



Bat activity response to fire regime depends on species, vegetation conditions, and behavior

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ABSTRACT

Disturbances such as fire play an important role in shaping forests and the wildlife they support. As such, forest managers employ prescribed fire to restore ecosystem function, promote forest biodiversity, and maintain wildlife habitat. To better understand how bats respond to variation in fire regime, we used acoustic recorders to quantify bat activity in forests maintained by frequent fire in southern Florida, USA and modelled this variation as a function of both fire regime and vegetation characteristics. Next, to better understand the mechanisms underlying these responses, we quantified variation in bat foraging efficiency and activity during the important early evening period. We found that even in regions historically maintained by frequent fire, bat activity was more closely associated with vegetation conditions, such as canopy cover and woody understory volume, than fire regime. When vegetation and fire frequency were considered together, the bat activity response was nuanced. Activity across the bat community was greater in forests that had burned more frequently in the previous two decades, but bats appeared more likely to encounter prey in forests that burned less frequently. Species-specific responses added additional complexity, potentially related to size and wing morphology, with larger bats responding more strongly to fire, whereas activity of smaller bats was primarily related to vegetation characteristics. Similarly, activity during the early-evening shifted as a function of fire frequency, but in different directions for different species. Our results suggest that investigations of occurrence or overall bat activity may provide an incomplete understanding of the complex responses to fire regimes that become more apparent when activity is partitioned into more refined metrics. These nuances have implications for management of fire-maintained forests. Though frequent burning may best promote the ecosystem services associated with insectivorous bat activity, a more heterogenous approach to fire management that considers bat species diversity, bat behavior, and vegetation conditions may provide additional benefits to bats.

1. Introduction

Disturbance is a fundamental driver of animal biodiversity and ecosystem function (He et al., 2019). Animal communities that reside in disturbance-dependent systems are influenced by the type, frequency, size, and severity of disturbances (i.e., the disturbance regime). In forested systems, disturbances from fire play an important role in shaping wildlife communities (Hutto et al., 2008). While humans have manipulated fire for millennia (Delcourt and Delcourt, 1997; Van de Water and Safford, 2011), only in recent decades has fire been managed to restore historical fire regimes and mitigate the negative effects of fire suppression (Van Lear et al., 2005; Van Wilgen et al., 2004). Effective

management of forests historically maintained by fire requires a better understanding of the links between fire management and the desired outcomes for promoting habitat of native wildlife communities.

The frequency of fires in forests influences plant composition and structure (Enright et al., 2015; Frost, 1995), which in turn, shapes wildlife habitat selection (Mills et al., 1991; Waldron et al., 2008). For example, in most fire-maintained forest systems, frequent fires result in a more open canopy, and less-frequent fires often allow for a more homogenous, closed canopy (Frost, 1995; Steel et al., 2015). In addition, the more open canopy and midstory resulting from repeated fires can allow more light to reach the forest floor, which can promote a denser ground cover of both herbaceous and woody plants. This variation in

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forest structure resulting from fire has important implications for the distribution and access of resources required by wildlife, such as food and shelter (McComb, 2007). Fire frequency can also influence the abundance of wildlife food resources, with fleshy fruits and diurnal, ground-dwelling insects decreasing in abundance with short fire return intervals (Chitwood et al., 2017; Lashley et al., 2015). Thus, the effects of fire regimes on vegetation have implications for wildlife distribution, but also the behavior, movement, and activity of diverse and mobile animal communities (Knapp et al., 2009).

To understand how variation in fire regimes shaped the activities of highly-mobile animals, we investigated bat communities in fire-maintained forests. Bats are vital to the health and function of many pyric systems and provide critical ecosystem services to humans, such as pest suppression (Boyles et al., 2011; Hughes et al., 2021). It is clear that bats respond to fire-altered changes to forest structure (Armitage and Ober, 2012; Bailey et al., 2019; Law et al., 2019; Loeb and Waldrop, 2008; Steel et al., 2019); however, the specific relationships between bats and vegetation structure vary across species. Generally, bats with smaller, broader, and more rounded wings are adapted for the quick agile flight required for capturing insects within more cluttered forests, compared to larger bats that commonly hunt above the canopy or in otherwise open habitats (Norberg and Rayner, 1987). In addition to affecting access to resources, fire may also influence the abundance of resources. For example, increases in bat activity immediately following fire are thought to be related to increased insect biomass (Braun de Torrez et al., 2018b). However, the influence of fire on the abundance of nocturnal, aerial insects (i.e., the insects most likely to be consumed by bats) remains unclear. Accordingly, it appears likely that bats' response to variation in fire is a function of their access to resources via vegetation structure. Variation in fire regime may also influence the availability and selection of roosting sites. Research conducted in temperate hardwood forests suggests that fire may facilitate the creation of snags used for roosting (O'Keefe and Loeb, 2017; Perry, 2012), but there is little evidence that this occurs in Florida's open pine (*Pinus* spp.) forests (Hanula et al., 2012; Lloyd et al., 2012). Instead, fire may facilitate roosting activity by increasing the quality of roosts by enhancing microclimates (Boyles and Aubrey, 2006) and roost accessibility.

To better understand the linkages between bat activity, fire regimes, and vegetation structure we used acoustic surveys to investigate the spatial and temporal variation in bat community activity across open-canopy pine forests subjected to varied fire regimes in South Florida, USA. First, we aimed to quantify the relative roles of vegetation structure and fire regime characteristics in driving bat activity at the community level and among individual species. Next, we aimed to better understand the mechanisms behind these responses by quantifying activity related to 1) foraging, using feeding buzzes, and 2) emergence, using activity within the earliest part of the night. We expected greater activity in forests that had burned more frequently, given the region's history of frequent fire (Landers et al., 1995) and observations of bats responding positively to fire (Boyles and Aubrey, 2006; Braun de Torrez et al., 2018b). However, we also expected considerable variation in the relative contribution of vegetation characteristics in explaining species-level activity, given the variation in the sensitivity of North-American bats to vertical vegetation density (Cox et al., 2016; Loeb and Waldrop, 2008).

