



Site occupancy of foraging bats on landscapes of managed pine forest



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ABSTRACT

The ability to fully evaluate potential relationships between forest management and bats is limited without information from relevant spatial scales. Further, knowledge of bat ecology in intensively managed forests is fairly limited even though these forests are a substantial portion of the forested landscape in the southeastern U.S. Therefore, we used occupancy models to examine influence of small-scale vegetation characteristics and large-scale spatial features on foraging patterns of bats within 6 managed-pine (*Pinus* spp.) forest landscapes in the southeastern U.S. Coastal Plain. We conducted repeated acoustic surveys to determine species presence/non-detection and evaluated a priori models relating detection probability and occupancy to site- and landscape-level metrics for 6 species/genera. Detection of big brown (*Eptesicus fuscus*) and eastern red (*Lasiurus borealis*)/Seminole (*L. seminolus*) bats (eastern red and Seminole bats combined) decreased with increasing basal area, and detection of big brown and Brazilian free-tailed bats (*Tadarida brasiliensis*) increased over the summer sampling period. Relationships between occupancy and habitat metrics were species-specific but consistent with previous studies. Occupancy for most bat species was lower at sampling sites with higher vegetation clutter and higher basal area. In contrast to most previous studies, occupancy of all bat species investigated was unrelated to or negatively influenced by distance to water. Although site- and landscape-level features influenced occupancy, our results indicate that site-specific features (vegetation clutter and basal area) influenced most species. Therefore, stand-level management activities that decrease vegetation structure, such as thinning intermediate-aged stands and/or controlling midstory vegetation (e.g., fire or herbicide applications), likely will maintain or increase suitability of managed pine forest stands and landscapes for many bat species in the southeastern Coastal Plain. The forest mosaics that we sampled, consisting primarily of managed pine stands intermingled with non-production habitat types, supported a large proportion of the bat community associated with forests of the Coastal Plain which suggests the compatibility of timber production and bat conservation objectives.

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1. Introduction

Forests are important to virtually all North American bat species and many use forests exclusively to fulfill life history requirements (Miller et al., 2003). Alteration of forest structure through forest management practices may enhance foraging habitat for some bat species thereby reducing it for others (Aldridge and Rautenbach, 1987; Patriquin and Barclay, 2003), making management decisions that benefit entire bat communities challenging. Differences in morphology and echolocation call structure among bats suggest that species are adapted to small-scale (within stand),

structural habitat features (Aldridge and Rautenbach, 1987; Brigham et al., 1997). However, bats are capable of commuting among habitat patches across the landscape (Bernard and Fenton, 2003) and likely perceive habitat conditions at large spatial scales (Zimmerman and Glanz, 2000). Because effects of forest management on bat foraging ecology are scale-dependent (Grindal and Brigham, 1999), simultaneous consideration of small- and large-scale habitat features is necessary when evaluating potential management effects (Erickson and West, 2003; Zimmerman and Glanz, 2000).

Small-scale habitat use by foraging bats is often attributed to amount of structural complexity (i.e., clutter; Brigham et al., 1997; Ford et al., 2005; Loeb and O'Keefe, 2006; Sleep and Brigham, 2003). The degree to which bats use cluttered habitat types is related to bat morphology, including body mass, wing

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loading, wing aspect ratio, and echolocation call characteristics (Aldridge and Rautenbach, 1987). In general, smaller species are better adapted to foraging in cluttered forest conditions (Sleep and Brigham, 2003) whereas larger bats often forage over the forest canopy (Menzel et al., 2005) or in forest openings (Ford et al., 2006; Menzel et al., 2005). Increased bat activity in areas of reduced vegetation structure has been documented in a variety of forested landscapes (Erickson and West, 2003; Ford et al., 2006; Humes et al., 1999; Loeb and O'Keefe, 2006; Loeb and Waldrop, 2008; Yates and Muzika, 2006). In intensively managed forests, vegetation structure is determined by a variety of factors including stand age, tree spacing, and midstory management (Guldin et al., 2007) which are influenced by stand-level silvicultural treatments (Wigley et al., 2007). Thus, with proper planning and consideration, forest management practices can improve conditions for foraging bats within landowner's management and economic constraints (Wigley et al., 2007).

Results of previous studies have generally concluded that landscape characteristics, such as amount of forest cover, proximity to water, and edge, influence bat occupancy or foraging activity (Duff and Morrell, 2007; Ford et al., 2006; Grindal and Brigham, 1999; Walsh and Harris, 1996; Yates and Muzika, 2006). However, extent of influence and relevant landscape features are species-specific. Foraging and commuting activities of some species may be related to specific features (e.g., open water), whereas others conduct activities over a range of stand conditions (Brigham, 1991; Elmore et al., 2004; Yates and Muzika, 2006). Some studies have suggested that landscape characteristics and habitat mosaics have a greater influence on bat habitat use in intensively-managed landscapes because of potential for reduced small-scale heterogeneity due to even-aged management of forest stands (Erickson and West, 2003; Ford et al., 2006; Miles et al., 2006). Under homogeneous forest conditions, foraging bats may have to travel farther from roost sites to find suitable foraging conditions. Additionally, managed forests may have lower roost availability for some species (Miles et al., 2006) which can influence foraging habitat selection (Crampton and Barclay, 1998).

Conducting foraging studies on bats is difficult because of their small size, vagility, and nocturnal nature (Duff and Morrell, 2007). Because radiotelemetry is expensive and logistically challenging, most studies examining habitat use by foraging bats rely on acoustic methods (Morris et al., 2011b). Morris et al. (2011b) cautioned against using acoustic methods to infer habitat selection at larger spatial scales because bat echolocation calls are more likely to be recorded (i.e., detected) in habitat types where bats echolocate more (e.g., those used for foraging) than in those where they echolocate less (e.g., those used for roosting). The resulting false absences (species is present but not detected; MacKenzie, 2005) may influence results and inferences unless accounted for in analyses (Gu and Swihart, 2004). Because bats are imperfectly detected and detection may be influenced by habitat characteristics, occupancy modeling has recently been applied to acoustic surveys for bats (Amelon, 2007; Gorreson et al., 2008; Hein et al., 2009; Weller and Baldwin, 2012; Yates and Muzika, 2006). Occupancy modeling allows simultaneous investigation of factors influencing occupancy and detection probabilities, improving the ability to make inferences about species use of landscape features (MacKenzie et al., 2002; MacKenzie, 2005).

