

# Bat winter foraging habitat use in working forests: a multispecies spatial occupancy approach

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## Keywords

Acoustics; bats; foraging; forest management; habitat use; imperfect detection; occupancy; *Pinus taeda*; spatial autocorrelation; species richness.

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Editor: Rahel Sollmann  
Associate Editor: Jennifer Moore

Received 10 May 2023; accepted 31 October 2023

doi:10.1111/acv.12924

## Abstract

Insectivorous bats in temperate zones have evolved strategies such as migration or hibernation to overcome challenges of reduced resource availability and increased energy demand during winter. In the southeastern United States Coastal Plain, bats are either year-round residents and remain active during winter or are migrants from colder areas seeking milder temperatures. Southeastern Coastal Plain forests also may represent important areas for remnant populations of species impacted by white-nose syndrome. Working pine (*Pinus* spp.) forests comprise a large proportion of southeastern Coastal Plain forests, yet winter bat habitat associations and how forest management affects bat use remain understudied. Hence, we used hierarchical multispecies spatial occupancy models to evaluate factors influencing winter bat occupancy and foraging habitat associations in working forests of the southeastern Coastal Plain. From January to March 2020–2022, we deployed Anabat Swift acoustic detectors and measured site- and landscape-level covariates on six working landscapes. We detected five species of bats and three species groups at 93% (224/240) of sites. We observed higher species richness at sites with high proportions of contiguous forest and low levels of basal area. At the species level, occupancy patterns were influenced by site and landscape covariates, which had varying effects on species with distinct foraging strategies. Temperature was an important predictor of detectability. Our findings offer new insights into the ecology of bats in working forest landscapes during winter, where we highlight positive responses in occupancy with contiguous forests and lower levels of basal area, as in previous summer work. By providing valuable information on winter community composition and foraging habitat associations, we hope to guide management decisions for forest attributes important to these species, thus increasing conservation opportunities within working forests.

## Introduction

Understanding how environmental variables drive species-level patterns and shape community structure is fundamental to ecology and conservation. In temperate regions, some species, including bats, have evolved thermoregulatory adaptations (e.g., torpor) to overcome winter challenges of reduced resource availability and increased energy demand by seasonally altering their active state (Humphries & Thomas, 2003; Humphries *et al.*, 2017; de Bruyn *et al.*, 2021). Alternatively, some bat species cope with cold winters by migrating to warmer regions for overwintering (Cryan, 2009; Grider *et al.*, 2016; Frazer, Brooks, & Longstaffe, 2017). Winter activity patterns are directly related to

climate conditions, particularly temperature, which influences both thermoregulatory behaviors and hibernation traits (Stawski & Geiser, 2011; Barros *et al.*, 2021), as well as whether their insect prey remain active (Grider *et al.*, 2016; Welti *et al.*, 2022). In temperate regions at lower latitudes, coinciding with winter destinations of migratory species, torpor breaks are frequent, allowing bats to be year-round residents and rely on a combination of activity and short periods of torpor (Boyles, Dunbar, & Whitaker, 2006; Barros, Ribeiro, & Cabral, 2017; Mas *et al.*, 2022). These species, however, are subject to changing environmental conditions and shifting insect availability, resulting in a diversity of winter activity patterns (Czenze & Willis, 2015).



Unlike regions farther north, warmer temperatures of the southeastern United States Coastal Plain favor resident bats that remain active year-round, and migratory bats that overwinter (Grider *et al.*, 2016). This region is characterized by its large expanse of working pine (*Pinus* spp.) forest landscapes (approximately 15.8 million ha), about 90% of which are privately owned (Oswalt *et al.*, 2019). In temperate regions, most bats are associated with forests for roosting or foraging, creating a need to understand how bat communities use forests and how forest management influences bat use (Brigham, 2007; Gallagher *et al.*, 2021). Forest management practices such as thinning, clearcutting, prescribed burning, and other activities can affect habitat use by bats (Wigley, Miller, & Yarrow, 2007; Bender *et al.*, 2015; Cox *et al.*, 2016; Węgiel *et al.*, 2019; Taylor *et al.*, 2020) by modifying forest structure, affecting distribution and abundance of living and dead trees used for roosting, and affecting the number of forest openings and edges used for foraging (Morris, Miller, & Kalcounis-Rueppell, 2010; Tena *et al.*, 2020).

Understanding bat community- and species-level habitat use is reliant upon the ability to effectively detect bat roost and/or foraging presence. The probability of detecting bats depends on several factors, such as species behavior and physical traits, forest structure, or survey-related characteristics, making some species more detectable than others (Devarajan, Morelli, & Tenan, 2020). Additionally, for elusive species such as bats, imperfect detection is an essential source of bias when assessing species richness among communities (Kéry & Schmidt, 2008; Dorazio, Gotelli, & Ellison, 2011). Recently, hierarchical multispecies detection/non-detection modeling was developed to address questions about habitat associations, including both community-level and species-specific responses, while addressing important complexities such as imperfect detection (MacKenzie *et al.*, 2002; Dorazio & Royle, 2005; Guillera-Aroita, Ridout, & Morgan, 2010), spatial autocorrelation (Finley, Banerjee, & McRoberts, 2009; Banerjee, Carlin, & Gelfand, 2014), and residual species correlations (Ovaskainen, Hottola, & Siitonen, 2010). Controlling for other sources of bias, such as spatial autocorrelation, is key to identifying underlying processes or factors that influence observed patterns. Thus, spatially explicit models are fundamental for conservation and management decisions (Bateman *et al.*, 2020).

Working forest owners and managers are increasingly committed to conserving biodiversity, as evidenced by voluntary enrollment in sustainable forestry certification programs that include biodiversity principles (Wigley, Miller, & Yarrow, 2007). Given the geographic scale and economic and social importance of privately owned working forests (Oswalt *et al.*, 2019), understanding how biodiversity can be conserved in managed landscapes is imperative (Demarais *et al.*, 2017; Yeiser *et al.*, 2018). However, limited data on foraging ecology and selection of foraging areas by bats in working forest landscapes, especially outside the growing season, hinders our ability to evaluate management decisions. Currently, management decisions are based largely on

knowledge of bat habitat relationships during summer. If and how these relationships are consistent with relationships in other seasons is poorly understood. Thus, investigations into winter habitat use are needed to ensure that management actions provide suitable habitat conditions year-round. Hence, we used a multispecies spatial occupancy modeling approach that explicitly accounts for imperfect detection, spatial autocorrelation, and species correlations to examine winter bat associations on working forest lands across the southeastern United States Coastal Plain. Previous studies have observed that bat communities are shaped by landscape features at different spatial scales (Loeb & O'Keefe, 2006; Bender *et al.*, 2015; Rodríguez-San Pedro & Simonetti, 2015). Therefore, we examined the influence of site- and landscape-level habitat characteristics on species richness to study the effect on winter bat community composition. We also determined species-specific winter foraging habitat occupancy at site- and landscape-levels.