2. Materials and methods

2.1. Study area

We studied the relative activity levels of bat communities in pine forests (mesic and hydric pine flatwoods) on managed land in South Florida. These forests historically were shaped by frequent fire, with a historical fire return interval of 2 to 4 years; however, contemporary fire return intervals typically are much longer, due to fire suppression and limited resources (Florida Natural Areas Inventory, 2010). We surveyed

bats in 2015 and 2016 at four conservation areas in South Florida, USA: Big Cypress National Preserve (BICY; 720 000 acres in Collier, Miami-Dade, and Monroe counties, managed by National Park Service), Fakahatchee Strand Preserve State Park (FSPSP; 74 000 acres in Collier County, managed by Florida Department of Environmental Protection), Fred C. Babcock-Webb Wildlife Management Area (BWWMA; 66 000 acres in Charlotte County, managed by Florida Fish and Wildlife Conservation Commission), and Florida Panther National Wildlife Refuge (FPNWR; 26 400 acres in Collier County, managed by US Fish and Wildlife Service) (Fig. 1). Within the broader region of South Florida, these forests occur within a matrix of agricultural production and dense human development, amplifying bats' value as insect predators.

There are eleven species of bats that likely occur in the study region, eight of which are in the family *Vespertilionidae* and three in the family *Molossidae*. These species vary in their foraging strategies (reflected by wing morphology), and their typical roosting structures (Table 1). The vespertilionids in the community include the big brown bat (*Eptesicus fuscus*, EPFU), northern yellow bat (*Lasiurus intermedius*, LAIN), Seminole bat (*L. seminolus*, LASE), red bat (*L. borealis*, LABO), evening bat (*Nycticeius humeralis*, NYHU), tricolored bat (*Perimyotis subflavus*, PESU), Southeastern myotis (*Myotis austroriparius*), and Rafinesque's big-eared bat (*Corynorhinus rafinesquii*, CORA). The big brown bat, southeastern myotis, red bat, and Rafinesque's big-eared bat are considered rare in southern Florida, and Rafinesque's big-eared bat, northern yellow bat, southeastern myotis, and tricolored bat are designated as species of greatest conservation need in the state (FWC, 2019). The three molossids are the Florida bonneted bat (*Eumops floridanus*, EUFL), endemic to southern Florida and listed as federally endangered (USFWS, 2013), the Brazilian free-tailed bat (*Tadarida brasiliensis*, TABR), and the velvety free-tailed bat (*Molossus molossus*, MOMO).

2.2. Site selection

We used land cover maps to delineate fire-maintained pine forests within which to sample bat communities using acoustic surveys. We randomly selected survey sites ≥ 100 m from the edge of fire management units, trails, roads, or adjacent vegetation communities, and ≥ 300 m from other survey sites (additional details about site selections can be found in Braun de Torrez et al., 2018c). In an effort to measure activity within stands, rather than long-distance commuting, we specifically avoided areas that were potential flyways. In total, we sampled 79 sites that represented each of three broad fire regimes defined according to the average fire return interval: short (0–3 years; $n = 40$), moderate (4–6 years; $n = 22$), and long (7–17 years; $n = 17$).

2.3. Acoustic sampling

At each site, we conducted acoustic surveys in 2015 and 2016 using one full spectrum Song Meter SM3BAT detector and SM3-U1 omnidirectional ultrasonic microphone (Wildlife Acoustics, Maynard, MA, USA) mounted at 3 m above the ground, as described in Braun de Torrez et al. (2018b). We programmed the detectors to record from 30 min before sunset to 30 min after sunrise. To account for seasonal variation in bat activity, we surveyed each site for two consecutive nights, four times between January and July, with each survey separated by ≥ 21 nights.

2.4. Acoustic analysis

Acoustic recordings were automatically grouped into distinct files using parameters we programmed into the detectors (trigger window: 3 s, trigger max: 15 s; see Supplemental Materials S1; Braun de Torrez et al., 2018a). We eliminated all acoustic files associated with nights when data were not recorded throughout the entire night due to equipment malfunction (4 detector nights). We used Kaleidoscope Pro 3.14B (Classifiers: Bats of Florida beta and Bats of the Neotropics;

