

Assessing the Influence of Prescribed Fire on Faunal Communities in a Pyric Landscape

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# **Assessing the Influence of Prescribed Fire on Faunal Communities in a Pyric Landscape**

**Marcelo Jorge**

## **ABSTRACT**

Understanding the link between environmental factors such as disturbance events, land cover, and soil productivity to spatial variation in animal distributions and vital rates is fundamental to population ecology and wildlife management. The Longleaf pine (*Pinus palustris*; hereafter, LLP) ecosystem is an archetypal fire-mediated ecosystem, which has seen drastic reductions in land area due to fire suppression. Current restoration utilizes prescribed fire and hardwood removal, but more research is needed to understand the influence of these restoration efforts on the wildlife that exist in that ecosystem. As such, we conducted field surveys on Camp Blanding Joint Training Center and Wildlife Management Area to understand how fire influences relative abundances of mammalian predators, occupancy and species richness of avian species, guilds and communities, and vital rates of white-tailed deer (*Odocoileus virginianus*) fawns.

Our results indicated that mammalian predator space use, and avian species richness were influenced by fire and land cover. Mammalian predator space use was altered by fire conditions and land cover. This mechanism may support predator management strategies that utilizes commonly management techniques for the restoration and conservation of the LLP ecosystem to indirectly alter predator distributions, which has the potential to positively affect the management of important species within this ecosystem. Some mammalian mesocarnivores historically common throughout the southeastern United States were rarely detected, suggesting more research is needed to identify the cause of the potential decline in mesocarnivores in the Southeastern United States.

Avian species richness at the community level was positively influenced by the heterogeneity of post fire conditions, or pyrodiversity. Avian species richness of the cavity nesting guild was negatively influenced by increasing time-since-fire. Our results suggest that managers can promote avian community diversity by reducing the size of burn units to create areas with multiple adjacent burn units, with unique fire histories and a mosaic of post-fire conditions.

Lastly, fawn recruitment was greater on the higher productivity site than the low productivity site on CB. However, within sites soil productivity did not have a demonstrable effect. In fact, we observed differences between sites, but did not observe any effects of covariates on spatial variation in density or survival of fawns within sites. Although we did not explicitly test the factors influencing our parameters between sites, we hypothesize that the variation in coyote activity rates as well as soil productivity and its subsequent effects (i.e. forage availability, concealment cover, and land cover type) likely drove the differences we saw between sites. These results are relevant to local managers and provide support for unit-specific, deer management on CB.

In conclusion, understanding the influence of fire in a frequently burned landscape allows us to better inform management of predators and avian communities using prescribed burns, and the differences in deer populations between areas allowed us to better inform managers on harvest quotas so that the magnitude of the effect of harvest can better match the population vital rates of each area.

# **Assessing the Influence of Prescribed Fire on Faunal Communities in a Pyric Landscape**

**Marcelo Jorge**

## **GENERAL AUDIENCE ABSTRACT**

Understanding the link between environmental factors such as fire, land cover and soil productivity is essential for wildlife managers to maintain healthy wildlife populations. The Longleaf pine (*Pinus palustris*) ecosystem requires frequent fire and has seen drastic reductions in land area due to fire suppression. Current restoration utilizes prescribed fire, controlled burning of an area, and hardwood removal, logging hardwood trees such as oaks, but more research is needed to understand how this restoration influences the wildlife in the longleaf pine ecosystem. As such, we collected data collected from Camp Blanding Joint Training Center and Wildlife Management Area to understand how fire influences the relative numbers of mammalian predators, the distribution and species richness (i.e. number of unique species) of avian species, guilds and communities, and vital rates (i.e. births, survival to a certain age) of white-tailed deer fawns.

Our results indicated that mammalian predator distributions, and avian species richness were influenced by fire and land cover. Mammalian predator space use was altered by fire conditions and landcover, which supports a predator management strategy that utilizes prescribed burning and hardwood removal used in restoration and conservation of the LLP ecosystem to indirectly alter predator distributions. Some mammalian mesocarnivores (i.e. foxes, skunks, weasels, etc.) historically common throughout the southeastern United States were rarely detected, suggesting more research is needed to identify the cause of the potential decline of cryptic mesocarnivores in the Southeastern United States.

Avian species richness, number of unique species, at the community level was positively influenced by pyrodiversity, the number of unique burn years in an area. This supports and further extends the ‘pyrodiversity begets biodiversity’ hypothesis for avian species, which states that greater pyrodiversity increases the diversity of bird species in that area. Avian species richness of cavity nesting birds decreased with increasing time since fire. Our results suggest that managers can promote avian community diversity by reducing the size of burn units to create areas with multiple adjacent burn units, with unique fire histories and a mosaic of post-fire conditions.

Lastly, fawn recruitment was greater on the higher productivity site than the low productivity site, however, within sites soil productivity did not seem to influence birth and recruitment. Although we did not statistically test the factors influencing our parameters between sites, we hypothesize that the variation in coyote activity rates as well as soil productivity and its subsequent effects (i.e. forage availability, concealment cover, and land cover type) likely drove the differences we saw between sites. These results are relevant to local managers and provide support for managing deer differently across both sites.

In conclusion, understanding the influence of fire in a frequently burned landscape allows us to better inform management of predators and avian communities using prescribed burns, and the differences in deer populations between areas allowed us to better inform managers on harvest quotas so that the magnitude of the effect of harvest can better match the population vital rates of each area.

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## Overall Introduction

In the United States, federal forest-fire management began in 1886 when the U.S. Army patrolled forests to suppress fires (Agee, 1974). In 1916, the U.S. Forest Service prioritized fire suppression, altering the trajectory of numerous ecosystems in North America (Van Lear and Harlow, 2002). Many systems experienced mesophication, whereby shade-tolerant species replace heliophytic (i.e. sun-loving) and fire-tolerant species and induce a positive feedback loop creating cool, damp microclimates (Nowacki & Abrams, 2008). Mesophication was likely most conspicuous on sites that historically had short fire return intervals as those sites experienced more rapid transformation relative to sites with longer return intervals. For example, frequently burned conifer ecosystems of the Southeast could rapidly transition to mesic hardwood systems within a decade.

The concept of using fire as a tool grew, and the U.S. Forest Service conducted the first prescribed fire on public lands on the Osceola National Forest in Florida in 1943 during an era of national fire suppression (Bickford and Newcomb, 1946). In the decades since, management agencies have slowly embraced fire as a tool to reduce the hazard wildfires posed to the public, achieve silvicultural objectives, and improve wildlife habitat (Stephens & Ruth, 2005).

The longleaf pine (*Pinus palustris*; LLP) ecosystem has one of the shortest fire return intervals in the world (Christensen, 1981). This ecosystem is characterized by structural attributes that facilitate frequent fires including fine-fuel inputs such as pine needles with high resin content (Hendricks et al. 2002) and bunch grasses providing needle elevation for fuel desiccation and well-ventilated fires (Myers, 1990). Fire suppression and conversion of lands to agriculture reduced the LLP ecosystem to 3% of its historical range (Frost, 1993), resulting in numerous threatened, endemic species. Two-thirds of all species of flora and fauna that are

threatened, endangered or in decline in the Southeast are associated with the LLP ecosystem (Kirkman and Mitchell, 2006), making LLP ecosystem restoration a high priority for conservation.

In the early 1900's LLP restoration primarily occurred on private lands managed for northern bobwhite quail (*Colinus virginianus*; Johnson and Gjerstad, 1998). However, the passage of two federal laws spurred restoration efforts on public lands. In 1968, the Endangered Species Act was passed and the red-cockaded woodpecker (*Leuconotopicus borealis*; RCW) was listed as endangered (Brockway et al. 2005). Its habitat requirements included open pine savannas, which are most efficiently maintained through frequent fire. The Sikes Act of 1960 mandated the Department of the Interior and the Department of Defense (DoD) to create Integrated Natural Resources Management Plans (INRMPs). The Sikes Act required that INRMPs include the protection of endangered species and profoundly influenced the management of LLP ecosystems on federal lands. The goals of the adaptive ecosystem management strategy were to support sustainable use of DoD lands, and to restore, sustain, and protect natural and cultural resources (Goran et al. 2002). The distribution of the LLP ecosystem is now at a fraction of its historical range; subsequently there is currently considerable effort aimed at LLP restoration.

Species specific management plans have system wide effects that are often understudied. Thus, understanding the impact of fire should incorporate multiple species to gain a community level understanding of the effects of fire on wildlife. As such, we evaluated how fire influences several suites of species to gain a better understanding of the influence of fire and how managers may be able to maximize the efficacy of their fire management prescriptions.

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## **Chapter 1: Fire, land cover, and soil productivity drive predator abundances in a Longleaf Pine Ecosystem.**

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### **Abstract**

Understanding the link between environmental factors such as disturbance events, land cover, and soil productivity to spatial variation in animal abundance is fundamental to population ecology and wildlife management. The Longleaf pine (*Pinus palustris*) ecosystem is an archetypal, fire-mediated ecosystem, which has seen drastic reductions in land area due to fire suppression. Current restoration utilizes prescribed fire and hardwood removal, but little is known regarding how these restoration efforts influence predator spatial distributions and predator-prey interactions. We conducted a study to investigate how fire, land cover, and soil productivity influence spatial distributions of predators in a fire-mediated ecosystem. We conducted a 34-camera survey across Camp Blanding Joint Training Center, a military installation in northern Florida, and utilized N-mixture models to estimate relative abundances of mammalian predators. To conceptualize our results relative to managed prey species, we categorized predators into white-tailed deer fawn predators [i.e. coyote (*Canis latrans*), bobcat (*Felis rufus*), and Florida black bear (*Ursus americanus floridanus*)] and nest predators [i.e. raccoon (*Procyon lotor*), Virginia opossum (*Didelphis virginiana*), and nine-banded armadillo (*Dasypus novemcinctus*)]. Coyote ( $P = <0.001$ ) and bobcat ( $P = 0.01$ ) relative abundances increased with decreasing pyrodiversity, the number of unique time-since-fire values. Raccoon relative abundance increased with distance from recent burns ( $P = 0.02$ ). Coyote ( $P = <0.001$ ) and bobcat ( $P = <0.001$ ) relative abundance also increased with proximity to hardwoods, while raccoon relative abundance decreased with proximity to pine ( $P = 0.02$ ). Interestingly, there was a lack of detections of mesopredators [i.e. red fox (*Vulpes Vulpes*), grey fox (*Urocyon*

*cinereoargenteus*), spotted skunk (*Mephitis mephitis*) and striped skunk (*Spilogale putorius*)] that were historically considered common throughout the Southeastern United States and longleaf pine ecosystems. Our results indicate that predator space use was altered by fire conditions and distances to pine and hardwood stands, which supports a predator management strategy that utilizes management tools commonly used in restoration and conservation of the LLP ecosystem to indirectly alter predator distributions, which has the potential to positively affect the management of important species within this ecosystem.

## **Keywords**

Prescribed fire; Pyrodiversity; Predator management; N-mixture model; longleaf pine; coyote; raccoon

## **1. Introduction**

Understanding the relationship between environmental factors such as disturbance events, land cover, and soil productivity and spatial variation in abundances of wildlife species is a fundamental topic in population and community ecology, as well as wildlife management. Prescribed fire is a management tool used to restore and maintain historical disturbance regimes, alter vegetation structure, and reduce fuel loads particularly in the southeastern USA where many endemic ecosystems are fire maintained (Waldrop et al. 1992). The Longleaf pine (LLP; *Pinus palustris*) ecosystem is an archetypal, fire-mediated ecosystem with one of the shortest fire return intervals of any system in North America (Christensen, 1981). This ecosystem is characterized by structural attributes that facilitate frequent fires including fine-fuel inputs such as pine needles with high resin content (Hendricks et al. 2002) and bunch grasses providing needle elevation for fuel desiccation and well-ventilated fires (Myers, 1990). Fire suppression has led to forest mesophication, whereby shade-tolerant species replace heliophytic and fire-tolerant species and induce a feedback loop creating cool, damp microclimates (Nowacki and Abrams, 2008).

Moreover, timber harvest and land conversion to agriculture or developments have reduced the LLP ecosystem to 3% of its historical range (Frost, 1993; Brockway, 2005). Consequently, two-thirds of all species of flora and fauna that are threatened, endangered or in decline in the Southeast are associated with the LLP ecosystem, making LLP ecosystem restoration a high priority for conservation (Kirkman and Mitchell, 2006). Current restoration efforts include prescribed fire (Landers et al 1995) and mechanical (Provencher et al. 2001, Kush et al. 2004) as well as chemical (Brockway and Outcalt, 2000) removal of scattered hardwoods within pine stands. Hardwood removal in LLP ecosystems consists of removal of encroaching mesophytic oak species such as water oak (*Quercus nigra*) and live oak (*Q. virginiana*) and retention pyrophytic oak species (i.e., *Q. falcate*, *Q. stellate*) which can begin to disrupt the mesophication feedback loop in LLP systems (Provencher et al. 2001).

Within LLP ecosystems, many managed and protected wildlife species can be negatively affected by predation including white-tailed deer (*Odocoileus virginianus*; Chitwood et al. 2015, Conner et al. 2016), northern bobwhite quail (*Colinus virginianus*; Rollins and Carroll, 2001, Palmer et al. 2019), wild turkey (*Meleagris gallopavo*; Kilburg et al. 2014), and gopher tortoise (*Gopherus Polyphemus*; Smith et al. 2013). Predator communities in LLP ecosystems have experienced considerable reorganization during the last 200 years (Conner and Cherry, 2017). Large carnivores including cougars (*Puma concolor*) and red wolves (*Canis rufus*) have been extirpated, potentially resulting in elevated predation through mesopredator release (Prugh et al. 2009). While the Florida subspecies of black bear (*Ursus americanus floridanus*) has seen a significant increase in population from 300 estimated bears in 1940 (McDaniel, 1974) to 3,916 in 2017 (Humm et al. 2017). Predator communities in LLP ecosystems are now characterized by generalist species that occur across wide distributions, but how fire influences spatial variation in

predator abundances within frequently burned systems is largely unknown and important for understanding variation in predation risk.

Fire can influence predator-prey interactions by rapidly modifying the distribution of concealment cover and food resources. Fire can facilitate predation through several mechanisms (Leahy et al. 2016) including increased prey vulnerability (Green and Sanecki, 2006; Conner et al. 2011), and predator activity (Soyumert et al. 2010, Birtsas et al. 2012, McGregor et al. 2014). Nonetheless, the Green Magnet Hypothesis suggests herbivores are attracted to recently burned areas to exploit improved foraging conditions (Christensen, 1977; Singh, 1993; Archibald, 2005). Rapid removal of concealment cover caused by fire can have variable effects on the predation risk dependent upon the prey's escape tactics and the predator's hunting mode, thereby explaining why herbivores do not universally follow the Green Magnet Hypothesis and why conflicting results can occur within a prey species (Lashley et al. 2015, Cherry et al. 2017; 2018). For example, white-tailed deer were attracted to recently burned areas in the Greater Everglades Ecosystem where the primary predator was the Florida panther (*Puma concolor coryi*), a stalking ambush predator that uses concealment cover to pursue and attack prey (Cherry et al. 2018). However, in systems where coyotes (*Canis latrans*), a cursorial predator that pursues prey in open areas, were the dominant predator, white-tailed deer avoided recently burned areas where they maintained elevated vigilance levels due to increased perceived predation risk mediated by a lack of cover (Cherry et al. 2017). White-tailed deer recruitment has declined in parts of the Southeast (Kilgo et al. 2010), largely due to predation of neonates (Epstein et al. 1985; Kilgo et al. 2012; Jackson and Ditchkoff, 2013; Shuman et al. 2017) and fawn survival rates are particularly low in LLP forests, potentially due to reduction in concealment cover post fire facilitating predation (Nelson et al. 2015, Chitwood et al. 2015). In LLP ecosystems, white-

tailed deer are depredated by bobcats (*Lynx rufus*), coyotes, and black bears (*Ursus americanus*; Epstein et al. 1983; Nelson et al. 2015). Fire can also influence the distribution of predators and has been suggested as a potential mechanism whereby predator space use can be altered to indirectly affect prey survival (Chamberlain et al. 2003, Jones et al. 2004).

