

Contents lists available at ScienceDirect

Forest Ecology and Management



journal homepage: www.elsevier.com/locate/foreco

# Frequent prescribed burns reduce mammalian species richness and occurrence in longleaf pine sandhills<sup> $\star$ </sup>

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## ARTICLE INFO

Keywords: Nest predator Invasive species Pinus palustris Occupancy Prescribed fire Intermediate disturbance hypothesis

# ABSTRACT

Prescribed fire is a critical forest management tool, the frequency and size of which can alter the composition of wildlife communities. In the longleaf pine ecosystem of the southeastern United States, frequent prescribed fire (1-3 year fire interval) is used to replicate natural processes that prevent woody encroachment and transition to alternate states. However, we have little understanding of how different scales and frequencies of fire influence medium and large mammals. To address this knowledge gap, we assessed the homogenizing influence of prescribed fire on mammal community composition at different fire frequencies and scales. We set 110 camera trap grids containing 990 individual camera points across conservation lands in north Florida and the Florida panhandle. We used a Bayesian multi-species occupancy modeling approach to assess the relationship between fire frequency and the occurrence of 11 mammal species across three spatial scales (0.2 ha, 12.57 ha, and 176.71 ha). Species richness was negatively associated with increased burn frequency at all scales and community occurrence was negatively associated with increased burn frequency at the two largest scales. Non-native ninebanded armadillos were negatively associated with increased burn frequency at all scales and non-native feral hogs were negatively associated with increased burn frequency at the two largest scales. Raccoons and opossums, both known nest predators, were negatively associated with increased burn frequency at the two largest scales. Our results indicate that prescribed fire applied at 1-3 year intervals could be used to reduce the occurrence of most non-native mammals and several prolific nest predators in longleaf pine sandhills, particularly at larger scales. However, these perceived benefits must be weighed against the concurrent loss of the ecosystem services and functions native generalist species provide.

#### 1. Introduction

Fire drives community composition in ecosystems across the globe (Pastro et al., 2014; Koltz et al., 2018; He et al., 2019). In savannas, fire may prevent succession to closed canopy forests by resetting secondary succession (Midgley et al., 2010). These fire-maintained savannas often support a diverse wildlife community (Loggins et al., 2019; Durigan and Ratter, 2016). However, fire frequency plays an important role in

determining the composition of these communities (He at al, 2019). There is considerable evidence that diversity in fire maintained systems peaks at intermediate levels of disturbance (intermediate disturbance hypothesis; Connell, 1978; He et al., 2019). However, how disturbance frequency influences diversity is less straightforward when non-native species are present (Hobbs and Huenneke, 1992) or when native communities are dominated by habitat generalists (Sullivan et al., 2016). Increased rates of disturbance may select for non-native species (Catford

https://doi.org/10.1016/j.foreco.2023.121596

Received 16 July 2023; Received in revised form 14 November 2023; Accepted 16 November 2023 Available online 28 November 2023 0378-1127/© 2023 Elsevier B.V. All rights reserved.

<sup>\*</sup> This research was funded by the Florida Fish and Wildlife Conservation Commission (agreement 11427), the University of Florida Institute of Food and Agricultural Sciences, and the USDA National Institute of Food and Agriculture (Hatch project FLA-WEC-005125).

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et al., 2012) while habitat generalists are likely insensitive to variable disturbance frequency. Therefore, changes in when peak biodiversity occurs with relation to the timing of disturbance may be driven by the presence of non-native species (Catford et al., 2012), confounding generally-accepted notions regarding the benefits of disturbance for biodiversity (Galil, 2007; Catford et al., 2012).

The longleaf pine (Pinus palustris) ecosystem is a fire-maintained pine-savanna ecosystem in the southeastern United States (Frost, 1993). Once spanning ~36,000,000 ha (Landers et al., 1995), disjunct patches comprising just 5 % of the original ecosystem remain (Oswalt et al., 2012; Miles, 2019). Restoration and maintenance guidelines recommend prescribed fire application at 1-3 year intervals (Howze et al., 2021) although longer intervals are common (Boone et al., 2017). How prescribed fire influences biodiversity within the longleaf pine ecosystem is well documented for plants (Brockway and Lewis, 1997; Kush et al., 1999; Glitzenstein et al., 2012), birds (Engstrom et al., 1984; Steen et al., 2013a), and some herpetofauna (Litt et al., 2001; Schurbon and Fauth, 2003; Steen at al, 2013b). However, implications for some mammalian inhabitants are incomplete or anecdotal (but see review by Darracq et al., 2016). Non-native mammalian inhabitants include three species: feral hogs (Sus scrofa), covotes (Canis latrans), and nine-banded armadillos (Dasypus novemcinctus). Feral hogs complicate restoration by killing up to 8320 longleaf pine seedlings per acre (Hanson and Karstad, 1959), spreading and aiding the establishment of invasive plants (Siemann et al., 2009; Bankovich et al., 2016), acting as a disease reservoir (Barrios-Garcia and Ballari, 2012), and depredating nests of game species (Sanders et al., 2020). Coyotes disproportionately impact game species, killing up to 37 % of white-tailed deer (Odocoileus virginianus) neonates and fawns (Kilgo et al., 2012; Nelson et al., 2015), killing wild turkey (Meleagris gallopavo) hens (Little et al., 2016), and depredating turkey nests (Lehman et al., 2008) as well as depredating nests of imperiled species (Malone et al., 2019). Nine-banded armadillos are comparatively less destructive, but also depredate nests of imperiled (Douglass and Winegarner, 1977) and game species (Staller et al., 2005; Dreibelbis et al., 2011) and are a disease reservoir (Sharma et al., 2015). The community of native mammals in longleaf pine savannas includes three habitat generalists including highly proficient nest predators like raccoons (Procyon lotor) and opportunistic nest predators like Virginia opossums (Didelphis virginiana) and bobcats (Lynx rufus; Staller et al., 2005; Malone et al., 2019). Raccoons depredate nests of economically important game species including northern bobwhite quail (Colinus virginianus; Staller et al., 2005) and wild turkey (Melville et al., 2014; Boone and Johnson, 2023) and imperiled species including gopher tortoises (Gopherus polyphemus; Landers et al., 1980; Moore et al., 2009). Yet, native meso (medium-sized) and large mammals are also critical to ecosystem functioning because of their role as seed dispersers (Willson et al., 1993; Steele and Koprowski, 2001), influence on vegetation structure via direct (consumption) and indirect (landscape of fear) manipulation (Rooney and Waller, 2003; Cherry et al., 2016), and participation in nutrient cycling (Pletscher et al., 1989) and disease transmission (Beineke et al., 2015).