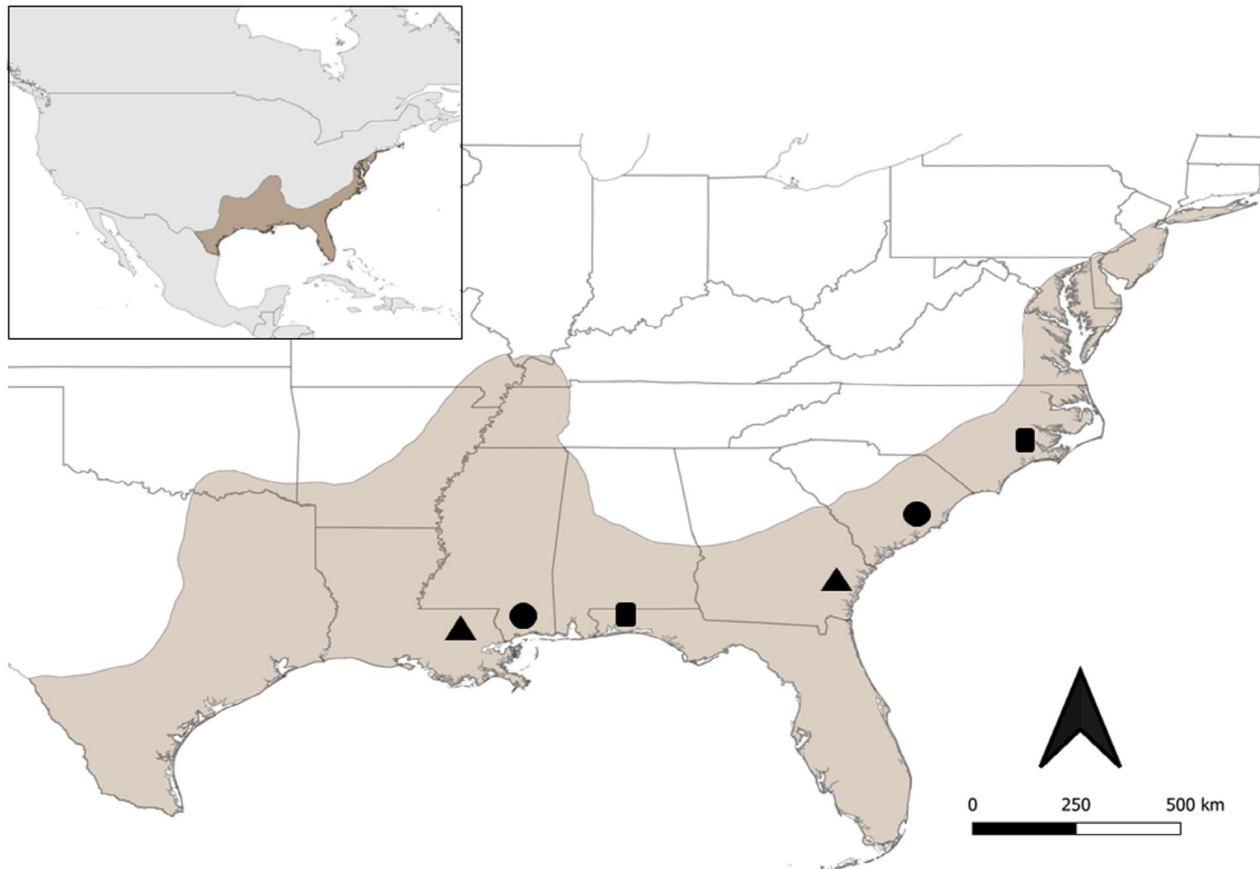
## Materials and methods

### Study area

We conducted our study on six working forest landscapes across six states (Florida, Georgia, Louisiana, Mississippi, North Carolina, and South Carolina) of the southeastern United States Coastal Plain during 2020–2022 (Fig. 1). All study areas consisted primarily of planted loblolly pine (*P. taeda*) stands interspersed with streamside management zones (predominantly mature hardwood trees), roads, and wildlife openings, with other non-forest areas accounting for the remaining land area. We selected study areas >3 000 ha and comprised primarily of upland planted pine with <15% in forested wetlands. Management activities were typical of commercial forestry operations in the region, including clearcutting at 20–35 years, mechanical and/or chemical site preparation, and planting 182–283 pine trees ha<sup>-1</sup> (Gresham, 2002). Competing vegetation was temporarily suppressed through herbicide applications, prescribed fire, or mechanically, with most stands being thinned at least once.

### Bat acoustic sampling

On each study area, we created a 900 × 900 m grid and used ArcGIS Pro 2.8.0 (ESRI, Redlands, California, USA) to randomly select grid intersections as sampling points. The grid spacing was selected to ensure that the distance between sampling points encompassed a core area that constituted much of an individual bat's foraging movements (Morris, Miller, & Conner, 2011; Bender *et al.*, 2015). We surveyed 40 sampling points randomly selected from the grid on each study area to ensure enough samples to adequately represent variation in stand age, stand size, and management history. We sampled all points at each study area within a 1-month period. We defined January–March as the winter sampling season as mean nightly temperatures are lowest (typically <10°C) during this time throughout most of the Coastal Plain region (NOAA [Climate.gov](https://www.climate.gov/), <https://www.climate.gov/>



**Figure 1** Locations of study sites in the southeastern United States Coastal Plain where bat acoustic sampling was conducted January–March 2020–2022. Sites sampled in 2020 are indicated by triangles, 2021 by circles, and 2022 by squares.

[maps-data/data-snapshots/averagetemp-monthly-1981-2010-cmb-0000-02-00?theme=Temperature](https://maps-data/data-snapshots/averagetemp-monthly-1981-2010-cmb-0000-02-00?theme=Temperature)).