Nest predation can limit avian productivity (Ricklefs et al. 1969) and has contributed to the decline of gopher tortoises (Smith et al. 2013). Fire has the potential to influence predation of nesting birds and herpetofauna by altering the distribution of mammalian carnivores (Roseberry and Klimstra, 1970; Vickery et al. 1992; Chamberlain et al. 2003, Jones et al. 2004). Many important nest predators consume soft mast during bird nesting season (Johnson, 1970; McManus, 1974; Lotze and Anderson, 1979) and soft mast production can be reduced by frequent fire (Lashley et al. 2015). For example, raccoon (*Procyon lotor*) reduced use of pine-dominated uplands following prescribed fire and mesic hardwood removal, two common silvicultural practices used for restoration and management of LLP uplands (Jones et al. 2004, Kirby et al. 2016). Thus, frequent fire may be a mechanism to decrease predator-nest encounters through reduced carnivore use of burned areas (Chamberlain et al. 2003, Jones et al. 2004). Conversely, fire occurring during the nesting season could negatively affect nest success by facilitating depredation or directly destroying nests (Kilburg et al. 2014). Fire facilitated predation may occur through decreasing concealment cover (Bowman and Harris, 1980; Badyaev, 1995; Moore, 2006). However, if predators avoid recently burned areas the probability of a predator encountering a nest may decrease, despite reduced concealment cover at the nest site. This may increase nest success for the numerous endemic species who nest in LLP dominated uplands. Therefore, it is important to establish the effects of fire on nest predator distributions and potential impacts on prey species.

Studies on the effects of fire on predators in LLP systems have primarily focused on habitat use and selection. In LLP systems, rarely burned hardwood forests are selected by multiple predator species including bobcats (Godbois et al. 2003), raccoons (Kirby et al. 2016), gray foxes (*Urocyon cinereoargenteus*; Deuel et al. 2017), and black bears (Stratman et al. 2001; Stratman and Pelton, 2007; Karelus et al. 2016). In North Carolina, coyotes selected open habitats and recently burned longleaf pine forests (Stevenson et al. 2018). Prescribed fire increases herbaceous cover (Lander and Mueller, 1986) attracting bobcat prey (Golley et al. 1965), which likely subsequently influences bobcat habitat use (Knick, 1990). Gray foxes selected rarely burned hardwood stands and showed no selection of frequently burned forests (Deuel et al. 2017). In LLP ecosystems, raccoons selected hardwood forests and areas with greater time-since-fire (Jones et al. 2004, Kirby et al. 2016). Little is known about the spatial ecology of other predators in LLP systems such as long-tailed weasels (*Mustela frenata*), spotted skunks (*Spilogale putorius*), striped skunks (*Mephitis Mephitis*), and Virginia opossum (*Didelphis virginiana*). Although some information exists regarding the habitat use and selection of predators in LLP systems, information regarding how fire influences spatial variation in abundance is limited.

Given the use of fire to maintain and restore LLP systems, the influence of fire on predator-prey interactions, and the potential of fire to be used in predator management, we evaluated the factors influencing the relative abundance of predator species common in LLP ecosystems. Common predators of LLP ecosystems include gray fox, red fox (*Vulpes Vulpes*), striped skunk, spotted skunk, long-tailed weasels, bobcat, coyote, black bear, raccoon, Virginia opossum, and nine-banded armadillo (*Dasypus novemcinctus*). To understand the importance of fire relative to other factors we also evaluated the effects of soil productivity and land cover on

predator abundances. We incorporated soil productivity because many predators consume soft mast and herbivore prey that are often affected by productivity (Harestad and Bunnell 1979, Senft et al. 1987, Mitchell and Powell 2004). While many of these predator species are common in systems with a wide range of fire regimes, we expect that fire will be an important predictor of abundance within LLP systems, because fire dramatically alters the distribution of food and cover resources. We predict that predator species abundances will vary with land cover and that abundances will be greater when associated with hardwood forests. To test these hypotheses, we evaluated the effects of fire, land cover, and soil productivity on relative abundances of predators using remote sensing camera surveys.

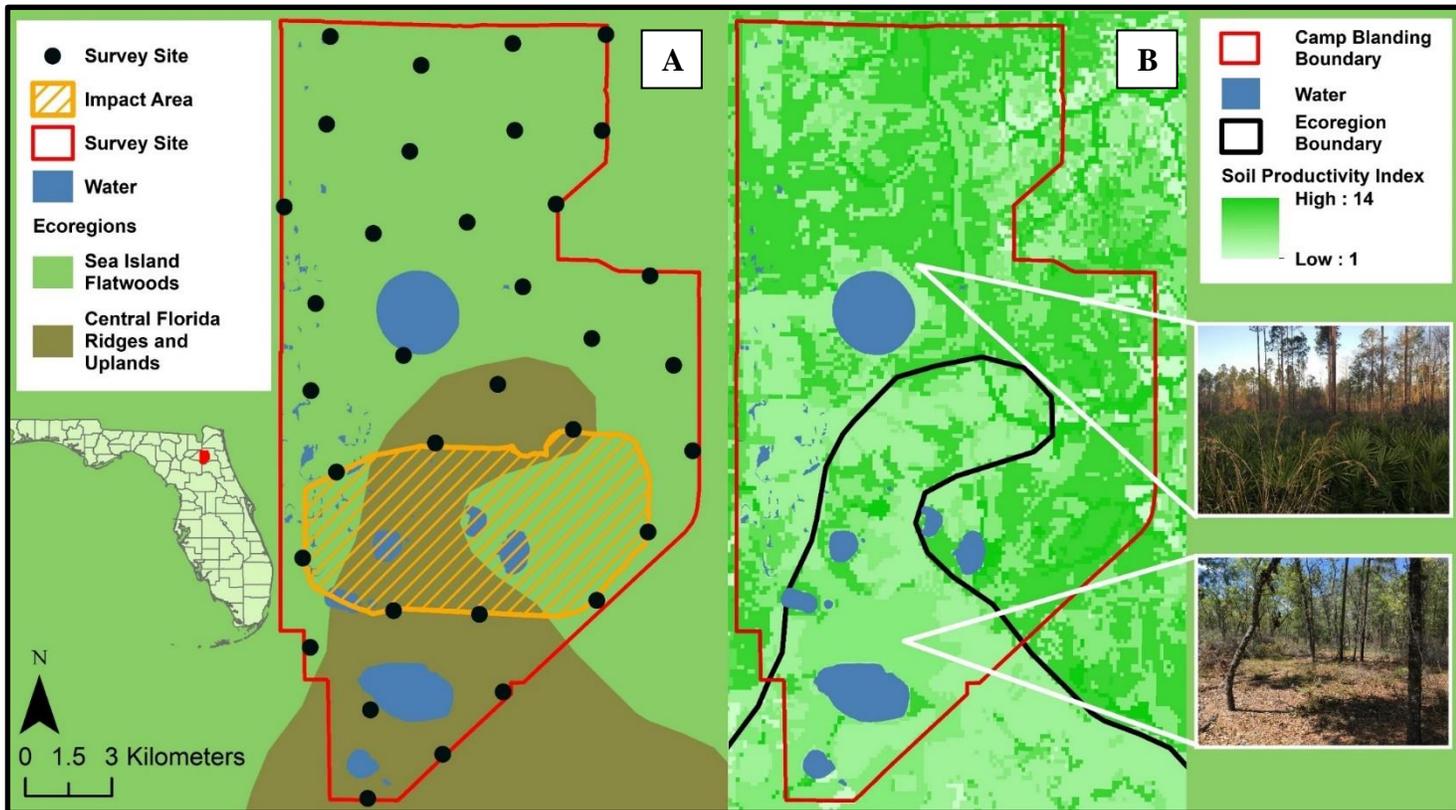
## **2. Methods**

### **2.1 Study Site**

We conducted this study at Camp Blanding Joint Training Center and Wildlife Management Area (CB), a 227 km<sup>2</sup> site ranging from 15 m to 74 m of elevation in northeastern Florida. Mean annual temperature was 20.5°C with a mean annual precipitation of 123.5 cm. Camp Blanding had a subtropical climate characterized by hot humid summers and mild winters. Land use for CB is designed for military training with a 6500-ha 'Impact Zone' where artillery strikes are targeted, forest management, sand mining, and wildlife habitat management. Prescribed burning is used for habitat restoration and averages a 3 to 5-year rotation dependent on forest stand composition. There is considerable variation in site soil productivity across CB, which occurred at the interface of the more productive Sea Islands Flatwoods ecoregion and the less productive Central Florida Ridges and Uplands ecoregion (Omernik and Griffith, 2014; Figure 1). Major forest types included mesic flatwoods dominated by uneven-aged longleaf pine woodlands, planted pine plantations, xeric sandhills, and bottomland hardwood forests. Archery,

gun, and dog accompanied hunting, as well as trapping and fishing were permitted within designated areas (FWC, 2017). Florida Fish and Wildlife Conservation Commission and Florida Department of Military Affairs cooperatively managed wildlife.

## 2.2 Study Design



**Figure 1.** 1 Location of 34 survey sites (A) in relation to the impact area, boundary line, water, ecoregions and the respective soil productivity (B) used in the 2017-2018 camera survey on Camp Blanding Joint Military Center, Starke, FL.

## 2.2 Study Design

### 2.2.1 Predator Camera Survey

We implemented a camera survey, in which we identified 34 survey sites separated by a minimum of 3 km, avoiding the Impact Area (Figure 1). At each of the 34 survey sites, we deployed a remote sensing trail camera (HCO Scoutgaurd SG565, TrailCamPro, Springfield, MO) to record images of wildlife. We programmed cameras to have normal sensitivity, capturing a 14-megapixel image upon each trigger with no delay between triggers. We

conducted continuous camera surveys from 4 June – 10 October 2017 and 14 May – 11 September 2018. We chose this survey period as it overlapped with the white-tailed deer fawning season and bird/herpetofauna nesting and neonate rearing season. We monitored cameras monthly to download data, clear trails of vegetation, and check batteries. We used image curation software, MediaPro (Phase One, Melville, NY) to categorize images and record wildlife detections and the associated date, time, and location data. We identified species using morphological features, and animals that could not be identified were categorized as unknown species.

### 2.2.2 Fire, land cover and soil productivity measures

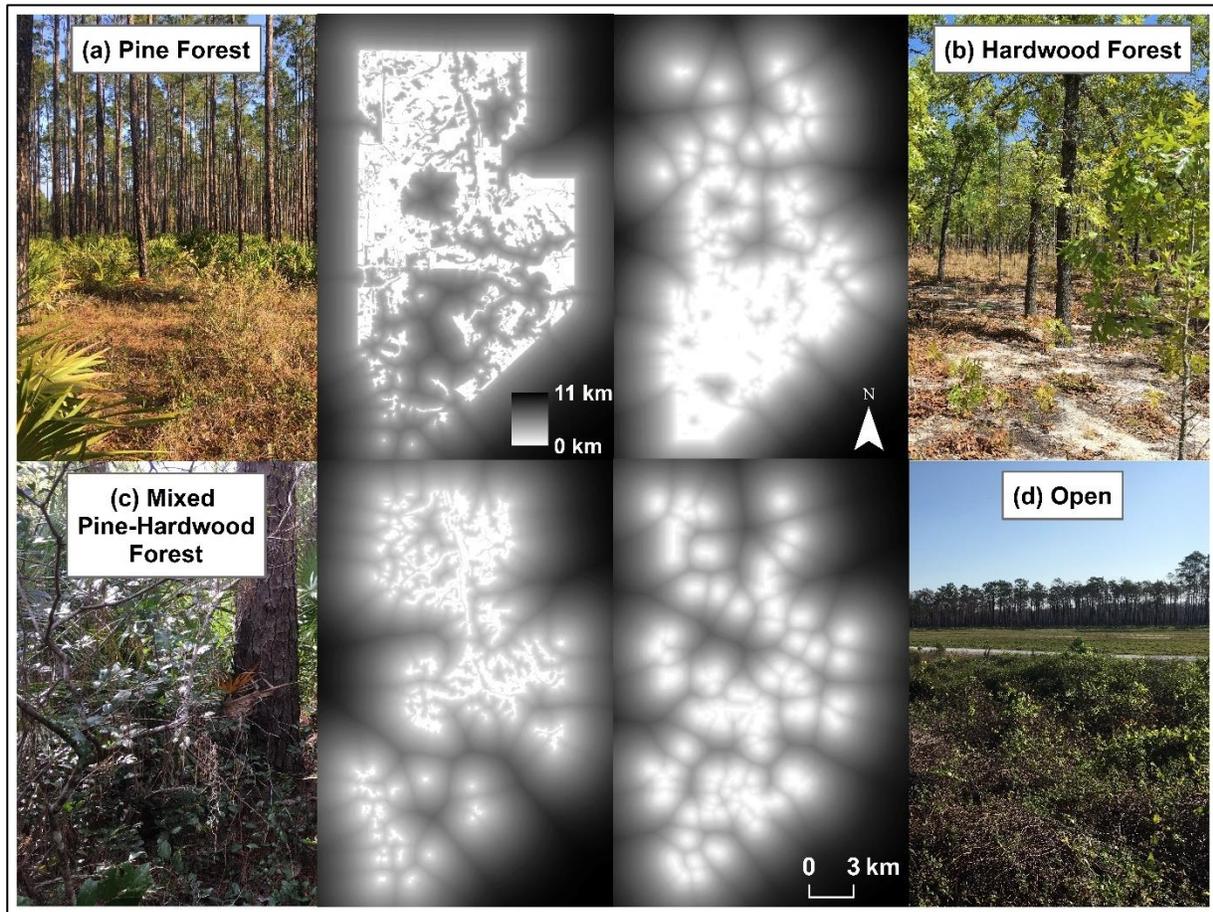
	Name	Description
Fire	Time-since-fire	Number of growing seasons since the last burn at the survey site.
	Pyrodiversity	Number of unique times since fire (years; 2001-2018) values at the time of the survey within a 500m buffer around the survey site.
	Mean fire return interval	Average number of days between burns since 2001 at each site ranging from 851 to 6148 days.
	Distance to recently burned stands	Distance (m) to the nearest 30m raster cell representing a forest during the first growing season following fire.
Cover type	Distance to cover type	Distance (m) to nearest 30m raster cell representing a given cover type (hardwood forests, pine forests, mixed pine-hardwood forest, open habitat) at each site.
Productivity	Soil productivity	United States Department of Agriculture measure of soil productivity based on soil taxonomic information ranging from 0 (least productive) to 19 (most productive; Schaetzl et al. 2012; Soil Survey Staff, 2017).

**Table 1. 1** Covariate names and descriptions for camera surveys conducted 4 June – 10 October 2017 and 14 May-11 September 2018, at 34 plots on Camp Blanding Joint Training Center, Starke, FL.

To evaluate the effects of environmental covariates on wildlife species, we created shapefiles and raster layers representing fire history, land cover type, and soil productivity using ArcGIS 10.3 (ESRI, Redlands, Ca; Table 1). We created spatiotemporally explicit fire covariates that reflect the fire conditions on site during 2017 and 2018 using fire history data

curated by CB Department of Military Affairs Environmental Division staff. To identify the time-since-fire at each survey site, we created a raster layer where each cell was characterized by the number of growing seasons since the most recent fire experienced at that location. Time-since-fire values ranged from 0-21 years, in which values 20 and 21 represent areas not burned since 2001 for 2017 and 2018, respectively. Because fire history data began in 2001, we assigned areas without data with the values of 20 years since fire for 2017 and 21 for 2018 to incorporate any burns prior to 2001. We did this instead of assigning the values of 17 for 2017 and 18 for 2018 as this would imply that everything without data was burned in 2000.

Pyrodiversity, or the heterogeneity in fire effects, can have important implications for wildlife populations and communities (Martin and Sapsis, 1992; He et al. 2019). To characterize pyrodiversity around a given survey site, we created a 500 m buffer around each survey site and identified the number of unique times since fire values within the buffer. Pyrodiversity values ranged from 0-5. We identified the mean fire return interval for each cell by extracting the fire history since 2001, calculating each fire return interval and creating an average from those values. Mean fire return interval represents longer term fire management that influenced current conditions. We created the variable distance to recently burned stands by creating a raster layer for each survey year where each cell was characterized by the distance (m) to nearest cell during the first growing season following fire. We created a land cover raster layer with 30 x 30 m raster layers by reclassifying CB's land cover dataset into four land cover types including hardwood forests, pine forests, mixed pine-hardwood forests, and open areas. We used the Euclidian distance function in ArcGIS 10.3 Spatial Analyst Tools (ESRI, Redlands, Ca) to create distance raster layers where each cell is populated with the distance to the nearest representative cell of a given land cover type (Figure 2).