Intensively managed pine (*Pinus* spp.) forests covers >12 million ha in the southeastern U.S. (Smith et al., 2009). Owners of managed forest lands are increasingly committed to conserving biodiversity as evidenced by voluntary enrollment in sustainable forestry certification programs which include biodiversity principles (Wigley et al., 2007). However, limited data on selection of foraging habitat in managed forest landscapes hinders our ability to evaluate management decisions that may influence bats. Therefore, we used

occupancy modeling to examine influence of site- and landscape-level characteristics on foraging bats in managed pine landscapes of the southeastern U.S. Coastal Plain. Elucidating factors influencing foraging habitat selection will complement existing limited data on foraging and roosting habitat selection in managed pine landscapes, allowing for more informed management decisions to maximize benefit to bat communities.

2. Methods

2.1. Study sites

We conducted our study on 6 intensively-managed forest landscapes in corporate ownership/management across five states (Butler Co., Alabama (Site AL); Ashley Co., Arkansas (Site AR); Decatur Co., Georgia (reference site in detection models); Brunswick (Site NC-1) and Beaufort/Martin Cos. (Site NC-2), North Carolina; Charleston and Dorchester Cos., South Carolina (Site SC) in the Coastal Plain of the southeastern U.S. The southeastern Coastal Plain is generally characterized by flat topography and sandy soils. Soils of the region are highly variable in the amount of organic matter and permeability (Hubbard et al., 2004) resulting in a diverse regional vegetation community. However, forests dominate the regional land cover and agriculture is the primary land use on non-forest lands within this physiographic region (Hubbard et al., 2004; Wear and Greis, 2002).

Our study landscapes consisted primarily of planted loblolly pine (*Pinus taeda*) forests interspersed with streamside management zones and other inclusions dominated by mature (>40 yrs old) hardwoods or mixed pine-hardwoods. Although specific management at study sites varied by individual landowner, typical management of planted pine forests included clear-cutting at 20–35 yrs, mechanical and/or chemical site preparation, and planting 1–2-yr-old nursery stock in raised beds at 182–283 trees/ha. Competing vegetation was temporarily suppressed through herbicide application (banded or broadcast spraying) the first growing season after stand establishment and potentially later during early- and mid-rotation, and most stands were commercially thinned at least once. All landowners were participating in a forest certification program (Guynn et al., 2004).

2.2. Acoustic detection and call classification

We conducted acoustic surveys at our study landscapes from May–August, 2007–2008. Bats were surveyed at 22–36 sample points on each landscape (mean = 26.3) once during the 2-yr study (3 sites/year) over an approximately 1-month period. Sample points were distributed across the landscape in a grid arrangement with 900 m between points. We selected a 900 m spacing to encompass a core area that constitutes much of an individual's foraging movements (Everson, 2005; Menzel et al., 2001a; Morris et al., 2011a; O'Donnell, 2001). Core foraging areas generally constitute a small percentage of an individual's home range (Morris et al., 2011a; O'Donnell, 2001; Zeale et al., 2012) and recent evidence suggests that home and core ranges are smaller in actively managed plantation forests than in landscapes where stands have not been harvested recently (Borkin and Parsons, 2014). Although spacing was consistent, grids were necessarily irregularly shaped because of the irregular shape of study sites. The order of sampling at each study site was based on proximity of sampling points, accessibility, and other logistical considerations to allow sampling multiple points each night. We generally conducted acoustic sampling for 2 consecutive nights to minimize temporal variability, but sampled additional nights opportunistically to improve occupancy and detection estimates.

We passively recorded bat echolocation calls using Anabat II detectors (Titley Scientific, East Brisbane, Australia) coupled with a zero-crossing interface module (ZCAIM) deployed at each sample point. We stored detector/ZCAIM combinations in waterproof plastic containers and placed them approximately 1.5 m above the forest floor on camera tripods. We directed microphones in the direction of least vegetation clutter, 45° from horizontal using a 5.1 cm PVC elbow (Weller and Zabel, 2002). We programmed detectors to begin sampling 30 min prior to sunset and end sampling 30 min after sunrise. Sunrise and sunset times were obtained from the U.S. Naval Observatory (accessible at <http://www.usno.navy.mil/USNO>) using the one year sunrise/sunset table for the nearest city or town. We did not sample during rain or strong wind. We randomly assigned detectors to sampling points to minimize equipment bias.

We considered 8 bat species/groups as potential residents of Coastal Plain forested landscapes based on published literature and our own captures. Our list of residents included big brown bat (*Eptesicus fuscus*), eastern red/Seminole bat group (*Lasiurus borealis* and *L. seminolus* combined; hereafter, red/Seminole bats), hoary bat (*L. cinereus*), evening bat (*Nycticeius humeralis*), tri-colored bat (*Perymyotis subflavus*), Rafinesque's big-eared bat (*Corynorhinus rafinesquii*), Brazilian free-tailed bat (*Tadarida brasiliensis*), and southeastern myotis (*Myotis austroriparius*). We used ANALOOK (v 4.9; Titley Scientific, East Brisbane, Australia) to create a custom filter to retain sequences containing ≥ 5 search phase calls following Britzke and Murray (2000). We used ANALOOK to extract 11 call parameters (O'Farrell et al., 2000) from retained files to increase objectivity and repeatability (Obrist et al., 2004). We used *k*-nearest neighbor (Buttrey and Karo, 2002) to quantitatively classify individual calls based on a reference library of calls from potential species. The *k*-nearest neighbor method is comparable in classification accuracy to alternative quantitative bat-call identification methods (Britzke et al., 2011) and produces posterior probabilities useful in evaluating classifications. Sequences recorded in the field that did not result in identification with a posterior classification probability ≥ 0.5 were eliminated.