Meso and large mammal community composition is likely influenced by the scale at which prescribed fire is applied. Frequent fires (1–3 year intervals) in the longleaf pine ecosystem have the potential to homogenize forest structure, plant diversity (Lashley et al., 2014), and resource availability (Darracq et al., 2016). Frequent fires can eliminate hard mast (turkey oak [*Quercus laevis*] acorns) and soft mast (blueberries [*Vaccinium spp.*] and saw palmetto [*Serenoa repens*] berries) vital to some wildlife (Martin, 1983; Stratman and Pelton, 1999; Stratman and Pelton, 2007; Lashley et al., 2014; Cherry et al., 2016). Likewise, the loss of structural diversity in vegetation limits resources associated with resting (Conner and Godbois, 2003), nesting, cover, and thermal regulation (Weigl et al., 1989) of mammalian inhabitants, including eastern gray squirrels (*Sciurus carolinensis*) and fox squirrels (*S. niger*). The effects of these changes may be amplified when prescribed fire is applied at increasing scales, subsequently homogenizing larger areas. The compositional and structural homogenization that results from larger, more frequent fire may select for generalist and non-native species.

Our understanding of the influence of fire frequency and scale on mammal communities remains limited because most studies have focused on a single species (Weigl et al., 1989; Sisson et al., 1990; Stratman and Pelton, 2007), lacked replication (Engstrom et al., 1984), investigated small spatial scales (Engstrom et al., 1984), or inferred species' responses using convenience data (Darracq et al., 2016). In particular, there is a gap in our knowledge of the response of the meso and large mammal community to the scale and frequency of fire in this system. To understand the relationship between fire, scale, and meso and large mammal use of longleaf pine sandhills, we investigated species occurrence in relation to fire frequency assessed at multiple spatial scales. We predicted that fire frequency would have minimal influence on community structure, because our suite of species was predominately composed of generalists capable of inhabiting a wide variety of vegetative communities (Werdelin, 1981; Gipson et al., 1998; Beasley et al., 2011; Walsh and Tucker, 2020). We predicted that non-native hog and covote occurrence would not be impacted by greater burn frequencies because of their high adaptive capacity (Gipson et al., 1998). Finally, due to the homogenizing effect of fire we also predicted that all species except non-native hogs and covotes would be negatively associated with increased fire frequency at the largest scale.

## 2. Material and methods

## 2.1. Survey area

We conducted field surveys at five sites within north-central Florida and the panhandle (Fig. 1). Our research sites included Camp Blanding Joint Training Center, Eglin Air Force Base, Jennings State Forest, Ocala National Forest, and St. Marks National Wildlife Refuge. Within each site, we confined our research to sandhill communities (Florida Natural Areas Inventory, 2014) characterized by well-drained sand ridges and drought-tolerant trees. The majority of each of our sites was actively burned by managers to reduce woody vegetation (burn interval ranged from 2.22 years to unburned in >20 years, burn histories are summarized in Table 1). Frequently burned (1–3 year burn interval) portions of our study sites had abundant longleaf pine, scattered pyrophytic oaks (as detailed in Hiers et al., 2014), and an understory of grasses, forbs, and small shrubs. Portions of our study sites that were burned less frequently had increased oak biomass, decreased herbaceous groundcover, and increased detritus.

#### 2.2. Scales of inference

We used a multi-scaled approach because (A) the optimal sampling scale is relative to a species' size (Thornton and Fletcher, 2014) and dispersal capabilities (Jackson and Fahrig, 2015), which varied considerably for the mammals we were studying, and (B) the homogenizing effect of frequent fire may be increasingly detrimental to wildlife as burn size increases by limiting resource availability and accessibility (Tiedemann et al., 2000). We measured the influence of burn frequency on mammalian occurrence at the localized scale of individual sampling points (0.20 ha; 25 m radius; point scale; Fig. 2), within patches of potential habitat (12.57 ha; 200 m radius around the center of a sampling grid; patch scale; Fig. 2), and at a neighborhood scale (176.71 ha; 750 m radius around the center of a sampling grid; neighborhood scale; Fig. 2).

#### 2.3. Field surveys

We conducted field surveys January-July, 2013 at St. Marks National Wildlife Refuge (January-February), Camp Blanding Joint Training Center (March), and Jennings State Forest (March–July), and in 2014 at Ocala National Forest (January-March) and Eglin Air Force Base (March–July). We measured the occurrence of mammals by placing nine



Fig. 1. Study sites (n = 5) located within the longleaf pine ecosystem of Florida, USA.

# Table 1

The minimum, average, and maximum number of fires that occurred in the preceding 20 years at the point (25 m radius around individual camera points), patch (200 m radius around grids of nine cameras), and neighborhood (750 m radius around grids of nine cameras) scales. Study sites included Camp Blanding Joint Training Center (1), Jennings State Forest (1), Eglin Air Force Base (2), Ocala National Forest (3), and St. Marks National Wildlife Refuge (4).