**Figure 1. 2** Distance rasters and representative photos of (a) pine forests, (b) hardwood forest, (c) mixed pine-hardwood forest, and (d) open habitat used in the 2017-2018 camera survey on Camp Blanding Joint Military Center, Starke, FL. Brighter areas denote closer distances to the given land cover type.

We created a spatially explicit soil productivity metric using the United States Department of Agriculture Productivity Index (Schaetzl et al. 2012) to identify soil productivity at different soil classifications (Soil Survey Staff, 2017). We characterized soil productivity of each survey site at multiple scales (100 m, 500 m, 1000 m, and 1500 m) using the zonal statistics function in ArcGIS 10.3 (ESRI, Redlands, Ca) to average productivity values within the various buffers around each survey site. We categorized predators into three buffer size groups based on their size and mobility: 1500 m buffers (bobcat, coyote, and black bear), 1000 m (raccoons, gray

foxes, red foxes), and 500 m buffers (Virginia opossum, nine-banded armadillo, spotted skunk and striped skunk, long-tailed weasel).

### **2.2.3 Data Analysis**

To estimate effects of land cover and fire conditions on relative abundance of predators we fit species-specific single-season hierarchical N-mixture models following Royle (2004). N-mixture models rely on the assumption of independence between sites, which requires that individuals cannot be detected at multiple sites within the survey period (Royle, 2004). We attempted to meet the assumption by ensuring 3 km spacing between survey sites (O'Connell et al. 2006, Cherry et al. 2017). We balanced maximizing the number of surveys sites, while attempting to satisfy the assumption of independence among survey sites required by our analysis (Royle, 2004). These models also assume independent detections, and to attempt to meet that assumption, we used detections separated by greater than 5 minutes (Tobler et al. 2008). Following Fuller et al. (2016), we considered each site - year combination to be a unique site as we focused on species abundance rather than turnover rate (i.e., colonization and extinction probabilities), and because we only had two years of data, temporal replication was limited for a dynamic model. Due to drought conditions prior to and early in the survey in 2017 and relatively moderate conditions during the 2018 survey, as well as temporal variation in fire history, we suggest this is a reasonable procedure despite sites being replicated by year.

We designed our study to evaluate relative abundance of a suite of predator species and many tradeoffs must be considered when designing such a study. Because we attempted to balance maximizing the number of sites and satisfying the assumption of independence among sites, we likely did not optimize either outcome. While we likely met the assumption of independence for most species in the study, for some species that have large home ranges or are

highly mobile (i.e. black bears, and coyotes), we likely violated this assumption. This violation would result in overestimated abundance for those species. It is important to note that the abundance estimates presented should not be considered abundances for CB, but rather relative abundances that allowed for analyses of factors driving the variation in abundances. While the parameters and precision of those estimates may be inflated, the assessment of the factors influencing these estimates is typically robust to such violations (O'Connell, 2006). Our goal was to improve understanding of factors influencing abundance, rather than provide actual abundance estimates and therefore we suggest our approach is sound but acknowledge potential for biased estimates.

We developed variables that represented our hypotheses regarding factors influencing species abundances and created models including a global, null, and all possible additive and linear combinations of variables, resulting in 256 candidate models for each species. Because we were interested in the factors influencing abundances rather than obtaining an estimate of true abundance, we focused on the differences in relative abundances across sites. To account for dependence between site-years, we included the effect of year on the detection and abundance for each model (Fuller et al. 2016). To test for collinearity in predictor variables, we used the Corr Function (Hankin, 2005) in program R (R Core Team, 2016). If variables were correlated at  $R^2 > 0.40$  we only retained one of the correlated variables (Mukaka, 2012). When choosing which covariate to retain, we kept the most biologically meaningful covariate across all species. We scaled and centered all covariates for analysis to aid in model convergence. We fit models in package unmarked (Fiske and Chandler, 2011) in program R (R Core Team, 2016). We used Akaike Information Criterion (AIC) to compare model weights to determine the top model (Akaike, 1973; Burnham and Anderson, 2002). For each species, we report AIC table for all

models with delta AIC values <2 in Appendix A. We assigned significance at alpha = 0.05, and marginal significance at alpha = 0.05 - 0.1.

### 3. Results

We recorded 12,248 and 9,993 animal detections for 2017 and 2018, respectively.

Detection histories for bobcat, coyote, black bear, raccoon, Virginia opossum and nine-banded armadillo were sufficient for analyses. The most frequently detected species across both years was coyote, while the least detected, of the species analyzed, was black bear (Table 2). We did not detect long-tailed weasel, red fox, or spotted skunk and only rarely detected gray fox, and striped skunk.

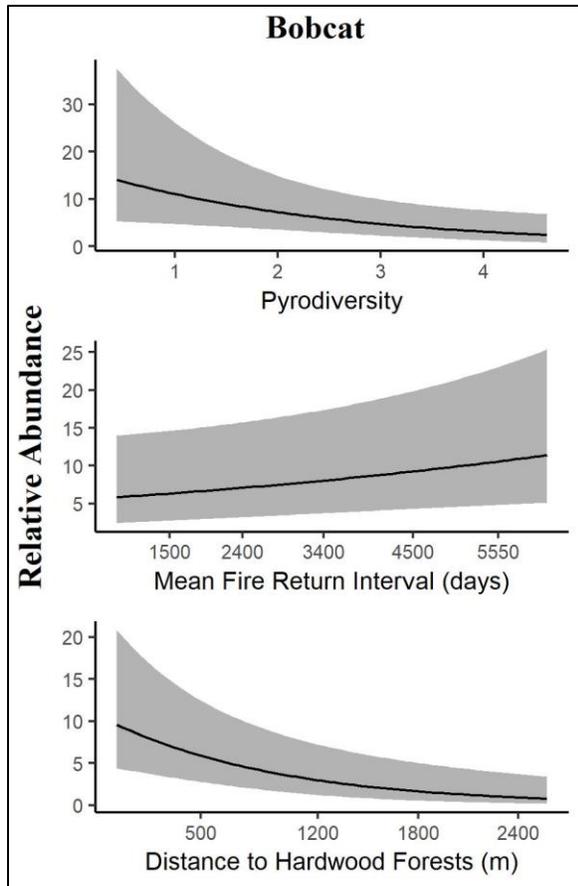
Species	Detections per 100 trap nights	Mean number of sites detected
Coyote	8.41	29
Raccoon	4.72	20.5
Bobcat	2.62	25
Virginia opossum	1.58	9.5
Nine-banded armadillo	1.57	19.5
Black bear	1.40	17
Grey fox	0.03	1
Striped skunk	0.03	1
Red fox	0.00	0
Spotted skunk	0.00	0
Long-tailed weasel	0.00	0

**Table 1. 2** Detections per one hundred trap nights, in descending order, and mean number of sites detected across years, for the species surveyed in 2017-2018 camera surveys conducted 4 June – 10 October 2017 and 14 May- 11 September 2018 at 34 plots on Camp Blanding Joint Training Center, Starke, FL. The dashed line represents the cutoff of species that had sufficient data to be analyzed with species below the line not having sufficient data.

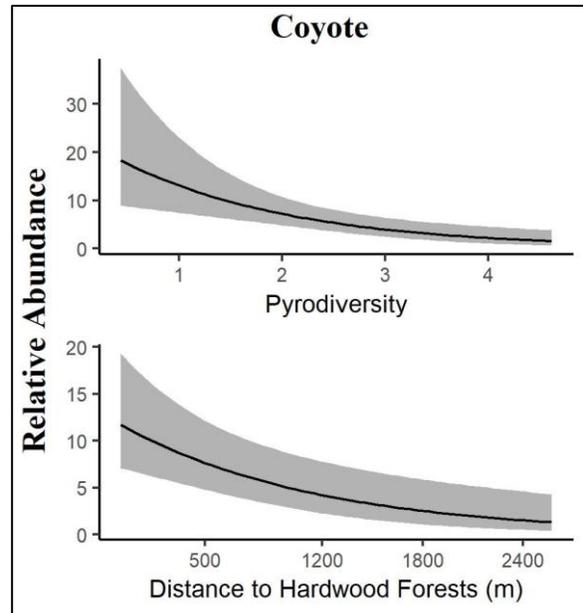
	Beta	SE	Z	P value
<b>Bobcat (<i>Lynx rufus</i>)</b>				
Distance to hardwood forests	-0.623	0.188	-3.31	<0.001
Pyrodiversity	-0.423	0.177	-2.39	0.017
Distance to recently burned stands	-0.312	0.186	-1.68	0.093
Mean fire return interval	0.274	0.139	1.98	0.048
<b>Coyote (<i>Canis latrans</i>)</b>				
Pyrodiversity	-0.594	0.174	-3.42	<0.001
Distance to hardwood forests	-0.545	0.164	-3.31	<0.001
Distance to recently burned stands	-0.266	0.154	-1.72	0.083
<b>Black Bear (<i>Ursus americanus floridanus</i>)</b>				
Distance to mixed pine-hardwood forests	-0.636	0.221	-2.87	0.004
Distance to pine forests	-0.390	0.248	-1.57	0.115
<b>Raccoon (<i>Procyon lotor</i>)</b>				
Distance to hardwood forests	-0.462	0.239	-1.93	0.053
Distance to recently burned stands	0.459	0.210	2.18	0.028
Distance to pine forests	0.404	0.175	2.31	0.020
<b>Virginia Opossum (<i>Didelphis virginiana</i>)</b>				
Soil productivity	-0.995	0.303	-3.29	0.001
Distance to mixed pine-hardwood forests	0.693	0.400	1.73	0.083
<b>Nine-banded Armadillo (<i>Dasypus novemcinctus</i>)</b>				
Pyrodiversity	0.827	0.265	3.11	0.001
Time-since-fire	0.473	0.235	2.01	0.044

**Table 1. 3** Beta estimates, standard errors, z-scores and p-values for informative parameters for top single-species, single season occupancy models fit to data collected during 2017-2018 camera surveys conducted 4 June – 10 October 2017 and 14 May- 11 September 2018 at 34 plots on Camp Blanding Joint Training Center, Starke, FL.

Our analyses revealed linkages between species-specific relative abundances and fire, land cover, or soil productivity for each of the six species (Table 3). The best model predicting bobcat abundance included distance to hardwood forests, pyrodiversity, mean fire return interval, which were strongly supported, and distance to recently burned stands which was only marginally supported. Bobcat abundance increased with proximity to hardwood forests ( $P < 0.0001$ ; Figure 3) and with increasing fire return interval ( $P = 0.048$ ). Bobcat abundance decreased with increasing pyrodiversity ( $P = 0.017$ ). We observed some support for increased

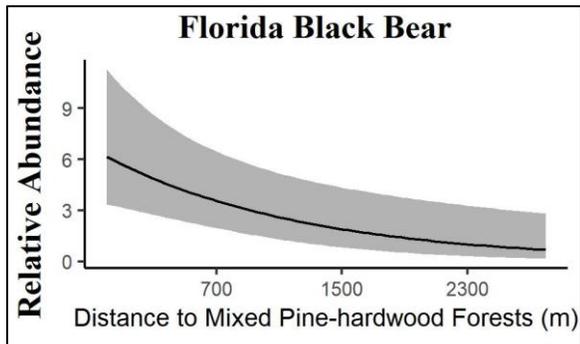


**Figure 1.3** Predicted bobcat relative abundance per site given pyrodiversity, mean fire return interval, and distance to hardwood forests from camera surveys conducted 4 June – 10 October 2017 and 14 May- 11 September 2018 at 34 plots on Camp Blanding Joint Military Center, Starke, FL. Grey shading denotes confidence intervals.

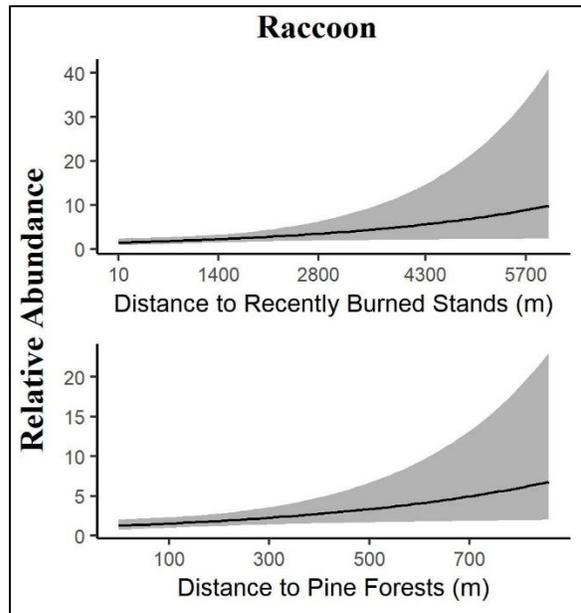


**Figure 1.4** Predicted coyote relative abundance per site given pyrodiversity, and distance to hardwood forests from camera surveys conducted 4 June – 10 October 2017 and 14 May- 11 September 2018 at 34 plots on Camp Blanding Joint Military Center, Starke, FL. Grey shading denotes confidence intervals.

bobcat abundance with proximity to recently burned stands ( $P=0.093$ ). The best model predicting coyote abundance included distance to hardwood forests, pyrodiversity, which were strongly supported, and distance to recently burned stands which was only marginally supported. Coyote abundance increased with proximity to hardwood forests ( $P<0.001$ ). Coyote abundance decreased with increasing pyrodiversity ( $P= <0.001$ ; Figure 4). We observed some support for increased coyote abundance with proximity to recently burned stands ( $P=0.083$ ). The best model predicting black bear abundance included distance to mixed pine-hardwood forests and distance to pine forests. Black bear abundance increased with proximity to mixed pine-hardwood forests, which was the only strongly supported variable ( $P=0.004$ ; Figure 5). The best model predicting raccoon abundance included distance to pine forests, recently burned stands, and hardwood forests. Raccoon abundance increased with increasing distance to pine forests ( $P=0.020$ ) and

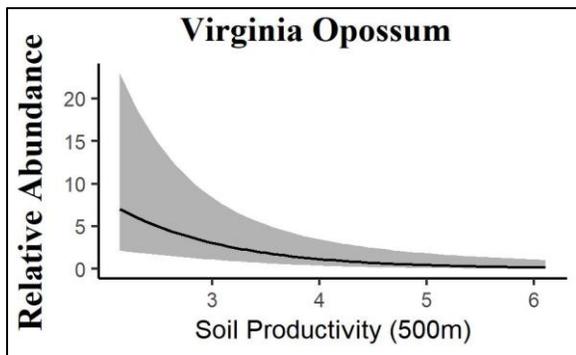


**Figure 1. 5** Predicted Florida black bear relative abundance per site given distance mixed pine-hardwood forests from camera surveys conducted 4 June – 10 October 2017 and 14 May- 11 September 2018 at 34 plots on Camp Blanding Joint Military Center, Starke, FL. Grey shading denotes confidence intervals.

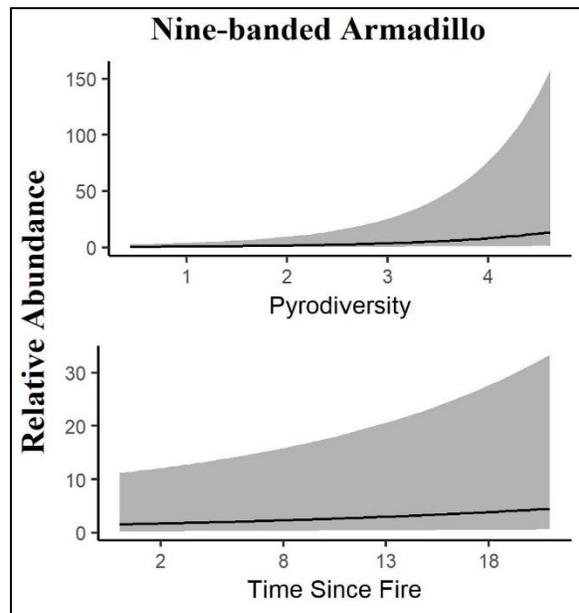


**Figure 1. 6** Predicted raccoon relative abundance per site given distance to recently burned stands, and distance to pine forests from camera surveys conducted 4 June – 10 October 2017 and 14 May-11 September 2018 at 34 plots on Camp Blanding Joint Military Center, Starke, FL. Grey shading denotes confidence intervals.

increased marginally with proximity to hardwood forests ( $P=0.053$ ; Figure 6). Raccoon abundance also increased with distance from recently burned stands ( $P=0.028$ ). The best model predicting Virginia opossum abundance included soil productivity, which was strongly supported, and distance to mixed pine-hardwood forests, which was not. Virginia opossum abundance decreased with increasing productivity ( $P=0.001$ ; Figure 7). The best model predicting nine-banded armadillo abundance included time-since-fire, and pyrodiversity, which were both strongly supported. Nine-banded armadillo abundance increased with increased pyrodiversity ( $P=0.001$ ; Figure 8) and time-since-fire ( $P=0.044$ ).