At each sampling point, we deployed Anabat Swift acoustic detectors with omnidirectional ultrasonic microphones US-OV2 and US-OV3 (Title Electronics, Ballina, New South Wales, Australia; Appendix S1: Table S1) for three consecutive nights, recording from 30 min before sunset to 30 min after sunrise (Reichert *et al.*, 2018). If rain occurred during the sampling period, we left detectors out for additional nights to ensure three nights of rain-free sampling. We placed detectors on poles with microphones 3 m above the forest floor pointed in the direction of the least vegetation clutter (Weller & Zabel, 2002). We coupled each detector with a temperature logger (HOBO Pendant G Acceleration Data Logger, Onset Computer Corp., Pocasset, Massachusetts, USA) programmed to record hourly temperature.

### Bat call analysis

We used auto ID software and subsequent visual vetting to identify calls to species, as recommended by the North American Bat Monitoring Program (NABat; Reichert *et al.*, 2018). We first used Kaleidoscope Pro 5.4.1 software (Wildlife Acoustics Inc., Maynard, Massachusetts, USA) to

filter noise files. We selected default filter setting parameters for bat analysis specifying a signal of interest between 8 and 120 kHz, 2 to 500 ms, and at least 2 pulses per sequence. We used the batch function in Kaleidoscope Pro to split each sequence to a maximum duration of 10 s for standardization. We selected the auto classifier of Kaleidoscope Pro with a balanced sensitivity level for classification to assist the visual vetting. Subsequently, we manually analyzed all remaining files using call structure, frequency of minimum and maximum energy, characteristic frequency, duration, inter-pulse interval, and slope (O'Farrell & Gannon, 1999; Szwczak *et al.*, 2011). We grouped bat passes into species groups for *Lasiurus borealis*/*L. seminolus*, *Eptesicus fuscus*/*Lasionycteris noctivagans*, and *Myotis austroriparius*/*M. septentrionalis* due to overlap in acoustic call characteristics between these species (Grider *et al.*, 2016; Johnson & Chambers, 2017; Kunberger & Long, 2022).

### Habitat and landscape metrics

We measured three components of vegetation structure at each sampling point (Appendix S1: Table S2). First, we used a convex spherical densiometer (Forestry Suppliers Inc., Jackson, Mississippi, USA) to measure percent canopy

openness, which can be managed via planting density, by averaging measurements taken at the acoustic point and four additional locations in each cardinal direction 5 m from the point. Second, we characterized vegetation clutter, which can relate to forest management through mechanical, chemical, and prescribed burning practices, using methods based on Nudds (1977) and modified by Bender *et al.* (2015). To do so, we estimated average percent coverage of a 1 m<sup>2</sup> panel raised 4.5 m above the ground and 5 m from the acoustic point in each cardinal direction and in the direction the microphone was oriented. Third, we used a 10-factor prism (Husch, Beers, & Kershaw, 2003) centered at the acoustic detector point to estimate basal area (m<sup>2</sup> ha<sup>-1</sup>) of overstory trees, which again can relate to planting density, thinning, and other forest management activities.

We used ArcGIS Pro and Fragstats v4.2 (McGarigal *et al.*, 2015) to calculate landscape metrics from landowner-provided and publicly available data (Appendix S1: Table S2). Although variables at this scale cannot be managed directly, they may be important for managers to consider when implementing landscape-scale planning. We measured proportions of forest and wetland cover types and determined total edge (m) as landscape composition metrics within a 450-m-radius circular buffer around sampling points. The 450-m buffer area represented the area that did not overlap with the buffers of neighboring sampling points. We defined edge as the boundary between any two of six cover types reclassified from the National Land Cover Database (Dewitz & U.S. Geological Survey, 2021). We grouped forest stands into growth stages (hereafter, stand age; 0–3 [early establishment], 4–7 [closing canopy], 8–13 [closed canopy, pre-thinned], 14–20 years [mid-rotation thinned], or 21+ years old [mature forest, semi-closed canopy; including streamside management zones/bottomland hardwood forests]) as it can relate to forest management activities (e.g., thinning, final harvest) and is easily interpreted by forest managers (Marshall *et al.*, 2022). Lastly, we measured distance (m) from sampling points to roads and permanent water using the Near tool in ArcGIS Pro.

## Multi-species modeling

We implemented the hierarchical multispecies spatial occupancy model developed by Doser *et al.* (2022). The hierarchical model, which consists of an ecological process model and an observation sub-model, accounts for residual species correlation in a joint species distribution model framework while considering imperfect detection. The model quantifies the probability of occupancy for each species by accounting for factors influencing detection (MacKenzie *et al.*, 2018). This hierarchical approach, in which species-specific effects are treated as random effects arising from a common community-level distribution, allows for inference of management effects on individual species and overall communities (Zipkin *et al.*, 2010). The ecological process model is  $z_i$ ,  $j$ , the true state of presence or absence of species  $i$  at sites  $j$ . Similar to Tikhonov *et al.* (2020), this model uses a spatial factor model along with Nearest Neighbor Gaussian

Processes (NNGP; Datta *et al.*, 2016) to ensure computational efficiency of species assemblages at different spatial locations. The observational sub-model (detection sub-model hereafter) separately models imperfect detection from the latent ecological process (see Doser, Finley, & Banerjee, 2022 for the modeling framework).

Occupancy covariates included a combination of site- (basal area, canopy openness, and vegetation clutter) and landscape-level (total forest, total wetland, total edge, distance to freshwater, distance to roads, and stand age). We expected the influence of covariates on bat species to differ depending on their foraging strategy (Appendix S1: Table S2). Detection covariates included basal area, temperature at sunset, vegetation clutter, and year. We standardized all continuous covariates for both ecological and survey processes to a mean of 0 and a standard deviation equal to 1 (Zipkin, DeWan, & Royle, 2009; Kéry & Royle, 2015). We tested for correlation among continuous predictor variables using Pearson's correlation coefficient to ensure that highly correlated ( $r \geq |0.7|$ ) variables were not included in the same model.