2.3. Habitat and landscape metrics

We measured 3 components of vegetation structure at each sample point (Table 1). We measured percent canopy cover using a convex spherical densiometer (Ben Meadows Company, Janesville, Wisconsin, USA) by averaging measurements taken at the

acoustic sample point and 4 additional locations 5 m from the point in each cardinal direction. We estimated basal area (m^2/ha) of overstory trees using a 10-factor prism centered at the acoustic detector point. We characterized vegetation clutter using methods based on Nudds (1977) by estimating percent coverage of a 1- m^2 panel raised approximately 4.5 m above the ground and 4.5 m from the sample point in each cardinal direction and in the direction the acoustic detector was oriented.

We used ArcMap 9.3 (ESRI, Redlands, California, USA) and Fragstats (McGarigal et al., 2002) to calculate landscape metrics from owner-provided and publicly available data (Table 1). We corrected data when ground-truthing indicated discrepancies (i.e., updated age of stands to reflect recent harvests). We measured landscape composition metrics using a 450-m-radius circular buffer around sample points and landscape configuration metrics using Euclidean distances (m). The 450-m buffer area surrounding each sample point represented the area around each point that did not overlap with the buffers of neighboring sample points. Edge was defined as the boundary between any two of six habitat classes including nonforest (i.e., roads, wildlife openings, utility right-of-ways, etc.) and age-based forest classes (0–9, 10–19, 20–30, 30–40, >40 yrs old). We did not investigate influence of distance to edge because we were primarily interested in large-scale factors. Previous research indicates that distance to edge has only localized effects on foraging bats (Krusic et al., 1996) so we accounted for edge at the landscape scale by measuring total edge within the 450 m buffer around each sample point. Predictor variable values were rescaled for analysis by multiplying/dividing by multiples of 10 to ensure ranges of values for each predictor were similar in scale (Donovan and Hines, 2007).

2.4. Statistical analyses

We developed models containing occupancy covariates to evaluate a priori hypotheses about influence of landscape and site variables on bat occupancy probability while simultaneously accounting for imperfect detection. Although our analyses were in an occupancy modeling framework (and we use the term “occupancy” throughout), our results should be interpreted as use because species presence at each point was assumed to vary randomly within sample season (i.e., duration encompassing repeated sampling visits; MacKenzie et al., 2006).

We determined the most parsimonious detection model for each species prior to evaluating occupancy hypotheses to avoid evalua-

Table 1

Variable names, descriptions, and hypotheses (including predicted effect) for site- and landscape-scale habitat variables used as covariates in bat occupancy analysis on 6 managed pine forest study sites in the Coastal Plain of the southeastern U.S., 2007–2008.

Scale/variable	Description	Hypothesis
<i>Site</i>		
BA	Basal area (m^2/ha) at sampling point	Reduces foraging efficiency (–)
%clutter	Percent vegetation clutter at sampling point	Reduces foraging efficiency (–)
<i>Landscape</i>		
Water	Euclidean distance (km) to nearest permanent water	Foraging/drinking habitat (–)
%0–9	Percent stands 0–9 yrs old within 450-m buffers around sample points	Promotes efficient foraging (+)
%thinned	Percent stands thinned within 5 yrs within 450-m buffers around sample points	Promotes efficient foraging (+)
Dist unthin 10–19	Euclidean distance (km) to nearest unthinned stand 10–19 yrs old	Reduces foraging efficiency (–)
%unthin 10–19	Percent unthinned stands 10–19 yrs old within 450-m buffers around sample points	Reduces foraging efficiency (–)
Dist 30plus	Euclidean distance (km) to nearest stand ≥ 30 yrs old	Roosting habitat (+)
%30plus	Percent stands ≥ 30 yrs old within 450-m circular buffers around each point	Roosting habitat (+)
Dist road	Euclidean distance (km) to nearest road	Foraging and navigation (+)
Rd density	Density of roads (linear km/ km^2) within 450 m buffers around sample points	Used for foraging and navigation (+)
PR	Richness of patch types within 450 m buffers around sample points	Fulfill multiple requirements (+)
SIDI	Simpson's index of diversity. Measure of patch richness and equitability within 450 m buffer that ranges from 0 (no diversity) to 1	Fulfill multiple requirements (+)
TE	Total edge (km) within 450 m buffer	Used for navigation, increased prey (+)

tion of an excessively large set of models (Hein et al., 2009; Long et al., 2011; Yates and Muzika, 2006). Our candidate set of 10 detection models included study site, basal area, and % clutter as variables to account for differences among study areas and structural clutter among sampling locations. We also included Julian date because study sites were sampled at different times during the sampling period and detection probability likely varies temporally during the active summer season (Hein et al., 2009). The candidate set of detection models represented individual and additive combinations of variables in addition to a null and global detection model.

We generated 19 candidate models based on hypotheses regarding factors that potentially influence site occupancy (Table 1) in addition to null and global models. Five of our candidate models included additive combinations of variables we considered plausible based on bat ecology in managed forests of the southeastern U.S. For example, many bat species forage over water (Vindigni et al., 2009) and roost in mature trees (Miles et al., 2006) in managed-pine landscapes. We considered it plausible that likelihood of occupancy would increase in areas where these resources were closely juxtaposed and commuting distances minimized. Therefore, we created a model that contained the variables distance to water and distance to stands >30 yrs old. Other multi-variable models were developed using similar rationale. We used only uncorrelated predictor variables in the same occupancy or detection model (Pearson's $|r| \leq 0.70$) to avoid multicollinearity. We eliminated canopy cover from all analyses because it was correlated with basal area, which we retained because it is readily available to forest managers.

We used PRESENCE (version 2.4; Hines, 2006) to calculate Akaike's information criterion adjusted for small sample sizes (AICc) that we subsequently used to determine relative plausibility of our models given our data. We used the bootstrap option in PRESENCE with 1000 bootstrapping events to assess goodness-of-fit with the most parameterized model for each species (Donovan and Hines, 2007; MacKenzie and Bailey, 2004). When lack of fit was indicated (c-hat value >1) we used quasi-AIC values (QAICc) to evaluate models. We inflated standard errors of parameter estimates by the square root of c-hat when QAICc values were used (Donovan and Hines, 2007; MacKenzie and Bailey, 2004).