**Figure 1. 7** Predicted Virginia opossum relative abundance per site given soil productivity at the 500m scale from camera surveys conducted 4 June – 10 October 2017 and 14 May- 11 September 2018 at 34 plots on Camp Blanding Joint Military Center, Starke, FL. Grey shading denotes confidence intervals.



**Figure 1. 8** Predicted nine-banded armadillo relative abundance per site given pyrodiversity and time-since-fire from camera surveys conducted 4 June – 10 October 2017 and 14 May- 11 September 2018 at 34 plots on Camp Blanding Joint Military Center, Starke, FL. Grey shading denotes confidence intervals.

## 4. Discussion

### 4.1 Evidence supports fire and hardwood removal to alter predator abundance

Our work revealed linkages between abundances of predators and environmental factors including fire, land cover and soil productivity. We had sufficient data to model the abundances of six predators which we categorized as fawn predators (i.e. coyote, bobcat, black bear) and nest predators (i.e. raccoon, Virginia opossum and nine-banded armadillo), acknowledging that fawn predators may also depredate on nests. We identified an effect of fire on all species except, black bear and Virginia opossum (Table 4).

Species	Fire			Land cover			Soil	
	Time since fire	Pyrodiversity	Recent burns	Mean fire return interval	Hardwood forest	Mixed pine-hardwood forest	Pine forest	Soil productivity
Bobcat		-		+	+			
Coyote		-			+			
Black Bear						+		
Raccoon			+				-	
Virginia Opossum								-
Nine-banded Armadillo	+	+						

**Table 1. 4** Predator abundance responses to fire, land cover and soil variables for camera surveys conducted 4 June – 10 October 2017 and 14 May- 11 September 2018, at 34 plots on Camp Blanding Joint Training Center, Starke, FL. Green plus sign denotes a significant ( $p < 0.05$ ) increase in abundance while red minus sign denotes significant decreases in abundance.

Interestingly we failed to detect or had low detection rates for carnivores assumed to be common in the region. We did not detect long-tailed weasel, red fox, or spotted skunk and only recorded two detections of gray foxes and two detections of striped skunks. Coyotes were the

most frequently detected predator and have been implicated in declines in foxes (Newsome and Ripple, 2014; Levi and Wilmers, 2012) and the rearrangement of carnivore communities (Crooks and Soule, 1999). Although our study did not examine interactions between carnivores, our results should be considered within the context that, coyotes were the dominant predator in terms of detections (Table 3) and body size (apart from black bears) in our system. Three important points emerge from this context. First, the distribution of coyotes is likely important for understanding spatial variation in predation in LLP systems. Second, given foxes, mustelids, and skunks were functionally absent, the mammalian nest predator guild in our study consisted largely of raccoons, the second most detected predator, Virginia opossums, and nine-banded armadillos. Finally, mesopredator species that are considered common in the region and in LLP systems were largely absent during our study and future work should investigate status of these species in LLP systems, and what role fire along with intraguild interactions have on these mesopredators.

Pyrodiversity was associated with decreased abundances of bobcats and coyotes. Areas characterized by greater pyrodiversity occur in areas where multiple burn units, with unique fire histories, are near one another, creating a mosaic of post-fire conditions. Bobcat abundance often decreases with fragmentation while home range size increases (Crooks, 2001; Tucker et al. 2008). In pine-dominated systems in the Southeast, coyote abundance decreased (Cherry et al. 2017) and fawn survival increased (Gulsby et al. 2017) with fragmentation. Nine-banded armadillo was the only predator to increase in abundance with pyrodiversity. Increasing the mosaic of fire conditions, and richness in fire history can be achieved by reducing the size of burn units, as well as facilitating heterogeneity in fire severity within a burn.

Raccoon abundance increased with distance from recently burned stands, whereas bobcat and coyote abundances increased marginally near recently burned stands. Our results support previous studies in LLP ecosystems suggesting that raccoons are strongly associated with less frequently burned forests (Kirby et al. 2016). Soft mast is an important food item for raccoons and many fruit producing plants do not produce soft mast until the second or third growing season following fire (Harlow and Van Lear, 1989; Lashley et al. 2015). Frequent fire could be used as a tool for reducing raccoon abundance in pine uplands, which may reduce predation on ground-nesting birds and herpetofauna (Chamberlain et al. 2003, Jones et al. 2004, Kirby et al. 2016). In systems where raccoons are a major predator of ground-nesting herpetofauna or birds (Butler and Sowell, 1997; Hernandez et al. 1997; Staller et al. 2005), these management techniques may reduce predation. While testing this hypothesis is beyond the scope of this study, our result that raccoon abundance was lower near recently burned stands provide support for the mechanism.

Bobcat, coyote, and raccoon abundances increased with proximity to hardwood forests, illustrating the importance of this land cover type to carnivores in LLP ecosystems. Hardwood stands are an important land cover type in pine-dominated landscapes, which are characterized by longer fire return intervals (Hiers et al. 2014) and are frequently used by bobcats for den sites, thermal refugia, and travel corridors (Conner et al. 1992). In a mixed pine-hardwood system in Georgia, hardwoods were the most selected land cover type for female coyotes during denning (Hickman et al. 2016). However, Hickman's (2016) result is contrary to Stevenson et al. (2018), who report that coyotes avoided densely vegetated hardwood drainages in a LLP ecosystem on Fort Bragg, North Carolina. The removal of hydric oak (*Quercus* spp.) species from LLP-dominated uplands has been suggested to manipulate space use or population dynamics of

raccoons (Kirby et al. 2016). Suppression of hardwood encroachment is a common management objective used to maintain and restore LLP ecosystems, and our results suggest this management may have indirect benefits on prey populations by reducing the abundances of important predators.

Black bear abundance was greater near mixed pine-hardwood stands. Karelus et al. (2016) reported that black bear home ranges on CB were associated with forested wetlands. Our categorization of mixed pine-hardwood forest is predominately associated with riparian moist soil forest types that include forested wetlands. Our results also support previous work that reported black bears select mixed hardwoods stands (Landers et al. 1979) to consume hard and soft mast (Maehr and Brady, 1986). These stands are often characterized by longer fire return intervals (i.e. 5+ years) than pine stands (i.e. 3-5 years) and likely provide more soft mast than more frequently burned forests, while also providing hard mast from hardwood species such as oaks and hickories (*Carya* spp.). Retention of these mixed hardwood forests and riparian areas may be an important management strategy for maintaining black bear populations.

## **4.2 Conclusions**

A better understanding of factors driving predator populations and communities can facilitate conservation decision-making, identify management potential and limitations of a site, and provide science-based justification for management actions. To improve this understanding, we developed a study that evaluated predator responses to manageable land conditions, such as fire history, as well as more inherent conditions, such as soil productivity and land cover.

Fire and silvicultural practices, such as hardwoods removal, has the potential to be used as a tool to alter abundances of predators in a pyric landscape. Common predators found across the United States may have specific adaptations to conditions on pyric landscapes. Our results

indicated predators were more abundant near hardwoods sites and with lower pyrodiversity, suggesting that hardwood removal within pine stands and mosaic burning of the LLP ecosystems would likely decrease fawn predator abundance potentially decreasing the likelihood of fawn predation. Furthermore, hardwood removal along with maintenance of pine stands and frequent burning would likely decrease nest predator abundance potentially decreasing the likelihood of nest predation. Our results showed that fire history and land cover type were the most influential factors influencing four species while soil productivity had little influence on predator abundances. Future work should focus on directly testing the efficacy of using fire as a predator management tool and should account for the timing of fire relative to the fawn rearing and nesting season (Kilburg et al. 2014). Our results support a predator management strategy that utilizes management tools commonly used in restoration and conservation of the LLP ecosystem to indirectly alter predator distributions, which has the potential to positively affect the management of important species within this ecosystem.

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## Appendix

**Appendix A.** Akaike Information Criterion (AIC) table with model name, the number of parameters (K), AIC, delta AIC, AIC weight, and cumulative weights only for delta AIC values < 2 from 2017-2018 camera surveys conducted 4 June – 10 October 2017 and 14 May- 11 September 2018 at 34 plots on Camp Blanding Joint Training Center, Starke, FL. Acronyms are as follows: p = detection parameter,  $\lambda$  = abundance parameter, MFRI = Mean Fire Return Interval, PD = Pyrodiversity, DHAR = Distance to Hardwood Forests, DPINE = Distance to Pine Forests, DMIX = Distance to Mixed Pine-Hardwood Forests, DRBS = Distance Recently Burned Stands, SP = Soil Productivity, TSF = Time-since-fire.

Model Name	K	AIC	delta	AIC weight	Cumulative weight
<b>Bobcat</b>					
p(year), $\lambda$ (MFRI + PD + DHAR + DRBS + year)	9	1764.96	0.00	0.08	0.08
p(year), $\lambda$ (MFRI + PD + DHAR + year)	8	1765.80	0.85	0.05	0.13
p(year), $\lambda$ (MFRI + PD + DPINE + DHAR + DRBS + year)	10	1766.61	1.65	0.04	0.17
p(year), $\lambda$ (MFRI + PD + DHAR + DRBS + DMIX + year)	10	1766.74	1.78	0.03	0.20
p(year), $\lambda$ (PD + DHAR + DRBS + year)	8	1766.85	1.89	0.03	0.23
p(year), $\lambda$ (MFRI + PD + SP + DHARs + DRBS + year)	10	1766.95	1.99	0.03	0.26
<b>Coyote</b>					
p(year), $\lambda$ (PD + DHAR + DRBS + year)	8	4076.03	0.00	0.05	0.05
p(year), $\lambda$ (PD + DPINE + DHAR + DRBS + year)	9	4076.06	0.03	0.04	0.09
p(year), $\lambda$ (PD + SP + DHARs + DRBS + year)	9	4076.58	0.55	0.03	0.12
p(year), $\lambda$ (MFRI + PD + DHAR + DRBS + year)	9	4076.61	0.58	0.03	0.16
p(year), $\lambda$ (PD + DPINE + DHAR + year)	8	4076.70	0.67	0.03	0.19
p(year), $\lambda$ (MFRI + PD + DHAR + year)	8	4076.75	0.73	0.03	0.22
p(year), $\lambda$ (PD + DHAR + year)	7	4076.84	0.81	0.03	0.25
p(year), $\lambda$ (MFRI + PD + DPINE + DHAR + DRBS + year)	10	4076.88	0.85	0.03	0.28
p(year), $\lambda$ (PD + DHAR + DRBS + DMIX + year)	9	4077.01	0.99	0.03	0.31
p(year), $\lambda$ (MFRI + PD + DPINE + DHAR + year)	9	4077.03	1.00	0.03	0.34
p(year), $\lambda$ (MFRI + PD + SP + DHAR + DRBS + year)	10	4077.23	1.21	0.03	0.36
p(year), $\lambda$ (PD + DPINE + DHAR + DRBS + DMIX + year)	10	4077.33	1.30	0.02	0.38
p(year), $\lambda$ (PD + SP + DHAR + DRBS + DMIX + year)	10	4077.35	1.32	0.02	0.41
p(year), $\lambda$ (PD + SP + DHAR + year)	8	4077.39	1.37	0.02	0.43
p(year), $\lambda$ (MFRI + PD + SP + DHAR + year)	9	4077.44	1.41	0.02	0.45
p(year), $\lambda$ (PD + SP + DPINE + DHAR + DRBS + year)	10	4077.52	1.49	0.02	0.47
p(year), $\lambda$ (MFRI + PD + DHAR + DRBS + DMIX + year)	10	4077.67	1.64	0.02	0.49
p(year), $\lambda$ (TSF + PD + DHAR + DRBS + year)	9	4077.98	1.95	0.02	0.51
p(year), $\lambda$ (PD + DHAR + DMIX + year)	8	4078.02	2.00	0.02	0.53
<b>Raccoon</b>					
p(year), $\lambda$ (DPINE + DHAR + DRBS + year)	8	2385.18	0.00	0.08	0.08
p(year), $\lambda$ (PD + DPINE + DHAR + DRBS + year)	9	2386.47	1.29	0.04	0.12
p(year), $\lambda$ (SP + DPINE + DHAR + DRBS + year)	9	2386.68	1.50	0.04	0.15
p(year), $\lambda$ (DPINE + DRBS + year)	7	2387.00	1.82	0.03	0.18
p(year), $\lambda$ (TSF + DPINE + DHAR + DRBS + year)	9	2387.13	1.95	0.03	0.21

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**Appendix A Conti.**

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**Black bear**

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p(year), $\lambda$ (DPINE + DMIX + year)	7	1087.48	0.00	0.04	0.04
p(year), $\lambda$ (SP + DMIX + year)	7	1087.69	0.21	0.03	0.07
p(year), $\lambda$ (SP + DPINE + DMIX + year)	8	1088.13	0.66	0.03	0.10
p(year), $\lambda$ (DMIX + year)	6	1088.30	0.83	0.03	0.13
p(year), $\lambda$ (DPINE + DHAR + DMIX + year)	8	1088.32	0.85	0.03	0.15
p(year), $\lambda$ (SP + DHAR + DMIX + year)	8	1088.32	0.85	0.03	0.17
p(year), $\lambda$ (DHAR + DMIX + year)	7	1088.35	0.87	0.03	0.20
p(year), $\lambda$ (TSF + SP + DMIX + year)	8	1088.58	1.11	0.02	0.22
p(year), $\lambda$ (TSF + SP + DHAR + DMIX + year)	9	1088.66	1.19	0.02	0.24
p(year), $\lambda$ (TSF + DHAR + DMIX + year)	8	1088.85	1.38	0.02	0.26
p(year), $\lambda$ (MFRI + SP + DMIX + year)	8	1088.89	1.41	0.02	0.28
p(year), $\lambda$ (TSF + DPINE + DMIX + year)	8	1089.03	1.55	0.02	0.30
p(year), $\lambda$ (MFRI + DPINE + DMIX + year)	8	1089.08	1.60	0.02	0.31
p(year), $\lambda$ (SP + DPINE + DHAR + DMIX + year)	9	1089.19	1.71	0.02	0.33
p(year), $\lambda$ (DPINE + DRBS + DMIX + year)	8	1089.28	1.80	0.02	0.35
p(year), $\lambda$ (TSF + DPINE + DHAR + DMIX + year)	9	1089.40	1.92	0.02	0.36
p(year), $\lambda$ (TSF + DMIX + year)	7	1089.41	1.93	0.01	0.38
p(year), $\lambda$ (PD + DPINE + DMIX + year)	8	1089.44	1.96	0.01	0.39
p(year), $\lambda$ (TSF + SP + DPINE + DMIX + year)	9	1089.45	1.97	0.01	0.40

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**Virginia opossum**

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p(year), $\lambda$ (SP + DMIX + year)	7	893.15	0.00	0.04	0.04
p(year), $\lambda$ (MFRI + SP + DMIX + year)	8	893.31	0.16	0.04	0.08
p(year), $\lambda$ (TSF + SP + DMIX + year)	8	893.70	0.56	0.03	0.10
p(year), $\lambda$ (PD + SP + DMIX + year)	8	894.01	0.86	0.03	0.13
p(year), $\lambda$ (TSF + PD + SP + DMIX + year)	9	894.40	1.25	0.02	0.15
p(year), $\lambda$ (TSF + MFRI + SP + DMIX + year)	9	894.46	1.31	0.02	0.17
p(year), $\lambda$ (SP + year)	6	894.55	1.40	0.02	0.19
p(year), $\lambda$ (MFRI + SP + DPINE + DMIX + year)	9	894.65	1.50	0.02	0.21
p(year), $\lambda$ (PD + SP + DPINE + DMIX + year)	9	894.75	1.61	0.02	0.23
p(year), $\lambda$ (SP + DPINE + DMIX + year)	8	894.81	1.66	0.02	0.24
p(year), $\lambda$ (PD + DPINE + DMIX + year)	8	894.86	1.71	0.02	0.26
p(year), $\lambda$ (MFRI + SP + DRBS + DMIX + year)	9	894.87	1.72	0.02	0.28
p(year), $\lambda$ (MFRI + PD + SP + DMIX + year)	9	894.92	1.78	0.02	0.29
p(year), $\lambda$ (MFRI + SP + year)	7	894.95	1.81	0.02	0.31
p(year), $\lambda$ (SP + DHAR + DMIX + year)	8	895.09	1.94	0.02	0.32
p(year), $\lambda$ (SP + DRBS + DMIX + year)	8	895.10	1.96	0.02	0.34

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**Nine-banded armadillo**

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p(year), $\lambda$ (TSF + PD + year)	7	1075.05	0.00	0.05	0.05
p(year), $\lambda$ (TSF + PD + DHAR + year)	8	1076.02	0.97	0.03	0.08
p(year), $\lambda$ (TSF + PD + DPINE + year)	8	1076.09	1.04	0.03	0.12
p(year), $\lambda$ (TSF + PD + DPINE + DHAR + year)	9	1076.38	1.33	0.03	0.14
p(year), $\lambda$ (TSF + PD + SP + year)	8	1076.75	1.70	0.02	0.17
p(year), $\lambda$ (TSF + PD + DRBS + year)	8	1076.76	1.71	0.02	0.19
p(year), $\lambda$ (PD + DPINE + DHAR + year)	8	1076.82	1.78	0.02	0.21

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**Appendix A Conti.**

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p(year), $\lambda(\text{TSF} + \text{PD} + \text{DMIX} + \text{year})$	8	1076.84	1.79	0.02	0.23
p(year), $\lambda(\text{PD} + \text{DPINE} + \text{year})$	7	1076.94	1.89	0.02	0.25
p(year), $\lambda(\text{PD} + \text{year})$	6	1077.00	1.95	0.02	0.27

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## **Chapter 2: Avian species richness and occupancy in a frequently burned ecosystem: A link between pyrodiversity and biodiversity**

*Formatted for Journal of Forest Ecology and Management*

### **Abstract**

Fire influences the distributions of ecosystems around the world, but the link between pyrodiversity, the diversity of post fire conditions, and biodiversity is just emerging.

