



# Effect of forest opening characteristics, prey abundance, and environmental factors on bat activity in the Southern Appalachians



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## ABSTRACT

Early successional habitat (ESH) is important for many wildlife species. Over the past century, land use changes have caused ESH to decline in hardwood forests of the eastern United States. Because of the decline of ESH and ESH dependent wildlife, ESH has recently received increased attention from land managers and scientists. Bats, which utilize ESH for foraging, are also a conservation concern, however little information is available on how ESH restoration affects bats. Our objective was to determine how ESH opening size, presence of edge, opening shape, prey abundance, vegetation structure, and environmental factors affect bat activity. In June–August 2014 and May–August 2015, we placed Anabat SD2 bat detectors at the interior and edge of small (0.2–1.6 ha), medium (2.1–5.6 ha), and large (6.2–18.5 ha) forest openings in the Nantahala National Forest, Cheoah Ranger District, Graham County, North Carolina. We used Townes-style Malaise insect traps to determine insect abundance and quantified vegetation structure. Differences in insect abundance, bat activity, and bat species richness were tested using mixed effects general linear models. Opening size and presence of edge did not affect total insect abundance, although density of trees >2 m in height and elevation had a negative effect on total insect abundance whereas mean nightly temperature had a positive effect. Similarly, overall bat activity did not vary with opening size or presence of edge, but was negatively related to density of trees >2 m high and elevation and positively related to the related circumscribing circle index (i.e., more elongated) and mean nightly temperature. Activity of open-adapted bat species was also negatively related to density of trees >2 m. These results suggest that opening size and prey abundance do not affect bat activity in the southern Appalachian Mountains. Open-adapted bats may select foraging patches with less vegetation structure because they can forage more efficiently in these environments, whereas clutter-adapted bats can forage efficiently in both cluttered and open environments. Thus, if creating ESH to benefit bats, land managers should maintain an open vegetation structure, focus on creating openings at lower elevations, and configure openings to maximize edge relative to opening area.

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## 1. Introduction

Early successional habitat (ESH), or recently disturbed forest with an open canopy structure and a vegetation community dominated by herbaceous plants and shrubs, is an important habitat type which is receiving increased attention from scientists and land managers (Askins, 2001; DeGraaf and Yamasaki, 2003; Greenberg et al., 2011a; Swanson et al., 2011). Historically, ESH

was created and maintained by natural disturbances such as wind storms, ice storms, wildfire, disease, and insect epidemics (Lorimer, 2001; Lorimer and White, 2003; Rogers, 1996; Swanson et al., 2011). After Europeans arrived in North America, large areas of land were cleared for agriculture and timber harvest (Askins, 2001) which created an abundance of ESH (Lorimer, 2001; Trani et al., 2001). By the mid-20th century, the intensity of timber harvest in hardwood forests had declined and agricultural land was allowed to regenerate into mature forest. At the same time, natural disturbance, especially wildfire, was suppressed (DeGraaf and Yamasaki, 2003; Lorimer, 2001; Trani et al., 2001). These changes in disturbance regimes led to a ~16% decline in the abundance of ESH in the eastern United States during the second half of the 20th century (Brooks, 2003; Shifley and Thompson, 2011).

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The decline of ESH is of management concern because ESH is critical habitat for many species. For example, the abundance of shade-intolerant herbs and fruiting plants, which serve as sources of food for both birds and mammals, are greater in recently disturbed forests (Elliott et al., 2011; Greenberg et al., 2011b). Reptiles utilize ESH for basking (Greenberg, 2001; McLeod and Gates, 1998) and 45% of bird species associated with forest openings are in decline (Hunter et al., 2001). Recently disturbed forest is also valuable habitat for some terrestrial mammals including many species of rodents and shrews (Kirkland, 1990; Urban and Swihart, 2011).

ESH is also important for many bat species because it provides open areas in which to forage for insect prey (Loeb and O'Keefe, 2011). For example, bat activity is higher in stands that have been recently cut compared to closed canopy forests (Ellis et al., 2002; Grindal and Brigham, 1999, 1998; Krusic et al., 1996; Menzel et al., 2002). However, only a limited number of studies have examined the effect of forest opening size on bat activity. Grindal and Brigham (1998) found that bat activity did not differ significantly across openings 0.5–1.5 ha in size. In contrast, Ford et al. (2005) found that little brown bats (*Myotis lucifugus*), big brown bats (*Eptesicus fuscus*), eastern red bats (*Lasiurus borealis*), and hoary bats (*L. cinereus*) were more likely to occur in larger canopy gaps (~0.07–0.10 ha) compared to smaller gaps (~0.01–0.03 ha). However, in both of these studies, the range of opening sizes sampled was small compared to forest openings created through operational scale forest management activities.

A number of factors may affect use and selection of foraging patches by bats, one of which is wing morphology. Bats with high wing aspect ratios and high wing loads (long narrow wings) are adapted for straight line, long distance flight (Norberg and Rayner, 1987). These open-adapted species may select larger openings that reduce the need to engage in costly aerobic flight. Alternatively, bats with low wing aspect ratios and low wing loads (short broad wings) are adapted for short distance, agile flight. These clutter-adapted species may be equally active in openings of all sizes because aerobic flight maneuvers are less costly. Bat wing morphology may also affect which parts of a forest opening a species may prefer. Bat activity at opening edges is higher than at opening interiors (Grindal and Brigham, 1999) and, although not statistically significant, peak activity of open-adapted species tends to be farther from the edge than that of clutter-adapted species (Jantzen and Fenton, 2013). Other factors that may affect selection of foraging patches include distance to water (Brooks, 2009; Krusic et al., 1996), elevation (Grindal and Brigham, 1999), and prey abundance (Morris et al., 2010; Tibbels and Kurta, 2003) although the relationship between bat activity and insect abundance is equivocal (e.g., Grindal and Brigham, 1998; Muller et al., 2012).