Although MacKenzie and Bailey (2004) suggested using the global set of occupancy parameters when determining the most plausible detection model if possible, PRESENCE was unable to reach convergence or produced nonsensical parameter estimates when the global set of occupancy parameters was used. Therefore, we used a 'general set' of predictor variables in the occupancy portion of all models (i.e., ψ = water + dist. unthin 10–19 + dist. roads + TE + % 30 plus + % 0–9 + % thinned + % clutter). The general set of occupancy variables included the maximum number of variables that allowed PRESENCE to reach convergence. For each species investigated, we incorporated the most plausible detection model into all occupancy models for that species. When assessing fit of occupancy models for each species, we typically used the global set of occupancy parameters along with the most plausible detection model previously determined. However, we used a reduced global model to assess fit when analyzing Brazilian free-tailed bat data because the full global model did not reach convergence in PRESENCE. We considered it possible that observations within study sites may be spatially autocorrelated (i.e., site-level effects), which would preclude using traditional regression techniques (Sokal and Rohlf, 1995). Therefore, we conducted analysis of variance on the residuals from the most parameterized occupancy model for each species using study site as the independent variable (Hein et al., 2009; Rieman et al., 2006). Because our results indicated no significant spatial dependence, we pooled data from all study sites and used traditional regression techniques rather than hierarchically structured models (Rieman et al., 2006). To

incorporate model selection uncertainty, we model-averaged parameter estimates and created a composite model for each species that included parameters from all plausible models (i.e., Akaike weights within 10% of the most plausible model).

3. Results

We detected bats at 80% (126/158) of sample points across all landscapes during 385 detector nights. Approximately 18% of sequences recorded in the field did not pass our ≥ 0.5 threshold for posterior classification probabilities and were eliminated from further analyses. Overall call classification accuracy, based on leave-one-out cross validation of our reference library, was 83% and mean species accuracy was 81%, ranging from 51% to 96% (Bender, 2011). However, species identifications during this project were based on posterior classification probabilities averaged across all calls within each sequence so that sequences rather than individual calls were assigned to a species. Therefore, we used three-fold cross validation of the reference library to estimate sequence classification accuracy. Sequence accuracies averaged across three iterations of the cross validation procedure ranged by species from 72% to 100% (see Bender, 2011 for more detailed discussion of the classification procedure and accuracy estimation).

We detected all species we considered residents at each of the 6 study areas except Rafinesque's big-eared and hoary bats, which were only detected at 2 and 3 study areas, respectively. Species detected at the greatest number of sample points were evening ($n = 99$) and red/Seminole ($n = 97$) bats. Species intermediate in sample points occupied (i.e., used) included tri-colored bats ($n = 71$), big brown bats ($n = 70$), southeastern myotis ($n = 54$), and Brazilian free-tailed bats ($n = 44$). We were unable to model influence of predictor variables on Rafinesque's big-eared and hoary bats because of the low number of sample points (2 and 11, respectively).

Goodness-of-fit tests indicated that data for all species were overdispersed (i.e., more variation than predicted by underlying statistical distributions). Therefore, QAICc values were used to evaluate model plausibility and standard errors were inflated by

Table 2

Quasi-Akaike's Information Criterion adjusted for small sample size (QAICc), delta QAICc, QAICc weight (ω_i), and number of parameters (K) for top performing (QAICc ≤ 2) site occupancy models of bats within managed pine forest landscapes of the southeastern U.S. Coastal Plain, May–August, 2007–2008. Models included occupancy (ψ) and detection (ρ) parameters. Variables are defined in Table 1.

Model	QAICc	Δ QAICc	ω_i	K
<i>Big Brown Bat</i>				
ψ (TE), ρ (Date, BA)	266.60	0.00	0.8875	5
<i>Red/Seminole Bat</i>				
ψ (Water), ρ (BA)	354.50	0.00	0.1589	4
ψ (PR), ρ (BA)	354.65	0.15	0.1474	4
ψ (BA), ρ (BA)	354.97	0.47	0.1256	4
ψ (%clutter), ρ (BA)	355.26	0.76	0.1087	4
ψ (TE), ρ (BA)	356.18	1.68	0.0686	4
ψ (.), ρ (BA)	356.50	2.00	0.0585	3
<i>Southeastern Myotis</i>				
ψ (%30plus, % unthin 10–19), ρ (BA)	206.80	0.00	0.2333	5
ψ (%30plus), ρ (BA)	207.24	0.44	0.1872	4
ψ (%clutter), ρ (BA)	207.91	1.11	0.1339	4
<i>Evening Bat</i>				
ψ (%clutter), ρ (BA)	292.81	0.00	0.6625	4
<i>Tri-colored Bat</i>				
ψ (%clutter), ρ (Site)	269.15	0.00	0.2918	8
ψ (Water), ρ (Site)	270.00	0.85	0.1908	8
ψ (% unthin 10–19), ρ (Site)	270.88	1.73	0.1229	8
<i>Brazilian Free-tailed Bat</i>				
ψ (BA), ρ (Date, Site)	134.53	0.00	0.5109	9

Table 3

Model averaged parameter estimates, standard errors (SE), and 90% confidence intervals (CI) for occupancy (ψ) and detection (ρ) parameters contained in species composite models and averaged over the confidence set of models (QAICc weight $\geq 10\%$ most plausible model) for bats in managed pine forests of the southeastern U.S. Coastal Plain, May–August, 2007–2008. For each species, variables following ψ and ρ intercepts in columns represent occupancy and detection probability parameters, respectively. Variables are defined in Table 1.