Biodiversity is commonly estimated through species richness, which can be assessed at multiple levels (e.g. community, guild) and spatial scales (e.g. regional, continental), but the factors influencing each level and scale may not be the same. The longleaf pine (*Pinus palustris*; hereafter, LLP) ecosystem is an archetypal fire-mediated ecosystem that lost much of its historical range due to fire suppression, resulting in current restoration strategies utilizing prescribed burning. This ecosystem supports a diverse avian community including threatened and endangered species, and promoting biodiversity is a common goal in wildlife management. We evaluated the effects of fire and stand conditions on avian occupancy and species richness in a LLP ecosystem in northeastern Florida. We deployed 34 programmable acoustic recorders, separated 3 km apart, to record three, 5-minute sessions per day for six days for two years. We identified species by their calls and grouped them by nesting and foraging behavior to assess factors influencing species richness and occupancy at the community, guild, and species levels. To evaluate the effects of environmental factors, we created spatial data representing fire history characteristics, pyrodiversity (i.e. the number of unique fires within a 500m buffer), land cover type, soil productivity, and forest structure. We estimated species richness at the community level and guild level whereby simultaneously estimating individual species occupancy, utilizing hierarchical, Bayesian multispecies occupancy models. At the community level, avian species richness increased with pyrodiversity ( $\beta = 0.136$ , 95% CrI= 0.009 – 0.260). At the guild level,

cavity nesting avian species richness decreased with increasing time-since-fire ( $\beta = -0.334$ , 95% CrI=  $-0.713 - 0.003$ ). Our work revealed how fire influenced fauna, the importance of pyrodiversity as a driver for biodiversity at a small scale, and provided management recommendation for promoting biodiversity in frequently burned forests.

## **Keywords**

Prescribed fire; Longleaf pine; Species richness; Florida; Community ecology; Bayesian multispecies occupancy models

### **1. Introduction**

Fire influences the extent and distribution of ecosystems around the world (Bond et al. 2005). Fire-mediated ecosystems are often characterized as global biodiversity hotspots (Myers et al. 2000) with high species richness (Bond and Parr, 2010, Rundel et al. 2018, Fernandes et al. 2018). Thus, understanding the interactions between fire, flora, and fauna is integral to the conservation of regional and global biodiversity in fire-maintained ecosystems. Environmental heterogeneity (e.g., climate and soil) is a primary driver of species richness, however fire's proposed role in the maintenance of heterogeneity (O'Brien, 1998) has been largely ignored until recently (Francis and Currie, 2003; Hawkins et al., 2003; Kreft and Jetz, 2007; Rundel et al. 2018, 2018; He et al. 2018; He et al. 2019).

Although species richness is a vital component to ecosystem function and can be assessed at multiple levels (e.g. community, guild) and spatial scales (e.g. regional, continental), often factors influencing species richness may not scale up to higher levels (Willis and Whittaker, 2002). Thus, estimations of richness should be conducted at multiple levels to gain a better understanding of the factors influencing community dynamics. Furthermore, species richness alone is insufficient to inform management and conservation decisions given the social, ecologic, economic, and conservation importance of individual species [e.g., wild turkey (*Meleagris*

*gallopavo*), red-cockaded woodpecker (*Dryobates borealis*)]. Thus, species-specific responses must also be considered. As such, the incorporation of species-specific responses to fire will allow for better conservation of sensitive, endemic, or game species.

Species- and guild-specific responses to fire are variable in both direction and effect size (Fontaine and Kennedy, 2012). This is because fire-mediated changes augment habitat structure and food resources for avian species, which have variable impacts on species as a function of species- or guild-specific life history traits. For example, prescribed fire generally increases nest success in cavity-nesting species (Saab and Powell, 2005) likely due to fire-mediated tree mortality creating snags for nest sites (Bock and Block, 2005). Shrub and tree-nesting species have lower abundance in severely burned blocks compared to unburned blocks, likely due to fire consuming foliage that these birds utilize for nesting and foraging (Smucker et al. 2005). But, specific-species responses within a nesting guild may still be variable due to other natural history traits influencing distribution. For example in western North America, occupancy probability for the seed specialist pine siskin (*Spinus pinus*) declined with prescribed fire, while the bark insectivore black-backed woodpecker (*Picoides arcticus*) responded positively, despite both being canopy nesters (Russell et al. 2009). Furthermore, in southern pine forests, avian diversity, abundance, and species richness have been shown to be greater in sites that experience frequent burning (Conner et al. 2002, Allen et al. 2006), despite guild and species-specific associations exhibiting variable responses. Accordingly, understanding species-, guild- and community specific responses to spatial variation in fire history may improve our understanding of avian community ecology and efficiency of restoration efforts designed to promote biodiversity.

The ‘pyrodiversity begets biodiversity’ hypothesis (Martin and Sapsis, 1992; Parr and Andersen 2006; Davies et al. 2012), which suggests diversity of post fire conditions (i.e.,

pyrodiversity) promotes biodiversity, has received increasing attention recently (Tingley et al. 2016, He et al. 2019). Pyrodiversity is characterized by heterogeneity in age, size, and/or intensity of fire. The fundamental mechanism driving biodiversity as a function of pyrodiversity is similar to the concept that landscape heterogeneity promotes biodiversity in that, the more niche space an area contains, the greater number of species it is able to support (*sensu* Hutchinsonian niche; Hutchinson, 1957). However, research evaluating this hypothesis have had variable results at various scales, contrasting from strong positive responses (Maravalhas and Vasconcelos, 2014; Ponisio et al. 2016, Tingley et al. 2016) to no response or negative responses (Parr and Andersen, 2006; Taylor et al. 2012; Andersen et al. 2014). Furthermore, many studies evaluating the influence of fire on biodiversity were largely considered at global, continental, and regional scales (Bond and Parr, 2010; Tingley et al. 2016; Taylor et al. 2012; Farnsworth et al. 2014; Sitters, 2014; Beale et al. 2018) with fewer studies conducted at local scales (Davies et al. 2012; Fontaine and Kennedy, 2012; Sitters et al. 2016), thus elucidating the need for research specifically at smaller spatial scales (e.g. wildlife management area) to inform fire management and wildlife conservation.

Prescribed fire is effectively used to reduce fuel loads, alter vegetative structure, and restore and maintain historical disturbance regimes (Landers et al. 1986; Wade and Lunsford, 1989; Shea, 1994). This management practice has been commonly utilized in the southeastern United States where many endemic ecosystems are fire-maintained (Waldrop et al. 1992). Longleaf pine (*Pinus palustris*, hereafter LLP) savannas are fire-mediated ecosystems that boast some of the shortest fire return intervals of any system in North America (Christensen, 1981). Fire suppression in LLP ecosystems has led to mesophication, whereby heliophytic and fire-tolerant species are replaced by shade-tolerant species inducing a positive feedback loop creating

cool, damp microclimates (Nowacki and Abrams, 2008). As a result, plant species diversity declines as fire-adapted species are replaced by a limited assemblage of shade-tolerant, fire-sensitive species, effectively deteriorating LLP ecosystem (Nowacki and Abrams, 2008). Concurrently, land conversion and timber harvest has reduced the LLP ecosystem to 3% of its historical range (Frost, 1993; Brockway et al. 2005). As a result of mesophication and habitat alterations, two-thirds of all southeastern species of flora and fauna that are threatened, endangered, or in decline are associated with the LLP ecosystem, making LLP ecosystem restoration a high priority for conservation (Kirkman and Mitchell, 2006).

We investigated the effects of fire history on avian community dynamics in a frequently burned LLP ecosystem. We tested the ‘pyrodiversity begets biodiversity’ hypothesis (Martin and Sapsis, 1992; Parr and Andersen 2006; Davies et al. 2012) by examining the effect of heterogeneity in time-since-fire on species richness at community and guild levels. Our system was ideal to test this hypothesis because, relative to studies which have fire effects that vary in size, intensity, and frequency (Saab et al. 2005), our site has experienced frequent low intensity prescribed fires resulting in limited heterogeneity in severity and burn unit size. This allowed us to isolate time-since-fire as a primary driver in post-fire conditions. Furthermore, the scale of investigation (i.e. 227 km<sup>2</sup>) was smaller than most tests of this hypothesis (but see, Davies et al. 2012; Fontaine and Kennedy, 2012; Sitters et al. 2016) and therefore provided an opportunity to test the limits of the hypothesis. The hypothesis may not be supported at smaller scales due to species-area relationships; as patch size decreases the number of species occupying that patch also decreases, which produces a theoretical upper limit to the hypothesis (He et al. 2019). Understanding the upper limit of the hypothesis is beneficial to managers who typically operate at smaller scales. Lastly, it has been suggested that the drivers that influence subsets of the

community may not scale up to the community as a whole (Harte, 2011; Supp et al. 2012; Supp and Ernest, 2014) and by combining factors that influence species richness at the community and guild levels, we address a call for analysis at multiple levels of biological organization.

To assess the effects of pyrodiversity on biodiversity and examine ecological drivers across several ecological levels (i.e., species, guilds, and communities) we employed a Bayesian hierarchical community occupancy analysis to estimate the effects of fire on avian species richness and occupancy. To understand the relative importance of fire history on avian community dynamics, we also examine effects of soil productivity, land cover, and habitat structure. Our overarching goal was to examine the influence of fire and heterogeneity in fire history (i.e. pyrodiversity) relative to other ecological drivers to facilitate management and improve our understanding of avian communities in frequently burned conifer ecosystems. We predicted pyrodiversity would increase species richness at the community level, but would have weaker effects at the guild level due to common adaptations within guilds. We predicted that fire history (i.e. time-since-fire, mean fire return interval and recently burned areas) would have greater effects on the guild level than pyrodiversity since members of the guild likely have similar responses to fire effects on nesting or foraging resources.

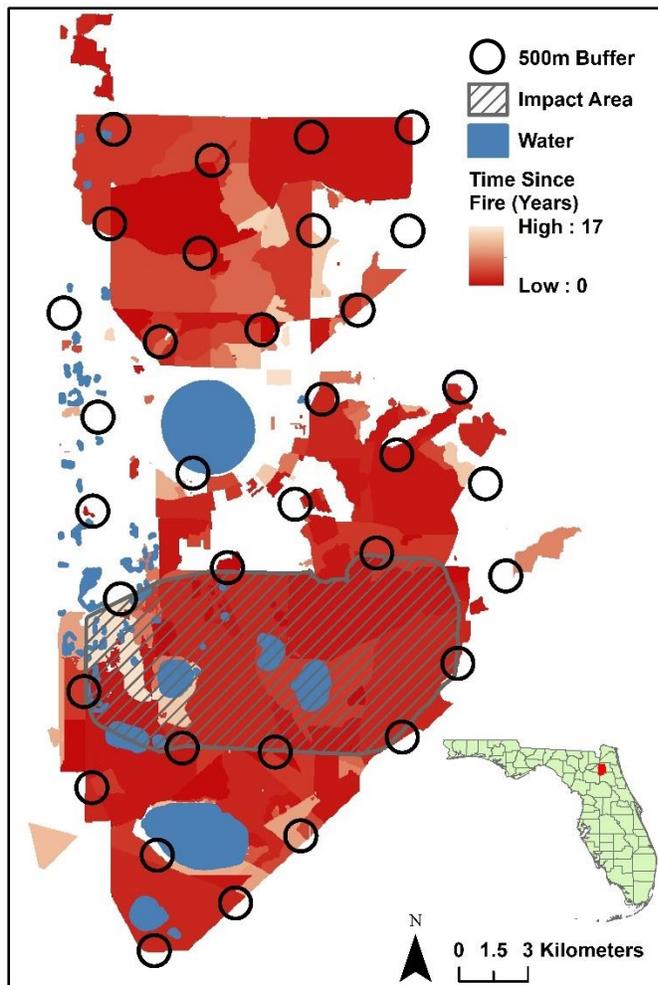
## **2. Methods**

### **2.1 Study Site**

Our study was located on Camp Blanding Joint Training Center and Wildlife Management Area (CB), a 227 km<sup>2</sup> site in northeastern Florida (Figure 1), where elevations ranged from 15 m to 74 m. Mean annual precipitation was 123.5 cm with a mean annual temperature of 20.5°C. The climate at CB was subtropical characterized by mild winters and hot humid summers. Land use on CB was designed for military training with a 6500-ha 'Impact

Zone' where artillery strikes are targeted, as well as forest management, sand mining, and wildlife habitat maintenance and restoration. Prescribed burning was used for habitat restoration and averaged a 3- to 5-year rotation dependent on forest stand composition and landform position. Soil productivity varied considerably across CB, which included the interface of the more productive Sea Islands Flatwoods ecoregion and the less productive Central Florida Ridges and Uplands ecoregion (Omernik and Griffith, 2014). Major forest types included mesic flatwoods dominated by longleaf pine woodlands and pine plantations, xeric sandhills, as well as bottomland hardwood forests. Florida Fish and Wildlife Conservation Commission and Florida Department of Military Affairs cooperatively manage wildlife on the base through hunting (FWC, 2017), as well as habitat maintenance and restoration through silviculture and prescribed fire.

## 2.2 Study Design



**Figure 2. 1** Locations of 34 avian acoustic monitoring sites, with 500 m buffer, in relation to time-since-fire in years (pyrodiversity), water features and impact area on Camp Blanding Joint Military Center, Starke, FL. Surveys were conducted 29 March – 3 April, 2017 and 3 April – 8 April, 2018.