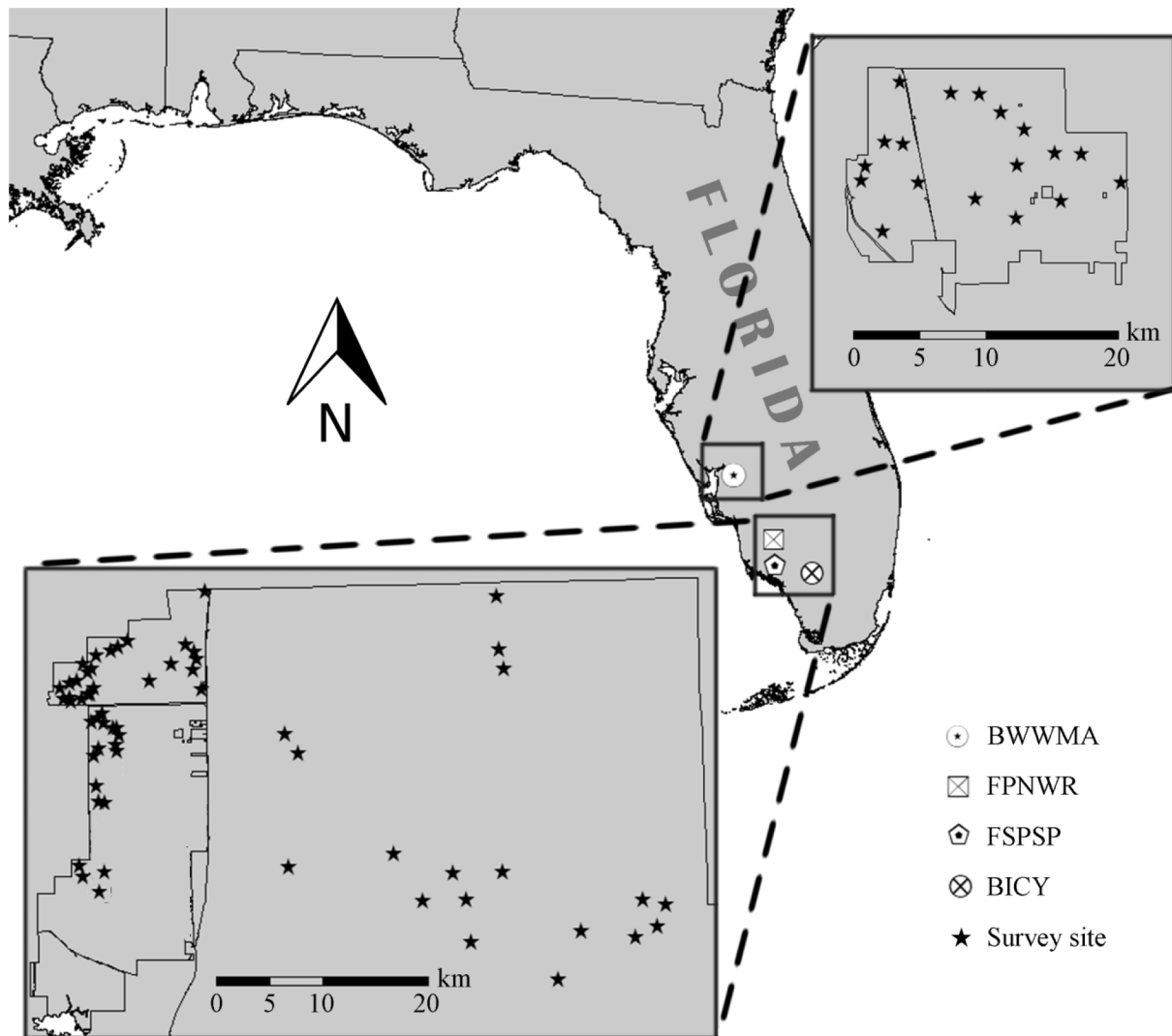


Fig. 1. Locations of sites in Florida, USA where bats were surveyed with acoustic detectors in 2015 and 2016 (BWWMA = Fred C. Babcock-Webb Wildlife Management Area, FPNWR = Florida Panther National Wildlife Refuge, FSPSP = Fakahatchee Strand Preserve State Park, and BICY = Big Cypress National Preserve).

Wildlife Acoustics, Inc.) for automated noise (non-bat ultrasound) filtering, initial species classification, and to manually review the spectrograms of acoustic files (Braun de Torrez et al., 2018a). We required that all files used in our analyses had ≥ 5 total calls and a match ratio of $\geq 75\%$ (percentage of the calls in each of these files that matched the ID assigned by Kaleidoscope Pro). We chose these strict criteria to maximize the accuracy of species identifications, knowing that many files would be excluded. Thus, our metrics of activity should be considered relative as opposed to absolute. To confirm species identifications of files that met our criteria, we manually reviewed: 1) all unexpected species classifications based on species range maps, and 2) any species with < 10 files at a given detector location. Due to their status as a rare and endangered species, we treated *E. floridanus* slightly differently by dropping the minimum number of required calls to 2 and eliminating the match ratio requirement from the automated classifier output. We manually reviewed all files classified by the software as *E. floridanus*, NoID, Noise, or those containing alternate species suggestions of *E. floridanus*, such that we maximized the likelihood of correctly identifying this species (Braun de Torrez et al., 2018a). For all files with uncertain species identification, we compared to available reference libraries of known species, had two independent researchers confirm species identification and consulted a second automated call analysis software (SonoBat 4). Our automated and manual validation

protocols were used consistently across detectors; thus, despite some expected identification error, we were able to compare relative bat species activity detected across sites.

We considered species with indistinguishable calls (eastern red bats, *Lasiurus borealis*, and Seminole bats, *L. seminolus*) as 1 species group; however, distribution maps indicate that Seminole bats were much more likely to occur in the study area than are eastern red bats (Florida Fish and Wildlife Conservation Commission, 2019). Further, based on testing with reference calls from known species, we determined that the classification software performed poorly when distinguishing between *L. intermedius* and *Eptesicus fuscus*, and combined these two species for all further analyses. For simplicity, we refer to these phonic groups as “species” throughout the remainder of the manuscript. We excluded all species with fewer than 20 files (velvety free-tailed bats [*Molossus molossus*], Rafinesque’s big-eared bats [*Corynorhinus rafinesquii*], southeastern myotis [*Myotis austroriparius*]) from our analysis because the sparse data precluded meaningful inferences about these species.

We further refined the acoustic analysis by identifying feeding buzzes to serve as a metric of foraging activity (Coleman and Barclay, 2013). Feeding buzzes are specific vocalizations characterized by a progressively increasing call rate and culminating in a rapid burst of calls as the bat attacks its prey (Fig. S1; Kalko, 1995). We manually examined a random subset of all files ($n = 6810$; 33% of total all files), independent

Table 1

Scientific name, common name, wing morphology, and typical roost structures for each bat species in South Florida, USA.

Scientific name	Common name	Wing aspect ratio ^a	Wing length	Roost structures
<i>Perimyotis subflavus</i>	Tricolored bat	Low	Short	foliage, cavity/bark, artificial
<i>Corynorhinus rafinesquii</i>	Rafinesque's big-eared bat	Low	Short	cavity, artificial
<i>Myotis austroriparius</i>	Southeastern myotis	Low	Short	cavity/bark, artificial
<i>Nycticeius humeralis</i>	Evening bat	Moderate	Moderate	foliage, cavity/bark, artificial
<i>Eptesicus fuscus</i>	Big brown bat	Moderate	Moderate	cavity/bark, artificial
<i>Lasiurus intermedius</i>	Northern yellow bat	Moderate	Moderate	foliage
<i>Lasiurus borealis</i>	Red bat	Moderate	Moderate	foliage
<i>Lasiurus seminolus</i>	Seminole bat	Moderate	Moderate	foliage
<i>Tadarida brasiliensis</i>	Brazilian free-tailed bat	High	Long	cavity/bark, artificial
<i>Eumops floridanus</i>	Florida bonneted bat	High	Long	cavity/bark, artificial
<i>Molossus molossus</i>	Velvety free-tailed bat	High	Long	cavity, artificial

^a Ratio of wing length to wing width.

of species, for those containing feeding buzzes. Using Kaleidoscope Pro, we manually reviewed (by listening and visually reviewing spectrograms) the subset of files for the presence of feeding buzzes. To ensure that the subset represented the same gradient of fire frequency of the full set of files, we first stratified the files according to three categories of fire frequency, then randomly selected 33% of files from each category to review for feeding buzzes. Thus, there was not an equal number of files in each category.