Understanding how bats select forest openings is important because many species of bats are in decline. Currently, the most serious threat facing bats in North America is white-nose syndrome (O'Shea et al., 2016) with infected populations declining as much as 75–90% (Turner et al., 2011). Wind energy is also a serious threat to bats (O'Shea et al., 2016) with an estimated 600,000 bats killed in 2012 due to interactions with wind turbines in the United States (Hayes, 2013). The emerging threats of WNS and wind energy are in addition to ongoing threats faced by bats such as habitat loss and fragmentation, intentional killing, and environmental contaminants (O'Shea et al., 2016).

Our objective was to determine how opening size, opening shape, presence of edge, prey abundance, and environmental factors affect bat activity in forest openings. We hypothesized that: (1) open-adapted bats (big brown bats, silver-haired bats [*Lasionycteris noctivagans*], hoary bats, and eastern red bats) would be more active in large openings than in small openings while clutter-adapted species (tri-colored bats [*Perimyotis subflavus*]

and *Myotis* spp.) would not respond to differences in opening size, and (2) activity of open-adapted bats would be greater at opening interiors while activity of clutter-adapted bats would be greater at opening edges. We further hypothesized that (3) bat activity would be positively related to opening elongation, insect abundance, and nightly temperature, and (4) negatively related to vegetation clutter, elevation, and distance to water.

## 2. Methods

### 2.1. Study area

The study took place in the Nantahala National Forest, Cheoah Ranger District, Graham County, North Carolina (Fig. 1). The Cheoah Ranger District is located in the southern Appalachian Mountains which are characterized by ridge and valley topography with high mountain peaks. The dominant vegetation type is mixed hardwood forest interspersed with pine stands and mountain balds. Common tree species include oaks (*Quercus*), maples (*Acer*), poplars (*Liriodendron*), hickories (*Carya*), and pines (*Pinus*). From May to August 2014 and 2015, the average monthly temperature was 21.4 °C and average monthly precipitation was 91.1 mm. Elevation in the Cheoah Ranger District ranges from 530 m to 1658 m above sea level.

### 2.2. Study design

We sampled 33 forest openings, however one opening was dropped from the analysis due to equipment failure. All openings had an open canopy structure and were dominated by shrubs, herbaceous plants, and bare ground. Openings included timber harvests, areas treated after a southern pine beetle (*Dendroctonus frontalis*) infestation, prescribed burns, and wildlife openings. Timber harvests were classified by the U.S. Forest Service as either shelterwood establishment or two-age shelterwood establishment harvests and were completed <5 years prior to sampling. Southern pine beetle areas were clear cut, burned, and replanted with short-leaf pine (*P. echinata*) and were <14 years old. Wildlife openings were clearings maintained for the benefit of wildlife through regular mowing. Prescribed burn openings were areas where high intensity fire had removed the understory and overstory. Prescribed burns were completed <7 years prior to sampling.

Prior to sampling, we examined the size distribution of available openings and, based on this preliminary analysis, defined three size classes: small (0.2–1.6 ha), medium (2.1–5.6 ha), and large (6.2–18.5 ha). In each sampling period, we selected one small, medium, and large opening to sample simultaneously. The three openings were chosen to minimize travel time between openings and were considered a block. The average distance between openings was 1.1 km with a range of 0.01–12.4 km.

### 2.3. Acoustic sampling

We used Anabat SD2 (Titley Scientific, Columbia, MO) acoustic bat detectors to measure bat activity in each opening from June 4 to August 2, 2014 and May 22 to August 13, 2015. The detector microphones were enclosed in weatherproof housings mounted atop 3.7 m poles. The microphones were connected to the detectors, which were enclosed in waterproof containers at the base of the poles, via a 6.1 m cable. Prior to the start of each field season, the sensitivities of the Anabat SD2 detectors were equalized to a detector with an internal sensitivity setting of 30 using the Anabat Equalizer (Titley Scientific, Columbia, MO).

We placed an Anabat SD2 detector near the edge and interior of each opening. The edge detector was positioned 5 m into the