We fit our models using Polya-Gamma data augmentation (Polson, Scott, & Windle, 2013) for computational efficiency in R version 4.4.1 (R Core Team, 2020) via package spOccupancy (function sfMsPOcc; Doser, Finley, & Banerjee, 2022). Accommodating sources of spatial dependence among observations is key to obtaining valid inferences about species occupancy (Doser, Finley, & Banerjee, 2022), thus we fit a spatial factor model to control for spatial correlations and residual spatial variation in species occurrence. We implemented spatial models using three replicate Markov chain Monte Carlo (MCMC) iterations to generate 10 000 samples from the posterior distribution of each model after discarding a “burn-in” of 5 000 samples, with a thinning rate of 50. We selected an exponential covariance to model spatial dependence structure among observations (Banerjee, Carlin, & Gelfand, 2014). We estimated model parameters and community summaries, setting default vague prior hyperparameter values: *hypermeans* to 0 and *hypervariances* to 2.72 (Banerjee, Carlin, & Gelfand, 2014) in Normal priors, and scale and shape parameters to 0.1 (Lunn *et al.*, 2013) in inverse-Gamma priors. To control spatial autocorrelation, the spatial decay  $\phi$  for each latent factor followed a uniform *Unif* (0, 10) distribution. We determined model convergence of Markov chains using R-hat statistic values (<1.1) for all parameters within the models (Brooks & Gelman, 1998). We used the Widely Applicable Information Criterion (WAIC; Watanabe, 2010) to compare our set of models and shortlist the best-performing models, with models with a  $\Delta$ WAIC < 2 being biologically plausible and relevant. To evaluate detection covariates, we constructed models of single and all possible additive combinations of variables and compared them by including an occupancy sub-model with only the spatial structure, and no covariates. Temperature at sunset was the top-ranked detection model (Appendix S1: Table S3) and was subsequently included as the only covariate in the detection sub-model. We then developed 25 spatial models that included single and additive combinations of covariates,

along with null and global models, in the occupancy sub-models and temperature at sunset in the detection sub-model (Appendix S1: Table S4). We calculated posterior mean and standard deviation of the model coefficients with 95% Bayesian credible intervals (BCI). Parameter estimates of covariates with BCI that did not cross 0 were considered important predictors of species occupancy, as this was reflective of a consistent relationship within model iterations. However, we also considered covariates as biologically meaningful if estimated 75% BCIs did not overlap zero, although the 95% BCIs overlapped zero (Cumming & Finch, 2005; Nakagawa & Cuthill, 2007; Tilker et al., 2020). We computed Bayesian *P*-values with Freeman-Tukey statistic to assess model fit, where a model with a good fit to the data had a value near 0.5, while values <0.1 or >0.9 suggested poor model fit (Gelman, Meng, & Stern, 1996; Hobbs & Hooten, 2015).

## Results

We identified 26 650 bat passes and detected bats at 93% (224/240) of sampling points across all study areas during 738 detector nights. We detected 5 species and 3 species groups: *Dasypterus intermedius*, *L. cinereus*, *Nycticeius humeralis*, *Perimyotis subflavus*, *Tadarida brasiliensis*, *E. fuscus/L. noctivagans*, *L. borealis/L. seminolus*, and *M. austroriparius/M. septentrionalis*. All species were detected at all study sites except *T. brasiliensis*, which was not detected in South Carolina. The most frequently detected species was *L. cinereus* (177/240), followed by *L. borealis/L. seminolus* (156/240) and *E. fuscus/L. noctivagans* (122/240). *Dasypterus intermedius* was detected at the fewest number of sampling sites (70/240) (Table 1).

Our model selection supported a single model (Table 2). Under the supported model, basal area was an important site-level predictor of bat occupancy, with negative effects on the bat community (Fig. 2, Appendix S1: Table S5) and all species except for *M. austroriparius/M. septentrionalis* (Fig. 3, Appendix S1: Table S6). Posterior probability distributions (95% BCIs) of *L. borealis/L. seminolus*, *N. humeralis*, and *T. brasiliensis* did not overlap zero. We observed biologically meaningful (75% BCIs that did not include 0) influences of basal area on occupancy of *E. fuscus/L. noctivagans*, *L. cinereus*, *D. intermedius*, and *P. subflavus*. At the landscape level, total forest and distance to roads were biologically meaningful, positively affecting the bat community (Fig. 2). Total forest also positively influenced occupancy of several species, being an important predictor for *E. fuscus/L. noctivagans* and biologically meaningful for *L. borealis/L. seminolus*, *N. humeralis*, and *P. subflavus* (Fig. 3). Distance to roads was a biologically meaningful predictor of occupancy with positive relationships for *D. intermedius*, *L. cinereus*, and *M. austroriparius/M. septentrionalis*. Three covariates that were not influential at the community level influenced occupancy of individual species/groups (Fig. 3, Appendix S1: Table S6). Distance to water had a positive influence on occupancy of *E. fuscus/L. noctivagans* and was biologically meaningful for *L. cinereus*. Total wetlands were

**Table 1** Summary of bat species ecomorphological characteristics, foraging strategies, and number of sampling sites (out of 240 total) where bats were detected during winter acoustic surveys in working forest landscapes of the southeastern United States Coastal Plain, 2020–2022

Phonic group	Species	Total sites detected	Foraging strategy
Low group $F_c > 30$ kHz duration >5 ms	<i>Dasypterus intermedius</i>	70	Open-space aerial foragers
	<i>Eptesicus fuscus/Lasionycteris noctivagans</i>	122	Open and edge-space aerial foragers
	<i>Lasiurus cinereus</i>	177	Open-space aerial foragers
	<i>Tadarida brasiliensis</i>	110	Open-space aerial foragers
Mid group $F_c$ 30–45 kHz duration >5 ms	<i>Lasiurus borealis/L. seminolus</i>	156	Edge-space aerial foragers
	<i>Nycticeius humeralis</i>	115	Edge-space aerial foragers
	<i>Perimyotis subflavus</i>	106	Edge-space aerial foragers
	<i>Myotis</i>	103	Narrow-space, aerial-gleaning forager
Myotis group $F_c > 40$ kHz duration < 5 ms	<i>Myotis austroriparius/M. septentrionalis</i>	103	Narrow-space, aerial-gleaning forager

Foraging strategies follow Norberg & Rayner (1987) and Denzinger & Schnitzler (2013).  $F_c$  is the characteristic frequency (kHz) at the lowest slope toward the end of the call or the lowest frequency for consistent FM sweeps. Duration is the call duration (ms) from the beginning to end

a biologically meaningful predictor of *E. fuscus/L. noctivagans*, negatively affecting occupancy. Lastly, total edge was biologically meaningful and negatively affected occupancy of *M. austroriparius/M. septentrionalis*. Temperature at sunset, the only covariate included in the detection sub-model, was an important predictor of detection at both the community (Appendix S1: Table S5) and species-specific levels (Appendix S1: Table S6), positively affecting both mean species detection and individual bat species.