2.5. Fire regime metrics

We used ArcGIS and the statistical software R, version 3.3.3 (R Development Core Team, 2017), to map the fires (wildfires or prescribed burns) that were reported to occur across the four conservation areas over the previous 18 years. We only considered fires that were greater than 40 ha in size and labeled successful by fire managers. Additionally, fires were only counted once per season, such that multi-day fires were considered to be one fire. Historical data from FSPSP, FPNWR, and BWWMA were recorded in distinct fire management units; thus, we calculated fire variables for each unit. Data from BICY consisted of GIS shapefiles representing the estimated area burned by each fire. Here we calculated burn frequency at each site based on the number of overlapping burn polygons (Braun de Torrez et al., 2018c). From the resulting fires, we then calculated two separate metrics to describe the fire regime, the time since last fire in years (TSF) and the fire frequency (number of fires in the 18-year period). We selected these metrics because TSF has been shown to influence the abundance of wildlife food resources (Chitwood et al., 2017; Lashley et al., 2015), whereas fire frequency is more likely to drive forest stand structure and access to resources (Armitage and Ober, 2012; Boyles and Aubrey, 2006; Waldrop et al., 1992). As such, TSF and fire frequency represent two components of the fire regime that may affect bat activity in different ways. When appropriate, we consider both TSF and fire frequency; however, for analyses where we only consider univariate effects (see species-specific activity and roosting activity below), we chose to investigate fire frequency because of its relevance for forest managers.

2.6. Vegetation conditions

We quantified vegetation composition and structure in a 15-m radius plot around each detector. Specifically, we measured percent canopy cover and woody understory volume because previous studies have shown woody vegetation structure influences bat activity (Cox et al., 2016; Loeb and Waldrop, 2008). Additionally, we measured herbaceous groundcover volume because of known relationships between fire, herbaceous cover, and arthropod abundance (Chitwood et al., 2017; Hahn and Orrock, 2014). We calculated percent canopy cover by averaging five spherical densiometer measurements, one at the center of the plot and one 10 m in each cardinal direction from the center. We characterized understory cover (defined as plants <3 m tall or with a DBH <10 cm) within each plot by first estimating the percent cover of the following plant groups: forbs, grasses (family *Poaceae*), shrubs, and small trees using five cover class categories (1 = 0–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80%, 5 = 81–100%). Using the median of each cover class category (1 = 10%, 2 = 30%, 3 = 50%, 4 = 70%, 5 = 90%), we calculated the sum of herbaceous groundcover (forbs, sawgrass, bunchgrass, and other grasses; hereafter “herbaceous cover”) and the sum of small tree and shrub cover (hereafter “woody cover”). We then averaged four height measurements for each of herbaceous and woody vegetation and multiplied these average heights by the respective areal cover to derive herbaceous and woody vegetation volume.

2.7. Bat community activity

Following previous studies of bat activity, we used the number of files containing bat calls per night as a metric of relative nightly bat activity (Braun de Torrez et al., 2018c; Buchalski et al., 2013; Cox et al., 2016; Loeb and Waldrop, 2008). To make inferences about the bat community as a whole, we calculated the mean number of files at each site per night for each species, then rounded these nightly means to whole numbers, and used a Poisson regression framework (for count data) to relate the number of files to characteristics of fire regimes and vegetation. Specifically, we used the *glmmTMB* function in the R package *glmmTMB* (Magnusson et al., 2020) to fit generalized linear mixed models using a log link function. To account for variation in activity across species, we incorporated the species identity as a random intercept in all models. The remaining predictor variables describing fire regime and vegetation were incorporated as fixed effects.

To understand how well fire regime and vegetation structure explained variation in bat activity, we developed a suite of “fire models” and “vegetation models.” For the suite of fire models, we considered all combinations of fire frequency and the time since fire (TSF). Additionally, we considered the quadratic effect of TSF, given that species' responses to fire may be non-linear (Taillie et al., 2018). Similarly, the suite of vegetation models included the linear effects of the three-vegetation metrics (canopy cover, volume of woody groundcover, and volume of herbaceous groundcover), as well as a quadratic effect of canopy cover because some species may be most active in forests with intermediate canopy cover (Bailey et al., 2019). We ranked the models according to the lowest Akaike's Information Criterion (AIC; Burnham and Anderson, 2002), and selected from the competing models (<2 ΔAIC) the model with the fewest parameters. To assess the relative influence of fire and vegetation characteristics on bat activity, we compared the AIC values of the top-ranked models from both suites of models. Lastly, to understand the relative strength of the vegetation and fire characteristics on bat activity, and to evaluate the explanatory power of both fire variability and vegetation structure on bat activity, we fit a composite model that included the effects from the top-ranked fire model and vegetation model together. In addition to using the magnitude and 95% confidence intervals of parameter estimates to evaluate the strength and uncertainty of predictor variables, we used the model to calculate predictions of activity, with prediction intervals, across the range of covariates covered by the sites (Magnusson et al.,

2020).

2.8. Species-specific activity

We then investigated species-specific activity responses to both fire and vegetation metrics, while accounting for variable and imperfect detection using the N-mixture hierarchical modeling framework (Royle, 2004). In contrast to the community-wide analysis above, we considered each detector night to be an independent sample and used the detection histories across nights to estimate the detection probability in a given night. Though this framework is more commonly used to model animal abundance with repeated counts of individuals (Royle, 2004), we followed previous studies that use vocalization counts to make inferences about animal activity (Caldwell et al., 2019; Shamoan et al., 2017). We fit a separate model for each species using the *pcount* function within the R package unmarked (Fiske and Chandler, 2011). We accounted for variation in detection over the course of a year by incorporating Julian date as an observation covariate with both linear and quadratic effects (Clement et al., 2014; Weller and Baldwin, 2012).

To determine the extent to which species varied in their response to fire regime, we included fire frequency as a linear effect for each species. We did not investigate the effect of TSF at the species level because our analysis at the community level suggested it was less relevant to bat activity. Similarly, we did not use a model selection approach at the species level. Instead, we fit the same two models for each species to facilitate the interpretation of our results and more directly compare the responses to fire regime across species. The first model included just the linear effect of fire frequency, and the second model included fire frequency, as well as the 3 vegetation metrics (canopy cover, woody understory volume, and herbaceous understory volume).

