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LETTER

At a fine scale, hardwood patches support wildlife diversity in longleaf pine woodlands

Adia R. Sovie[1,2] | L. Mike Conner[3] | Robert A. McCleery[2]

[1]Department of Wildlife and Fisheries, Michigan State University, Lansing, USA

[2]Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida, USA

[3]Wildlife Lab, The Jones Center at Ichauway, Newton, Georgia, USA

Correspondence
Adia R. Sovie, Department of Wildlife and Fisheries, Michigan State University, Lansing, MI, USA.
Email: sovieadi@msu.edu

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Abstract

Restoring and maintaining biodiversity in a changing world is increasingly challenging due to the competing needs of species for suitable space and resources. One ecosystem that has seen considerable anthropogenic changes in extent and structure is the longleaf pine (*Pinus palustris*) ecosystem. Understanding how wildlife responds to restoration is important to informing forest restoration and conservation. We monitored game birds and mid-large-sized mammal occupancy in and around hardwood patches embedded within a longleaf pine woodland at The Jones Center at Ichauway in Newton, GA. We found that 11 species use the transition zone between the longleaf pine and hardwood hammocks. Gray squirrels (*Sciurus carolinensis*), Virginia opossums (*Didelphis virginiana*), and nine-banded armadillos (*Dasypus novemcinctus*) occupancy increased along the gradient while fox squirrel (*Sciurus niger*) declined. Our results suggest that oak patches and transitional zones are important to maintaining biodiversity within the longleaf pine ecosystem.

KEYWORDS
community, edges, hardwoods, longleaf pine, mammal

INTRODUCTION

Restoring and maintaining biodiversity in a changing world is increasingly challenging due to the competing needs of wildlife species for suitable space and resources (Goodrich & Buskirk, 1995; Thompson et al., 1999). These tensions are particularly pronounced in the southeastern United States where endemism is high and the amount of land under protection is small (Jenkins et al., 2015). Within the southeastern United States, one ecosystem that has undergone considerable anthropogenic change, increasing fragmentation, and restoration effort, is the longleaf pine (*Pinus palustris*) forest. Historically, longleaf pine forests covered much of North America's southeastern Coastal Plain (Frost, 1993), but only 3% of its historic range remains (Landers et al., 1995). Much of the remaining longleaf pine forest is fragmented and invaded by hardwoods (Landers et al., 1995; Provencher et al., 2001). These structural shifts change the vertebrate communities in the longleaf pine, favoring generalist and closed canopy specialists over open canopy species (Darracq et al., 2016; Sovie et al., 2021). As a result, aggressive hardwood management is common within the longleaf pine system, resulting in homogeneous savanna-like conditions with limited areas of oak canopy. Historically, longleaf pine forests likely included patches of dryland oaks (Frost, 1993) and it is unclear if these patches produce important resources for native wildlife (Hiers et al., 2014) or have negative ecological consequences due to changing predation risk and facilitating species invasions (Sovie et al., 2021).

Hardwood edges within the longleaf pine matrix may provide fine-scale resources where animals shelter from predators, rear young (Huegel et al., 1986), and forage (Boone et al., 2017). Recent research suggests that some "longleaf-pine specialists" will utilize resources within and around hardwood patches (Sovie et al., 2021). Further, animals that utilize closed canopy areas can persist within the longleaf pine woodland if some hardwood patches remain. Several studies have identified fine-scale heterogeneity as important for maintaining bird, small mammal, invertebrate, and reptile diversity, but rarely for larger vertebrates (Batary & Baldi, 2004; Hurst et al., 2013; Lang et al., 2002; Magura, 2002; Reynolds et al., 2018). Understanding how species respond to edges at fine scales is important in maintaining diverse wildlife communities within longleaf pine ecosystems and can improve restoration efforts (Goodrich & Buskirk, 1995; Linnell & Strand, 2000; Means, 2007).

The goal of this study was to understand how upland game birds and mid-large-sized mammals use the edges of hardwood patches at fine scales within a larger longleaf pine matrix. We used closely spaced game cameras to detect fine-scale habitat associations that can be missed using radio collars or trapping. Specifically, we focused our study on a 20 m transect where open pineland transitions to a closed canopy hammock. While most mammalian species can traverse this area quickly, their preferential utilization of fine-scale changes in vegetation structure can influence a species' ecological role (Steele et al., 2015), survival (Manning & Edge, 2004), and fitness (Bloom et al., 2013). We chose to focus our study on upland game birds and mid-larger bodied mammals because these species are often the focus of management and conservation efforts and are reliably monitored using game cameras. We also included the eastern chipmunk (*Tamias striatus*) and Southern flying squirrel (*Glaucomys volans*) in our analysis due to their role as species of management concern in our system. Eastern chipmunks are a unique remnant population in our study area and flying squirrels are frequently managed in longleaf pine woodlands due to their competition with red-cockaded woodpeckers (*Leuconotopicus borealis*) (Laves & Loeb, 1999). We predicted that species considered longleaf pine specialists (e.g., fox squirrels [*Sciurus niger*] and Northern bobwhites [*Colinus virginianus*]) would utilize the edges of hardwood patches but not the interior of these areas. However, generalists and hardwood specialists (e.g., Nine-banded armadillos [*Dasypus novemcinctus*], gray foxes [*Urocyon cinereoargenteus*], gray squirrels [*Sciurus carolinensis*], coyotes [*Canis latrans*], Virginia opossums [*Didelphis virginiana*], white-tailed deer [*Odocoileus virginianus*], raccoons [*Procyon lotor*], feral hogs [*Sus scrofa*], eastern chipmunks, and eastern cottontails [*Sylvilagus floridanus*]) would make use of the transition between hardwood patches and the surrounding longleaf pine.