## Discussion

Our results add to the sparse literature regarding winter habitat associations for bats in working forest landscapes in the southeastern United States Coastal Plain. Like previous work conducted during summer, we found winter bat community richness and occupancy for most individual species/groups were positively associated with forest management practices that promote open canopy conditions. Forest thinning is a common mid-rotation management practice during which trees are selectively removed (thereby reducing basal area) to allocate resources to remaining trees (Verschuyl et al., 2011). Consequently, thinning promotes bat activity in mid-rotation stands by creating open space below the canopy for foraging. Furthermore, we found areas surrounded by a greater

**Table 2** Effective number of parameters (pD), Widely Applicable Information Criterion (WAIC), and difference in WAIC value between the model and the model with the lowest value ( $\Delta$ WAIC) for the top 5 models of bat community occupancy ( $\psi$ ) and detection probability ( $p$ ) during winter 2020–2022 in working forest landscapes of the southeastern United States Coastal Plain

Model	pD	WAIC	$\Delta$ WAIC
$\psi$ (basal area + distance road + distance water + total edge + total forest + total wetland), $p$ (temperature)	243.34	5597.86	0.00
$\psi$ (basal area + clutter + distance road + distance water + total edge + total forest + total wetland), $p$ (temperature)	249.98	5606.01	8.15
$\psi$ (basal area + clutter + distance road + distance water + stand class + total edge + total forest + total wetland), $p$ (temperature)	259.32	5610.25	12.39
$\psi$ (distance water + total forest + total wetland), $p$ (temperature)	242.76	5614.89	17.03
$\psi$ (total wetland), $p$ (temperature)	237.79	5616.69	18.83

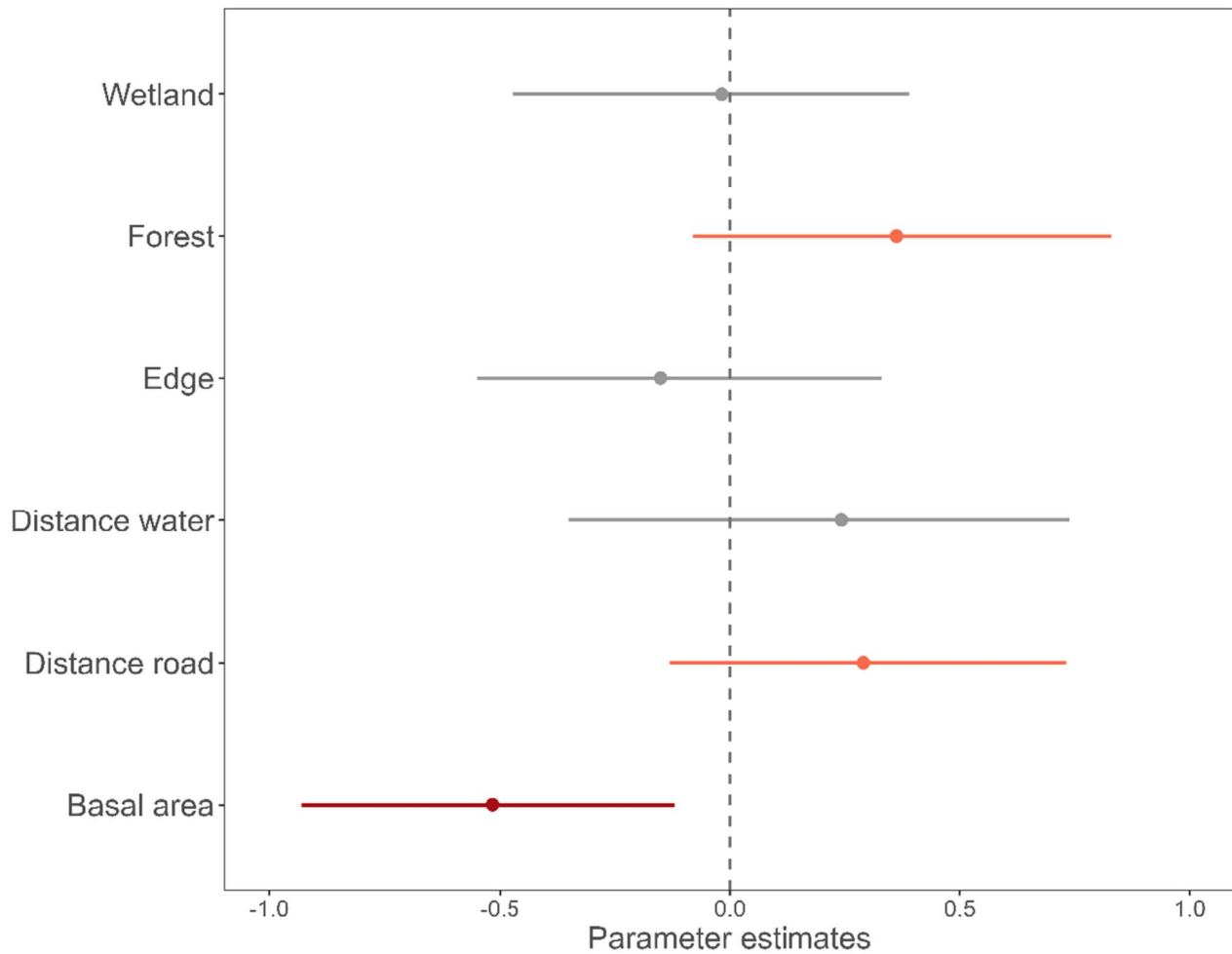
proportion of forest increased community and species occupancy. The primary objective of most working forest owners and managers is to provide a continuous, sustainable supply of wood products (Miller, Wigley, & Miller, 2009). As a result, working landscapes are comprised of forests of various ages and structural conditions, but with contiguous forests as the predominant land cover. Thus, consistent with results from summer studies (Loeb & O’Keefe, 2006; Brigham, 2007; Bender *et al.*, 2015), our results indicate that standard management practices in working forests also provide suitable forest conditions for bats during winter.