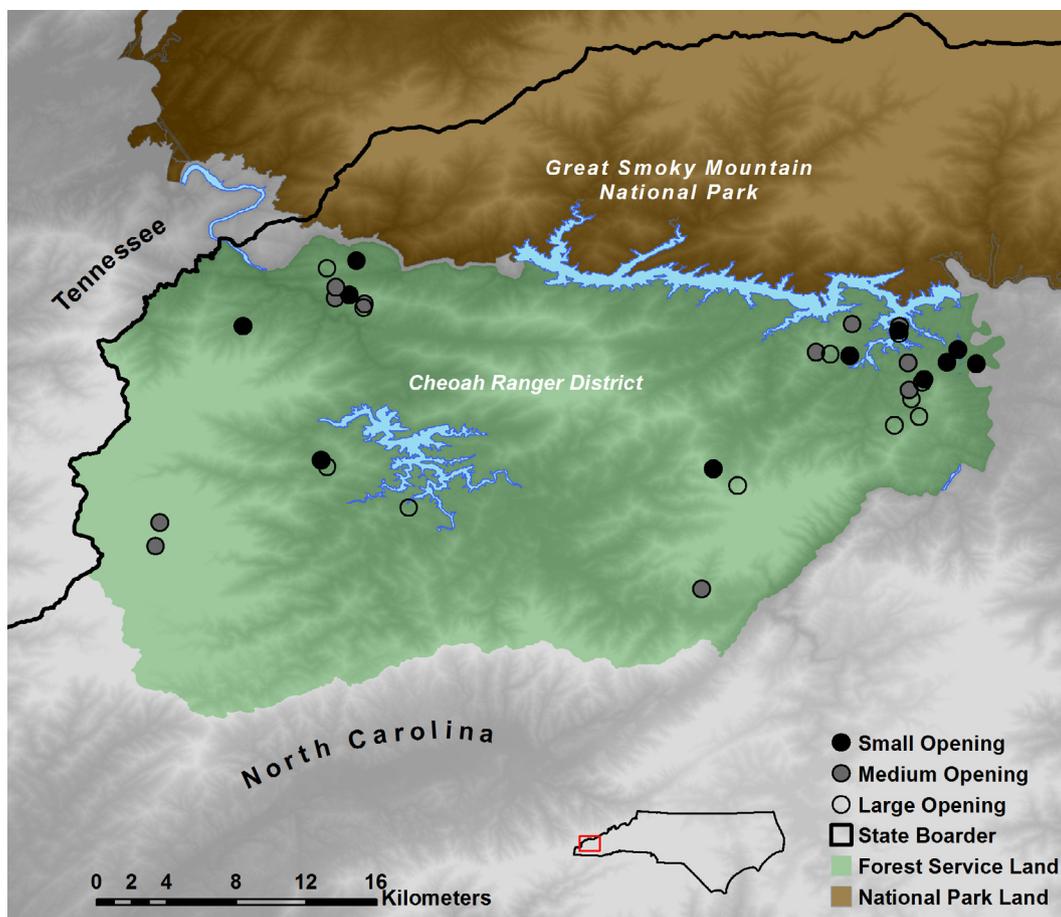


Fig. 1. Study area in Nantahala National Forest Cheoah Ranger District, Graham County, NC and location of forest openings sampled.

opening from the boundary between the forest and the opening. The second SD2 was placed 20–70 m from the forest edge into the opening interior depending on opening size and shape. Because the edge effect for bats extends 40 m into forest openings (Jantzen and Fenton, 2013), placing detectors 70 m into the opening was sufficient to avoid edge effects in the larger openings. We also maintained a distance >20 m between the edge and interior detectors to prevent both detectors from simultaneously recording the same bat. Each detector was programmed to begin recording 15 min prior to sunset and to stop recording 15 min after sunrise. Bat activity was monitored for at least three nights in each opening. We discarded data collected on nights with heavy rain or when rain lasted more than 30 min. An iButton temperature logger (Embedded Data Systems, Lawrenceburg, KY) was also placed on a Malaise insect trap (see Section 2.4) approximately 5 m from each detector. The temperature loggers recorded ambient temperature at 10 min intervals throughout the night.

Call files were downloaded from the SD2 detector using CFCreate (Titely Scientific, Columbia, MO) with a division ratio of eight, smooth of 50, and maximum time between calls (max TBC) of 5 s. We used an automated filter algorithm (noise filter) in AnaLookW (Titely Scientific, Columbia, MO) to remove files that did not contain bat calls. Files that passed the noise filter were manually reviewed to confirm the presence of bat calls. Each file that contained at least one bat call was considered a bat pass and we used these files as a measure of overall bat activity. Files that passed the noise filter were then run through a more rigorous filter (ID filter) which removed files with <5 call pulses or that were of otherwise low quality. We also manually reviewed files that passed this filter to ensure that they contained only search phase calls. We used

Kaleidoscope Pro Version 3.1.0 (Wildlife Acoustics, Maynard, MA) to identify each file to species. Settings used in Kaleidoscope Pro can be found in Supplemental Table 1. Species assignments made by Kaleidoscope were manually reviewed and identifications were corrected if necessary. If we did not agree with the identification assigned by Kaleidoscope but could not confidently identify the species, the file was dropped from the analysis. Identified files were counted to determine species level activity. Because it can be difficult to differentiate between some species even with the use of an automated classifier, we grouped files classified as big brown bats and silver-haired bats, eastern red bats and evening bats, and *Myotis* spp. Although eastern red bats tend to be more open-adapted than evening bats, evening bats are rare at our study location (O'Keefe et al., 2009; O'Keefe and Loeb, 2017) and most likely did not contribute significantly to activity of this group.

#### 2.4. Insect sampling

A Townes-style Malaise insect trap, which captures flying insects, was paired with each bat detector. The traps were positioned in an open area approximately 5 m from the bat detector as terrain and vegetation allowed. Insect traps paired with bat detectors at opening edges were also positioned approximately 5 m from the edge. A small LED headlamp was hung on the collection head of each trap. As close to recording start time as possible, we attached collection bottles filled ~1/8 full of 80% ethanol to the traps and illuminated the LED headlamps. We removed the bottles from the insect traps the following morning as close to recording stop time as possible. At least two nights of insect trapping were completed at each location sampled. We transferred insects from

the collection bottles to storage containers filled with 80% ethanol and counted and identified specimens to order with the aid of a dissecting scope based on keys found in Johnson and Triplehorn (2004). A small percentage of insects could not be identified because specimens were damaged beyond recognition.

### 2.5. Habitat and landscape characteristics

We conducted vegetation surveys at each detector location to quantify vegetation structure. Within a 5 m radius (78.5 m<sup>2</sup>) plot centered on each bat detector, we counted the number of trees <1 m, 1–2 m, and >2 m in height, visually estimated percent cover of shrubs <0.5 m, 0.5–1.5 m, and >1.5 m, percent cover of herbaceous plants <1 m, 1–2 m, and >2 m, and percentage of bare ground. Estimates of cover and bare ground were made to the nearest 5% and were conducted by the same person (JDB) to eliminate variation due to multiple observers. In addition to the 5 m radius plots, we also measured basal area of live and dead trees using a ten-factor prism.