METHODS

Study area

We monitored wildlife in and around five hardwood patches at The Jones Center at Ichauway in Newton, GA (Figure 1). The Jones Center at Ichauway is a 12,000 ha property managed for conservation and scientific research. At the time of our study, Ichauway was comprised of a range of ecological communities which included stands of longleaf, slash (*P. elliottil*), and loblolly pine (*P. taeda*), as well as mixed pine hardwoods, riparian hardwood forests, depressional wetlands, and shrub-scrub uplands. Over 7000 ha of the property was open canopy upland pine-grassland vegetation comprised of second-generation longleaf pine, and managed with frequent prescribed fire and silviculture, which included removal of "off site" hardwoods. Less common on the property were closed canopy hardwood patches composed of a diverse array of oak species including *Quercus incana, Q. falcata, Q. laevis, Q. stellata, Q. virginiana, and Q. hemisphaerica* (Jacqmain et al., 1999; Loudermilk et al., 2013). The hard transitions from open canopy pine to closed canopy hardwood hammocks occurring on The Jones Center provide excellent conditions to investigate the role of oak hammocks in other longleaf and open pine systems.

Practitioner points

- Patches of closed-canopy hardwoods embedded within longleaf pine woodlands support a variety of wildlife species.
- Future management and restoration of longleaf pine systems may be improved by retaining small patches of hardwoods in the open pine matrix to support a wider diversity of species.
- Similar practices may be considered in other open canopy systems that are maintained via disturbance which create heterogeneous landscapes that enhance biodiversity—like oak patches impeded in the longleaf pine ecosystem.

Animal activity

We randomly selected five 4–10 ha hardwood patches in the northern sector of the Jones Center to monitor with camera traps (Figure 1a). Within each patch, we then randomly selected four points along the edge to center a perpendicular transect of cameras; we placed transects at least 25 m apart to improve independence. To investigate how animals respond to the edge at a fine scale we placed a camera 10 m into the longleaf pine, one at the patch edge, and one 10 m into the hardwood patch (Figure 1b). At each camera location, we assessed visual obstruction using a modified Robel pole (Robel et al., 1970; Sovie et al., 2016). We installed each camera 50 cm above the ground and angled it towards a bait pile of pecans and cracked corn (Greene et al., 2016). We deployed cameras in each patch five times with each deployment lasting 10–15 days and replaced bait every 5 days. We stopped collecting community composition data in two of the patches after two deployments because we manipulated gray squirrels for a related study (Sovie et al., 2021). We programmed cameras to take three photos every time the camera was tripped using the camera's normal sensitivity setting and rest for 3 min between bursts. We considered photos of animals of the same species taken >20 min apart as independent observations (Greene et al., 2016).