Vegetation structure, specifically basal area, negatively influenced community richness and occupancy of most species. While information regarding the effects of vegetation structure on bat community richness in working Coastal Plain forests is limited, higher levels of basal area negatively influencing communities have previously been observed for phonic groups (i.e., categorization of species with similar ecomorphological characteristics based on similar call frequency; Beilke, Blakey, & O’Keefe, 2021; Gallagher *et al.*, 2021). For example, summer occupancy probability was negatively related to increased basal area for all phonic groups on managed forest lands in the northeastern United States, regardless of their foraging strategies (Gallagher *et al.*, 2021). Negative responses of bats to increased basal area typically are attributed to reduced flight ability and greater difficulty detecting insect prey (Meyer, Schwarz, & Fahr, 2004; Bender *et al.*, 2021). Although insect abundance, along with vegetation characteristics, is an important predictor of bat activity during summer in Coastal Plain regions (Moore & Best, 2018; Bender *et al.*, 2021), in winter, when temperatures are lower, bats may restrict foraging to areas

where insects are present (Shute, Loeb, & Jachowski, 2021). In addition to seasonal changes in foraging, bat activity in forests is mainly determined by the interaction between flight accessibility and prey availability, whereas in open spaces such as forest gaps, prey availability is the primary factor driving activity (Adams, Law, & French, 2009; Tiago Marques, Ramos Pereira, & Palmeirim, 2016; Tena *et al.*, 2020; Erasmy *et al.*, 2021). In contrast, the *M. austroriparius*/*M. septentrionalis* species group was not affected by higher levels of basal area. The *Myotis* species we documented are clutter-adapted and thus likely exhibit flexibility in their foraging strategy inside of forests (Norberg & Rayner, 1987; Henderson & Broders, 2008; Beilke, Blakey, & O’Keefe, 2021).

The relationship between summer bat activity and forest composition (i.e., proportion of forest and wetlands) in the southeastern United States Coastal Plain is well established (Hein, Castleberry, & Miller, 2009; Bender *et al.*, 2015; Taylor *et al.*, 2020). Importantly, our study demonstrated similar associations between occupancy and prevalence of forested landcover during winter, even for species in different foraging guilds. Greater species richness within larger forest patches is not surprising as all bat species in the region use forests for roosting and/or foraging (Brigham, 2007; Taylor *et al.*, 2020). Consequently, we found occupancy of several species associated with higher forest cover. Positive occupancy probabilities for *L. borealis*/*L. seminolus* and *P. subflavus* at sites with higher proportions of forests were expected as these species typically forage along edges adjacent to forests or within forest gaps (Dixon, 2011; Schimpp, Li, & Kalcounis-Rueppell, 2018; Beilke, Haulton, & O’Keefe, 2023). Although little is known about *L. noctivagans* foraging habitat selection, the positive relationship between occupancy of *N. humeralis* and *E. fuscus* and proportion of forest we observed, supports previous studies which reported *N. humeralis* and *E. fuscus* using forested areas interspersed with edges and open areas (Duchamp, Sparks, & Whitaker Jr, 2004; Johnson, Gates, & Ford, 2008; Schimpp, Li, & Kalcounis-Rueppell, 2018; Andersen *et al.*, 2022). The lack of a relationship with wetlands observed for most species and lower occupancy of *E. fuscus*/*L. noctivagans* was surprising as most studies have demonstrated positive relationships (Mas *et al.*, 2021). Our results may be related to the structural conditions of wetlands in our study areas, which were primarily forested wetlands as opposed to open-water wetlands. Similarly, Andersen *et al.* (2022) observed that bat activity was negatively related to forested wetlands in Coastal Plain working forests during winter. Although bats may forage along the edges, high basal area within forested wetlands likely decreases the probability of occupancy for open/edge space foragers like *E. fuscus*/*L. noctivagans*.

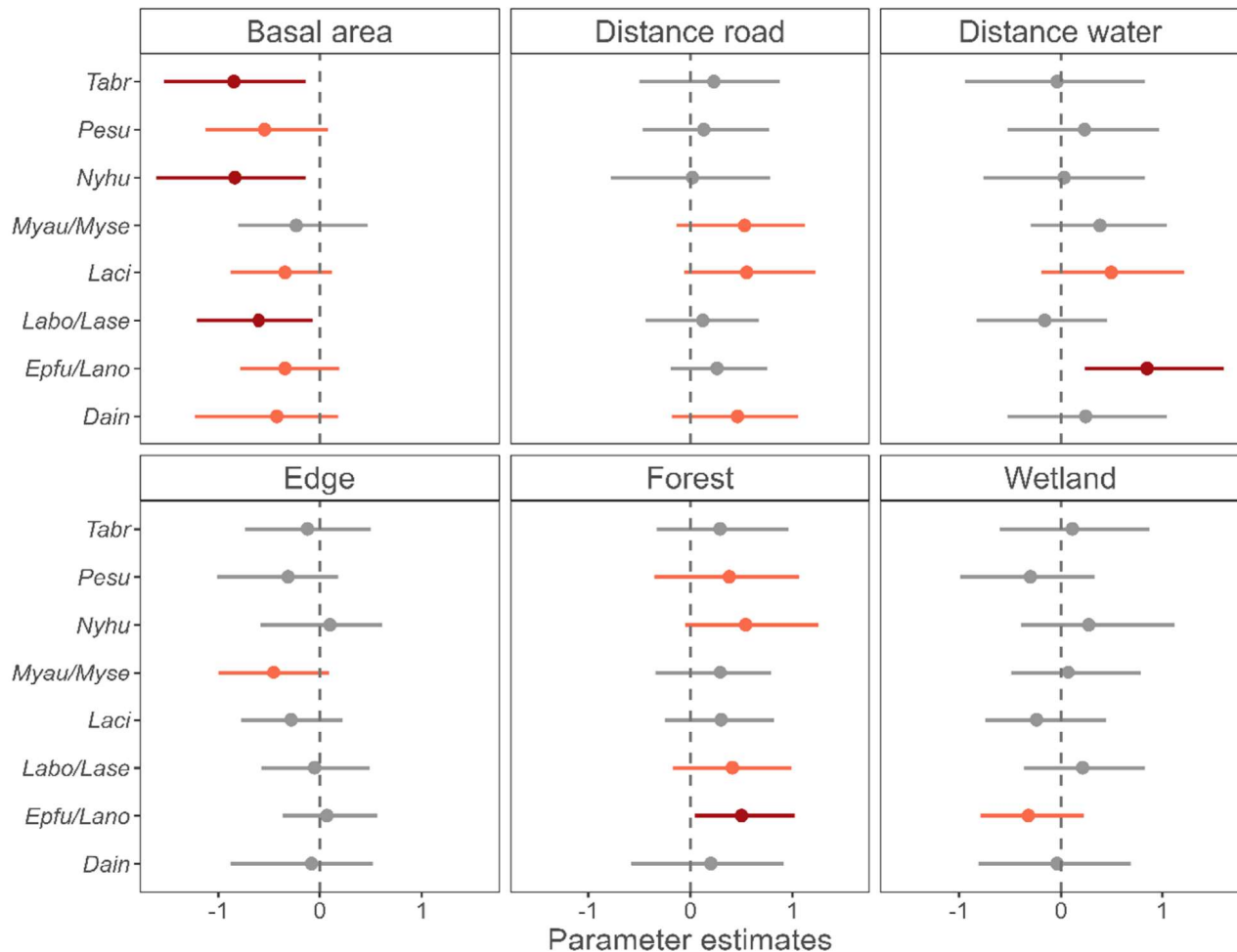
Distance to freshwater is often important in bat habitat selection (e.g., Ford *et al.*, 2005; Rainho & Palmeirim, 2011; Janzen & Fenton, 2013), but we found no relationship with bat occupancy at the community level and few at the species level. Where we did find species-level relationships (*E. fuscus*/*L. noctivagans* and *L. cinereus*), they were contrary to