We recorded the position of each bat detector using a Trimble GeoExplorer 2008 GPS (Trimble, Sunnyvale, CA) which had a horizontal accuracy of <2 m. GPS files were post-processed using Pathfinder Pro 5.60 (Trimble, Sunnyvale, CA) and were imported into ArcMap 10.1 (ESRI, Redlands, CA). The elevation of each point was extracted using a digital elevation model (<https://gdg.sc.egov.usda.gov>). Distance to the nearest permanent water source was also determined in ArcMap using the National Hydrography Dataset (<https://gdg.sc.egov.usda.gov>). To quantify the amount of edge relative to patch area, we used the related circumscribing circle (RCC) index (McGarigal et al., 2012). The RCC is defined as  $RCC = 1 - \frac{a_p}{a_c}$ , where  $a_p$  is the area of the opening and  $a_c$  is the area of the smallest circumscribing circle. The RCC index was appropriate because it is not sensitive total patch area. The RCC of each opening was calculated using FRAGSTATS (McGarigal et al., 2012).

### 2.6. Statistical analysis

All analyses were conducted using SAS University Edition (SAS Institute, Cary, NC). To determine if vegetation structure varied systematically across our treatments, we conducted a non-metric multidimensional scaling (NMDS) analysis. The matrix of similarity values was generated by PROC DISTANCE using the Bray-Curtis similarity index (SAS Institute Inc., 2016, pp. 2355–2397). This

matrix was then used as an input for PROC MDS which performed the NMDS (SAS Institute Inc., 2016, pp. 5908–5945). These results were then plotted and examined for clustering or gradient patterns.

We used a mixed effects general linear models (PROC GLIMMIX) to test for differences in insect abundance among opening sizes and locations within openings. We analyzed both total abundance of insects and the abundance of the five insect orders most commonly preyed upon by bats: Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera (Whitaker, 2004). Fixed effects were opening size (small, medium, large), location (interior, edge), and size \* location and random effects were block, block \* size, and location(block \* size). The block effect incorporated both the sampling block and the year in which the block was sampled because some blocks were sampled in both years. Because the NMDS analysis did not indicate a pattern in vegetation structure across our treatments, we chose to include density of trees >2 m tall and live basal area in our models. These measure of vegetation structure were selected because they are most likely to affect bats. RCC, elevation, distance to water, and mean nightly temperature were also included as covariates. We assumed a Poisson distribution with a log link function and used an offset to account for differences in sampling period length. Denominator degrees of freedom were calculated using the Kenward-Rogers method (Kenward and Roger, 1997). We examined a plot of the residuals to assess whether the data met model assumptions. We used a significance level of  $\alpha = 0.1$  for all statistical tests and assessed significant fixed effects using a Fisher's Least Significant Difference test. Mean values reported are the inverse link function applied to the estimated population marginal means (LSMEANS)  $\pm 1$  S.E. To determine if total insect abundance could be used to summarize insect abundance or if it was necessary to examine each order, we conducted a pairwise correlation analysis of the five insect orders (PROC CORR) and found that the abundance of most orders was significantly correlated (Supplemental Table 2). Therefore, we used total insect abundance as a covariate in subsequent models.

We used the same model as was used for total insect abundance to test for differences in overall bat activity, species-level bat activity, and species richness except we added total insect abundance as a covariate. For overall bat activity we assumed a Poisson distribution with a log link function, for species/species group activity we assumed a negative binomial distribution with a log link function, and for bat species richness we assumed a multinomial distribution with a cumulative logit link function. We defined four

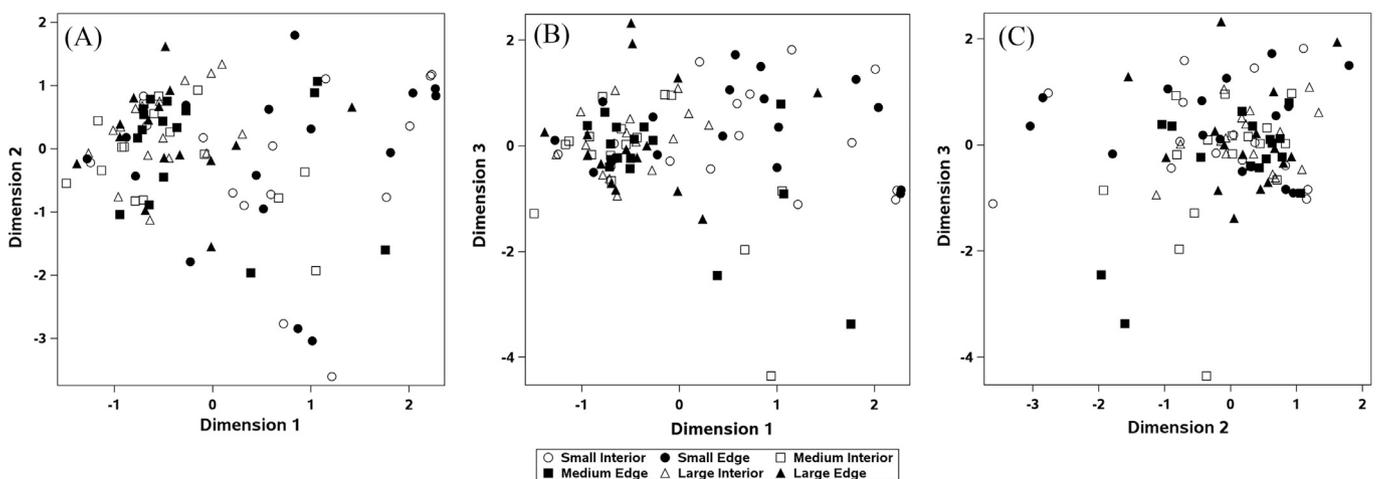


Fig. 2. Results of the NMDS analysis of the vegetation structure data collected at opening interiors and edges in the Nantahala National Forest, NC May–August 2014–2015 for axes (A) axes 1 and 2, (B) axes 1 and 3, and (C) axes 2 and 3.

categories of species richness: zero species/species group, one species/species groups, two species/species groups, and  $\geq 3$  species/species groups. We examined odds ratios to aid in interpreting species richness model results.

