2006; Bender et al., 2015; Cox et al., 2016), these species are also often regarded as generalists (Ford et al., 2005; Menzel et al., 2005). The positive response we observed between LABO/NYHU occupancy and increasing measures of structure support this assumption and indicate that while LABO/NYHU may benefit from a reduction in structure after burning, they may be able to exploit an array of forest conditions regardless of clutter (Brigham, 1991; Menzel et al., 2005; Morris et al., 2010; Smith and Gehrt, 2010).

Although both Kalcounis-Rüppell et al. (1999) and Krusic et al. (1996) found differences in bat activity among forest types, like Loeb and O'Keefe (2006) we found little support for the importance of forest type in our analyses. This may indicate that burn history and forest structure more strongly impact foraging use than forest composition. However, in burned MOH forests we found significantly lower polewood/sawlog and sapling densities, stand basal areas, and canopy closure, and observed significantly higher EPFU/LANO occupancy. This suggests that the effect of burning on forest structure may depend on forest type, which in turn appears to affect occupancy of larger bat species in our study area.

In the Northern Hemisphere, higher elevation forests with southwesterly aspects are more prone to ignition as they are generally drier than forests on north and east-facing slopes and burn more consistently with greater intensity (Desta et al., 2004; Kane et al., 2007; Thomas-Van Gundy et al., 2007; Harper et al., 2016). Less vegetation after burning at high elevations with southwesterly facing slopes likely enhances use by clutter-intolerant species. However, we found an effect of elevation on occupancy for smaller species of bats (MYSP and PESU) as well as the largest species (LACI). While we are not sure why there was a positive association between MYSP and PESU, the positive association of elevation and westerly aspect on LACI occupancy in burned sites suggests that the effects of prescribed burning may be especially favorable for large bat species.

Of the three burn parameters examined, only burn severity had a significant effect on bat occupancy within burned sites. Both MYSP and PESU were more likely to use low severity burn sites than moderate severity burn sites. Our findings contrast with those of Lacki et al. (2017) who found no effect of burn severity on bat activity in similar forest types in Kentucky. The lack of response that Lacki et al. (2017) observed may have resulted from the high (minimum > 34 kHz) or low-frequency (maximum ≤ 34 kHz) categories the study used to classify echolocation pulses. This phonic grouping may have obscured the individual species responses we observed after instead classifying call files to species/species' group. For example, by including LABO/NYHU in the high-frequency group, Lacki et al. (2017) may have masked the effects of burn severity on MYSP and PESU. Our results suggest that a threshold may exist for clutter-adapted species where the positive effects of burning cease and fire becomes less favorable. Higher severity fires may only be beneficial to more clutter-intolerant species (Armitage and Ober, 2012; Buchalski et al., 2013). The lack of a significant effect of burn severity on occupancy for any of the larger species may have been due in part to the absence of high severity burns in our study area (Armitage and Ober, 2012; Buchalski et al., 2013). Moreover, a significant interaction between burn severity and aspect for PESU occupancy indicates that the effect of fire can be further complicated by the influence of topography.

Although we found no support for the importance of either repeated burn entries or time since last burn on occupancy for any of our species/species groups, these factors may still be influential in determining bat use in mixed pine-oak forests. In our study, the majority of burned sites

sampled (93%) had been burned within the past 7 years. Therefore, sufficient variation may not have existed among burned sites to adequately test the temporal effects burning may have had on occupancy. Though few studies have assessed the importance of frequency or recency of burn on bat occupancy or activity, NYHU occurrence in Missouri hardwood forests is positively related to frequency of fire (Starbuck et al., 2015). Additionally, fire frequency and intensity (a burn metric closely related to severity) appear to be important for bat activity in hardwood forests in Illinois (Smith and Gehrt, 2010). Armitage and Ober (2012) observed a strong relationship between fire frequency and bat activity in Florida longleaf pine (*P. palustris*) stands, with activity of larger-bodied species sharply declining in sites burned > 8 years before the study occurred. They attributed the decreased activity to a substantial increase in vegetative structure in these sites.

Although not a primary parameter of interest, we included detection probability in our models to correct for imperfect detection. While some studies have found little influence of structural clutter on detectability of bats in forests (Patriquin and Barclay, 2003; Yates and Muzika, 2006; Amelon, 2007; Titchenell et al., 2011), we found negative relationships between detection probability and vegetation structure for all five species/species groups we examined. Further, we found that burn history (i.e., whether a site had been burned) also significantly influenced detection for some species. Consequently, we suggest our results are robust to the effects of vegetation structure and burn history on detection, and encourage future studies of the effects of prescribed fire on bats account for variable detection, as even low levels of non-detection can influence interpretation of significant results (Gu and Swihart, 2004).

5. Summary and management implications

As managers increasingly use prescribed burning as a tool to minimize wildfire risk, maximize timber yield, and propagate native biodiversity and forest health in southeastern pine and oak forests (Swift et al., 1993; Vose et al., 1994; Brose et al., 2001; Flatley et al., 2013, 2015), concern over fires' effect on declining bat populations has also increased. However, prescribed burning may instead be compatible with management for healthy bat populations. Our findings of a positive association between occupancy of all species/species groups examined and burning, coupled with the lower structural complexity in burned sites, supports the use of fire treatments to maintain open forests and increase the suitability of foraging habitat for bats. Although the relationship between bat occupancy and forest structure was complex, we identified vegetative structure as an important predictor of use for several species. While this study only investigated the effects of prescribed fire, our findings generally support other studies that have found silvicultural practices that reduce vegetative structure (e.g., thinning treatments and harvest), are positively associated with bat occurrence and foraging activity of bats (Brigham et al., 1997b; Ford et al., 2006; Loeb and O'Keefe, 2006; Yates and Muzika, 2006; Loeb and Waldrop, 2008).

An increased understanding of bats' response to fire is of particular interest for species that are vulnerable to the impacts of WNS, and therefore of greatest conservation concern, such as the federally listed northern long-eared bat and Indiana bat, and severely declining little brown and tri-colored bats. The positive relationships we observed between MYSP and PESU occupancy and burning suggests that this forest management practice may be beneficial even for these clutter-adapted species and may promote species conservation. However, because occupancy of MYSP and PESU was negatively associated with sites that had received moderate severity burns compared to low severity burns, caution should be exercised when using fire where these species exist.

We suggest that managers concerned with bat conservation strive for landscape heterogeneity when burning. Although use was higher in burned sites, we still observed use of unburned sites, although our data demonstrate that the response of bats to structure varies by species. Furthermore, some effects of fire can differ by species depending on conditions of the habitat burned. Therefore, to encompass optimal foraging conditions (and possibly diverse roosting opportunities) in mixed pine-oak forests for both clutter-adapted and clutter-intolerant bats, we suggest managers retain some unburned forest as well as mosaics of lower and higher severity burns across the landscape to provide optimal habitat for a wide variety of bat species.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.05.024.

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