**Figure 2** Mean beta coefficients for bat community-level occupancy in working forest landscapes of the southeastern United States Coastal Plain winter 2020–22, estimated with a spatial community occupancy model fit to acoustic detector data. Gray bars show relationships in which the 75% Bayesian credible interval (BCI) overlaps zero, orange bars indicate that the 75% BCI does not overlap zero but the 95% BCI does overlap zero, and red bars indicate that the 95% BCI does not overlap zero.

our expectations and from previous studies during summer that found higher bat activity closer to water (e.g., Kalcounis-Rüppell, Psyllakis, & Brigham, 2005; Ford *et al.*, 2006; Ancillotto *et al.*, 2019). Water availability is typically high in the southeastern Coastal Plain, due to high annual rainfall, especially during winter (Bosch, Sheridan, & Davis, 1999), and therefore may not be a limiting factor for bats. Additionally, due to lower rates of evaporative water loss than in summer (Cryan & Wolf, 2003), frequent access to water may be less important for bats during winter. Furthermore, bats commonly feed on emergent insects over water in summer, but insect availability typically is lower during winter (Corbet, 1964). Alternatively, due to the difficulty of mapping small and often ephemeral freshwater sources, our analysis only included water sources from available spatial data layers, which could have hindered our ability to detect relationships and gave us results contrary to those expected (Bender *et al.*, 2015; Perea, Morris, & Castleberry, 2022).

Although distance to roads increased probability of occupancy at the community level, the relationship was inconsistent among species. Unimproved roads like those in working forests likely do not represent fragmentation to bats, but often separate stands of different ages and structural characteristics. Thus, we contend that roads serve as an indicator of fragmentation despite there being continuous forest cover. Positive occupancy probabilities with distance to roads for *M. austroriparius*/*M. septentrionalis* is consistent with the well-documented preference for continuous mature stands for both foraging and roosting and avoidance of fragmented forests (*M. septentrionalis*: Henderson & Broders, 2008), typical of clutter-adapted species (Denzinger & Schnitzler, 2013; Beilke, Blakey, & O’Keefe, 2021). In contrast, the observed positive response for *D. intermedius* and *L. cinereus*, two of the largest bat species in North America, is not intuitive but may be associated with their ecomorphological characteristics as open-space foraging species (Norberg & Rayner, 1987; Denzinger & Schnitzler, 2013). As open-space foragers



**Figure 3** Mean beta coefficients for bat species-level occupancy in working forest landscapes of the southeastern United States Coastal Plain winter 2020–22, estimated with a spatial community occupancy model fit to acoustic detector data. Gray bars show relationships in which the 75% Bayesian credible interval (BCI) overlaps zero, orange bars indicate that the 75% BCI does not overlap zero but the 95% BCI does overlap zero, and red bars indicate that the 95% BCI does not overlap zero. Species codes: *Lasiurus cinereus* (*Laci*), *Dasypterus intermedius* (*Dain*), *Eptesicus fuscus*/*Lasionycteris noctivagans* (*Epfu/Lano*), *Lasiurus borealis*/*Lasiurus seminolus* (*Labo/Lase*), *Myotis austroriparius*/*Myotis septentrionalis* (*Myau/Myse*), *Nycticeius humeralis* (*Nyhu*), *Perimyotis subflavus* (*Pesu*), and *Tadarida brasiliensis* (*Tabr*).

(Veilleux *et al.*, 2009; Shute, Loeb, & Jachowski, 2021; Perea, Morris, & Castleberry, 2022), *D. intermedius* and *L. cinereus* forage above the canopy and in large canopy openings across the landscape likely without regard to roads. Thus, the observed relationship may be merely a result of greater area in interior forest compared to roads increasing the likelihood of foraging in areas farther from roads. However, further studies are needed to investigate how forest gaps and openings in mature forests are used by open-space foraging species (Loeb & O’Keefe, 2011; Tena *et al.*, 2020).

Previous summer studies have generally found positive associations between bat activity and edge regardless of species’ ecomorphological characteristics (Morris, Miller, & Kalcounis-Rueppell, 2010; Janzen & Fenton, 2013). However, in our winter study, occupancy of the community and all but one species/group was not associated with edge. Consistent with previous studies, we observed a negative

relationship between occupancy probability and edge for *M. austroriparius*/*M. septentrionalis*, species that commonly forage within forest stands and avoid edges (Henderson & Broders, 2008; Morris, Miller, & Kalcounis-Rueppell, 2010). However, the varying and equivocal relationships between edge and other bat species were counter to our expectations. Based on wing morphology and echolocation call characteristics *L. borealis*/*L. seminolus*, *N. humeralis*, and *P. subflavus* are predicted to be edge foragers, which has been demonstrated in previous studies (Norberg & Rayner, 1987; Morris, Miller, & Kalcounis-Rueppell, 2010). Use of edges for foraging is typically attributed to avoidance of vegetation clutter and greater insect abundance (Morris, Miller, & Kalcounis-Rueppell, 2010). In one of the few studies that examined bat foraging habitat use in winter, Shute, Loeb, & Jachowski (2021) observed that vegetation characteristics related to *P. subflavus* occupancy changed from summer to



winter possibly in response to temporal and spatial changes in prey availability or environmental conditions. Because we also found these species/groups associated with higher forest cover, we suggest that species considered edge foragers in summer may restrict activity to areas with higher prey availability or more suitable environmental conditions during winter (Shute, Loeb, & Jachowski, 2021).