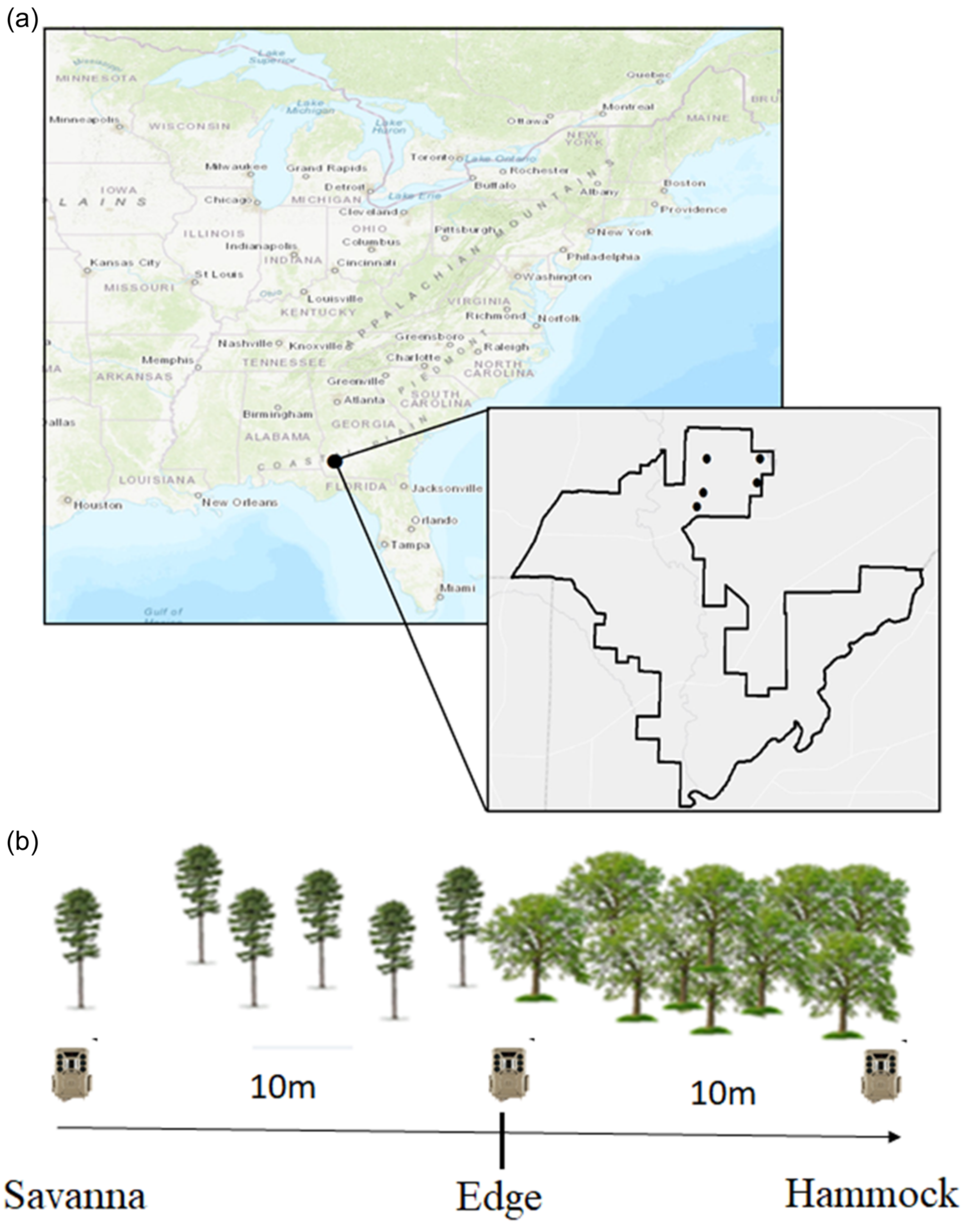

FIGURE 1 (a) Location of study patches within The Jones Center at Ichauway in Newton, GA. (b) Example of camera placement along the savanna to hardwood gradient. Adapted from Sovie et al. (2021).

We treated camera failure as missing data (Foster & Harmsen, 2012) and assumed failures were randomly distributed and do not affect our analysis (Little & Rubin, 2014). We followed the American Society of Mammalogists guidelines (Sikes and Animal Care and Use Committee of the American Society of Mammalogists, 2016) for studying mammals. The University of Florida Institutional Animal Care and Use Committee (IACUC) approved our study (Protocol #: 201709855).

Data analysis

We visually identified species in pictures and extracted metadata (date/time) from each photograph. We produced detection history matrices for each camera based on a sampling occasion of 5 days (0 = species not detected; 1 = species detected; NA = inactive sampling unit or occasion). We collapsed our detection data to 5-day sessions to reduce the complexity of the detection matrix and improve model performance (Nichols et al., 2008). Due to the close spatial distribution of camera traps, statistical tests between cameras in the same transect and patch may be biased due to autocorrelations in the data (Koenig, 1999). To test for spatial autocorrelation, we fit a spline correlogram using the function spline.correlog() in package ncf and considered values < 0.2 lacking autocorrelation (Bjornstad & Falck, 2001; McMurry & Politis, 2010). A spline correlogram estimates spatial dependence as a continuous function of distance. We found no indication of spatial autocorrelation between measures taken from a camera on different days or among cameras within transects. Thus, within a patch, we pooled cameras in the hardwood patch interior together, cameras at the edge together, and cameras in the pineland together. For species with >20 observations, we examined how the pineland to hardwood transition influenced species occupancy. Using a hierarchical Bayesian multispecies occupancy model, we accounted for differences in occupancy and detectability among species (Dorazio et al., 2006; MacKenzie et al., 2006). We treated each species in the community as a random variable and estimated species-specific and whole-community effects. Our modeling approach also allowed us to measure how environmental variables affect occupancy on species-specific and whole-community levels. We defined the probability of occupancy as Ψ_{ik} for species k at site i and defined detection probability as p_{ijk} over sampling period j. To account for potential spatial autocorrelation among cameras we modeled patch as a random effect centered on 0 with a variance from the common distribution. We also estimated how visual obstruction affected capture success for different species. We modeled detection probability as:

$$\mathrm{logit}(p_{ijk}) = \alpha_{\mathrm{k}} + \alpha 1_{\mathrm{k}} * \text{visual obstruction}_i.$$

We assumed that Ψ would vary across species along the pineland to hardwood gradient. First, we investigated if any of our focal species responded to the pineland to hardwood gradient in a nonlinear way by incorporating a quadratic effect. For all species, we found that the 95% credible intervals (CRI) for the polynomial effect crossed 0, thus we focused on linear relationships. We modeled Ψ with location on the savanna to hardwood gradient (0 = pineland, 1 = Edge, 2 = Hammock) as a continuous fixed effect. We used a logit link function formulated for the global model as:

$$\mathrm{logit}(\psi_{\mathrm{ik}}) = \beta \mathrm{k} + \beta 1_{\mathrm{k}} * \mathrm{gradient}_{\mathrm{i}} + \beta 2_{\mathrm{k}} * \mathrm{patch}_i.$$