Study site	Point min	Point mean	Point max	Patch min	Patch mean	Patch max	Neighborhood min	Neighborhood mean	Neighborhood max
1	1.00	2.98	7.09	0.98	2.93	6.88	1.23	2.77	6.36
2	2.00	5.06	8.00	2.00	5.06	7.91	2.24	4.77	7.12
3	0.00	5.33	10.12	0.90	5.28	10.00	0.23	4.37	9.36
4	0.00	5.63	8.50	0.56	5.62	8.01	0.35	4.81	6.79



Fig. 2. We measured the influence of covariates collected at three scales on mammalian occurrence. These scales were the (A) point scale – 25 m radius around individual camera points, (B) patch scale – 200 m radius around grids of nine cameras, and (C) neighborhood scale – 750 m radius around grids of nine cameras.

camera traps (Trophy Cam®, Bushnell Outdoor Products, Overland Park, Kansas) in a  $3 \times 3$  arrangement on each grid with 100 m spacing between each camera point (Greene et al., 2016). We attached camera traps to the nearest tree at each point (< 10 m from point), or to a wooden stake when no tree was available, ~45 cm above the ground, allowing us to capture a large variety of meso and large mammals. We did not bait cameras to avoid biasing mammal occurrence by attracting animals from surrounding areas. We removed vegetation within 10 m of the camera to decrease the number of misfires caused by vegetation movement in windy conditions, and to increase mammal detection. We deployed cameras for four consecutive days at each point, and tallied the number of days (n  $\leq$  4 days) that cameras functioned properly as a measure of point-level survey effort (TotalCamDays) and cumulatively for each 9-point grid for the patch and neighborhood scales (n < 36days). We selected locations for grids using a stratified random sampling approach and placed them so their edges were at least 150 m apart. We stratified the placement of grids by three burn intervals: (A) frequent (> 0 but < 3 year burn interval), (B) intermediate (> 3 but < 5 year burn interval), and (C) infrequent (> 5 year burn interval; Darracq et al., 2016). We ran three grids at a time and, with few exceptions, these concurrently-run grids included one grid from each of the three burn intervals to minimize the influence of seasonal change or stochastic events (cold fronts, storms, etc.) on the results. We calculated burn interval for all locations using data provided by land managers for the previous 20 years. We randomly selected 35-39 grids in each of the three burn intervals using ArcGIS® v. 10.4.1 (ESRI, Redlands, California), for a total of 110 locations.

#### 2.4. Prescribed fire characteristics

We obtained burn history shapefiles from land managers and merged them into a single layer of total burns in ArcGIS®. We then rasterized this layer so cell size was  $1 \text{ m}^2$  and each cell contained a count value representative of the burn total over the previous 20 years. When burn total varied across a cell, the cell value was representative of the burn total covering the largest portion of the area. We then used the zonal statistics tool in ArcGIS® to calculate the average 20-year burn total (*BurnTotal*) within each point (n = 990; 0.20 ha; 25 m radius), patch (n = 110; 12.57 ha; 200 m radius around the center of a sampling grid), and neighborhood (n = 110; 176.71 ha; 750 m radius around the center of a sampling grid) buffer. We omitted portions of polygons lying outside the boundaries of our five research sites because burn data were not available for these areas.

#### 2.5. Vegetative characteristics

To determine if vegetation influenced detection probability, we measured shrub density (*ShrubDensity*) using the line-intercept method (Cook and Stubbendieck, 1986). We measured shrub density at the height of cameras (~45 cm) along four transects extending 10 m in each cardinal direction from each camera. We also generated a 9-point aggregate average of shrub density for the patch and neighborhood scales.

#### 2.6. Data analysis

In order to assess differences in the mammal community across fire frequency regimes, we used multi-species hierarchical occupancy modeling (Dorazio and Royle, 2005). This approach leverages detection non-detection data collected across all observed species to estimate species richness while accounting for heterogeneity in detection probabilities and covariate relationships among species (Dorazio et al., 2011). We treated each day that a camera was active in the field as a non-independent survey effort. At the point scale, we estimated species-specific detection probabilities for each day (Dorazio and Royle, 2005). At the patch and neighborhood scales, we aggregated detection non-detection data for each 9-point grid (if a species was observed anywhere on a grid, it was recorded as being present).

We employed a Bayesian hierarchical modeling approach to investigate point, patch, and neighborhood scale characteristics that we believed would affect species-specific and cumulative community occurrence and detection probabilities (Dorazio and Royle, 2005; Russell et al., 2009). Cumulative community occurrence and detection probabilities were the average occurrence and detection probabilities of the full suite of species. We fit a single full model for each of three spatial scales (point, patch, and neighborhood). We did not run additive models of multiple scales because we were interested in comparing between scales. We modeled the effects of survey effort (TotalCamDays) and micro-habitat structure (ShrubDensity) on the probability of detecting a species and cumulative community detection probability. We tested for the effects of BurnTotal on species-specific and community probability of site occupancy. We standardized (z-transformation) covariates on detection and site occupancy and modeled them with random effects, with species-level variation drawn from a common distribution with an estimated mean and variance (i.e. hyperparameters). To account for the spatial clustering of nine points within a grid, we included grid as a random effect in the point scale model. To account for the spatial clustering of grids within each site, because metrics summarized at the neighborhood scale sometimes resulted in overlap of sampled area within a site and because there was seasonal variation between when sites were sampled, we included site as a random effect in the patch and neighborhood scale models. We considered Camp Blanding Joint Training Center and Jennings State Forest a single site because they shared a border and their burn plans were managed jointly. We did not include site in the point scale model due to model non-convergence.