### 2.2.1 Avian Acoustic Survey

To record detections of avian species, we monitored 34 survey sites, separated by a minimum of 3 km, throughout CB, excluding the Impact Area (Figure 1). At each site, we mounted a programmable acoustic recorder (PAR; Song Meter 2 and Song Meter 3, Wildlife Acoustics, Concord, MA) to record avian vocalizations (i.e., songs, calls, and chirps). Acoustic surveys were conducted from 29 March – 3 April 2017 and from 3 April – 8 April 2018 to

coincide with breeding and chick-rearing season. Recorders were mounted 2.4 - 3m off the ground and programmed to record three, five-minute surveys per day for six days. Surveys occurred at sunrise, one hour after sunrise, and two hours after sunrise. We selected 53 target species common in frequently burned pine forests in Florida and grouped them by nesting behavior (ground = 15, cavity = 13, tree = 15, shrub = 9, human structure = 1) and foraging behavior defined by hunting strategy and diet (ground-omnivore = 5, ground-granivore = 6, ground-insectivore = 10, aerial-insectivore = 4, bark-insectivore = 7, foliage-insectivore = 13; Sullivan et al. 2009; Appendix A). We chose nesting behavior as a grouping variable because we surveyed during nesting season and nesting is an important life history stage in avian population dynamics, which is likely to be influenced by fire (Ricklefs 1969, Martin 1993). We chose foraging behavior as another grouping variable because foraging guilds have been shown to respond differently to restoration (i.e. prescribed burning and silviculture; Davis et al. 2000). We excluded cedar waxwing (*Bombycilla cedrorum*), sandhill crane (*Grus canadensis*), and pine siskin (*Spinus pinus*) from the foraging guild as their foraging behavior (i.e. foliage-frugivore, probing-omnivore, and foliage-granivore, respectively) did not match any guild nor could they be grouped by foraging behavior. After researchers had completed 10 hours of song identification training, we interpreted acoustic files by identifying species heard in each five-minute session, while identifying species researchers were able to consult publicly available recordings to verify identifications.

## 2.2.2 Fire, land cover, soil productivity and forest structure measures

**Table 2. 1** Covariate names and descriptions for occupancy models fit to the 2017-2018 avian community acoustic survey conducted 29 March – 3 April 2017 and 3 April – 8 April 2018 at 34 survey sites on Camp Blanding Joint Training Center, Starke, FL.

	Name	Description
Fire	Time-Since-Fire	Number of growing seasons since the last burn at the survey site.
	Pyrodiversity	Number of unique times since fire (years; 2001-2018) values, based on growing seasons, at the time of the survey within a 500m buffer around the survey site.
	Mean Fire Return Interval	Average number of days between burns since 2001 at the survey site.
	Distance to Recently Burned Stands	Distance (m) to the nearest 30m raster cell representing a forest during the first growing season following fire.
Cover Type	Distance to Cover Type	Distance (m) to nearest 30m raster cell representing a given cover type (hardwood forests, pine forests, open habitat) at each site.
Productivity	Soil Productivity	United States Department of Agriculture measure of soil productivity based on soil taxonomic information ranging from 0 (least productive) to 19 (most productive; Schaetzl et al. 2012; Soil Survey Staff, 2017).
Forest Structure	Forest Canopy Cover	Amount of cover within a 500 m buffer around each survey site determined by a vertical projection of the tree canopy onto a two-dimensional horizontal surface (LANDFIRE, 2018).

To evaluate the effects of environmental covariates on avian species richness and occupancy, we generated a 500 m buffer around each survey site and created spatial data representing fire history characteristics, land cover type, soil productivity and forest structure using ArcGIS 10.3 (ESRI, Redlands, CA; Table 1). We created spatiotemporally explicit fire covariates that reflected the fire conditions on site for 2017 and 2018 with fire history data curated by CB’s Department of Military Affairs Environmental Division. We evaluated time-since-fire at each site by creating a raster layer where each 30 m cell was characterized by the number of growing seasons since the most recent fire. We chose to evaluate time-since-fire at

the annual scale based on personal observations of pronounced variation in stand structure as a function of the number of growing seasons since fire (Figure 2).

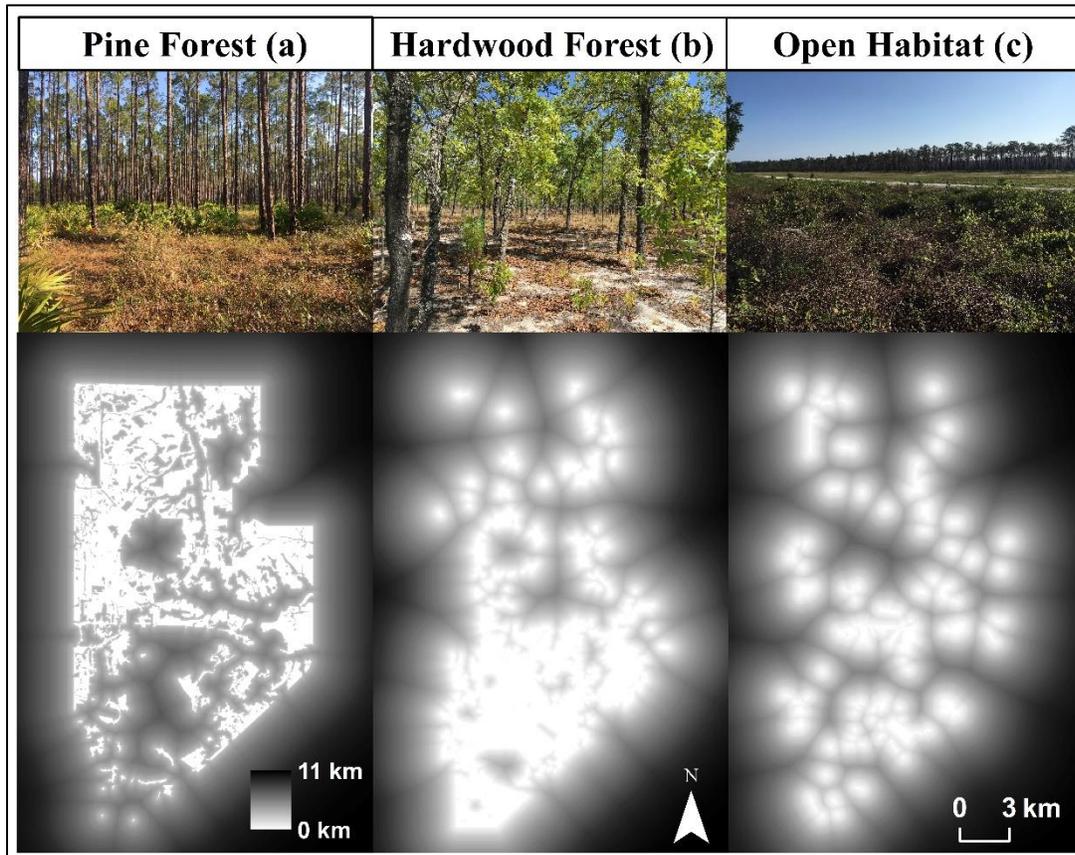


**Figure 2. 2** Representative images of a pine stand during (A) the first and (B) the second growing season following fire at the same location on Camp Blanding Joint Military Center, Starke, FL.

To characterize pyrodiversity, we identified the number of unique time-since-fire within each buffer. To evaluate the influence of long-term fire management on environmental conditions, we characterized the mean fire return interval for each site by extracting the fire history data since 2001, calculating each fire return interval and averaging those values within each location. We evaluated distance to recently burned stands by creating a raster layer for each

survey year where each cell was characterized by the Euclidean distance (m) to nearest cell containing a fire with the maximum of one growing season following fire. We developed a land cover raster layer by reclassifying CB's land cover into three land cover types: hardwood forests, pine forests, and open areas. We created distance raster layers using the Euclidian distance function in ArcGIS 10.3 Spatial Analyst Tools (ESRI, Redlands, CA), which created raster layers where each cell is populated with the distance to the nearest representative cell of a given land cover type (Figure 3). We created a spatially explicit soil productivity metric using the United States Department of Agriculture Productivity Index (Schaetzl et al. 2012) to identify soil productivity, which we then combined to spatially explicit soil classifications (Soil Survey Staff, 2017). We characterized soil productivity of each survey site at a 500 m scale using the zonal statistics function in ArcGIS 10.3 (ESRI, Redlands, CA) to average productivity values within the buffer around each survey site. We chose to analyze pyrodiversity and soil productivity at the 500 m scale as testing of different scales has shown 500 m to predict well across multiple species (Niemi et al. 2004, Grinde et al. 2017). We created a spatially-explicit, percent canopy cover metric using 2014 LANDFIRE (2018) data. This dataset uses a land cover raster based on predictive models derived from Landsat imagery and spatially-explicit ground vegetation assessments to create numerous variables associated with forest structure. We extracted percent canopy cover values from this dataset to characterize forest structure that may be important to avian communities (Dickson et al. 1991; Gates and Giffin, 1991).

### 2.2.3 Data Analysis



**Figure 2. 3** Euclidean distance rasters and representative photos of (a) pine forests, (b) hardwood forest, and (c) open habitat used in the 2017-2018 avian community acoustic survey conducted 29 March – 3 April 2017 and 3 April – 8 April 2018 on Camp Blanding Joint Military Center, Starke, FL. Brighter areas denote closer distances to the respective land cover type.

To estimate effects of land cover, fire conditions, pyrodiversity and canopy cover on avian occupancy, we fit hierarchical Bayesian multispecies site-occupancy models (Dorazio and Royle, 2005) with parameter-expanded data augmentation (Dorazio et al. 2006). These models estimated the effects of variables on the occupancy of individual species, which is used to estimate the effects of those variables on species richness. The advantage of using this over more traditional occupancy analyses is that this approach accounts for both species-level effects as well as aggregated effects of variables at the community-level or guild-level, providing

information at the species and aggregated levels simultaneously. We used occupancy models due to their ability to account for imperfect detection of species (Mackenzie et al. 2002). We surveyed for six days with three surveys per day for a total of 18 occasions per year. We created species-specific capture histories for avian species detected during automated point counts. Each site-occasion was assigned a '1' if the species was detected and a '0' if the species was not detected. Further, data augmentation allowed us to make inferences on species that were never detected by adding additional all-zero detection histories to our data for undetected species (Kery and Royle, 2015). We added five all-zero detection histories to our data to account for potentially missed species, based on the number of target species we were unable to detect. These models rely on the assumption of independence between sites, which requires that individuals cannot be detected at multiple sites within the survey period. We attempted to meet the assumption by ensuring 3 km spacing between survey sites, although slightly less than another study (5.35 km) we needed to balance spacing with maximizing the number of sites (Furnas and Callas, 2015). We considered each site and year combination to be a unique site (i.e. 68 sites) as we focused on species occupancy rather than turnover rate (i.e., colonization and extinction probabilities), and temporal replication was limited for a dynamic model because we only collected two years of data (Fuller et al. 2016). Due to temporal variation in fire history covariates as well as drought conditions during the 2017 survey and moderate conditions in the 2018 survey, we suggest this is a reasonable procedure despite sites being replicated by year. We developed variables that represented our hypotheses regarding factors influencing species occupancy and created models including a global, null, and all possible additive combinations of variables, resulting in 256 candidate models. Models consisted of one Markov chain Monte Carlo (MCMC) chains run for 25,000 iterations with every 10<sup>th</sup> iteration thinned and 5,000 burn-

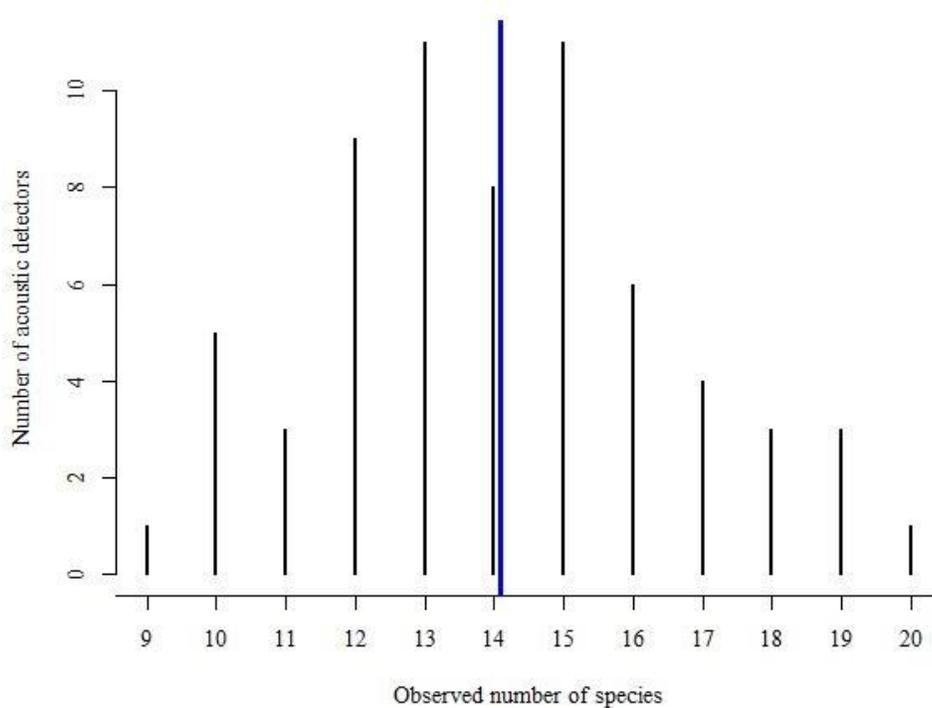
in, using Just Another Gibbs Sampler (JAGS; Plummer, 2013) in the JagsUI package (Kellner, 2015) in R programming language (R Core team, 2016). We fit all models to the entire dataset as well as subsets of the data based on nesting and foraging guilds, except for the building nesting guild as it consisted of only one species [i.e. Eastern phoebe (*Sayornis phoebe*)]. Because we were interested in the factors influencing occupancy rather than obtaining an estimate of true occupancy, we focused on the differences in relative use across sites. To account for dependence between site-years, we included the effect of year on the detection and occupancy portion of each model (Fuller et al. 2016). To test for collinearity, we utilized the Corr Function from the emulator package (Hankin, 2005) in program R (R Core Team, 2016), of which the analyzed covariates did not exceed an  $R^2$  values of 0.40 (Mukaka, 2012). We scaled and centered all covariates for analysis to aid in model convergence. We considered models converged when all Rhat values were less than 1.1. We used Deviance Information Criterion (DIC; Spiegelhalter et al. 2002) to determine the top model (Appendix B1-11). We assigned significance when credible intervals (CrI) for a given parameter did not overlap zero.

We designed a study to evaluate a broad range of avian species and many tradeoffs must be considered with such a design. Thus, we note and acknowledge certain limitations when considering these results. Our approach for estimating species occupancy relied on the assumption that sites were independent, meaning an individual would not be detected at multiple survey sites. Although we likely met this assumption for most species, a few species had large home ranges or were highly mobile (e.g. American crows, and wild turkeys), which may have violated this assumption. This violation would result in overestimated occupancy for those species. It is important to note that occupancy estimates presented should not be considered true occupancy for CB, but rather relative site use that allowed for analyses of factors driving the

variation in those parameters. Whereas the estimates themselves and precision of those estimates may be inflated, the assessment of factors influencing estimates and subsequent management implications are typically robust to violation of this assumption (O’Connell, 2006).