We adapted code from Kery and Royle (2016) and Loggins et al. (2019) and used JAGS 4.0 (Plummer, 2003) via the R package *r2jags* to build our models. We used noninformative priors for all parameters and ran 100,000 Markov Chain Monte Carlo (MCMC) iterations with three chains, using 12,000 samples (thin rate = 10, burn-in = 60,000) and assumed chains converged if Rhat<1.2 (Gelman et al., 2013). For each species, we evaluated each parameter coefficient and considered coefficients with 95% CRIs that did not cross zero to indicate a clear relationship.

RESULTS

From 24 May 2017 to 24 December 2017, we collected 4,166 independent captures of 16 species (Supporting Information: 1). We detected nearly all the game and mid-large-sized mammals that occupy the longleaf pine ecosystem (Darracq et al., 2016) with exception of black bears (*Ursus americanus*), and striped and spotted skunks (*Mephitis mephitis* & *Spilogale putorius*). We recorded most species in all patches, although we only captured coyotes, wild turkeys, and bobcats in one patch each. Nine-banded armadillos, Virginia opossums, gray squirrels, and raccoons were abundant across study patches.

We analyzed the occupancy of 11 species with >20 observations (Supporting Information: 1). Species varied in detection probability ranging from 0.01 for eastern cottontails to 0.50 for raccoons (Supporting Information: 2). Visual obstruction reduced detection of most species, although the 95% confidence interval of these estimates crossed 0 (Supporting Information: 3). Fox squirrel detection increased with visual obstruction (positive 95% CRI). Species varied in their occupancy as a function of the pineland to hardwood gradient (Figures 2 and 3). Occupancy for gray squirrels, opossums, and armadillos increased along the pineland to hardwood gradient (positive 95% CRI, Figure 2). Wild turkey, raccoon, Eastern cottontail, Northern bobwhite, flying squirrel, white-tailed deer, and eastern chipmunk occupancy also tended to increase along the gradient, but

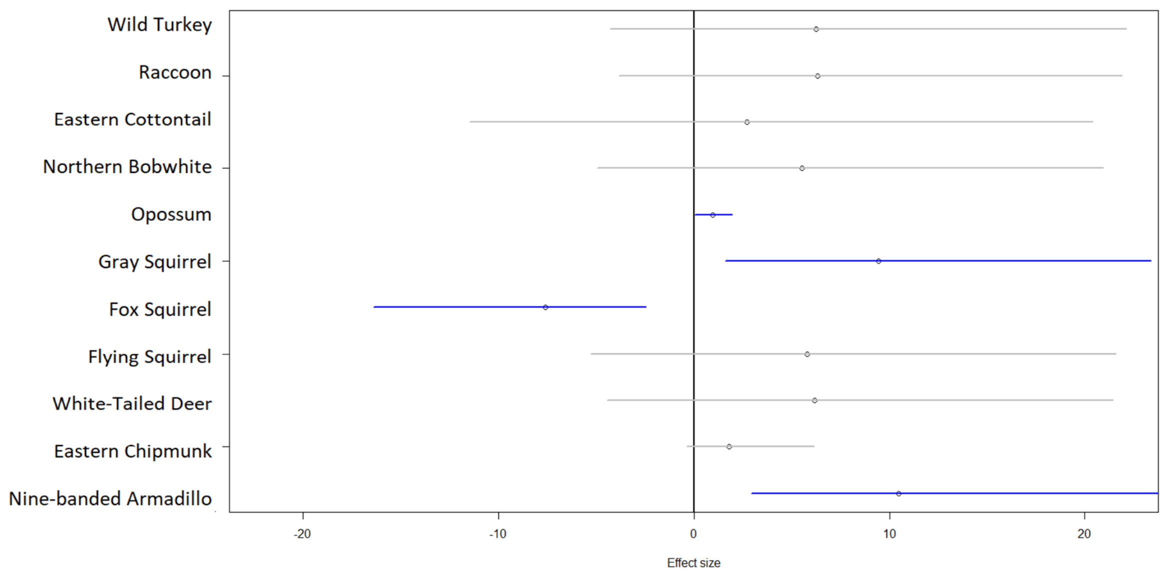

FIGURE 2 Species-level coefficients from multispecies occupancy model. Blue bars indicate significance based on non-overlapping 95% credible intervals. Values represent relationships between species occurrence and location on the savanna-edge-hammock gradient.