We used a mixed effects general linear model with size, location, and size \* location as fixed effects and block, block \* size, and location(block \* size) as random effects to determine if the noise and ID filters removed files consistently across all opening sizes and locations. For this test, we assumed a binomial distribution with a logit link function.

### 3. Results

We sampled 20 openings in 2014 and 27 openings in 2015; 15 of the openings were sampled in both years.

#### 3.1. Vegetation structure

Examination of plots generated during the NMDS analysis showed no pattern in vegetation structure across opening sizes or locations (interior or edge) along all three axes (Fig. 2). The badness of fit criterion (i.e., stress) was 0.11 which indicates that three dimensions were reasonable for these data.

#### 3.2. Insect abundance

We collected insects during 1207 trap hours in 2014 and 1519 h in 2015 and identified 27,243 and 48,863 specimens in 2014 and 2015, respectively. Insect orders identified were Coleoptera, Collembola, Diptera, Ephemeroptera, Hemiptera, Hymenoptera, Lepidoptera, Mecoptera, Neuroptera, Odonata, Orthoptera, Plecoptera, Psocoptera, Thysanoptera, and Trichoptera.

In 2014, Diptera was the most abundant order (79.8%) followed by Lepidoptera (5.8%), Hymenoptera (4.2%), Hemiptera (3.8%), Coleoptera (2.8%), and Collembola (1.5%). All other orders comprised <2.2% of insects captured. In 2015, Diptera was again the most abundant order (71.1%) followed by Lepidoptera (7.6%), Hemiptera (6.8%), Hymenoptera (5.7%), Thysanoptera (3.4%), and Coleoptera (3.3%). All other orders comprised <9.0% of insects captured.

Total insect abundance and the abundance of the five insect orders modeled did not differ significantly among opening sizes, however Hymenoptera abundance varied significantly with location (Table 1). Mean Hymenoptera abundance was  $0.95 \pm 0.15$  individuals/hour at opening interiors and  $1.22 \pm 0.15$  individuals/hour at opening edges. Total insect abundance and the abundance of all five orders were positively related to mean nightly temperature. Total insect abundance and the abundance of Diptera, Lepidoptera, and Coleoptera were negatively related to elevation and total insect abundance and Hemiptera abundance were negatively related to density of trees >2 m tall. None of the insect groups examined responded to live basal area or RCC.

#### 3.3. Bat activity and species richness

We recorded a total of 28,098 files during 1470 detector hours in 2014 and 23,965 files during 1692 detector hours in 2015. Of the 52,063 files recorded in both years, 27.7% contained bat calls (23.6% in 2014, 31.8% in 2015); we were able to identify 48.7% of those files to species (47.9% in 2014, 49.4% in 2015). The proportion of calls passing the noise filter differed significantly by opening size and there was a significant size \* location effect (Table 2). A significantly smaller proportion of calls passed the noise filter at interiors of medium openings than at all other locations (Fig. 3). The proportion of calls passing the ID filter did not vary signifi-

cantly among opening sizes or between interiors and edges (Table 2).

In 2014, big brown/silver-haired bats were the most frequently detected species group (49.8%) followed by tri-colored bats (23.8%), eastern red/evening bats (23.1%), *Myotis* spp. (1.7%), and hoary bats (1.6%). In 2015, eastern red/evening bats were the most frequently detected species group (43.7%) followed by big brown/

**Table 1**

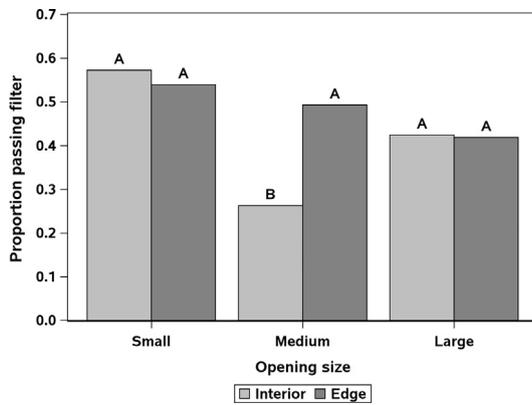
Results of mixed effects general linear models for total insect abundance and five insect orders commonly preyed upon by bats in the Nantahala National Forest, NC May–August 2014–2015.