We estimated model parameters based on posterior distributions generated using Markov chain Monte Carlo (MCMC) implemented in WinBugs (v1.4.3, http://www.mrc-bsu.cam.ac.uk/software/bugs/, accessed 10 February 2018) accessed through R2WinBUGS (Sturtz et al., 2005) in program R (v3.4.2, R Core Team, 2017). We used uninformative (uniform) priors (Gelman et al., 1995; Gilks et al., 1996) and generated three chains of 50,000 iterations with a burn-in of 10,000 iterations and a thinning rate of 50, yielding 3000 samples. We assessed convergence of MCMC chains based on trace plots and the Gelman-Rubin diagnostic (Rhat), where values < 1.1 indicated convergence (Gelman and Hill, 2007). We considered model covariates to be relevant predictors of occurrence and detection when their 95 % Bayesian credibility intervals (CRI) did not include zero. We evaluated species-specific and community occurrence slope ( $\beta$ ) at each scale to assess the rate of change associated with change in fire frequency (Nekola and White, 1999).

We calculated species richness, which is the number of species present, at each spatial scale (individual point, patch, or neighborhood) using the Z matrix method (Kéry and Royle, 2016). We then calculated the relationship between fire frequency and species richness at each scale by regressing the sampling unit measures of species richness against their respective fire frequency using generalized linear models. To account for sampling and model uncertainty, we repeated this analysis for each of the 3000 retained MCMC samples (Reichert et al., 2017). We then assessed significance based on the distribution of slope coefficients where those with a 95 % CRI not inclusive of zero were considered relevant predictors of species richness. We evaluated slope ( $\beta$ ) at each scale to assess the rate of species richness change associated with change in fire frequency (Nekola and White, 1999).

#### 3. RESULTS

In total, we conducted 3960 days and nights of camera trapping across 110 camera grids containing 990 individual camera points. We sorted > 600,000 photos to remove camera trap misfires, retaining 14,958 photos of mammals. We detected 13 species of mammal (black bear [*Ursus americanus*], bobcat, coyote, eastern cottontail [*Sylvilagus*]

*floridanus*], eastern gray squirrel, feral hog, fox squirrel, gray fox [*Urocyon cinereoargenteus*], nine-banded armadillo, raccoon, striped skunk [*Mephitis mephitis*], Virginia opossum, and white-tailed deer). We excluded black bear and striped skunk from analysis due to their low detection rates (observed during <0.10 % of game camera surveys). Observed species richness ranged from 0 to 5 at the point scale and 0-8 at the patch/neighborhood scales.

At all scales mammalian community occurrence probability was lower in areas that experienced an average of 10 burns in the previous 20 years (2-year burn interval) compared to areas that experienced zero burns (reduction by scale: point 84 %; patch 89 %; neighborhood 87 %; Fig. 3). Likewise, across all scales richness of studied mammalian species was reduced by > 50 % in areas with a 2-year burn interval compared to areas unburned in the previous 20 years (reduction by scale: point 52 %; patch 58 %; neighborhood 61 %; Fig. 4).

At the point scale, cumulative mammalian community detection probability was positively associated with increased *TotalCamDays* ( $\beta$ 1.27; CRI 0.05 – 2.48; Rhat 1.01), but *ShrubDensity* ( $\beta$  – 0.25; CRI –0.62 to 0.09; Rhat 1.00) was not a relevant predictor. *AvgBurnTotal* ( $\beta$  – 0.48; CRI –1.15 to 0.14; Rhat 1.00) was not a relevant predictor of community occurrence at the point scale, yet community occurrence decreased from 0.18 to 0.03 as *AvgBurnTotal* increased from zero to 10 (Fig. 3). Species richness at the point scale was negatively associated with *AvgBurnTotal* ( $\beta$  – 0.24; CRI –0.28 to –0.20; Fig. 4). Species richness decreased from 4.64 to 2.23 when *AvgBurnTotal* increased from zero to 10 (Fig. 4). Fox squirrel occurrence increased with *AvgBurnTotal*, while occurrence of the gray fox, gray squirrel, and nine-banded armadillo decreased (Fig. 3; Table A.1). At this smallest scale, burn frequency was not a relevant predictor of occurrence of the seven other mammals found on the study sites (Fig. 3; Table A.1).

At the patch scale, neither *TotalCamDays* ( $\beta$  0.02; CRI -0.10 to 0.17; Rhat 1.00) nor *ShrubDensity* ( $\beta$  - 0.30; CRI -0.73 to 0.13; Rhat 1.00) were relevant predictors of cumulative mammalian community detection. Community occurrence and species richness were negatively associated with *AvgBurnTotal* ( $\beta$  - 0.74; CRI -1.38 to -0.13; Rhat 1.00;

Fig. 3 and  $\beta$  – 0.48; CRI –0.58 to –0.39; Fig. 4, respectively). As *Avg-BurnTotal* increased from zero to 10 community occurrence decreased from 0.65 to 0.07 (Fig. 3) and species richness decreased from 8.27 to 3.48 (Fig. 4). Occurrence of all species, except the fox squirrel, were negatively associated with increased *AvgBurnTotal* at the patch scale (Fig. 3; Table A.2). *AvgBurnTotal* was a relevant predictor of gray squirrel, feral hog, nine-banded armadillo, opossum, and raccoon occurrence (Fig. 3; Table A.2).

At the largest (neighborhood) scale, neither *TotalCamDays* ( $\beta$  0.04; CRI –0.09 to 0.20; Rhat 1.00) nor *ShrubDensity* ( $\beta$  – 0.27; CRI –0.69 to 0.14; Rhat 1.00) were relevant predictors of cumulative mammalian community detection. Community occurrence and species richness at the neighborhood scale were negatively associated with *AvgBurnTotal* ( $\beta$  – 0.66; CRI –1.21 to –0.16; Rhat 1.00; Fig. 3 and  $\beta$  – 0.48; CRI –0.58 to –0.39; Fig. 4, respectively). As *AvgBurnTotal* increased from zero to 10 community occurrence decreased from 0.57 to 0.07 (Fig. 3) and species richness decreased from 7.99 to 3.15 (Fig. 4). Occurrence probabilities of all 11 species were negatively associated with increased *AvgBurnTotal* at the neighborhood scale (Fig. 3; Table A.3). *AvgBurnTotal* was a relevant predictor of gray squirrel, feral hog, nine-banded armadillo, opossum, and raccoon occurrence (Fig. 3; Table A.3).