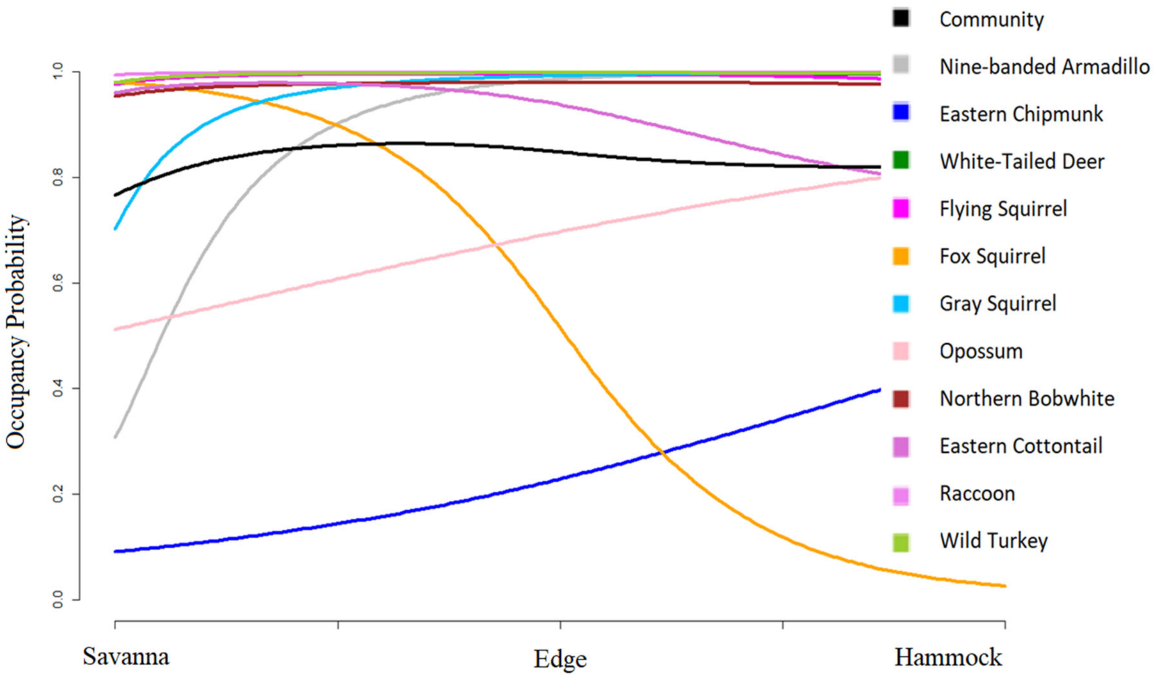

FIGURE 3 Posterior probabilities of the global model for community (black line) and species-level effect of location along the savanna to hardwood gradient.

the 95% CRI included zero, indicating that location on the gradient was not a clear predictor of Ψ. Fox squirrel occupancy declined (negative 95% CRI) along the gradient (Figure 3).

DISCUSSION

Edges and oak hammocks are important for maintaining biodiversity within the longleaf pine ecosystem we studied. We detected almost all the game species and mid-large-sized mammals known to utilize the longleaf pine ecosystem in this narrow band of transitional habitat. Further, we observed high levels of occupancy for most species across the pineland to hardwood gradient. We also documented many species considered longleaf pine specialists (fox squirrels and Northern bobwhite) within the hardwoods, suggesting these areas contain important resources for these species. Our results support the findings of Magura et al. (2017), specifically that anthropogenically maintained edges are often porous to open-habitat species, allowing them to utilize the forest.

While we documented many species utilizing the transition zone between longleaf pinelands and hardwood patches, animals responded to the hardwood patches in a variety of ways. Some species, such as the fox squirrel, rarely utilize hardwood interiors while others, such as the armadillo and gray squirrel, made extensive use of them. This suggests that hardwood patches support a unique assemblage of species within the longleaf pine, contributing to beta diversity. This supports findings by Darracq et al. (2016) that longleaf pine ecosystems with moderate (>3–5 year) burn intervals support the highest diversity. We also found that several species considered generalists use some habitat features more than expected. For example, raccoon occupancy was greatest in the interior of hardwood patches. This supports research that found that raccoons use openings, edges, and forest interiors (Byrne & Chamberlain, 2011) but select for mature hardwoods during the breeding season (Chamberlain et al., 2002). We predicted that game species such as deer, wild turkey, and bobwhite, for which managers typically consider edges to be beneficial, would increase their activity at the habitat edge or at intermediate levels of canopy cover; however, most species utilized the edge gradient equally. Transitional ecotones can support increased biodiversity due to the availability of resources in these areas (Manral et al., 2022).

These species may respond to the habitat edge at large scales (Alverson et al., 1988); however, their high occupancy across the gradient indicates these areas are important features in the landscape for them.

For wildlife, fine-scale vegetation structure can alter predation risk, movement corridors, and connectivity; these changes greatly alter how wildlife move through the landscape and interact with the environment (Loggins et al., 2019; Potash et al., 2019; Spirito et al., 2020). For example, we found that opossums and armadillos both preferentially utilized the interior of hammocks, suggesting these areas may provide important linkages across the landscape for these species. One of the negative consequences of fragmentation and the creation of edges is facilitating the incursion of invasive and/or generalist species into areas occupied by specialists (Loggins et al., 2019; Paton, 1994). We observed armadillos, wild pigs, and coyotes utilizing the pineland to oak hammock edge. These species did not historically occur in the southeastern United States (Engeman et al., 2000; Hody & Kays, 2018; Taulman & Robbins, 2014), and closed canopy oak patches may facilitate their expansion into the longleaf pine. The Jones Center actively controls wild pigs within their forest and the state of Georgia manages coyotes as an invasive species, partly explaining why coyotes and hogs were rare (only one observation each) in our study. However, raccoons and armadillos were common in our study and are important Northern bobwhite nest predators (Staller et al., 2005). Increased nest predation near habitat edges is a possible negative consequence of maintaining hardwood patches in the longleaf pine. However, we observed that Northern bobwhite had high occupancy rates across the pineland to hardwood gradient, indicating these areas remain important to them despite possible increased predation risk.