Effect	DF	F	P	Coefficient
<i>Total</i>				
Size	69.10	0.47	0.628	–
Location	68.06	0.79	0.377	–
Size * location	66.37	0.10	0.901	–
Trees > 2 m	77.53	3.15	0.080	–0.010
Live BA	73.88	0.47	0.495	0.029
RCC	79.13	0.01	0.904	0.096
Elevation	82.78	3.38	0.069	–0.001
Water distance	81.98	1.00	0.319	–0.001
Temperature	176.00	1550.64	<0.001	0.163
<i>Diptera</i>				
Size	68.71	0.40	0.670	–
Location	67.82	1.03	0.314	–
Size * location	65.73	0.23	0.794	–
Trees > 2 m	78.08	2.14	0.148	–0.010
Live BA	74.41	0.81	0.370	0.044
RCC	75.68	0.02	0.901	0.112
Elevation	82.50	3.25	0.075	–0.001
Water distance	81.30	1.34	0.251	–0.002
Temperature	176.00	1235.52	<0.001	0.166
<i>Lepidoptera</i>				
Size	62.20	2.02	0.142	–
Location	65.03	0.89	0.349	–
Size * location	61.69	0.83	0.439	–
Trees > 2 m	71.55	1.90	0.173	–0.007
Live BA	67.52	0.26	0.610	–0.018
RCC	75.97	2.16	0.146	–0.997
Elevation	93.63	8.52	0.004	–0.001
Water distance	76.99	0.04	0.841	$-2.0 \times 10^{-4}$
Temperature	176.00	78.24	<0.001	0.135
<i>Hymenoptera</i>				
Size	25.97	0.19	0.831	–
Location	46.51	3.08	0.086	–
Size * location	39.27	0.28	0.760	–
Trees > 2 m	42.03	1.97	0.167	–0.008
Live BA	64.63	0.29	0.595	–0.021
RCC	38.51	0.29	0.592	–0.419
Elevation	37.64	1.37	0.250	–0.001
Water distance	43.32	0.55	0.463	0.001
Temperature	176.00	41.10	<0.001	0.114
<i>Hemiptera</i>				
Size	25.79	1.41	0.263	–
Location	49.70	1.27	0.265	–
Size * location	41.89	0.03	0.968	–
Trees > 2 m	51.14	7.64	0.008	–0.022
Live BA	60.69	1.22	0.274	–0.053
RCC	37.41	0.99	0.326	1.141
Elevation	43.23	2.61	0.113	–0.001
Water distance	50.64	3.34	0.073	–0.003
Temperature	176.00	182.56	<0.001	0.272
<i>Coleoptera</i>				
Size	22.05	0.15	0.860	–
Location	53.77	0.43	0.513	–
Size * location	43.27	0.16	0.853	–
Trees > 2 m	38.85	2.12	0.153	–0.009
Live BA	65.88	0.35	0.557	0.025
RCC	35.45	0.88	0.354	0.749
Elevation	45.76	3.37	0.073	–0.001
Water Distance	40.24	0.19	0.663	–0.001
Temperature	176.00	95.96	<0.001	0.251

**Table 2**

Mixed effects general linear model results for mean number of files removed by the noise and ID filters for calls collected in interior and edges of small, medium, and large forest openings in the Nantahala National Forest, NC May–August 2014–2015.

Effect	Df	F	P
<i>Noise filter</i>			
Size	29.81	3.06	0.062
Location	43.70	2.47	0.124
Size * location	43.67	3.90	0.028
<i>ID filter</i>			
Size	43.15	2.31	0.111
Location	50.45	0.97	0.329
Size * location	49.91	0.59	0.556



**Fig. 3.** Mean proportion of bat files that passed the noise filter by opening size and location within openings in the Nantahala National Forest, NC May–August 2014–2015. Bars with different letters are significantly different ( $P \leq 0.10$ ).

silver-haired bats (33.2%), tri-colored bats (20.8%), hoary bats (1.2%), and *Myotis* spp (1.0%). Big brown/silver-haired bats and eastern red/evening bats occurred at 100% of sites surveyed in 2014, tri-colored bats occurred at 81.6% of sites, *Myotis* spp. occurred at 39.5% of sites, and hoary bats occurred at 13.2% of sites. In 2015, eastern red/evening bats occurred at 98.2% of sites surveyed, big brown/silver-haired bats occurred at 90.7% of sites, tri-colored bats occurred at 75.9% of sites, *Myotis* spp. occurred at 38.9% of sites, and hoary bats occurred at 22.2% of sites.

Overall bat activity and activity of the five species/species groups was not significantly different across opening sizes or between interiors and edges (Table 3). There was, however, a significant negative effect of density of trees >2 m for overall bat activity, big brown/silver-haired activity, eastern red/evening bat activity, and tri-colored bat activity. Overall bat activity, eastern red/evening bat activity, and tri-colored bat activity was also higher at lower elevations and overall bat activity and eastern red/evening bat activity was higher in more elongated openings (Table 3). Tri-colored bats were more active on warmer nights. Hoary bats were the only species that responded to insect abundance (Table 3) with a positive relationship between hoary bat activity and insect abundance. *Myotis* spp. responded to none of the factors we examined, however the residual plots for hoary bats and *Myotis* spp. showed evidence of a high frequency of zero counts indicating model assumptions may not have been met and caution should be used in interpreting results for these species.

Species richness in forest openings ranged from zero to five species/species groups. Bat species richness did not differ significantly among opening sizes or between interiors and edges (Table 4). There was a significant negative effect of density of trees >2 m high and a significant positive effect of insect abundance on bat species richness. As the density of trees >2 m increased by one unit, the

**Table 3**

Results of mixed effects linear models for overall bat activity and species/species group activity at the interior and edge of small, medium, and large openings in the Nantahala National Forest, NC May–August 2014–2015.