## 4. Discussion

In contrast to other disturbance dependent systems (Lepczyk et al., 2008; He et al., 2019), we found that community occurrence and species richness peaked at low levels of disturbance (fire) for a mammal community dominated by habitat generalist and non-native species. Counter to our prediction, we found reductions of cumulative community occurrence and species richness with increased burn frequencies across most spatial scales. Mammal species richness showed greater reductions at larger spatial scales when burn frequency was high (1–3 year burn intervals). At the largest scale, all 11 meso and large mammal species (five significantly) displayed negative associations with increased burn frequency. These results highlight the complexity and importance of



**Fig. 3.** The predicted relationship between the average 20 year burn total and the occurrence probability of 11 mammalian species inhabiting longleaf pine forests at three spatial scales. The black line depicts the model average (community occurrence). Statistically significant (p < 0.05) species-specific relationships are depicted with unique patterns in black, while non significant relationships are shown in solid gray. Spatial scales included point (0.20 ha; 25 m radius), patch (12.57 ha; 200 m radius around the center of a sampling grid), and neighborhood (176.71 ha; 750 m radius around the center of a sampling grid).

![](_page_5_Figure_2.jpeg)

**Fig. 4.** The predicted relationship between the average 20 year burn total and mammalian species richness at three scales in longleaf pine forests. The black line depicts the model average. All depicted relationships were statistically significant (p < 0.05). Spatial scales included point (0.20 ha; 25 m radius), patch (12.57 ha; 200 m radius around the center of a sampling grid), and neighborhood (176.71 ha; 750 m radius around the center of a sampling grid).

understanding the understudied role of fire in shaping wildlife communities across multiple spatial scales.

Native mammals are important contributors to ecosystem services, maintenance, and biodiversity. Gray squirrels, which were negatively associated with increased burn frequency at all 3 scales, and fox squirrels, which were only positively associated with increased burn frequency at the smallest scale, aid seed dispersal and influence the structure of future forests (Steele et al., 2005). Gray and fox squirrels also disperse fungal spores (Steele and Koprowski, 2001; Zaharick et al., 2015) and are a food source for many species (Koprowski, 1994a; Koprowski, 1994b). Reduced gray and fox squirrel occurrence could alter the composition and distribution of tree, fungal, and predator communities. Opossums likewise perform ecosystem services, including aiding carrion removal (Sawyer et al., 2022). Their negative association with increased burn frequency at the 2 largest scales indicates that increased burn frequency could increase prevalence of diseases associated with carrion persistence. Gray foxes consume crop pests (Greenberg et al., 1988; Wilson and Thomas, 1999), scarify and disperse seeds (Wilson and Thomas, 1999; Rubalcava-Castillo et al., 2020), and are already in decline throughout portions of their range (Bauder et al., 2020; Allen et al., 2021). Their negative association with increased burn frequency at the smallest scale suggests increased burn frequencies alter their distributions by removing preferred habitat, which could

exacerbate their decline if habitat is limiting at larger scales.

Of the species that had a negative association to increasing burn frequency, two were non-native (feral hog, nine-banded armadillo) while the third non-native species (coyote) had no association. Feral hogs cause considerable damage in the longleaf pine ecosystem, including seedling destruction that impedes forest regeneration (Hanson and Karstad, 1959), nest predation (northern bobwhite quail: Perez, 2020; wild turkey: Sanders et al., 2020), and the spread of invasive plants (Siemann et al., 2009; Bankovich et al., 2016) and zoonotic diseases (Barrios-Garcia and Ballari, 2012). Feral hogs responded negatively to increased fire frequency at the two largest scales. Similarly, frequent fires applied at any of the three tested scales reduced occurrence of nine-banded armadillos. However, unlike feral hogs, armadillos provide notable services. Armadillos promote nutrient cycling (Sawyer et al., 2012), influence forest structure and dynamics (Sawyer et al., 2012), are a prev source for mesocarnivores (Bueno and Motta-Junior, 2004; Bianchi et al., 2010), and their burrows likely provide refuge for native wildlife species, as has been found for other armadillo species (Desbiez and Kluyber, 2013). While this negative association between armadillos and fire is not novel (Jorge et al., 2020), it had not been shown to be consistent across multiple spatial scales, as in this study.

Five mammal species negatively associated with fire frequency (raccoon, feral hog, nine-banded armadillo, gray fox, and opossum) prey on nests and imperiled species. Raccoons eat the eggs of federally threatened gopher tortoises (Landers et al., 1980; Moore et al., 2009) and raccoons (Butler and Sowell, 1996) and feral hogs (Burton et al., 2012) eat juvenile gopher tortoises. Gopher tortoises are ecosystem engineers, whose burrows support at least 60 vertebrate and 302 invertebrate species, including imperiled species (Jackson and Milstrey, 1989; Potash et al., 2020b). Many of the mammal species negatively associated with fire are also known predators of wild turkeys, the second most popular game species throughout most of their range (United States Department of the Interior, United States Fish and Wildlife Service, United States Department of Commerce, 2018), accounting for \$4.4 billion in total economic activity in 2003 (\$7.08 billion in 2022 dollars; Southwick Associates, 2003). Raccoons (Davis et al., 1995; Melville et al., 2014; Sanders et al., 2020; Boone and Johnson, 2023), feral hogs (Sanders et al., 2020), opossums (Kozicky, 1948; Melville et al., 2014), gray foxes (Davis et al., 1995; Sanders et al., 2020), and nine-banded armadillos (Melville et al., 2014; Sanders et al., 2020) predate turkey nests, poults, or simulated turkey nests. Nest predation, nest abandonment, and poult predation frequently claim > 75 % of all nests laid (Haegen et al., 1988; Dreibelbis et al., 2008). Reducing nest failure and turkey poult mortality caused by predation could help mitigate recent turkey population declines observed throughout much of the southeastern U.S. (Tapley et al., 2011; Eriksen et al., 2015; Chamberlain et al., 2022).