Species/parameter	Estimate	SE	90% LOWER CI	90% UPPER CI
<i>Big Brown Bat</i>				
ψ intercept	3.9279	1.2241	1.9204	5.9354
TE	-4.5749	1.4348	-6.9279	-2.2219
ρ intercept	-2.4883	0.5119	-3.3278	-1.6489
Date	0.0193	0.0020	0.0160	0.0226
BA	-1.6167	0.3471	-2.1860	-1.0474
<i>Red/Seminole Bat</i>				
ψ intercept	1.6891	1.0989	-0.1132	3.4913
Water	1.1578	0.7519	-0.0753	2.3909
PR	-6.6082	3.6770	-12.6385	-0.5778
BA	-1.0601	0.4518	-1.8011	-0.3191
%clutter	-1.9980	0.9794	-3.6042	-0.3917
TE	-1.3031	0.8414	-2.6829	0.0768
Dist 30plus	0.0836	1.2760	-2.0091	2.1763
%unthin 10–19	-1.6585	1.3401	-3.8562	0.5393
Rd density	-1.6820	1.8969	-4.7929	1.4289
SIDI	-1.5912	2.2787	-5.3283	2.1458
%30plus	0.8509	1.4371	-1.5060	3.2077
Dist unthin 10–19	0.1490	0.4538	-0.5952	0.8932
Dist road	-0.6089	2.7382	-5.0995	3.8817
%0–9	0.1866	1.0188	-1.4842	1.8575
%thinned	-0.1006	1.4925	-2.5483	2.3472
ρ intercept	1.2854	0.2663	0.8486	1.7222
BA	-1.2127	0.3348	-1.7617	-0.6637
<i>Southeastern Myotis</i>				
ψ intercept	-0.0983	0.7991	-1.4089	1.2123
% 30plus	2.8565	1.4954	0.4041	5.3089
%unthin 10–19	-2.2775	1.4394	-4.6381	0.0832
%clutter	-2.5128	1.2658	-4.5887	-0.4369
BA	-1.2116	0.8280	-2.5695	0.1464
Water	0.9426	0.7479	-0.2839	2.1691
TE	-1.3264	0.9134	-2.8243	0.1715
PR	-3.8328	2.9169	-8.6165	0.9510
Dist 30plus	-1.2371	1.1748	-3.1637	0.6895
Dist unthin 10–19	0.4946	0.4759	-0.2860	1.2751
ρ intercept	-0.7548	0.4652	-1.5177	0.0082
BA	0.8755	0.5778	-0.0720	1.8231
<i>Evening Bat</i>				
ψ intercept	2.1388	0.4285	1.4360	2.8416
%clutter	-3.9275	1.1430	-5.8020	-2.0530
BA	-1.8691	0.5331	-2.7434	-0.9948
ρ intercept	1.5120	0.5861	0.5508	2.4732
BA	-1.1940	2.8519	-5.8711	3.4831
<i>Tri-colored Bat</i>				
ψ intercept	0.4495	0.6002	-0.5348	1.4338
%clutter	-2.5336	1.0281	-4.2197	-0.8476
Water	1.0992	0.5682	0.1675	2.0310
%unthin 10–19	-2.7962	1.3029	-4.9330	-0.6594
BA	-0.7805	0.3815	-1.4062	-0.1548
Dist 30plus	-0.3675	1.0101	-2.0240	1.2891
% 30plus	-0.2654	1.4349	-2.6187	2.0879
Rd density	-2.7530	1.8282	-5.7512	0.2453
ρ intercept	-0.2543	0.5348	-1.1314	0.6229
Site AR	2.6992	1.0782	0.9309	4.4675
Site SC	1.0934	0.6991	-0.0530	2.2399
Site AL	-1.4246	0.8552	-2.8272	-0.0221
Site NC-1	0.3804	0.7283	-0.8140	1.5749
Site NC-2	0.8861	0.7071	-0.2736	2.0458
<i>Brazilian Free-tailed Bat</i>				
ψ intercept	1.4829	1.2693	-0.5989	3.5646
BA	-1.9140	0.8565	-3.3186	-0.5093
%clutter	-3.0647	2.0200	-6.3774	0.2481
PR	-8.7249	7.6321	-21.2416	3.7919
ρ intercept	-8.2255	1.0711	-9.9821	-6.4689
Date	0.0436	0.0030	0.0387	0.0485
Site AR	0.8400	1.2232	-1.1660	2.8459

Table 3 (continued)

Species/parameter	Estimate	SE	90% LOWER CI	90% UPPER CI
Site SC	-2.1480	1.1712	-4.0688	-0.2273
Site AL	-0.2985	1.4095	-2.6102	2.0131
Site NC-1	-0.3907	1.1406	-2.2612	1.4798
Site NC-2	-1.5833	1.1653	-3.4943	0.3278

the square root of the c-hat parameter estimated from 1000 bootstraps (MacKenzie and Bailey, 2004).

3.1. Detection

Basal area was included in the detection portion of species' models for 4 of the 6 species/groups and was the single detection parameter in models for 3 species/groups (red/Seminole, southeastern myotis, and evening bats; Table 2). Model-averaged estimates and 90% confidence intervals indicated that increasing levels of basal area had a negative effect on probability of detecting red/Seminole bats (Table 3). The direction of effect on southeastern myotis and evening bats was uncertain because of confidence intervals that overlapped zero (Table 3). Increasing basal area had a negative effect on detection of big brown bats, whereas later dates positively influenced detection (Table 3). The positive relationship between later dates and probability of detection was similar for Brazilian free-tailed bats. Sampling site was included in the most plausible detection model for Brazilian free-tailed and tri-colored bats (Table 3), but estimates were imprecise and the direction of effect was largely uninterpretable (i.e., confidence intervals overlapped 0).

3.2. Occupancy

Data supported plausibility of a single occupancy model for big brown bats that included total edge as the single parameter estimated (Table 2). This model received a QAICc weight >0.88 indicating substantial support as the most plausible among the candidate set investigated. Increasing amounts of edge in the surrounding landscape had a negative effect on big brown bat occupancy (Table 3). The model was at least 15 times more likely to be the best model (i.e., QAICc weight of best model/QAICc weight of alternative model ≥ 15) than the other models investigated.

Data indicated strong support (i.e., $\Delta QAICc \leq 2$) for 6 red/Seminole bat occupancy models (Table 2), including the null model, and 18 models were included in the confidence set. The top model was 1.1 and 9.8 times more likely to be the best model than the two alternative models in the confidence set. Parameter estimates in the composite model with confidence intervals that did not overlap zero included patch richness, vegetation clutter, and basal area; all were negatively related to probability of occupancy (Table 3). Estimates and confidence intervals suggested a positive influence of distance to water and a negative influence of total edge on probability of occupancy, but estimates were imprecise (i.e., large confidence intervals). The direction of effect for remaining parameters in the composite model was indistinguishable (Table 3).