Effect	Df	F	P	Coefficient
<i>Overall</i>				
Size	41.55	1.92	0.160	–
Location	46.93	1.09	0.302	–
Size * location	39.50	1.66	0.204	–
Trees > 2 m	71.78	16.58	<0.001	–0.026
Live BA	59.34	0.61	0.438	0.029
Elevation	45.87	5.17	0.028	–0.001
Water distance	56.88	0.01	0.919	$1.0 \times 10^{-4}$
RCC	42.28	3.10	0.086	1.442
Temperature	156.00	96.00	<0.001	0.108
Insect abundance	156.00	1.89	0.171	$9.0 \times 10^{-4}$
<i>Big brown/silver-haired bats</i>				
Size	41.63	1.64	0.207	–
Location	54.34	0.11	0.740	–
Size * location	41.04	1.87	0.167	–
Trees > 2 m	77.68	9.87	0.002	–0.036
Live BA	60.66	0.76	0.388	–0.055
Elevation	50.58	2.68	0.108	–0.002
Water distance	64.06	0.28	0.597	0.001
RCC	47.11	0.70	0.406	1.350
Temperature	129.50	0.76	0.386	0.049
Insect abundance	100.10	0.23	0.636	0.001
<i>Eastern red/evening bats</i>				
Size	38.37	0.18	0.838	–
Location	54.81	1.24	0.270	–
Size * location	43.76	1.94	0.156	–
Trees > 2 m	75.11	3.48	0.066	–0.020
Live BA	56.21	1.17	0.284	0.063
Elevation	50.86	8.65	0.005	–0.003
Water distance	54.61	1.99	0.164	0.003
RCC	42.84	3.02	0.090	2.342
Temperature	110.80	1.31	0.255	0.058
Insect abundance	107.20	0.38	0.539	0.002
<i>Hoary bat</i>				
Size	83.18	0.47	0.628	–
Location	34.57	0.10	0.757	–
Size * location	33.58	0.58	0.568	–
Trees > 2 m	129.80	0.06	0.815	0.012
Live BA	71.20	2.61	0.111	–0.557
Elevation	77.63	1.61	0.209	0.006
Water distance	45.95	0.52	0.474	–0.007
RCC	102.50	2.48	0.119	11.692
Temperature	29.46	0.13	0.718	–0.079
Insect abundance	51.17	6.09	0.017	0.027
<i>Myotis</i> spp.				
Size	72.07	0.52	0.598	–
Location	57.88	0.00	0.956	–
Size * location	54.60	0.43	0.651	–
Trees > 2 m	156.00	1.43	0.234	–0.025
Live BA	73.65	0.81	0.371	0.108
Elevation	111.6	0.81	0.371	$4.0 \times 10^{-4}$
Water distance	98.98	0.93	0.337	–0.004
RCC	76.24	0.05	0.832	–0.492
Temperature	29.41	1.38	0.289	–0.124
Insect abundance	156.00	0.13	0.719	–0.002
<i>Tri-colored bat</i>				
Size	35.53	0.42	0.660	–
Location	59.64	0.86	0.357	–
Size * location	43.53	1.17	0.320	–
Trees > 2 m	70.97	3.76	0.057	–0.028
Live BA	73.09	0.17	0.678	0.035
Elevation	73.34	3.50	0.065	–0.004
Water distance	51.02	0.97	0.329	–0.003
RCC	38.08	0.90	0.348	1.649
Temperature	126.30	21.57	<0.001	0.305
Insect abundance	82.53	0.00	0.967	$-2.0 \times 10^{-4}$

odds of observing more bat species decreased by 0.966 and as insect abundance increased by one unit, the odds of observing more bat species increased by 1.009.

**Table 4**

Results of mixed effects general linear models for species richness recorded in small, medium, and large forest openings in the Nantahala National Forest, NC May–August 2014–2015.

Effect	DF	F	P	Coefficient	Odds Ratio
Size	29.04	1.42	0.259	–	–
Location	51.87	1.23	0.272	–	–
Size * location	42.23	0.75	0.480	–	–
Trees > 2 m	51.54	6.54	0.014	–0.034	0.966
Live BA	69.32	0.10	0.749	–0.030	0.970
Elevation	41.76	1.09	0.303	–0.001	0.999
Water distance	47.43	0.85	0.361	–0.003	0.997
RCC	39.06	0.01	0.937	0.134	1.143
Temperature	38.58	0.05	0.818	0.018	1.019
Insect abundance	171.00	2.74	0.100	0.009	1.009

#### 4. Discussion

The lack of response by bats and insects to opening size may have been due to the large size of the openings we examined in this study. For example, Ford et al. (2005) surveyed openings with mean canopy gap diameters ranging from 16.6 m to 35.1 m (~0.02–0.10 ha) and found that big brown bats, eastern red bats, hoary bats, and little brown bats were more likely to occur in larger openings. The smallest opening we surveyed was 0.2 ha, which is twice the size of the largest opening surveyed by Ford et al. The range of opening sizes we surveyed is more similar to those examined by Grindal and Brigham (1998) who did not observe a response by bats to openings 0.5–1.5 ha. Thus, at the scale of operational harvesting and other management activities in the Southern Appalachians, factors other than size may be more important in determining use of ESH patches by bats and insects.

The lack of response by bats and insects to presence of edge in our study is in contrast to results of other studies. For example, open-adapted and clutter-adapted species show a preference for opening edges in the Coastal Plain of North Carolina (Hein et al., 2009; Morris et al., 2010) and Ontario, Canada (Jantzen and Fenton, 2013). The lack of response by bats in our study may have been due to lower detection probabilities at opening edges. Dense vegetation is known to reduce call detection and quality (Parsons, 1996; Patriquin and Barclay, 2003) and bats flying near clutter often alter their echolocation calls (Broders et al., 2004; Wund, 2006). However, the number of calls removed by the noise and ID filters at edges was the same or higher than at opening interiors which increases our confidence that the lack of a preference for edges was not due to lower detection.