Of the species detected, the occurrence of species with the smallest home ranges (gray squirrels, nine-banded armadillos, and opossums; Don, 1983; Layne and Glover, 1977; Lay, 1942) decreased at high fire frequencies as scale increased. This suggests that burning at increased spatial scales may make some resources hard to find or too energetically expensive to obtain within their home range. This could explain the observed pattern of reduced species-specific and community occurrence of meso and large mammals when the largest scale had a history of frequent fires. Research on other vertebrate communities suggests similar patterns of decreasing occurrence and species richness with increasing burn frequency (Conner et al., 1999; Schurbon and Fauth, 2003; Allen et al., 2006; Smith et al., 2006; Stratman and Pelton, 2007).

Prescribed fire is vital to the restoration and maintenance of the longleaf pine ecosystem. However, management objectives must inform the frequency and spatial scale at which prescribed fire is applied. Frequent fire applied at large scales can select for habitat specialists and imperiled species, but our findings suggest that in return generalist species may decline or be eliminated. While specialists and imperiled species conservation is an important and common management goal, the contributions of generalist species to biodiversity, ecosystem function, and ecosystem services should not be ignored.

Frequent fires (1–3 year intervals) applied at increasing spatial scales homogenize vegetative communities and reduce shrub cover (but see Hiers et al., 2014 for nuanced discussion) and, as our findings demonstrate, can reduce the occurrence of generalist native species. This outcome may be desirable if the management objective prioritizes endemic, specialist, and imperiled species (e.g. birds, Whiting et al., 2007; amphibians, Klaus and Noss, 2016; snakes, Howze and Smith, 2021). Likewise, if management objectives prioritize reducing nest predator and non-native species occurrence, large, frequent prescribed fires may be desirable.

A mosaic approach where burns occur at smaller spatial scales and burn intervals vary between burn units is necessary if these generalist mammal species and their ecosystem functions and services are to be retained. An ideal example includes gray and fox squirrels. While fox squirrels are found in many vegetative communities (Greene and McCleery, 2017), they are often associated with longleaf pine forests managed with prescribed fire (Perkins and Conner, 2004; Boone et al., 2017; Potash et al., 2020a). Fox squirrels have a size-based competitive advantage over eastern gray squirrels when accessing resources within the park-like vegetative structure produced by 1–3 year burn intervals, but gray squirrels become dominant as tree and shrub density increase at longer burn intervals (Sovie et al., 2020; Sovie et al., 2021). Efforts to ensure that both species occur across the landscape may require a mosaic management approach that includes patches of frequently burned park-like areas and patches of moderate or infrequently burned areas with higher shrub and tree densities. Our work suggests that assessing the efficacy of these efforts could be most appropriate when conducted at larger spatial scales.

A major criticism of mosaic fire management approaches is that mosaics may provide habitat for species, such as nest predators, that are detrimental to the conservation of imperiled or otherwise prioritized species. While evidence does exist to support this assertion (Chamberlain et al., 2002; Kirby et al., 2017; Jorge et al., 2020), our finding that the occurrence of many nest predators decreased at scales as small as the patch scale (12.57 ha) suggests nest predator occurrence could be reduced in frequently burned areas even if fires are relatively small. Additionally, a 1–2 year burn interval produces nesting and brood cover important to northern bobwhite quail (Brooke et al., 2017). While eastern wild turkey nest site selection does not appear to be influenced by how recently prescribed fire occurred, areas burned within the last two years are selected for by wild turkey broods (Wood et al., 2019). Increasing the distance between frequently burned areas and infrequently burned areas and increasing the size of frequently burned patches could allow for the simultaneous conservation of disturbance-dependent imperiled species and generalist species, to the benefit of landscape-scale biodiversity.

While our study did investigate the influence of fire frequency across multiple scales on meso and large mammal occurrence, it did not directly measure the scale of each fire. Additionally, we investigated the average number of burns at each scale. While informative, this metric does have limitations (e.g. this metric does not differentiate between one fire that burns an entire scale once in 20 years and two fires that each burn 50 % of a scale once in twenty years. Both would be interpreted as one burn per 20 years). Additional research is needed to assess how fire size (as a continuous variable) and burn unit configuration influence meso and large mammal occurrence in longleaf pine sandhills.

## CRediT authorship contribution statement

Wesley Boone: Conceptualization, Data Collection, Methodology, Formal analysis, Writing. Britany Bankovich: Formal analysis, Review, Editing. Brian Reichert: Formal analysis, Visualization, Review, Editing. Mandy Watson: Formal analysis, Review, Editing. Robert McCleery: Funding acquisition, Supervision, Conceptualization, Methodology, Review, Editing.

# **Declaration of Competing Interest**

The authors have no competing interests to disclose.

#### Data availability

Data will be made available on request.

#### Acknowledgements

We thank the Florida Fish and Wildlife Conservation Commission, Camp Blanding Joint Training Center, Eglin Air Force Base, Jennings State Forest, Ocala National Forest, and St. Marks National Wildlife Refuge, especially B. Camposano, C. Sekerak, J. Perkins, J. Preston, R. Felix, M. Keys, and T. Peacock. We thank the numerous volunteers, technicians, and lab members that helped with field research. We thank Daniel Greene for numerous conversations that benefitted project design and implementation. This research was funded by Florida's State Wildlife Grant through Florida's Wildlife Legacy Initiative, the University of Florida Institute of Food and Agricultural Sciences, and the USDA National Institute of Food and Agriculture, Hatch project FLA-WEC-

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005125. We thank 2 anonymous reviewers for providing helpful comments on this manuscript. We thank Hazel-rah for raspberries and inspiration!.