The confidence set for southeastern myotis contained 11 models including the null model, with three receiving strong support (Table 2). The most plausible model was approximately 1.2 times more likely than the second best model and 9.9 times more likely than the least plausible within the confidence set. Composite model parameter estimates indicate that percent of stands aged 10–19 generally had a positive relationship to occupancy, whereas remaining parameter estimates generally exhibited a neg-

ative relationship (Table 3). However, only percent stands aged ≥ 30 yrs and percent vegetation clutter had parameter estimates with confidence intervals that did not overlap zero.

A single occupancy model for evening bats that included only percent vegetation clutter received strong support (Table 2). The composite model for evening bat included two measures of vegetation structure (basal area and percent clutter) at the sample point as occupancy parameters (Table 3). Parameter estimates indicate that both measures of increasing vegetation structure negatively influenced probability of occupancy. The percent clutter model was approximately 3 times more likely than the basal area model and ≥ 23 times more likely than alternative models to be the most plausible given our data. There was little evidence to support plausibility of other models.

Three occupancy models for tri-colored bats received strong support (Table 2), and the confidence set included 8 models that were 9.7–1.5 times less likely than the best model. In the composite model, probability of occupancy declined as amount of basal area, vegetation clutter, and percentage of unthinned stands aged 10–19 increased (Table 3), and occupancy increased with increasing distance to water. The remaining parameter estimates included in the composite model had confidence intervals that overlapped zero.

Basal area was the single occupancy parameter in the only model for Brazilian free-tailed bats that received strong support (Table 2). The top model was 7 times more likely than the second

best model and 9.7 times more likely than the least plausible among those in the confidence set used to generate the composite model. Probability of occupancy was negatively related to all 3 parameters included in the composite model; basal area, vegetation clutter, and patch richness (Table 3). Parameter estimates for basal area had confidence intervals that did not overlap zero, indicating a consistent negative effect on probability of occupancy. Confidence intervals for parameter estimates of vegetation clutter and patch richness overlapped zero, indicating that direction of the effect was not always negative.

Overall, measures of vegetation structure at the sample point (vegetation clutter and basal area) were the most common occupancy parameters in composite species models. Each of these parameters was present in the composite model for all species investigated, except big brown bats, and consistently indicated that increasing vegetation clutter and/or basal area negatively affected occupancy probability (Figs. 1 and 2). Total edge, patch richness, percent unthinned stands aged 10–19, and percent stands ≥ 30 yrs, distance to stands ≥ 30 yrs old, and distance to water were each found in three composite models. Increasing distance to water consistently had a positive relationship to occupancy whereas increasing amounts of edge, patch richness, and % unthinned stands aged 10–19 consistently had a negative effect. All remaining occupancy parameters were only present in a single composite model, had confidence intervals that overlapped zero, or the effect varied by species.

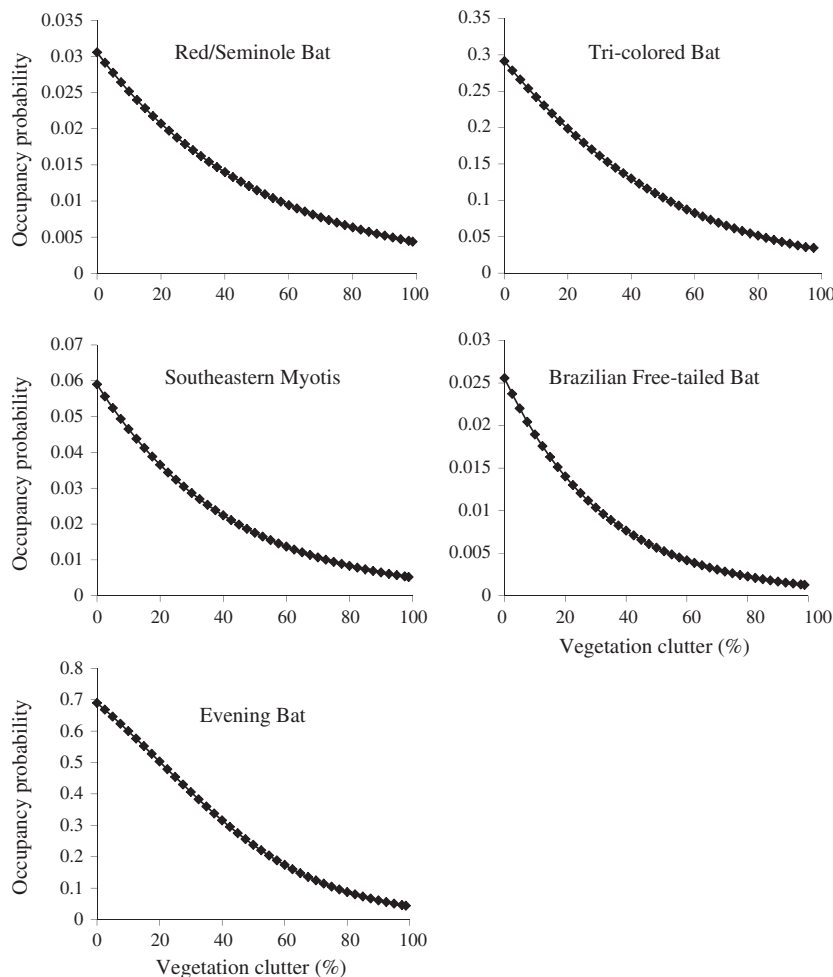


Fig. 1. Influence of percent vegetation clutter on probability of occupancy for 5 bat species on managed-pine landscapes in the southeastern Coastal Plain, 2007–2008.