2.9. Foraging activity

We investigated the relationship between foraging and fire frequency, TSF, and vegetation using logistic regression with the presence/absence of a feeding buzz within each of the reviewed files as the binary response variable. Because we selected a subset of files to review for feeding buzzes, we were unable to determine the total sampling effort, which precluded comparison of the total number of feeding buzzes. Thus, our analysis reflects the likelihood of encountering prey, given a certain level of activity. Analogous to the community activity model above, we included the same predictor variables as fixed effects, as well as a random effect of species identity. We fit all possible combinations of the fixed effects and ranked models according to the minimum AIC. We considered all models within $\Delta\text{AIC} \leq 2.0$ of the best model (and outperforming the null) to be competitive models (Burnham and Anderson, 2002). For all parameters in competitive models, we calculated 95% confidence intervals and identified informative parameters as those with confidence intervals that did not contain 0 (Arnold, 2010). To investigate species-specific foraging responses, we also fit the top-ranked model for each species separately.

2.10. Emergence activity

Within a given night, we investigated the variation in activity over the course of the night to make inferences about the critical early-evening period during which many species are most active (Adams and Thibault, 2006; Hayes, 1997). We obtained the sunset end and sunrise start times for each night and the following day using the *getSunlightTimes* function in the package *suncalc* (Theurmel and Elmarhraoui, 2019) and applied a correction factor to the time signature of each call file to account for differences in night length over the study (Sovie et al., 2019). We first calculated the difference between the sunset time and the time of the given vocalization to obtain the vocalization's time-after-sunset. We then calculated a night length for each survey night at each point as the time duration from sunset on the start of the survey

night to sunrise the following morning. We calculated the ratio of the longest night in our study period to every sampling night to create a correction factor (Sovie et al., 2019). We then multiplied each vocalization's time-after-sunset by its correction factor to obtain a standardized measure of each vocalization's time-after-sunset (hereafter: Call_Time). A Call_Time of 0 corresponded with the bat activity occurring exactly at sunset, while negative or positive values indicated that a call occurred before or after sunset, respectively.

Given the potential for fire frequency to affect quality of and accessibility of roosting sites in snags, we investigated the relationship between fire frequency and emergence activity. We used directional regression to fit the response variable (Call_Time) to the linear predictor (fire frequency) using a von Mises kernel distribution (Sovie et al., 2019; Xu et al., 2011). The von Mises distribution is a flexible, circular distribution that can be used for analyzing temporal animal activity patterns from passively collected data (Ridout and Linkie, 2009). We used bootstrapping with 999 iterations to estimate 95% confidence intervals (CI) around each fitted model. The confidence intervals provide a null envelope of bat activity that assumes no effect of time of night (Xu et al., 2011). Fitted values that fall above or below the 95% CI indicate a significant ($p < 0.05$) positive or negative relationship, respectively, between bat activity at the given time and fire frequency (Xu et al., 2011). Given bats typically emerge from roosts within 90 min of sunset (Braun de Torrez et al., 2020; Reichard et al., 2009), we considered the relationship between fire frequency and roosting activity to be significant when this portion (i.e. the first 90 min after sunset) of each species' activity curve fell outside of the 95% CI. We fit these models and estimated CIs using the *fitlincirc* function in the R package *Activity* (Rowcliffe et al., 2014). In contrast to the analyses described above, we did not investigate emergence activity at the community level because we could not account for the differences in activity across species using this modelling framework. As such, fitting the model to the data pooled across species were strongly biased toward the most active species (*T. brasiliensis*).

3. Results

Acoustic analysis of the raw audio resulted in 133,234 total files. After filtering out files that were not bats or could not be reliably identified to species based on our conservative protocol, 20,431 files were used in subsequent statistical analyses. Of the six species included in our analyses, all but *P. subflavus* were detected at >90% of the 79 survey locations (Table 2). The greatest number of files were detected and identified to *T. brasiliensis* ($n = 11,180$), and the least-detected species was *P. subflavus* ($n = 509$; Table 2).

At the community level, we observed that vegetation characteristics described variation in bat activity better than fire regime. The top-ranked vegetation model included a negative quadratic effect of canopy cover, and positive linear effects of both woody and herbaceous understory volume (Table 3). Among the fire models, the 2 models

Table 2

Species, number of sites at which the species was detected, and the number of files containing call sequences identified for each of six species^a of bats analyzed across four conservation areas in South Florida, USA (2015–2016).

Code	Scientific Name	# Sites Detected	Total Files
EPFU/LAIN	<i>Eptesicus fuscus/Lasiurus intermedius</i>	79	2,919
EUFL	<i>Eumops floridanus</i>	75	2,509
LABO/ LASE	<i>Lasiurus borealis/Lasiurus seminolus</i>	78	2,390
NYHU	<i>Nycticeius humeralis</i>	77	924
PESU	<i>Perimyotis subflavus</i>	54	509
TABR	<i>Tadarida brasiliensis</i>	76	11,180

^a Some species were combined into phonic groups due to difficulty distinguishing vocalizations.

within 2 AIC of the best model were comprised of an effect of fire frequency (the best model), plus additional parameters that were not significant (included 0 in 95% CI) and did not improve model parsimony. Accordingly, we considered the top-ranked model that included fire frequency as the only main effect to be the only competing model (Burnham and Anderson, 2002). Though vegetation conditions provided the best explanation of variation in bat community activity, fire frequency explained additional variation when included in the composite model, as evidenced by the decrease in AIC and the confidence interval of fire frequency that did not contain 0 in the composite model (Tables 3, 4). Specifically, bats were more active in forests that burned more frequently (Fig. 2).

At the species level, responses by bats to fire frequency varied among species. Two species (*T. brasiliensis* and *E. floridanus*) were more active in areas that had burned more frequently in the past 18 years, regardless of vegetation characteristics (Table 5). In contrast, we observed little evidence for a response to fire frequency for both *L. borealis*/*L. seminolus* and *N. humeralis* (Table 5). For both *E. fuscus*/*L. intermedius* and *P. subflavus*, the relationship between activity and fire frequency was strongly dependent on the inclusion of vegetation characteristics in the model. Similar to *T. brasiliensis* and *E. floridanus*, *P. subflavus* was more active in forests that burned more frequently, but this relationship was not significant when vegetation characteristics were included in the model (Table 5). Also, *E. fuscus*/*L. intermedius* was the only species for which activity was lower in forests that burned more frequently, but this relationship became slightly positive when vegetation characteristics were included (Table 5).