## Appendix

## Table A1

Species-specific and community summaries of covariate effects on occupancy (psi) and detection (p) at the point scale (25 m radius). Mean, standard deviation (SD), and Bayesian credibility interval (CRI) are based on model averaged posterior samples. We considered model covariates to be relevant predictors of species occurrence and detection when 95 % CRI's did not cross zero. We assessed model convergence using the Gelman-Rubin diagnostic (Rhat), where values < 1.1 indicated convergence (Gelman and Hill, 2007).

Species	Common name	Covariate	Mean	SD	95 % CRI	Rhat
Community (all species)	na	Psi(burn total)	-0.48	0.34	-1.15 – 0.14	1.00
		P(total cam days)	1.27	0.61	0.05 - 2.48	1.01
		P(shrub density)	-0.25	0.18	-0.62 - 0.09	1.00
Canis latrans	Coyote	Psi(burn total)	-0.30	0.17	-0.63 - 0.02	1.01
	-	P(total cam days)	0.21	0.19	-0.15 – 0.59	1.00
		P(shrub density)	-0.13	0.06	-0.24 0.02	1.00
Dasypus novemcincyus	Armadillo	Psi(burn total)	-1.48	0.49	-2.630.72	1.01
		P(total cam days)	0.83	0.92	-0.25 – 3.37	1.01
		P(shrub density)	-0.01	0.17	-0.35 – 0.34	1.00
Didelphis virginiana	Virginia opossum	Psi(burn total)	0.12	0.16	-0.17 – 0.44	1.00
		P(total cam days)	0.62	0.49	-0.12 - 1.81	1.01
		P(shrub density)	0.15	0.09	-0.01 - 0.32	1.00
Lynx rufus	Bobcat	Psi(burn total)	-0.13	0.51	-1.26 – 0.79	1.03
		P(total cam days)	0.86	0.87	-0.14 - 3.26	1.01
		P(shrub density)	-0.65	0.27	-1.220.16	1.00
Odocoileus virginianus	White-tailed deer	Psi(burn total)	-0.17	0.17	-0.51 – 0.17	1.00
		P(total cam days)	0.98	1.06	-0.14 - 3.85	1.00
		P(shrub density)	0.16	0.19	-0.20 - 0.53	1.00
Procyon lotor	Raccoon	Psi(burn total)	-0.28	0.68	-1.78 – 1.05	1.01
		P(total cam days)	0.80	0.87	-0.33 – 3.13	1.01
		P(shrub density)	0.16	0.25	-0.29 - 0.68	1.01
Sciurus carolinensis	Eastern gray squirrel	Psi(burn total)	-1.22	0.19	-1.61 - 0.86	1.00
		P(total cam days)	1.01	1.09	-0.15 – 4.16	1.02
		P(shrub density)	-0.11	0.14	-0.37 – 0.18	1.00
Sciurus niger	Fox squirrel	Psi(burn total)	0.57	0.25	0.08 - 1.06	1.00
		P(total cam days)	0.96	0.94	-0.05 – 3.50	1.03
		P(shrub density)	-0.87	0.24	-1.38 0.43	1.00
Sus scrofa	Feral hog	Psi(burn total)	-0.33	0.18	-0.69 – 0.02	1.00
		P(total cam days)	0.97	1.07	-0.16 – 3.97	1.00
		P(shrub density)	-0.07	0.16	-0.38 – 0.26	1.00
Sylvilagus floridanus	Eastern cottontail	Psi(burn total)	-0.24	0.17	-0.57 – 0.10	1.01
		P(total cam days)	0.56	0.48	-0.19 – 1.70	1.00
		P(shrub density)	-0.56	0.15	-0.88 0.29	1.00
Urocyon cinereoargenteus	Gray fox	Psi(burn total)	-1.79	0.39	-2.66 1.13	1.01
		P(total cam days)	0.88	0.97	-0.25 – 3.66	1.01
		P(shrub density)	-0.91	0.27	-1.50 0.43	1.00

#### Table A2

Species-specific and community summaries of covariate effects on occupancy (psi) and detection (p) at the patch scale (200 m radius). Mean, standard deviation (SD), and Bayesian credibility interval (CRI) are based on model averaged posterior samples. We considered model covariates to be relevant predictors of species occurrence and detection when 95 % CRI's did not cross zero. We assessed model convergence using the Gelman-Rubin diagnostic (Rhat), where values < 1.1 indicated convergence (Gelman and Hill, 2007).

Species	Common name	Covariate	Mean	SD	95 % CRI	Rhat
Community (all species)	na	Psi(burn total)	-0.74	0.32	-1.380.13	1.00
		P(total cam days)	0.02	0.07	-0.10 - 0.17	1.00
		P(shrub density)	-0.30	0.22	-0.73 - 0.13	1.00
Canis latrans	Coyote	Psi(burn total)	-0.40	0.72	-1.83 - 1.00	1.00
		P(total cam days)	0.02	0.11	-0.20 - 0.26	1.00
		P(shrub density)	-0.62	0.26	-1.16 0.14	1.00
Dasypus novemcincyus	Armadillo	Psi(burn total)	-1.52	0.49	-2.700.70	1.00
		P(total cam days)	0.08	0.16	-0.14 - 0.48	1.00
		P(shrub density)	-0.06	0.26	-0.54 - 0.49	1.00
Didelphis virginiana	Virginia opossum	Psi(burn total)	-0.67	0.27	-1.260.17	1.00
		P(total cam days)	0.03	0.09	-0.15 - 0.23	1.00
		P(shrub density)	-0.03	0.25	-0.49 - 0.49	1.00
Lynx rufus	Bobcat	Psi(burn total)	-0.56	0.70	-2.12 - 0.75	1.00
		P(total cam days)	0.07	0.16	-0.16 - 0.45	1.01
		P(shrub density)	0.07	0.33	-0.54 - 0.80	1.00
Odocoileus virginianus	White-tailed deer	Psi(burn total)	-0.90	0.62	-2.20 - 0.26	1.00

(continued on next page)