### 3. Results

We recorded 2,590 and 2,690 bird detections during the 6-day sampling periods in 2017 and 2018, respectively. We detected 48 of 53 target species at least once during the survey. The five species we did not detect were Florida scrub jay (*Aphelocoma coerulescens*), Florida grasshopper sparrow (*Ammodramus savannarum floridanus*), killdeer (*Charadrius vociferus*), hermit thrush (*Catharus guttatus*), and black-and-white warbler (*Mniotilta varia*). The American Crow (*Corvus brachyrhynchos*) was the most frequently detected avian species. The mean community occupancy probability was 36% and the average species detection probability was



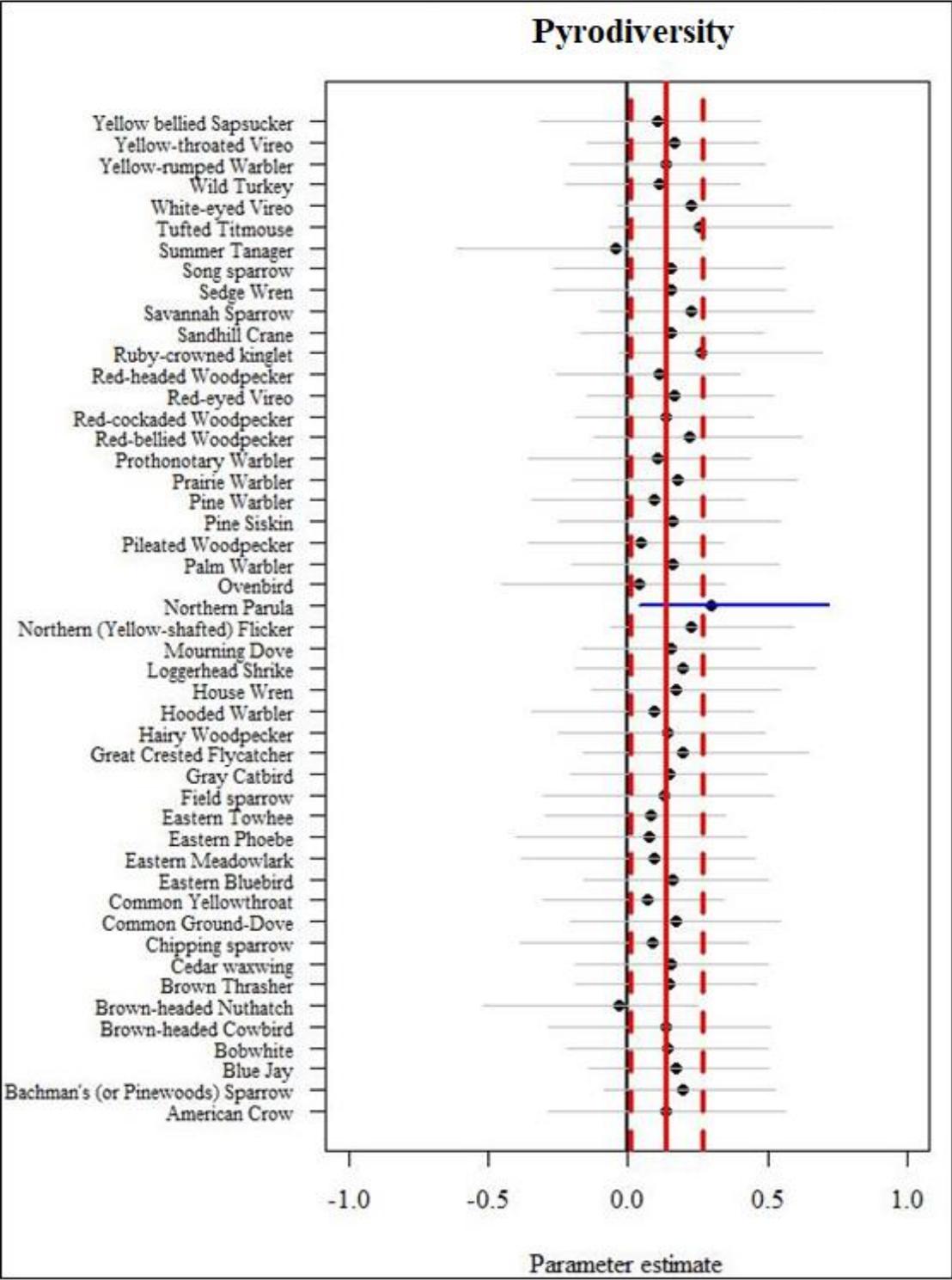
**Figure 2. 4** Naïve local species richness from the 2017-2018 wildlife community acoustic survey conducted 29 March – 3 April 2017 and 3 April – 8 April 2018 at 34 survey sites on Camp Blanding Joint Military Center, Starke, FL. Estimates are averages from 2017 and 2018 results, average naïve species richness across all sites and years is denoted by blue line.

17%. Naïve mean species richness for the 48 detected species was 14.09 species per site (Figure 4).

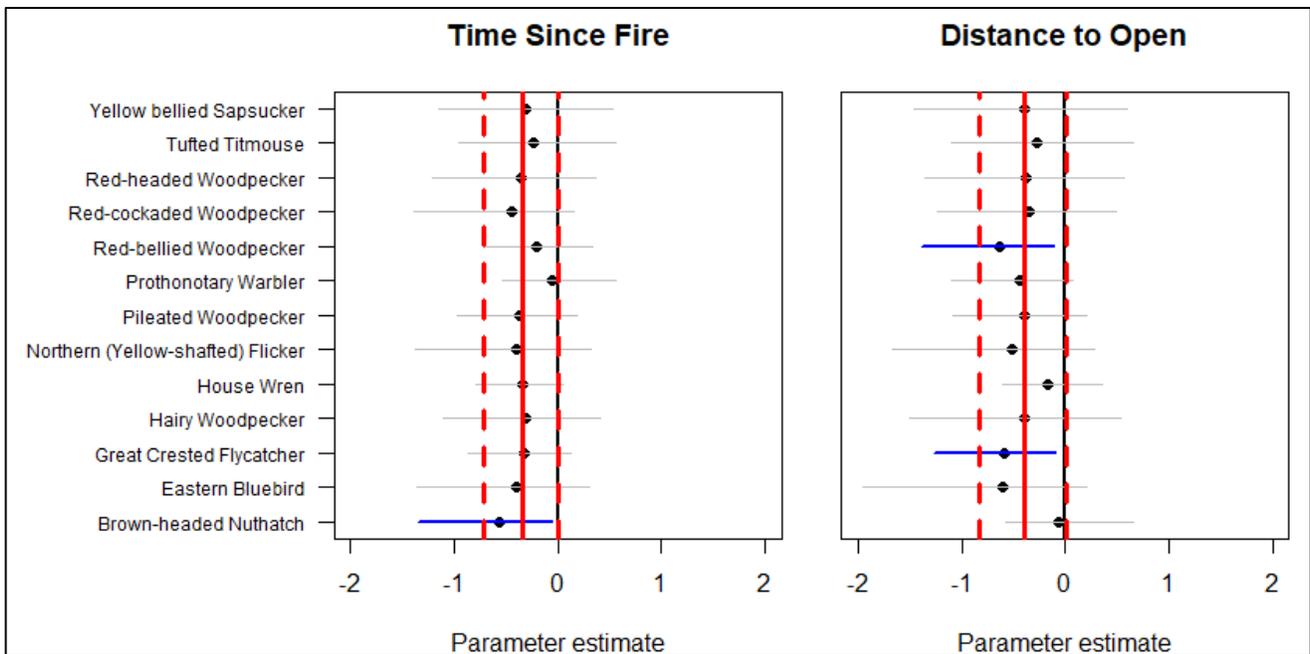
The top model predicting species richness at the community level included pyrodiversity, distance to pine forest, distance to hardwood forest, and canopy cover with a fixed effect of year on both the occupancy and detection portion of the model. At the community level, species richness increased with pyrodiversity ( $\beta = 0.136$ , 95% CrI = 0.009 – 0.260; Figure 5). Although included in the top model, the credible intervals for distance to hardwood forests, distance to pine forests, canopy cover, and survey year overlapped zero and were considered uninformative parameters. At the species level, within the community model, only the probability of Northern Parula (*Setophaga americana*) occupancy increased with pyrodiversity ( $\beta = 0.299$ , 95% CrI = 0.042 – 0.718, Figure 5). The probability of occupancy increased for White-eyed Vireos (*Vireo griseus*;  $\beta = 0.524$ , 95% CrI = 0.055 – 1.00) and House Wrens (*Troglodytes aedon*;  $\beta = 0.426$ , 95% CrI = 0.007 – 0.941) from 2017 to 2018. Finally, the probability of detection increased from 2017 to 2018 for American Crows ( $\beta = 0.617$ , 95% CrI = 0.378 – 0.854), Mourning Doves (*Zenaida macroura*;  $\beta = 0.297$ , 95% CrI = 0.022 – 0.578), and decreased for Blue Jays (*Cyanocitta cristata*;  $\beta = -0.454$ , 95% CrI = -0.715 – -0.199), Northern Flickers (*Colaptes auratus*;  $\beta = -0.629$ , 95% CrI = -1.26 – -0.066), Pileated Woodpeckers (*Dryocopus pileatus*;  $\beta = -0.584$ , 95% CrI = -1.05 – -0.124), red-headed woodpeckers (*Melanerpes erythrocephalus*;  $\beta = -0.681$ , 95% CrI = -1.47 – -0.082), and white-eyed Vireos ( $\beta = -0.491$ , 95% CrI = -0.818 – -0.172).

We found only weak effects at the guild level with no foraging guilds strongly influenced by our covariates and only one nesting guild influenced by our covariates. Despite a lack of support for strong covariate effects, ground foraging granivores' top model included only percent canopy cover which trended negative for all species except for the Bachman's sparrow (*Peucaea*

*aestivalis*), resulting in a trend of decreasing species richness for this guild with increasing canopy cover ( $\beta = -0.419$ , 95% CrI= -1.305 – 0.219). Out of the four nesting guilds analyzed (i.e., tree, shrub, ground, and cavity) only the cavity nesting guild was significantly influenced by covariates. The top model for cavity nesters included time-since-fire, distance to open habitats, soil productivity, and canopy cover with a fixed effect of year on both occupancy and detection. Cavity guild species richness decreased with increasing time-since-fire ( $\beta = -0.334$ , 95% CrI= -0.713 – -0.003; Figure 6). Although included in the top model, the credible intervals for distance to open habitats, soil productivity, canopy cover, and survey year overlapped zero and were considered uninformative parameters, although species richness trended towards decreasing with increasing distance to open habitats ( $\beta = -0.389$ , 95% CrI= -0.833 – 0.013; Figure 6). Within this guild, at the species level, all species occupancy estimates were negatively associated with increasing time-since-fire and distance to open habitat, but only Brown-headed nuthatch (*Sitta pusilla*) occupancy strongly decreased with increasing time-since-fire ( $\beta = -0.569$ , 95% CrI= -1.33 – -0.063; Figure 6), and the great crested flycatcher ( $\beta = -0.586$ , 95% CrI= -1.26 – -0.091) and red-bellied woodpecker ( $\beta = -0.636$ , 95% CrI= -1.38 – -0.114) probability of occupancy strongly decreased with increasing distance to open habitats.



conducted 29 March – 3 April 2017 and 3 April – 8 April 2018 at 34 plots on Camp Blanding Joint Military Center, Starke, FL. Estimates are averages from 2017 and 2018 results. Red lines denotes the community posterior mean (solid) and credible interval (dashed) while the blue line denotes individual species credible interval that do not overlap zero.



**Figure 2. 6** Comparison between cavity nesting bird guild and individual cavity nesting species response of occupancy probability to time-since-fire and distance to open habitats, for the 13 observed species, from a Bayesian multi-species occupancy model, for the 2017- 2018 wildlife community acoustic survey conducted 29 March – 3 April 2017 and 3 April- 8 April 2018 at 34 plots on Camp Blanding Joint Military Center, Starke, FL. The blue line represents the significant positive effect for the brown-headed nuthatch to increasing time-since-fire as well as a negative effect for the red-bellied woodpecker and great crested flycatcher to distance to open habitats. The community mean effect is denoted by the red line with the credible interval in red dashed lines.

## 4. Discussion

### 4.1 Evidence supports use of fire to promote avian diversity at the site level

We found support for the pyrodiversity begets biodiversity hypothesis at the community level and that the hypothesis was supported at our smaller spatial scales, indicating that the theoretical upper limit to number of species supported at small patch sizes was not likely reached even at smaller scales. Furthermore, we found that factors influencing guild level species richness did not scale up to the community level, as predicted.

Our work revealed linkages between avian species richness and environmental factors including fire and land cover. We modeled richness for the entire avian community and also had sufficient data to model occupancy of 48 avian species and species richness of four nest guilds,

and six foraging guilds. At the community level, we identified a positive effect of pyrodiversity on species richness; the diversity of conditions in areas with greater pyrodiversity likely provided greater numbers of ecological niche spaces. This supports and further extends the ‘pyrodiversity begets biodiversity’ hypothesis for avian species to smaller spatial scales that are more applicable to management decisions occurring on more local-level scales. Previous studies have produced equivocal results (Sitters et al. 2014, Tingley et al. 2016, Taylor et al. 2012) and we suggest this is due to variability in multiple fire characteristics (i.e. size, intensity, horizontal spread, vertical spread, seasonality and interval), cause (i.e. wildfire vs. prescribed), and spatial scale. Utilizing the low intensity prescribed burns common to LLP restoration and management allowed us to minimize the variability in some fire characteristics relative to studies with mixed severity fires. Our study supports the findings that pyrodiversity benefits avian biodiversity at smaller spatial scales (Davies et al 2012; Fontaine and Kennedy, 2012; Sitters et al. 2016). Furthermore, concurrent research found coyotes (*Canis lupus*) and bobcats (*Lynx rufus*) had lower relative abundances in areas of greater pyrodiversity and that raccoons (*Procyon lotor*) had lower relative abundances near recently burned areas (Jorge, M., [2017-2018], In Review), suggesting that the use of fire in our study system may also have altered predator distributions, further promoting avian species richness. The use of fire has been shown to promote avian species richness (Provencher et al. 2001, 2003), and has been shown to alter predator distributions or activity (Kirby et al. 2016, McGregor et al. 2014), but our study is unique in that we tested these hypothesis concurrently under the same prescribed fire prescriptions and study site.

Our results support previous studies that found that the factors influencing one level (e.g. guild) do not always scale up to higher levels (e.g. community; Willis and Whittaker, 2002;

Harte, 2011; Supp et al. 2012; Supp and Ernest, 2014). At the guild level, time-since-fire had a negative effect on cavity nesting guild species such that richness declined with increasing time-since-fire. Similarly, in southwestern Idaho, cavity nesting species occupancy probability was greater in more recent burns (i.e. 1-4 years), perhaps due to the influence of fire on prey availability and lack of nest predators (Saab et al. 2004). Furthermore, in the LLP sandhills of northern Florida, the occupancy probability of cavity nesting species increased post treatment of prescribed burns (Steen et al. 2013). The beneficial attributes of recent burns likely dissipate or change as time-since-fire increases, which likely decreases the number of species benefitting within the cavity nesting guild. We did not detect any significant effects of environmental covariates on other nesting guilds (i.e. ground, tree, and shrub) nor foraging guilds. This may have been due to a greater variability of individual species responses within each guild. For example, the cavity nesting guild consists of mostly insectivores and one omnivore making them a more homogenous guild than other guilds as they often rely on one another for cavities (i.e., primary cavity nesters create cavities for secondary cavity nesters). Therefore individual species' occupancy probabilities for cavity nesters were likely being driven by similar effects. Contrastingly, the tree nesting guild had a much more variability in diet (i.e., omnivore, insectivore, granivore, frugivore), which likely created more variability in their responses to covariates. Our results suggest that mosaic and frequent burning benefits avian diversity and the cavity nesting guild in particular, both suggestions can be done simultaneously under one management prescription.

At the individual species level, we identified positive effects of increasing pyrodiversity on northern Parula occupancy. In central Georgia, northern Parula abundance was greater in burned areas versus unburned areas, likely due to the increased availability of insects following

fire (White et al. 1999). Northern Parulas likely benefit from a diversity of fire conditions as recently burned stands provide abundant foraging opportunities, while less frequently burned stands provide important nesting resources. Therefore, Northern Parulas benefit from pyrodiversity because it supplies both foraging and nesting resources in close proximity. We found negative effects of increasing time-since-fire on Brown-headed nuthatch occupancy. Brown-headed nuthatches have been known to benefit from fire and timber management implemented for red-cockaded woodpeckers (Lucas, 1993; Wilson et al. 1995, Burger et al. 1998). For example, prescribed burns are frequently applied to clear understory, which maintains relatively short times since fire when managing for red-cockaded woodpeckers.

We identified negative effects of increasing distance to open habitats on great crested flycatcher occupancy. Great crested flycatchers have been suggested to reside in forest interior habitat but utilize more open wooded conditions (Hamel, 1992). Open habitats in our study were surrounded by forests, which may function similarly to an open woodland condition within a forest interior habitat. We identified negative effects of increasing distance to open habitats on red-bellied woodpecker occupancy. Red-bellied woodpeckers are more generalist species occupying dry to wet habitats from hardwood to mixed pine-hardwood forests to pine savanna habitats (Shackelford et al. 2000). Although seemingly contrary to our results, red-bellied woodpecker foraging microhabitat may vary depending on forage availability (Shackelford et al. 2000). Thus one potential explanation for our observation of greater occupancy near open habitats may have been the increased foraging opportunities through hawking for arthropods and feeding on fruits, berries, and seeds in open habitats which, at our site, were surrounded by forests more commonly associated with this species.