Although presence of edge did not affect bat activity, higher levels of activity in elongated openings suggests that bats preferentially selected openings with more edge relative to the opening area. This result supports previous work showing bat activity is greater in linear landscape elements (Verboom and Huitema, 1997; Law and Chidel, 2002; Hein et al., 2009). It has been suggested that bat activity is greater at edges because they provide bats with protection from wind (Verboom and Spoelstra, 1999), abundant prey (Whitaker et al., 2000), refuge from predators (Lima and O'Keefe, 2013; Walsh and Harris, 1996), navigational landmarks (Verboom et al., 1999) and flight conduits (Kalcounis-Rueppell et al., 2013). Therefore, even though bats did not forage close to edges in our study, foraging in openings with easy access to edges may hold many benefits for bats.

Vegetation structure was also a significant factor in determining bat activity. Similar to previous studies, bat response to vegetation structure was related to wing morphology and echolocation call structure (Aldrige and Rautenbach, 1987; Bender et al., 2015; Brooks, 2009; Erickson and West, 2003; Ford et al., 2005; Loeb and O'Keefe, 2006; Mehr et al., 2012; Norberg and Rayner, 1987; Owen et al., 2004; Patriquin and Barclay, 2003) as larger species

such as big brown/silver-haired bats and eastern red/evening bat activity showed a negative response to structural complexity (i.e., density of tall trees) while smaller species (*Myotis* spp.) did not. Although tri-colored bats are classified as clutter-adapted based on wing morphology (e.g., Menzel et al., 2005), they also tend to frequent more open environments (Bender et al., 2015; Loeb and O'Keefe, 2006; Yates and Muzika, 2006). In contrast, hoary bats, an open adapted species, did not respond to vegetation structure. This may have been due to the low number of detections of hoary bats rather than the actual effect of vegetation structure. Alternatively, hoary bats may not have responded to vegetation structure because they were foraging well above the vegetation (Brigham et al., 1997). The negative response of overall bat activity to vegetation structure was likely driven by big brown/silver-haired bats and eastern-red/evening bats which made up a large proportion of the calls identified.

Abiotic environmental factors were also useful in predicting bat activity. Although there were some exceptions among bat species/species groups and insect orders, in general, bat activity and insect abundance were positively related to temperature and negatively related to elevation. Several studies have found a positive relationship between bat activity and temperature (Erickson and West, 2002; Hayes, 1997; Wolbert et al., 2014; Wolcott and Vulinec, 2012) although only a few studies have examined the effects of elevation (Grindal and Brigham, 1999; Wolbert et al., 2014). Separating the effects of temperature and elevation is difficult as they are often correlated. Higher insect abundance and reduced thermoregulation costs at higher temperatures and lower elevations may have resulted in higher bat activity levels at lower elevations.

Although elevation and temperature were useful for explaining bat activity, distance to water was not. A number of studies have found that bat activity is higher closer to water (Brooks, 2009; Ford et al., 2006; Menzel et al., 2005), but other studies have found only a limited effect of distance from water on bat occupancy (Hein et al., 2009; Yates and Muzika, 2006). One explanation for the lack of response to water in our study is that water is such a ubiquitous resource in the Southern Appalachians that there may be no need for bats to aggregate around it. The average distance of our sites to water was 147.7 m and ranged from 5.7 m to 508.7 m despite making an effort to avoid openings near water. However distance to water may be a more important parameter in more arid landscapes or in drier years.

The positive relationship between bat species richness and insect abundance was likely due to openings with higher insect abundances drawing in more bats including less common species. Because of the higher insect abundance, these patches may have been more desirable foraging patches for bats. We also found a negative relationship between species richness and vegetation clutter. We would expect to find clutter-adapted bats in more cluttered openings, but our data indicate that open-adapted bats were found in most openings and clutter-adapted bats were only found

in a few openings. One explanation for the negative relationship between clutter and species richness is that detection of clutter-adapted species was lower at more cluttered sites due to their higher frequency and less intense echolocation calls.

The conclusions we make regarding bat habitat use should be understood within the context of the methods we used. One of the limitations of acoustical studies is that bat acoustical activity is assumed to be a relative index for habitat preference, but this assumption ignores the possibility that bats need to spend more time in lower quality habitats (Hayes, 2000). We were also not able to account for potential differences in detection among opening sizes or between edges and interiors using standard techniques (e.g. Mackenzie et al., 2002) because of the split-plot design of this study. Results from studies which do not incorporate differences in detection should be interpreted cautiously. A number of factors can affect detection in studies using acoustical detectors including vegetation structure and call intensity (Duchamp et al., 2006; Patriquin and Barclay, 2003; Sleep and Brigham, 2003). We attempted to control for differences in detection by placing bat detectors in areas with the most open vegetation structure available and elevating microphones above ground vegetation. We also limited comparisons to within species/species groups which have similar call structure. However, a significantly greater proportion of calls were removed by the noise filter from detectors at medium interiors indicating detection may have varied across some of our treatments. Further, we only sampled vegetation and insect availability near our detectors and bats may be responding to both at larger spatial scales. However, the openings we sampled were relatively homogenous in terms of vegetation structure as demonstrated by a lack of difference in vegetation structure between edges and interiors (Fig. 2). While insect availability may be variable in space and time, we were not able to set and check additional Malaise traps within the time frame necessary to capture only nocturnal insects due to logistical constraints. However, we note that use of one trap per stand or site is common in studies similar to ours (e.g., Armitage and Ober, 2012; Cox et al., 2016; Ober and Hayes, 2008; Summerville and Crist, 2002).

## 5. Summary and management implications

The results of this study indicate that restoring ESH may create foraging opportunities for bats, especially open-adapted species. However, these species require an open vegetation structure. For forest openings to benefit these species, open vegetation structures should be maintained. Managers should also consider restoring ESH at lower elevations where bat activity is higher. Although the size of ESH patches does not seem to affect bat activity, configuring patches to maximize the amount of edge relative to the patch area may further benefit bats.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.05.045>.

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