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## Table A2 (continued)

Species	Common name	Covariate	Mean	SD	95 % CRI	Rhat
		P(total cam days)	-0.02	0.08	-0.20 - 0.13	1.01
		P(shrub density)	0.20	0.12	-0.02 - 0.44	1.00
Procyon lotor	Raccoon	Psi(burn total)	-0.60	0.28	-1.190.07	1.00
		P(total cam days)	-0.01	0.09	-0.21 - 0.16	1.00
		P(shrub density)	-0.77	0.20	-1.17 0.40	1.00
Sciurus carolinensis	Eastern gray squirrel	Psi(burn total)	-1.66	0.34	-2.351.03	1.00
		P(total cam days)	0.07	0.11	-0.11 - 0.34	1.00
		P(shrub density)	-0.06	0.19	-0.39 – 0.35	1.00
Sciurus niger	Fox squirrel	Psi(burn total)	0.14	0.42	-0.73 - 0.89	1.00
		P(total cam days)	0.01	0.09	-0.19 - 0.20	1.00
		P(shrub density)	-1.11	0.30	-1.730.55	1.00
Sus scrofa	Feral hog	Psi(burn total)	-1.41	0.50	-2.520.55	1.00
		P(total cam days)	-0.03	0.12	-0.33 – 0.17	1.00
		P(shrub density)	-0.89	0.37	-1.630.17	1.00
Sylvilagus floridanus	Eastern cottontail	Psi(burn total)	-0.44	0.27	-1.00 - 0.06	1.00
		P(total cam days)	0.02	0.09	-0.16 - 0.20	1.00
		P(shrub density)	-0.17	0.14	-0.43 - 0.10	1.00
Urocyon cinereoargenteus	Gray fox	Psi(burn total)	-0.07	0.25	-0.57 – 0.45	1.00
		P(total cam days)	0.03	0.12	-0.18 - 0.31	1.00
		P(shrub density)	0.21	0.27	-0.30 – 0.75	1.00

#### Table A3

Species-specific and community summaries of covariate effects on occupancy (psi) and detection (p) at the neighborhood scale (750 m radius). Mean, standard deviation (SD), and Bayesian credibility interval (CRI) are based on model averaged posterior samples. We considered model covariates to be relevant predictors of species occurrence and detection when 95 % CRI's did not cross zero. We assessed model convergence using the Gelman-Rubin diagnostic (Rhat), where values < 1.1 indicated convergence (Gelman and Hill, 2007).

Species	Common name	Covariate	Mean	SD	95 % CRI	Rhat
Community (all species)	na	Psi(burn total)	-0.66	0.28	-1.21 - 0.16	1.00
		P(total cam days)	0.04	0.08	-0.09 - 0.20	1.00
		P(shrub density)	-0.27	0.21	-0.69 - 0.14	1.00
Canis latrans	Coyote	Psi(burn total)	-0.39	0.64	-1.63 - 0.96	1.00
	-	P(total cam days)	0.03	0.11	-0.18 - 0.27	1.00
		P(shrub density)	-0.62	0.26	-1.170.15	1.00
Dasypus novemcincyus	Armadillo	Psi(burn total)	-1.14	0.44	-2.12 - 0.43	1.00
		P(total cam days)	0.11	0.17	-0.12 - 0.58	1.01
		P(shrub density)	0.01	0.27	-0.47 - 0.58	1.00
Didelphis virginiana	Virginia opossum	Psi(burn total)	-0.85	0.28	-1.430.34	1.00
		P(total cam days)	0.04	0.10	-0.14 - 0.26	1.00
		P(shrub density)	-0.10	0.25	-0.52 - 0.42	1.00
Lynx rufus	Bobcat	Psi(burn total)	-0.55	0.51	-1.67 - 0.36	1.00
		P(total cam days)	0.09	0.16	-0.13 - 0.51	1.01
		P(shrub density)	0.06	0.33	-0.58 - 0.76	1.00
Odocoileus virginianus	White-tailed deer	Psi(burn total)	-0.80	0.52	-1.88 - 0.16	1.00
		P(total cam days)	-0.02	0.09	-0.21 - 0.13	1.00
		P(shrub density)	0.21	0.12	-0.01 - 0.44	1.00
Procyon lotor	Raccoon	Psi(burn total)	-0.66	0.27	-1.21 - 0.15	1.00
		P(total cam days)	-0.002	0.09	-0.20 - 0.17	1.00
		P(shrub density)	-0.77	0.19	-1.160.41	1.00
Sciurus carolinensis	Eastern gray squirrel	Psi(burn total)	-1.33	0.30	-1.960.77	1.00
		P(total cam days)	0.09	0.12	-0.10 - 0.39	1.00
		P(shrub density)	-0.01	0.19	-0.37 - 0.40	1.00
Sciurus niger	Fox squirrel	Psi(burn total)	-0.02	0.44	-0.91 - 0.79	1.00
		P(total cam days)	0.02	0.10	-0.19 - 0.22	1.00
		P(shrub density)	-1.14	0.30	-1.74 - 0.57	1.00
Sus scrofa	Feral hog	Psi(burn total)	-0.93	0.40	-1.830.26	1.00
		P(total cam days)	-0.01	0.13	-0.31 - 0.21	1.00
		P(shrub density)	-0.75	0.37	-1.550.06	1.00
Sylvilagus floridanus	Eastern cottontail	Psi(burn total)	-0.40	0.25	-0.91 - 0.08	1.00
		P(total cam days)	0.03	0.10	-0.16 - 0.24	1.00
		P(shrub density)	-0.17	0.14	-0.44 - 0.10	1.00
Urocyon cinereoargenteus	Gray fox	Psi(burn total)	-0.02	0.25	-0.53 - 0.46	1.00
		P(total cam days)	0.05	0.12	-0.18 - 0.33	1.00
		P(shrub density)	0.22	0.27	-0.31 – 0.75	1.00

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