Based on results of previous summer studies, we expected canopy openness, vegetation clutter, and stand age to influence bat occupancy during winter, but none were included in our top model. Although basal area and canopy openness were not strongly correlated, we chose not to include them in the same models because forest management affects them simultaneously (e.g., thinning reduces basal area and increases canopy openness). Previous studies have demonstrated a negative relationship between bat activity and canopy cover (Ford *et al.*, 2005; Froidevaux *et al.*, 2016), but those studies were not in working forests and were conducted during summer. In one of the few studies conducted in working forests during winter, Andersen *et al.* (2022) found that canopy cover did not influence bat activity. Although the reason is uncertain, it appears that basal area has a greater influence on bat occupancy than canopy openness during winter. Stand age likely was not an important predictor of occupancy because bats can forage within or above all stand ages in working forests. Pre-thinned pine stands ( $\leq 13$  years) are closed canopy with little uncluttered space for bats to forage. As a result, the bats we detected in those stands were foraging above the canopy. Once stands are thinned ( $\sim 14$  years), basal area is reduced allowing efficient foraging conditions within and below the canopy (Verschuyl *et al.*, 2011). The reduction in basal area associated with thinning apparently outweighed the influence of stand age. The lack of influence of vegetation clutter was surprising as most studies have demonstrated a negative response (Loeb & O'Keefe, 2006; Loeb & Waldrop, 2008; Bender *et al.*, 2015) but was likely due to management prescriptions in working forests. Following thinning, stands typically are managed with herbicides and/or prescribed fire to reduce competing trees in the midstory (Greene *et al.*, 2016), which consequently reduces vegetation clutter, allowing efficient foraging conditions for bats (Verschuyl *et al.*, 2011). Thus, the reduced basal area and subsequent midstory vegetation control associated with thinning in working forests appeared to diminish the influence of clutter in our study.

We found that temperature was an important factor in explaining detectability at the community and species levels, which should be considered when conducting winter bat studies. Our findings are consistent with previous studies assessing the influence of environmental conditions on bat activity (Brooks, 2009; Bender & Hartman, 2015; Parker, Li, & Kalcounis-Rueppell, 2020; Barros *et al.*, 2021). In temperate regions, winter temperatures can fluctuate weekly, or even daily, causing bats to enter short-term torpor bouts (Johnson *et al.*, 2012; Meierhofer *et al.*, 2019). Winter bat activity in the southeastern United States Coastal Plain is strongly influenced by temperature (Parker, Li, & Kalcounis-Rueppell, 2020). Grider *et al.* (2016) observed that

differences in mean nighttime temperature of  $\sim 1.5^{\circ}\text{C}$  influenced winter bat activity in North Carolina. In addition, temperature also affects availability of insect prey (Welti *et al.*, 2022), as it must be warm enough for insect prey to remain active. Thus, low temperatures negatively affect the probability of detecting bats during winter, which may limit our ability to obtain unbiased occupancy estimates if temperature is not considered. However, it is important to note that although our study confirms that temperature significantly influences bat detection, other possible environmental factors (e.g., humidity or atmospheric pressure) should be considered in future work.

Our results provide new insights into bat ecology in working forest landscapes during winter, where we highlight similar responses to site and landscape covariates as previous summer work. Although bat species' richness generally does not change throughout the year, occupancy can change for some species. For example, we observed drastically higher occupancy for *L. cinereus* when compared to a similar study conducted in the Coastal Plain during summer (Bender *et al.*, 2015). We consider these results of particular importance, as management decisions based on data collected during summer may positively support bat communities during winter. As previously observed during summer, promoting forests with low levels of basal area will increase occupancy at both the community and species levels. While forest thinning reduces basal area in mid-rotation stands promoting efficient foraging, the influence of low basal area was also supported in young pine stands, as we frequently recorded bats foraging over the canopy. Our study is one of the few that considers imperfect detection while controlling for spatial autocorrelation and residual correlation among bat species (Browning *et al.*, 2022), which provides robust estimates of occupancy and richness of wintering bats. Our results will inform managers of vegetation characteristics important to wintering bats, thereby increasing knowledge of wintering bat foraging ecology and conservation opportunities within working forests.

## Acknowledgments

This work was supported by the National Council of Air and Stream Improvement, Inc. and the University of Georgia, D. B. Warnell School of Forestry and Natural Resources. We thank Weyerhaeuser Company, Resource Management Service, and The Westervelt Company for logistical support. We thank Stephen Todd, Blake Ledbetter, Jeremy Vandenberg, Brandi Stevenson, and Jade Samples for assistance with data collection. We thank Dr. Cecil Jennings, Dr. Kamal J. K. Gandhi, and Dr. Darren Miller for comments and suggestions in early versions of this work. Finally, we want to thank the editor and reviewers that considerably improved this paper.

## Author contributions

SP, ALG, DG, SBC, and CD conceived the ideas and designed methodology; SP collected the data; SP, GF, and RC analyzed the data; SP and SBC led the writing of the

manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## Conflict of interest statement

The authors declare no conflict of interest.

## Data availability statement

Data collected on or derived from data collected on privately owned properties are sensitive and cannot be provided publicly. We will provide publicly available data and code on Dryad.

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## Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table S1.** Anabat Swift acoustic detectors with omnidirectional ultrasonic microphones US-OV2 and US-OV3 (Titley Electronics, Ballina, New South Wales, Australia) settings.

**Table S2.** Variable names, descriptions, and hypotheses (including predicted effect for each phonic group) for site- and landscape-scale habitat variables used as covariates in bat occupancy analysis during winter 2020–2022 in working forest landscapes of the southeastern United States Coastal Plain.

**Table S3.** Confidence set of 5 best-preselected detection sub-models ( $P$ ) with a null occupancy ( $\psi$ ) term, including the effective number of parameters ( $pD$ ), WAIC, and  $\Delta$ WAIC during winter 2020–2022 in working forest landscapes of the southeastern United States Coastal Plain.

**Table S4.** Models evaluated to examine bat community

occupancy ( $\psi$ ) and detection probability ( $P$ ) during winter 2020–2022 in working forest landscapes of the southeastern United States Coastal Plain. Models are ranked by WAIC value.

**Table S5.** Community mean coefficient estimates (posterior means with standard deviation (SD) and 95% Bayesian credible intervals (BCI)) of the best-supported model used to predict bat occupancy ( $\psi$ ) and detectability ( $p$ ) in working

forest landscapes of the southeastern United States Coastal Plain winter 2020–2022.

**Table S6.** Summary of species-specific parameter coefficients for occupancy ( $\psi$ ) and detection ( $p$ ) covariates for eight bat species/species groups detected during winter acoustic surveys in working forest landscapes of the southeastern United States Coastal Plain, 2020–2022.