Our results may be limited by our use of baited camera traps over a relatively small area. Baited cameras may artificially inflate the frequency of visitation and some age and sex classes are more likely to visit bait stations than others (Meek et al., 2014). However, repeated survey hierarchical models appear to be robust to within-species difference in detection probabilities (Veech et al., 2016). Further, although we tested for spatial autocorrelation between our cameras, some larger species could visit each bait station in succession. This would result in inflated occupancy estimates across the gradient such as those we observed for white-tailed deer. Further, while cameras can be used to monitor flying squirrels (Diggins et al., 2022) and chipmunks (Perkins-Taylor & Frey, 2018), in our study we can only detect these species if they are on the ground. Traveling on the ground is risky for small mammals and they may only visit bait stations with high canopy cover (Loggins et al., 2019). Thus, we may be observing changes in behavior due to perceived risk and not necessarily occupancy in these species. In addition, many of our species had low detection probabilities which may skew our results. However, our long survey duration (13 camera trapping sessions) means that even for species with a 0.1 detection probability we had a 75% chance of detecting at least one individual, if they are present, over the course of our survey. We did not find that visual obstruction affected detection probability except for fox squirrels. Fox squirrel detection increased with visual obstruction, which may reflect increased fox squirrel activity in the longleaf pine where canopy cover is low but herbaceous cover is high (Potash et al., 2019; Sovie et al., 2021).

Understanding how landscape patterns provide adequate resources to a range of wildlife is critical to maintaining diversity in the future. Although the broad-scale removal of hardwood patches has occurred in many protected areas, we found that these patches are important to supporting a broad diversity of wildlife. Future restoration of longleaf pine ecosystems may be improved by considering the services provided by hardwood patches (Hiers et al., 2014).

AUTHOR CONTRIBUTIONS

Adia R. Sovie: Conceptualization (lead); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); writing—original draft (equal); writing—review and editing (equal). **L. Mike Conner**: Conceptualization (equal); funding acquisition (equal); project administration (equal); resources (lead); supervision (equal); writing—original draft (equal); writing—review and editing (equal). **Robert A. McCleery**: Conceptualization (equal); supervision (lead); writing—original draft (equal); writing—review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data and supporting code will be available on Dryad. Data are available on Dryad: https://doi.org/10.5061/dryad.c59zw3rdb.

ORCID

Adia R. Sovie https://orcid.org/0000-0002-4253-2465
Robert A. McCleery http://orcid.org/0000-0001-7018-005X

REFERENCES

Alverson, W.S., Waller, D.M. & Solheim, S.L. (1988) Forests too deer: edge effects in northern Wisconsin. *Conservation Biology*, 2(4), 348–358.

Batary, P. & Baldi, A. (2004) Evidence of an edge effect on avian nest success. *Conservation Biology*, 18(2), 389–400.

BjØrnstad, O.N. & Falck, W. (2001) Nonparametric spatial covariance functions: estimation and testing. *Environmental and Ecological Statistics*, 8, 53–70.

Bloom, P.M., Clark, R.G., Howerter, D.W. & Armstrong, L.M. (2013) Multi-scale habitat selection affects offspring survival in a precocial species. *Oecologia*, 173, 1249–1259.

Boone IV, W.W., McCleery, R.A. & Reichert, B.E. (2017) Fox squirrel response to forest restoration treatments in longleaf pine. *Journal of Mammalogy*, 98(6), 1594–1603.

Byrne, M.E. & Chamberlain, M.J. (2011) Seasonal space use and habitat selection of adult raccoons (Procyon lotor) in a Louisiana Bottomland Hardwood Forest. *The American Midland Naturalist*, 166(2), 426–434.

Chamberlain, M.J., Conner, L.M. & Leopold, B.D. (2002) Seasonal habitat selection by Raccoons (Procyon lotor) in intensively managed pine forests of Central Mississippi. *The American Midland Naturalist*, 147(1), 102–108.

Darracq, A.K., Boone, W.W. & McCleery, R.A. (2016) Burn regime matters: a review of the effects of prescribed fire on vertebrates in the longleaf pine ecosystem. *Forest Ecology and Management*, 378, 214–221.

Diggins, C.A., Lipford, A., Farwell, T., Eline, D.V., Larose, S.H., Kelly, C.A. et al. (2022) Can camera traps be used to differentiate species of North American flying squirrels? *Wildlife Society Bulletin*, 46(3), 1323.

Dorazio, R.M., Royle, J.A., Söderström, B. & Glimskär, A. (2006) Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology*, 87, 842–854.