Activity related to foraging and emergence was generally greater in forests that burned less frequently. For foraging activity at the community level, the top-ranked and most parsimonious model included only the effect of fire frequency for all species combined (Table 6). The second-best model was within 2 AIC and consisted of the top-ranked model with the addition of the effect of TSF (Table 6), which was not significant (95% CI included 0). As such, we considered the top-ranked model to be the best and most parsimonious model (Arnold, 2010). The probability that a recorded call file contained a feeding buzz was negatively associated with fire frequency ($\beta = -0.09$, 95% CI: $-0.17 - -0.03$), reflecting that bats were more likely to encounter prey in forests that had burned less frequently. At the species level, *E. fuscus*/*L. intermedius* and *T. brasiliensis* were the only two species for which foraging activity was related to fire frequency (Table 7). For both species, the probability that a given call file contained a feeding buzz was greater in forests that burned less frequently (Table 7). We observed a relationship between fire frequency and emergence activity for three of the six bat

Table 3
Ranking according to minimum AIC of Poisson linear mixed effects models fit to observations of average nightly vocalization counts across the bat community in South Florida (2015–2016). Species was also included in each model as a random intercept.

Model Suite	Main Effects	AIC	ΔAIC
Fire	FireFrequency	3554.0	0
	FireFrequency + TSF + TSF ²	3554.4	0.37
	FireFrequency + TSF	3555.6	1.56
	TSF	3563.4	9.39
	TSF + TSF ²	3564.0	9.97
Vegetation	Canopy + Canopy ² + Woody + Herb	3461.2	0
	Canopy + Canopy ² + Woody	3467.9	6.63
	Canopy + Canopy ²	3497.1	35.90
	Herb + Woody	3518.8	57.55
	Woody	3520.6	59.35
	Herb	3561.9	100.70
	Canopy	3562.3	101.05
Composite	Canopy + Canopy ² + Woody + Herb + FireFrequency	3439.7	0

Table 4

Parameter estimates, standard error, and p-values from the composite (fire regime and vegetation) model of bat activity in South Florida pine forests (2015–2016).

	Estimate	SE	z value	Pr(> z)
Intercept	1.34	0.41	3.28	0.00
FireFrequency	0.11	0.02	4.93	0.00
Canopy	0.00	0.02	-0.09	0.93
Canopy ²	-0.12	0.02	-5.54	0.00
Woody	0.17	0.02	7.52	0.00
Herb	0.06	0.02	3.08	0.00

species we investigated (Fig. 3). Emergence activity for *E. floridanus* was greater in forests that burned more frequently, whereas emergence activity for *N. humeralis* and *T. brasiliensis* was greater in forests that burned less frequently (Fig. 3).

4. Discussion

We observed that variation in bat activity at the community level was most strongly related to forest vegetation structure, not fire regime. Specifically, bats were most active in forests that had intermediate canopy cover, greater woody understory volume, and to a lesser extent, greater herbaceous understory volume. This combination of better access to resources in more open forests and greater abundance of resources in forests with greater woody understory volume likely explains the curvilinear relationship between bat activity and canopy cover and the increased activity with increasing woody understory volume. Previous studies have shown that vegetation structure can mediate access to insect resources independent of their abundance (Adams et al., 2009; Cox et al., 2016). In forests with greater canopy cover, cluttered vegetation conditions hinder bats' ability to forage beneath the canopy, despite potentially high insect abundance (Adams et al., 2009). This limitation may be particularly important for larger bats (Menzel et al., 2005; Norberg and Rayner, 1987). In contrast, bats may be less active in open areas due to less abundant food resources and less cover from predators. Bat responses to understory vegetation volume may reflect differences in resource abundance, as complex vertical structure may promote insect abundance and diversity (Dodd et al., 2012; Ober and Hayes, 2008; Wickramasinghe et al., 2004); however, previous efforts linking bat activity with insect abundance have been inconclusive (Armitage and Ober, 2012; Cox et al., 2016). Nonetheless, insect abundance does increase with the successional development of vegetation following disturbance (Summerville and Marquis, 2017).

We observed that the metrics of fire regime we measured were less important to explaining variation in bat activity than vegetation characteristics, but that fire frequency did appear to contribute to explaining additional variation in habitat use by bats. As we predicted, bat activity was greater in forests that burned more frequently; however, the mechanism is unclear. Given the many ways in which fire frequency shapes vegetation composition and structure (Glitzenstein and Streng, 2003), bat responses to fire frequency could have resulted from vegetation characteristics we did not measure, such as understory species composition, which could lead to differences in the composition of insect prey. Alternatively, fire has been shown to stimulate a flux of insects from aquatic to terrestrial environments, which were then related to increased bat activity independent of forest vegetation (Malison and Baxter, 2010). Thus, fire may affect bat habitat quality via alteration to other aspects of the system such as soil chemistry, litter accumulation, and nutrient cycling, which may in turn influence prey abundance (Addington et al., 2015; Coates et al., 2018; Richter et al., 1982). Further study is needed to understand the mechanisms by which fire influences bat habitat quality and food resources.

Although the bat community in aggregate responded to greater understory vegetation volume and increased fire frequency, we observed variation among bat species that likely reflects their differences in

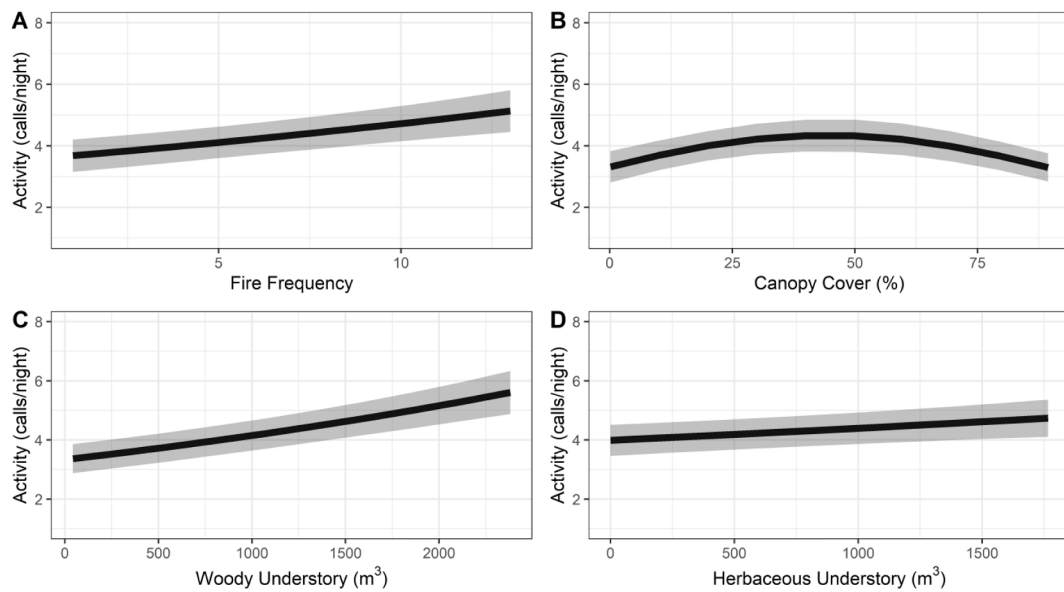


Fig. 2. Predicted bat community activity in fire-maintained pine forests in South Florida (2015–2016) as a function of fire frequency (number of fires that occurred in previous 18 years; (A), canopy cover (B), woody understory volume (C), and herbaceous understory volume (D) according to the best model of vegetation and fire regime characteristics, with 95% confidence intervals shown as shaded regions.