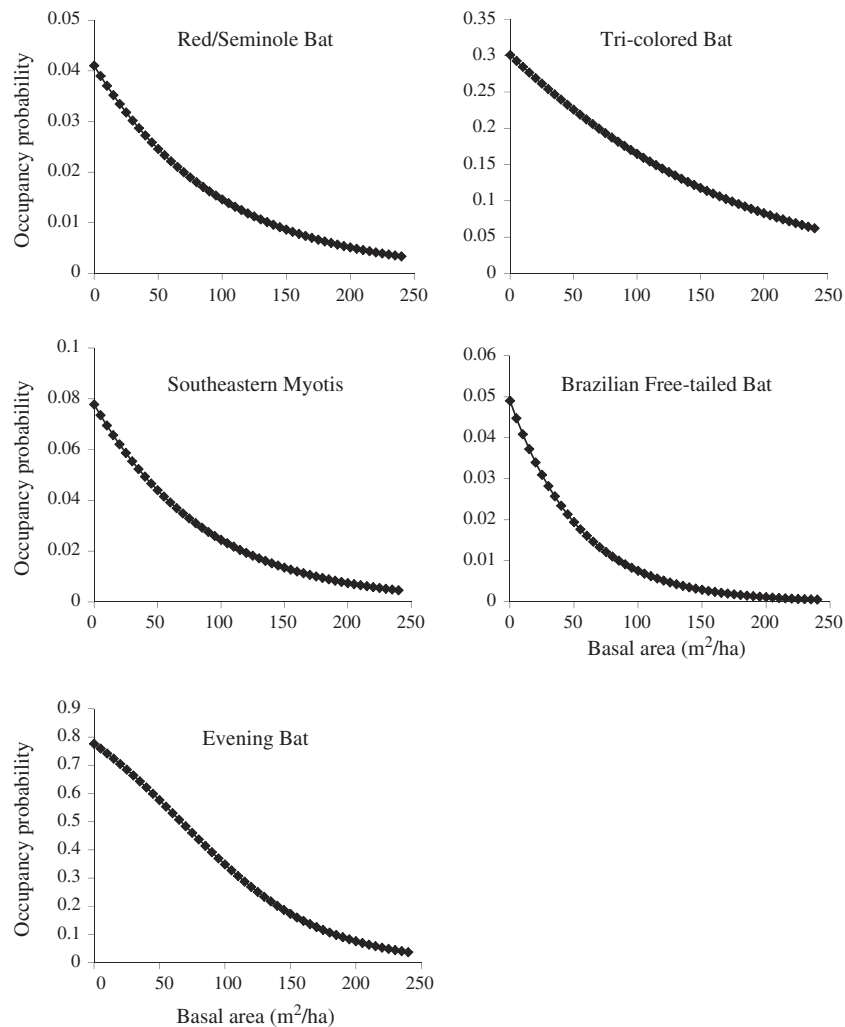


Fig. 2. Influence of basal area (m^2/ha) on probability of occupancy for 5 bat species on managed-pine landscapes in the southeastern Coastal Plain, 2007–2008.

4. Discussion

4.1. Detection

Although a negative effect of vegetation clutter on presence (Ford et al., 2006; Loeb and O'Keefe, 2006; Patriquin and Barclay, 2003) and activity (Ford et al., 2005; Humes et al., 1999; Ober and Hayes, 2010) is well-documented for some bat species, studies that have examined detection probability relative to vegetation clutter have found little influence (Amelon, 2007; Yates and Muzika, 2006; but see O'Keefe et al., 2014). Although basal area was included in detection models for 4 species/groups we examined, direction of relationship could only be determined for red/Seminole and big brown bats. Of 8 species examined by Amelon (2007), including 4 species present in our analyses, only eastern red bat detection was negatively influenced by vegetation clutter. Yates and Muzika (2006) found no relationships between detection and vegetation clutter for any of the 5 species they examined. Although clutter is expected to attenuate echolocation calls and reduce detection distance, bats may exhibit mechanical and perceptual adaptations to foraging in cluttered environments (Schnitzler and Kalko, 2001). Foraging bats also may increase echolocation call emission rate in background-cluttered environments compared to uncluttered environments (Schnitzler and Kalko, 2001). An increase in rate of search signals emitted may

compensate for attenuation from clutter explaining the general lack of influence of vegetation clutter on detection.

The temporal influence (Julian date) on detection we observed for big brown and Brazilian free-tailed bats supports previous research demonstrating a positive influence of sampling date in summer for some species (Hein et al., 2009; Seidman and Zabel, 2001). Increases in bat activity from early to late summer may be related to higher temperatures (Hayes, 1997), greater prey availability (Black, 1974), or juvenile bats entering the volant population (Yates and Muzika, 2006). Because we did not examine these factors relative to detection, causative factors for increased probability of detection for these species is unknown.

4.2. Occupancy

With the exception of big brown bats, we found that increasing amounts of vegetation at sample points (basal area and vegetation clutter) negatively influenced occupancy probability regardless of species' ecomorphology. Although some studies have found a negative effect of clutter on big brown bats (Loeb and O'Keefe, 2006), they are typically considered generalists capable of exploiting a range of stand conditions (Brigham, 1991; Morris et al., 2010). Yates and Muzika (2006) found that occurrences of eastern red and tricolored bats in Missouri, USA, both of which are categorized as clutter-adapted species (Menzel et al., 2005), were inversely

related to basal area. The benefits of reduced clutter in forest landscapes for most aerial foragers has been demonstrated experimentally (Brigham et al., 1997; Sleep and Brigham, 2003) and in field studies (Ford et al., 2006; Loeb and O'Keefe, 2006; Loeb and Waldrop, 2008). Whether decreased use of areas with higher clutter is due to decreased navigational ability or decreased prey abundance is unclear. Insect abundance can vary across a range of clutter conditions (Kalcounis and Brigham, 1995; Tibbels and Kurta, 2003) and influence of vegetation on bat foraging may be largely independent of insect abundance (Adams et al., 2009; Morris et al., 2010). Thus, negative influence of clutter is likely related to difficulties associated with tracking prey while simultaneously monitoring location of obstacles (Simmons et al., 1979) rather than decreased prey abundance.

We found that points across the landscape characterized by greater abundance of or closer proximity to unthinned stands 10–19 yrs old had a reduced probability of occupancy by tri-colored bats and parameter estimates suggest the same effect for the red/Seminole group and southeastern myotis. Similar relationships have been documented at the stand-level and have been attributed to inefficient foraging conditions (Loeb and O'Keefe, 2006), although foraging may take place above the canopy (Kalcounis-Rüppell et al., 1999; Menzel et al., 2005) or at stand margins (Morris et al., 2010). At the landscape-scale, Perry et al. (2008) found that diurnal roosts were less likely to be located in managed pine landscapes with increasing amounts of closed canopy stands. Because roost site selection may be influenced by proximity to food resources (Kunz and Lumsden, 2003), observations made by Perry et al. (2008) may have been influenced by an aversion to foraging in closed canopy stands that were functionally similar to unthinned 10–19 yr old stands on our study areas.