Engeman, R.M., Constantin, B., Nelson, M., Woolard, J. & Bourassa, J. (2001) Monitoring changes in feral swine abundance and spatial distribution. *Environmental Conservation*, 28(3), 235–240.

Foster, R.J. & Harmsen, B.J. (2012) A critique of density estimation from camera-trap data. *The Journal of Wildlife Management*, 76(2), 224–236.

Frost, C.C. (1993) Four centuries of changing landscape patterns in the longleaf pine ecosystem. In *Proceedings of the Tall Timbers fire ecology conference*, 18, 17–43.

Gelman, A., Carlin, J.B., Stern, H.S. & Rubin, D.B. (2013) *Bayesian data analysis, third edition (texts in statistical science)*. Boca Raton, FL: Chapman and Hall/CRC Press.

Goodrich, J.M. & Buskirk, S.W. (1995) Control of abundant native vertebrates for conservation of endangered species. *Conservation Biology*, 9(6), 1357–1364.

Greene, D.U., McCleery, R.A., Wagner, L.M. & Garrison, E.P. (2016) A comparison of four survey methods for detecting fox squirrels in the southeastern United States. *Journal of Fish and Wildlife Management*, 7(1), 99–106.

Hiers, J.K., Walters, J.R., Mitchell, R.J., Varner, J.M., Conner, L.M., Blanc, L.A. et al. (2014) Ecological value of retaining pyrophytic oaks in longleaf pine ecosystems. *The Journal of Wildlife Management*, 78(3), 383–393.

Hody, J.W. & Kays, R. (2018) Mapping the expansion of coyotes (*Canis latrans*) across North and Central America. *ZooKeys*, 759(759), 81–97.

Huegel, C.N., Dahlgren, R.B. & Gladfelter, H.L. (1986) Bedsite selection by white-tailed deer fawns in Iowa. *The Journal of Wildlife Management*, 50(3), 474–480.

Hurst, Z.M., McCleery, R.A., Collier, B.A., Fletcher, Jr. R.J., Silvy, N.J., Taylor, P.J. et al. (2013) Dynamic edge effects in small mammal communities across a conservation-agricultural interface in Swaziland. *PLoS One*, 8(9), e74520.

Jacqmain, E.I., Jones, R.H. & Mitchell, R.J. (1999) Influences of frequent cool-season burning across a soil moisture gradient on oak community structure in longleaf pine ecosystems. *The American Midland Naturalist*, 141(1), 85–100.

Jenkins, C.N., Van Houtan, K.S., Pimm, S.L. & Sexton, J.O. (2015) US protected lands mismatch biodiversity priorities. *Proceedings of the National Academy of Sciences*, 112(16), 5081–5086.

Kery, M. & Royle, J.A. (2016) *Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in R and BUGS*. Cambridge, MA: Academic Press.

Koenig, W.D. (1999) Spatial autocorrelation of ecological phenomena. *Trends in Ecology & Evolution*, 14(1), 22–26.

Landers, J.L., Van Lear, D.H. & Boyer, W.D. (1995) The longleaf pine forests of the southeast: requiem or renaissance? *Journal of Forestry*, 93(11), 39–44.

Lang, J.D., Powell, L.A., Krementz, D.G. & Conroy, M.J. (2002) Wood Thrush movements and habitat use: effects of forest management for Red-cockaded Woodpeckers. *The Auk*, 119(1), 109–124.

Laves, K.S. & Loeb, S.C. (1999) Effects of southern flying squirrels *Glaucomys volans* on red-cockaded woodpecker *Picoides borealis* reproductive success. *Animal Conservation*, 2(4), 295–303.

Linnell, J.D.C. & Strand, O. (2000) Interference interactions, co-existence and conservation of mammalian carnivores. *Diversity & Distributions*, 6(4), 169–176.

Little, R.J. & Rubin, D.B. (2014) *Incomplete data*. John Wiley & Sons, Inc.

Loggins, A.A., Shrader, A.M., Monadjem, A. & McCleery, R.A. (2019) Shrub cover homogenizes small mammals' activity and perceived predation risk. *Scientific Reports*, 9(1), 1–11.

Loudermilk, E.L., Scheller, R.M., Weisberg, P.J., Yang, J., Dilts, T.E., Karam, S.L. et al. (2013) Carbon dynamics in the future forest: the importance of long-term successional legacy and climate–fire interactions. *Global Change Biology*, 19(11), n/a.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. & Hines, J.E. (2006) *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Cambridge, MA: Academic Press.

Magura, T. (2002) Carabids and forest edge: spatial pattern and edge effect. *Forest Ecology and Management*, 157(1–3), 23–37.

Magura, T., Lövei, G.L. & Tóthmérész, B. (2017) Edge responses are different in edges under natural versus anthropogenic influence: a meta-analysis using ground beetles. *Ecology and Evolution*, 7(3), 1009–1017.

Manning, J.A. & Edge, W.D. (2004) Small mammal survival and downed wood at multiple scales in managed forests. *Journal of Mammalogy*, 85(1), 87–96.

Manral, V., Bargali, K., Bargali, S.S., Jhariya, M.K. & Padalia, K. (2022) Relationships between soil and microbial biomass properties and annual flux of nutrients in Central Himalayan forests, India. *Land Degradation & Development*, 12, 2014–2025.