Table 5

Species-specific parameter estimates and 95% confidence intervals for the effect of fire frequency on activity when modeled as the only fixed effect and when included with vegetation characteristics: canopy cover, herbaceous understory volume, and woody understory volume in South Florida, USA (2015–2016).

Species	Fire Frequency Only			Fire Frequency and Veg		
	Estimate	Lower	Upper	Estimate	Lower	Upper
EPFU/LAIN	-0.07	-0.12	-0.02	0.05	0	0.11
EUFL	0.09	0.04	0.15	0.08	0.01	0.14
LABO/LASE	-0.02	-0.08	0.03	-0.06	-0.12	0.01
NYHU	0.05	-0.04	0.13	0	-0.11	0.1
PESU	0.21	0.11	0.32	-0.06	-0.19	0.08
TABR	0.16	0.13	0.18	0.15	0.12	0.18

Table 6

Model selection table for logistic regression models used to investigate the effect of fire frequency (FireFrequency), time since fire (TSF), canopy cover, woody understory volume (Woody), and herbaceous understory volume (Herb) on the probability that a given bat call file contained a feeding buzz in South Florida, USA across all species (2015–2016).

Model	k	AIC	ΔAIC	weight
FireFrequency	3	5498.2	0	0.597
FireFrequency + TSF	4	5500	1.82	0.24
FireFrequency + TSF + TSF ² + Canopy + Canopy ² + Woody + Herb	9	5503.6	5.47	0.039
TSF	3	5504	5.85	0.032
TSF + TSF ²	4	5504.2	6.01	0.03
Null	2	5504.7	6.52	0.023

morphology. Previous studies suggest that differences in wing morphology play a role in determining a given bat species’ sensitivity to vegetation characteristics (Menzel et al., 2005; Norberg and Rayner, 1987). Specifically, dense canopy cover and midstorey cover can inhibit movement of larger, less maneuverable species of bats (e.g., *E. fuscus*), whereas smaller, more maneuverable bats (e.g., *P. subflavus*) may be more active in cluttered forests (Armitage and Ober, 2012). Despite the long wings, high aspect ratio and low maneuverability of *E. floridanus* and *T. brasiliensis*, we observed the inclusion of vegetation had little effect on their response to fire frequency, which suggests vegetation

Table 7

Parameter estimates, standard error, and p-values for the effect of fire frequency from the logistic regression model used to estimate the probability that a given call file contained a feeding buzz for each bat species detected in South Florida, USA (2015–2016).

Species	Estimate	SE	Z	Pr(> z)
EPFU/LAIN	-0.09	0.04	-2.32	0.02
EUFL	-0.06	0.06	-0.91	0.36
LABO/LASE	-0.05	0.07	-0.73	0.46
NYHU	0.03	0.11	0.29	0.77
PESU	0.01	0.08	0.18	0.86
TABR	-0.03	0.01	-2.06	0.04

characteristics are less important to their habitat selection than fire regime alone. Previous work investigating variation in bat activity at different heights above the ground revealed that activity of “open-adapted” species was significantly greater above the forest canopy, compared to within or below (Menzel et al., 2005). Thus, the lack of response to vegetation characteristics we observed likely reflects these species’ tendency to forage above the canopy, where they are less affected by variation in fine-scale forest structure. In agreement with previous work investigating relationships between pyrodiversity and biodiversity (Kelly et al., 2017; Martin and Sapsis, 1992; Tingley et al., 2016), these varied responses among bat species suggest that a shifting mosaic approach to fire management may serve to most effectively promote bat diversity.

Our analysis of feeding buzzes and early-evening activity suggests that variation in bat activity across fire regimes is in part related to roosting/emergence and foraging. However, these behavior-linked measures appeared to indicate different patterns of habitat selection than measures of bat community activity more broadly. Despite less overall community activity in forests that burned less frequently, bats appear to encounter prey more frequently in these forests. Although the mechanism for this discrepancy is unclear, it could explain why previous attempts to link bat activity to insect abundance have been inconclusive. One possible explanation is that bats use more open, frequently-burned forests for activities other than foraging, such as commuting, socializing, or investigating potential roosts while still being protected from predators. Alternatively, they may also forage in these sites but not encounter