The observed negative relationship between occupancy and distance to water for tri-colored bats contradicts the general belief that bats are more likely to be found closer to water. Numerous studies have documented that close proximity to water increases likelihood of use by bats for roosting (Kalcounis-Rüppell et al., 2005) and foraging (Brooks and Ford, 2005; Ford et al., 2006; Krusic et al., 1996; Menzel et al., 2005). However, water sources in our data only included those available on GIS data layers and did not include small and ephemeral sources. As clutter-adapted species (Menzel et al., 2005), it is likely that these species foraged over and drank from small water sources (e.g., flooded road ruts) that were common across the study areas but were not included in our data set due to the difficulty of mapping these small and often temporary water sources. The lack of any observed relationship for remaining species may reflect the abundance of larger water bodies (e.g., permanent ponds) typically found on intensively managed landscapes in the southeastern Coastal Plain (Vindigni et al., 2009).

Also contrary to other studies, increasing amounts of edge in the landscape surrounding a sample point had a negative influence on big brown bat occupancy. At small-scales, edges represent preferred foraging areas for many species (Grindal and Brigham, 1999; Hein et al., 2009), likely as a result of concentrated insect abundances (Lewis, 1970; Pasek, 1988) and navigational ease (Simmons et al., 1979) that permits efficient foraging (Grindal and Brigham, 1999; Morris et al., 2010). However, variables that influence foraging preferences at small scales may not have the same effect across all relevant spatial scales (Stephens et al., 2003). At the landscape-scale, the positive influence of edge for big brown bats appeared to diminish as amount of edge increased. The big brown bat is a habitat generalist, foraging in stand interiors and along edges (Brigham, 1991; Morris et al., 2010) and may select foraging areas that balance edge with interior habitat patches. Additionally, we did not differentiate between hard edges (i.e., edges between stands that differ substantially in structure

such as the edge between a recently harvested stand and an adjacent unmanaged stand 30 yrs old) and soft edges (i.e., edges between stands similar in structure such as the edge between a stand 20 yrs and a stand 24 yrs) that may differ in their foraging suitability (Morris et al., 2010).

Southeastern myotis occupancy was positively related to percent of the landscape composed of stands ≥ 30 yrs old. In the absence of caves, southeastern myotis roosts in large, hollow hardwood trees in bottomland forests (Carver and Ashley, 2008). On our study areas, suitable southeastern myotis roost sites were found in streamside management zones which typically were classified as >30 yrs old and often contained trees in much older age classes. Thus, roost preference of this species may have influenced its foraging habitat selection as has been demonstrated for other bat species (Crampton and Barclay, 1998).

Although increased patch richness has the potential to positively influence bat occupancy because multiple habitat features are available in a localized area, most studies, including ours, have found no positive influence of landscape-level measures of patch richness and diversity in forested environments (Elmore et al., 2005; Erickson and West, 2003; Ford et al., 2006; Yates and Muzika, 2006). Because forest cover dominates managed forest landscapes, importance of patch diversity and configuration likely are diminished compared to highly fragmented agricultural or urban landscapes in which individual patches (e.g., forests) may be critical features (Ford et al., 2006). Similarly, our data did not support roads as a landscape feature influencing probability of occupancy. Roads are well-documented as a habitat feature used for foraging and commuting by bats (Grindal and Brigham, 1999; Hein et al., 2009), but importance of roads to bat presence at the landscape scale has received little support (Loeb and O'Keefe, 2006). Studies that have documented use of roads by foraging bats directly surveyed road corridors (Grindal and Brigham, 1999; Hein et al., 2009) whereas landscape-level studies typically conduct surveys systematically throughout the study areas and measure metrics of roads in relation to survey points (Loeb and O'Keefe, 2006). Bats likely perceive roads as linear edge, and edge created by roads represented a small percentage of the total edge on our study areas which, except for big brown bats, did not influence bat occupancy.

4.3. Management implications

Our objective was to provide information on site- and landscape-scale bat foraging habitat relationships that would be broadly applicable to managed pine forests in the southeastern Coastal Plain. Although all of our study sites were managed for pine production, sites varied in landscape context, vegetation communities, silvicultural activities, and management objectives. This variability may have reduced our ability to detect some relationships, but by examining multiple managed landscapes under variable ownership across the Coastal Plain we gained ability to make inferences at a broad geographic scale. Information on bat habitat relationships that can be applied at large geographic scales may be more realistically incorporated into forest management plans than information about species- or site-specific relationships, thus increasing the overall benefit to bat communities in managed landscapes.

Although we found occupancy by foraging bats was influenced by site- and landscape-level features, stand-level variables, namely basal area and vegetation clutter, influenced the greatest number of species. Thus, stand-level activities, such as thinning intermediate-aged stands, appear to have the greatest potential to increase habitat suitability for foraging bats on managed forest landscapes of the southeastern Coastal Plain. Additionally, the landscape feature with the greatest influence, percentage of unthinned intermediate-aged stands, can be influenced by stand-level management

activities. Although a positive influence of thinning on bats has not been universally demonstrated (Patriquin and Barclay, 2003; Tibbels and Kurta, 2003), management activities that decrease vegetation structure likely will increase suitability of managed forest landscapes for most bats (Brigham et al., 1997; Ford et al., 2006; Loeb and O'Keefe, 2006; Loeb and Waldrop, 2008; Yates and Muzika, 2006). When considered along with roosting studies on managed landscapes (Elmore et al., 2004; Menzel et al., 1998, 2001b; Miles et al., 2006; Perry et al., 2008; Hein et al., 2008), our results on foraging bat occupancy suggest that managed forest mosaics, consisting of a mix of intensively managed pine stands of various age and structural conditions intermingled with stream-side management zones and inoperable areas, support a large proportion of the bat community associated with forests of the Coastal Plain.

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