McMurry, T.L. & Politis, D.N. (2010) Banded and tapered estimates for autocovariance matrices and the linear process bootstrap. *Journal of Time Series Analysis*, 31(6), 471–482.

Means, D.B. (2007) Vertebrate faunal diversity of longleaf pine ecosystems, *The longleaf pine ecosystem*. New York, NY: Springer. pp. 157–213 In.

Meek, P.D., Ballard, G., Claridge, A., Kays, R., Moseby, K., O'brien, T. et al. (2014) Recommended guiding principles for reporting on camera trapping research. *Biodiversity and Conservation*, 23(9), 2321–2343.

Nichols, J.D., Bailey, L.L., O'Connell, Jr. A.F., Talancy, N.W., Campbell Grant, E.H., Gilbert, A.T. et al. (2008) Multi-scale occupancy estimation and modelling using multiple detection methods. *Journal of Applied Ecology*, 45(5), 1321–1329.

Paton, P.W.C. (1994) The effect of edge on avian nest success: how strong is the evidence? *Conservation Biology*, 8(1), 17–26.

Perkins-Taylor, I.E. & Frey, J.K. (2018) Ecological factors associated with site occupancy of an endemic chipmunk. *The Journal of Wildlife Management*, 82(7), 1466–1477.

Plummer, M. (2003) JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. 3rd International Workshop on Distributed Statistical Computing (DSC 2003), Vienna, Austria.

Potash, A.D., Conner, L.M. & McCleery, R.A. (2019) Vertical and horizontal vegetation cover synergistically shape prey behaviour. *Animal Behaviour*, 152, 39–44.

Provencher, L., Herring, B.J., Gordon, D.R., Rodgers, H.L., Tanner, G.W., Hardesty, J.L. et al. (2001) Longleaf pine and oak responses to hardwood reduction techniques in fire-suppressed sandhills in northwest Florida. *Forest Ecology and Management*, 148(1–3), 63–77.

Reynolds, C., Fletcher, R.J., Carneiro, C.M., Jennings, N., Ke, A., LaScaleia, M.C. et al. (2018) Inconsistent effects of landscape heterogeneity and land-use on animal diversity in an agricultural mosaic: a multi-scale and multi-taxon investigation. *Landscape Ecology*, 33(2), 241–255.

Robel, R.J., Briggs, J.N., Dayton, A.D. & Hulbert, L.C. (1970) Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management*, 23, 295–297.

Sikes, R.S. & Animal Care and Use Committee of the American Society of Mammalogists. (2016) 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy*, 97(3), 663–688.

Sovie, A.R., Conner, L.M., Brown, J.S. & McCleery, R.A. (2021) Increasing woody cover facilitates competitive exclusion of a savanna specialist. *Biological Conservation*, 255, 108971.

Sovie, A.R., McCleery, R.A., Fletcher, R.J. & Hart, K.M. (2016) Invasive pythons, not anthropogenic stressors, explain the distribution of a keystone species. *Biological Invasions*, 18, 3309–3318.

Spirito, F., Rowland, M., Wisdom, M. & Tabeni, S. (2020) Tracking native small mammals to measure fine-scale space use in grazed and restored dry woodlands. *Global Ecology and Conservation*, 24, e01348.

Staller, E.L., Palmer, W.E., Carroll, J.P., Thornton, R.P. & Sisson, D.C. (2005) Identifying predators at northern bobwhite nests. *Journal of Wildlife Management*, 69(1), 124–132.

Steele, M.A., ROMPRÉ, G., Stratford, J.A., Zhang, H., Suchocki, M. & Marino, S. (2015) Scatterhoarding rodents favor higher predation risks for cache sites: the potential for predators to influence the seed dispersal process. *Integrative Zoology*, 10, 257–266. Available from: https://doi.org/10.1111/1749-4877.12134

Taulman, J.F. & Robbins, L.W. (2014) Range expansion and distributional limits of the nine-banded armadillo in the United States: an update of Taulman & Robbins (1996). *Journal of Biogeography*, 41(8), 1626–1630.

Thompson, F.R., Finch, D.M., Probst, J.R., Gaines, G.D. & Dobkin, D.S. (1999) Multi-resource and multi-scale approaches for meeting the challenge of managing multiple species. In: Bonney, R., Pashley, David N., Cooper, Robert J. & Niles, L. (Eds.) *Strategies for bird conservation: The partners in flight planning process*. Ithaca, NY: Cornell University, Cornell Lab of Ornithology. Available from: https://www.birds.cornell.edu/pifcapemay/thompson_etal.htm

Veech, J.A., Ott, J.R. & Troy, J.R. (2016) Intrinsic heterogeneity in detection probability and its effect on N-mixture models. *Methods in Ecology and Evolution*, 7(9), 1019–1028.

AUTHOR BIOGRAPHY

Adia R. Sovie is a Research Associate at Michigan State University. She obtained her PhD in Wildlife Ecology and Conservation from the University of Florida and her research interests include wildlife response to global change and quantitative ecology.

SUPPORTING INFORMATION

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

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