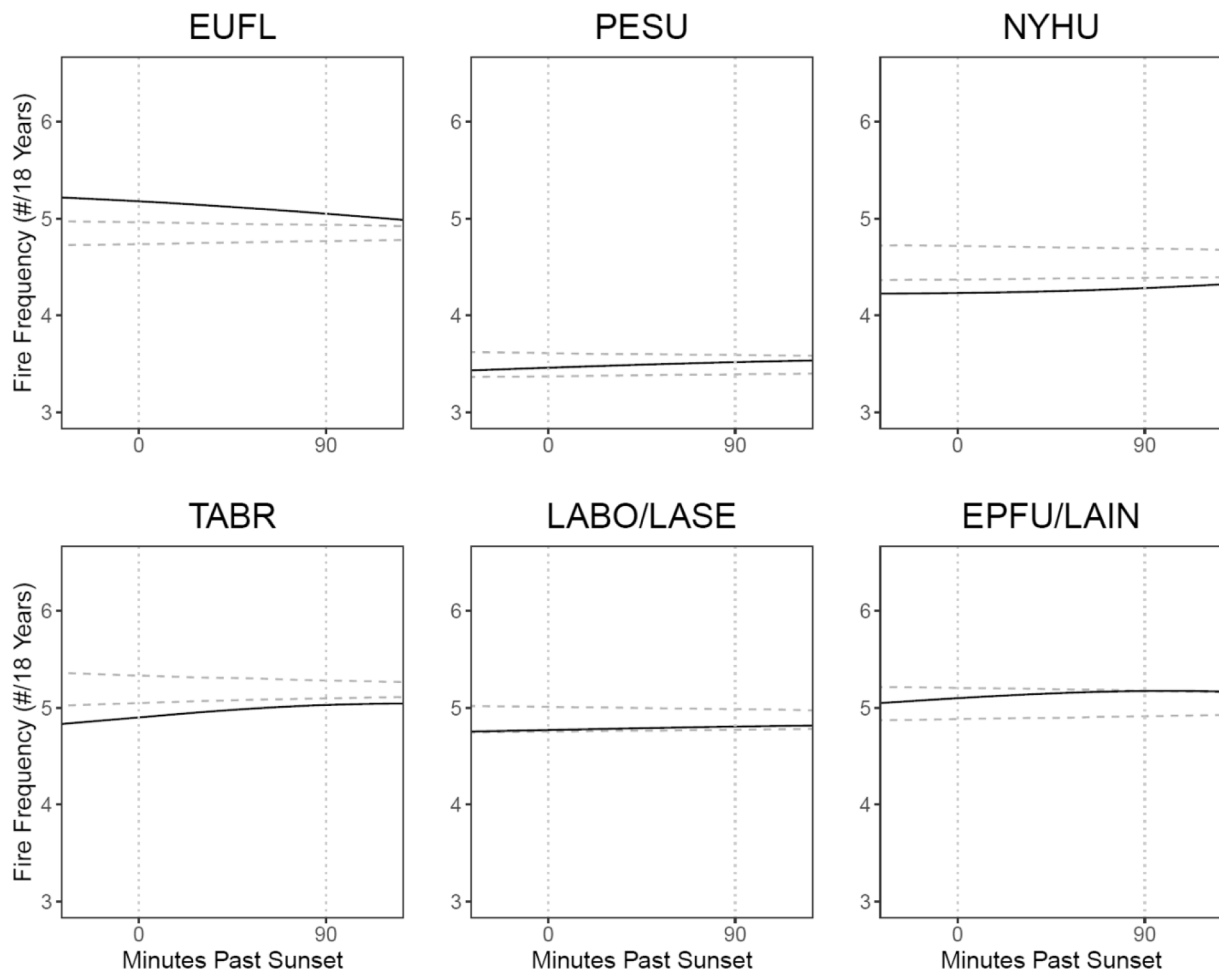


Fig. 3. Fitted relationship (solid line) from linear-circular regression between fire frequency and temporal activity over a night for six bat species complexes observed in South Florida pine forests, with the 95% confidence interval null envelope (dotted lines). Vocalization times were adjusted to the length of the longest night in our study period (807.25 min), and we present the responses over the first 90 min following sunset to represent emergence from roosts. Areas where the fitted relationship falls outside and above the null envelope represent a significant positive relationship between fire frequency and emergence activity at the given time of night, whereas areas where the fitted relationship falls below the null envelope represents a significantly negative relationship.

prey as frequently. Thus, insects may be more abundant in forests that burn less often, but bat activity remains lower because access is limited due to clutter. Granted previous work found little evidence that fire frequency influenced insect abundance in xeric pine forests, so further study is needed to understand the links between fire, insects, and bats. In regards to emergence, we found early-evening activity for both *N. humeralis* and *T. brasiliensis* was reduced in forests that burned more frequently, contrary to previous work showing prescribed fire promoted roosting conditions for cavity-roosting bats (Boyles and Aubrey, 2006). Though fire may promote favorable roosting conditions relative to unburned forests, recurring fire over time may consume snags, resulting in lower snag densities and fewer potential roosting sites (Armitage and Ober, 2012; Parnaby et al., 2010). Alternatively, bats may be selecting roosting habitat to minimize the risk of fire (Jorge et al., 2021a). In contrast to other species, *E. floridanus* may be uniquely adapted to ephemeral roosts, given its restricted range and association with fire-dependent forests in Florida (Braun de Torrez et al., 2018c). Alternatively, peak activity in the early-evening may be influenced by other behaviors such as drinking water or socializing. The labor-intensive task of identifying day roosts (Jorge et al., 2021a) would allow for better inferences about the effects of fire on roosting, though this approach may not be practical across multiple landscapes for multiple species.

Our results suggest that bat activity and occurrence, measured on a nightly basis, may provide an incomplete understanding of their complex responses to fire regimes. Because bats may select different habitat

conditions for roosting and foraging (Brigham, 1991), linking activity measures to these specific behaviors appears to be critical to better understanding their use of forests. The continued advancement of acoustic technology for studying bats has increased the ability of researchers to understand the factors influencing bat activity, but we suggest that failure to link activity to associated behaviors may provide an incomplete picture (Altendorf and Laundre, 2001; Smith and Banks, 2014). While increasing fire frequency to restore historical fire regimes has many important benefits for fire-maintained forests (Van Lear et al., 2005) and appears to promote bat activity broadly, unburned patches, such as those occurring on more mesic soils, may provide important resources for bats, such as roosts and insect prey (Jorge et al., 2021a; Jorge et al., 2021b). More generally, our results are consistent with previous studies that show that patches of less-frequently burned forests can provide critical resources for wildlife within a broader landscape of forests that have burned frequently (Lashley et al., 2015).

5. Conclusions

Forest managers aiming to maximize bat activity and thus ecosystem services like pest control, should aim to maintain canopy cover at 40–50% and burn frequently. However, varying the fire intensity or retaining unburned patches of forest within the burn perimeter may provide additional benefits. At a broader scale, considering the fire regime and burn schedule of adjacent forest units may be requisite to

most effectively manage fire-dependent forests for bats.

CRedit authorship contribution statement

P.J. Taillie: Formal analysis, Visualization, Writing – original draft. **E.C. Braun Torrez:** Conceptualization, Investigation, Writing – review & editing. **A.D. Potash:** Formal analysis, Writing – review & editing. **W. W. Boone IV:** Formal analysis, Writing – review & editing. **M. Jones:** Formal analysis, Writing – review & editing. **M.A. Wallrichs:** Investigation. **F. Schellenberg:** Investigation. **K. Hooker:** Formal analysis, Writing – review & editing. **H.K. Ober:** Conceptualization, Funding acquisition, Writing – review & editing. **R.A. McCleery:** Conceptualization, Funding acquisition, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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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.2021.119722>.

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