Our results highlight the importance of studying multiple levels of organization simultaneously to gain a more complete understanding of the effects of fire on avian community dynamics. We offer evidence in support of the linkage between pyrodiversity and biodiversity at a local scale that is readily translated to conservation actions. Our results and characterization of pyrodiversity suggests that managers can promote avian community diversity by reducing the size of burn units to create areas with multiple adjacent burn units, with unique fire histories and a mosaic of post-fire conditions. An important next step is to test the effect of diversity of other fire attributes including seasonality and severity on biodiversity to determine what fire attributes are most important to diversify to promote avian biodiversity. The underlying mechanisms behind the ‘pyrodiversity beget biodiversity’ hypothesis remains an open question and identifying these mechanisms will benefit managers and conservationists in promoting avian biodiversity. This study further supported and expanded the importance of pyrodiversity as a driver of biodiversity, highlighted the importance of estimating species richness at multiple levels due to differences in guild groupings (i.e. nesting v. foraging and guild v. community), and assessed impacts of covariates at a spatial scale that can be utilized by managers and conservationists to better promote avian diversity.

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## Appendix

**Appendix A.** Scientific name, common name, and nesting behavior categorized by for the 53 species selected for the 2017- 2018 wildlife community acoustic survey from Camp Blanding Joint Training Center, Clay County, FL.

Scientific name	Common Name	Nesting	Foraging
<i>Sayornis phoebe</i>	Eastern Phoebe	Buildings	Insectivore - Fly Catching
<i>Melanerpes erythrocephalus</i>	Red-headed Woodpecker	Cavity	Omnivore - Fly Catching
<i>Myiarchus crinitus</i>	Great Crested Flycatcher	Cavity	Insectivore - Fly Catching
<i>Sphyrapicus varius</i>	Yellow bellied Sapsucker	Cavity	Insectivore - Bark Forager
<i>Dryocopus pileatus</i>	Pileated Woodpecker	Cavity	Insectivore - Bark Forager
<i>Melanerpes carolinus</i>	Red-bellied Woodpecker	Cavity	Insectivore - Bark Forager
<i>Picoides villosus</i>	Hairy Woodpecker	Cavity	Insectivore - Bark Forager
<i>Picoides borealis</i>	Red-cockaded Woodpecker	Cavity	Insectivore - Bark Forager
<i>Sitta pusilla</i>	Brown-headed Nuthatch	Cavity	Insectivore - Bark Forager
<i>Troglodytes aedon</i>	House Wren	Cavity	Insectivore - Foliage Gleaner
<i>Protonotaria citrea</i>	Prothonotary Warbler	Cavity	Insectivore - Foliage Gleaner
<i>Parus bicolor</i>	Tufted Titmouse	Cavity	Insectivore - Foliage Gleaner
<i>Colaptes auratus</i>	Northern (Yellow-shafted) Flicker	Cavity	Insectivore - Ground Forager
<i>Sialia sialis</i>	Eastern Bluebird	Cavity	Insectivore - Ground Forager
<i>Mniotilta varia</i>	Black-and-white Warbler	Ground	Insectivore - Bark Forager
<i>Passerculus sandwichensis</i>	Savannah Sparrow	Ground	Insectivore - Ground Forager
<i>Spizella pusilla</i>	Field sparrow	Ground	Insectivore - Ground Forager
<i>Setophaga palmarum</i>	Palm Warbler	Ground	Insectivore - Ground Forager
<i>Charadrius vociferous</i>	Killdeer	Ground	Insectivore - Ground Forager
<i>Sturnella magna</i>	Eastern Meadowlark	Ground	Insectivore - Ground Forager
<i>Seiurus aurocapilla</i>	Ovenbird	Ground	Insectivore - Ground Forager
<i>Catharus guttatus</i>	Hermit Thrush	Ground	Insectivore - Ground Forager
<i>Ammodramus savannarum floridanus</i>	Florida Grasshopper Sparrow	Ground	Insectivore - Ground Forager
<i>Meleagris gallopavo</i>	Wild Turkey	Ground	Omnivore - Ground Forager
<i>Pipilo erythrophthalmus</i>	Eastern Towhee	Ground	Omnivore - Ground Forager
<i>Colinus virginianus</i>	Bobwhite	Ground	Granivore - Ground Forager
<i>Columbina passerine</i>	Common Ground-Dove	Ground	Granivore - Ground Forager
<i>Aimophila aestivalis</i>	Bachman's (or Pinewoods) Sparrow	Ground	Granivore - Ground Forager
<i>Grus canadensis</i>	Sandhill Crane	Ground	Omnivore - Probing
<i>Dendroica discolor</i>	Prairie Warbler	Shrub	Insectivore - Foliage Gleaner
<i>Vireo griseus</i>	White-eyed Vireo	Shrub	Insectivore - Foliage Gleaner
<i>Wilsonia citrina</i>	Hooded Warbler	Shrub	Insectivore - Foliage Gleaner
<i>Geothlypis trichas</i>	Common Yellowthroat	Shrub	Insectivore - Foliage Gleaner
<i>Melospiza melodia</i>	Song sparrow	Shrub	Insectivore - Ground Forager
<i>Cistothorus platensis</i>	Sedge Wren	Shrub	Insectivore - Ground Forager

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**Appendix A. Continued**

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<i>Dumetella carolinensis</i>	Gray Catbird	Shrub	Insectivore - Ground Forager
<i>Toxostoma rufum</i>	Brown Thrasher	Shrub	Omnivore - Ground Forager
<i>Spizella passerine</i>	Chipping sparrow	Shrub	Granivore - Ground Forager
<i>Lanius ludovicianus</i>	Loggerhead Shrike	Tree	Insectivore - Aerial Diver
<i>Dendroica pinus</i>	Pine Warbler	Tree	Insectivore - Bark Forager
<i>Vireo olivaceus</i>	Red-eyed Vireo	Tree	Insectivore - Foliage Gleaner
<i>Vireo flavifrons</i>	Yellow-throated Vireo	Tree	Insectivore - Foliage Gleaner
<i>Setophaga coronata</i>	Yellow-rumped Warbler	Tree	Insectivore - Foliage Gleaner
<i>Piranga rubra</i>	Summer Tanager	Tree	Insectivore - Foliage Gleaner
<i>Parula americana</i>	Northern Parula	Tree	Insectivore - Foliage Gleaner
<i>Regulus calendula</i>	Ruby-crowned kinglet	Tree	Insectivore - Foliage Gleaner
<i>Cyanocitta cristata</i>	Blue Jay	Tree	Omnivore - Ground Forager
<i>Aphelocoma coerulescens</i>	Florida Scrub Jay	Tree	Omnivore - Ground Forager
<i>Corvus brachyrhynchos</i>	American Crow	Tree	Omnivore - Ground Forager
<i>Molothrus ater</i>	Brown-headed Cowbird	Tree	Granivore - Ground Forager
<i>Zenaida macroura</i>	Mourning Dove	Tree	Granivore - Ground Forager
<i>Bombycilla cedrorum</i>	Cedar waxwing	Tree	Frugivore - Foliage Gleaner
<i>Spinus pinus</i>	Pine Siskin	Tree	Granivore - Foliage Gleaner

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**Appendix B1.** Deviance Information Criterion (DIC) and effective number of parameters (pD), from Bayesian multispecies occupancy models, for the top five models for all 48 species detected from 2017 and 2018 automated point counts conducted 29 March – 3 April 2017 and 3 April- 8 April 2018 at 34 plots on Camp Blanding Joint Training Center, Clay County, FL. P = detection parameter, psi = occupancy parameter.

Model	DIC	pD
p(Year), psi(Pyrodiversity + Distance to pine forests + Distance to hardwood forests + Forest canopy cover + Year)	20125.66	1113.11
p(Year), psi(Pyrodiversity + Distance to pine forests + Distance to hardwood forests + Distance to open forests + Year)	20134.59	1121.74
p(Year), psi(Distance to pine forests + Distance to hardwood forests + Distance to open forests + Year)	20138.27	1126.59
p(Year), psi(Distance to pine forests + Distance to hardwood forests + Canopy cover + Year)	20140.76	1129.48
p(Year), psi(USDAPI + Distance to pine forests + Distance to open forests + Forest canopy cover + Year)	20147.18	1134.21

**Appendix B2.** Deviance Information Criterion (DIC) and effective number of parameters (pD), from Bayesian multispecies occupancy models, for the top five models for 13 cavity nesting species detected from 2017 and 2018 automated point counts conducted 29 March – 3 April 2017 and 3 April- 8 April 2018 at 34 plots on Camp Blanding Joint Training Center, Clay County, FL. P = detection parameter, psi = occupancy parameter.

Model	DIC	pD
p(Year), psi(Time-since-fire + Soil Productivity + Distance to open habitats + Percent canopy cover + Year)	3548.32	232.10
p(Year), psi(Mean fire return interval + Distance to hardwood forests + Distance to open habitat + Year)	3550.46	235.08
p(Year), psi(Time-since-fire + Distance to open forests + Year)	3552.29	238.78
p(Year), psi(Soil productivity + Distance to open + Canopy cover + Year)	3552.46	237.94
p(Year), psi(Distance to hardwood + Year)	3553.33	241.70

**Appendix B3.** Deviance Information Criterion (DIC) and effective number of parameters (pD), from Bayesian multispecies occupancy models, for the top five models for 14 tree nesting species detected from 2017 and 2018 automated point counts conducted 29 March – 3 April 2017 and 3 April- 8 April 2018 at 34 plots on Camp Blanding Joint Training Center, Clay County, FL. P = detection parameter, psi = occupancy parameter.

Model	DIC	pD
p(Year), psi(Time-since-fire + Mean fire return interval + Distance to open habitats + Year)	7771.05	269.90
p(Year), psi(Distance to hardwood forests+ Canopy cover + Year)	7776.96	278.02
p(Year), psi(Mean fire return interval + Soil productivity + Year)	7777.79	279.02
p(Year), psi(Distance to hardwood + Distance to open + Canopy cover + Year)	7778.02	277.54
p(Year), psi(Time-since-fire + Mean fire return interval + Distance to hardwood + Year)	7778.86	279.93

**Appendix B4.** Deviance Information Criterion (DIC) and effective number of parameters (pD), from Bayesian multispecies occupancy models, for the top five models for 9 shrub nesting species detected from 2017 and 2018 automated point counts conducted 29 March – 3 April 2017 and 3 April- 8 April 2018 at 34 plots on Camp Blanding Joint Training Center, Clay County, FL. P = detection parameter, psi = occupancy parameter.

Model	DIC	pD
NULL	1879.77	231.10
p(Year), psi(Distance to pine forests + Year)	1904.57	253.37
p(Year), psi(Distance to open habitat + Canopy cover + Year)	1905.38	254.02
p(Year), psi(Distance to open habitat + Year)	1907.03	255.80
p(Year), psi(Pyrodiversity + Year)	1908.21	256.52

**Appendix B5.** Deviance Information Criterion (DIC) and effective number of parameters (pD), from Bayesian multispecies occupancy models, for the top five models for 11 ground nesting species detected from 2017 and 2018 automated point counts conducted 29 March – 3 April 2017 and 3 April- 8 April 2018 at 34 plots on Camp Blanding Joint Training Center, Clay County, FL. P = detection parameter, psi = occupancy parameter.

Model	DIC	pD
p(Year), psi(Canopy cover + Year)	8038.04	176.39
p(Year), psi(Soil productivity + Distance to pine forests + Distance to open habitat + Year)	8038.73	177.60
p(Year), psi(Distance to pine forests + Distance to hardwood forests + Canopy cover + Year)	8039.16	176.63
p(Year), psi(Soil productivity + Distance to pine forests + Distance to hardwood forests + Year)	8040.16	178.31
p(Year), psi(Soil productivity + Distance to pine forests + Canopy cover + Year)	8041.212	178.54

**Appendix B6.** Deviance Information Criterion (DIC) and effective number of parameters (pD), from Bayesian multispecies occupancy models, for the top five models for five Omnivorous ground foraging species detected from 2017 and 2018 automated point counts conducted 29 March – 3 April 2017 and 3 April- 8 April 2018 at 34 plots on Camp Blanding Joint Training Center, Clay County, FL. P = detection parameter, psi = occupancy parameter.

Model	DIC	pD
p(Year), psi(Distance to hardwood forests + Year)	4132.57	64.91
p(Year), psi(Distance to open habitat + Year)	4133.26	65.82
p(Year), psi(Pyrodiversity + Year)	4135.04	67.73
p(Year), psi(Time-since-fire + Year)	4135.55	67.92
p(Year), psi(Soil productivity+ Year)	4136.93	69.23

**Appendix B7.** Deviance Information Criterion (DIC) and effective number of parameters (pD), from Bayesian multispecies occupancy models, for the top five models for six granivore ground foraging species detected from 2017 and 2018 automated point counts conducted 29 March – 3 April 2017 and 3 April- 8 April 2018 at 34 plots on Camp Blanding Joint Training Center, Clay County, FL. P = detection parameter, psi = occupancy parameter.

Model	DIC	pD
p(Year), psi(Canopy cover + Year)	2209.93	180.31
p(Year), psi(Soil productivity + Canopy cover + Year)	2214.92	184.95
p(Year), psi(Distance to open habitat + Canopy cover + Year)	2216.32	186.50
p(Year), psi(Soil productivity + Year)	2219.86	191.47
NULL	2225.28	195.93

**Appendix B8.** Deviance Information Criterion (DIC) and effective number of parameters (pD), from Bayesian multispecies occupancy models, for the top five models for four insectivore aerial foraging species detected from 2017 and 2018 automated point counts conducted 29 March – 3 April 2017 and 3 April- 8 April 2018 at 34 plots on Camp Blanding Joint Training Center, Clay County, FL. P = detection parameter, psi = occupancy parameter.

Model	DIC	pD
p(Year), psi(Pyrodiversity + Distance to open habitat + Year)	2061.65	48.89
p(Year), psi(Mean fire return interval + Distance to open habitat + Year)	2062.22	47.60
p(Year), psi(Soil productivity + Distance to open habitat + Canopy cover + Year)	2062.26	49.69
p(Year), psi(Soil productivity + Year)	2064.35	51.29
p(Year), psi(Time-since-fire + Mean fire return interval + Distance to hardwood forests + Distance to open habitat + Year)	2064.41	50.11

**Appendix B9.** Deviance Information Criterion (DIC) and effective number of parameters (pD), from Bayesian multispecies occupancy models, for the top five models for ten insectivore ground foraging species detected from 2017 and 2018 automated point counts conducted 29 March – 3 April 2017 and 3 April- 8 April 2018 at 34 plots on Camp Blanding Joint Training Center, Clay County, FL. P = detection parameter, psi = occupancy parameter.

Model	DIC	pD
NULL	1290.26	230.69
p(Year), psi(Time-since-fire + Distance to open habitat + Canopy cover + Year)	1303.54	235.00
p(Year), psi(Distance to open habitat + Year)	1305.08	238.78
p(Year), psi(Canopy cover + Year)	1310.16	244.38
p(Year), psi(Mean fire return interval + Distance to open habitat + Canopy cover + Year)	1310.37	240.91

**Appendix B10.** Deviance Information Criterion (DIC) and effective number of parameters (pD), from Bayesian multispecies occupancy models, for the top five models for seven insectivore bark foraging species detected from 2017 and 2018 automated point counts conducted 29 March – 3 April 2017 and 3 April- 8 April 2018 at 34 plots on Camp Blanding Joint Training Center, Clay County, FL. P = detection parameter, psi = occupancy parameter.

Model	DIC	pD
NULL	4497.91	200.70
p(Year), psi(Distance to open habitat + Year)	4517.43	216.09
p(Year), psi(Time-since-fire + Year)	4526.89	225.68
p(Year), psi(Pyrodiversity + Year)	4533.67	230.26
p(Year), psi(Canopy cover + Year)	4536.24	234.38

**Appendix B11.** Deviance Information Criterion (DIC) and effective number of parameters (pD), from Bayesian multispecies occupancy models, for the top five models for thirteen insectivore foliage foraging species detected from 2017 and 2018 automated point counts conducted 29 March – 3 April 2017 and 3 April- 8 April 2018 at 34 plots on Camp Blanding Joint Training Center, Clay County, FL. P = detection parameter, psi = occupancy parameter.

Model	DIC	pD
p(Year), psi(Mean fire return interval + Soil productivity + Canopy cover + Year)	5216.86	157.13
p(Year), psi(Time-since-fire + Mean fire return interval + Soil productivity + Distance to open habitat + Year)	5217.73	157.83
p(Year), psi(Time-since-fire + Pyrodiversity + Distance to hardwood forests + Year)	5218.15	157.91
p(Year), psi(Time-since-fire + Soil productivity + Year)	5218.86	159.13
p(Year), psi(Pyrodiversity + Soil productivity + Year)	5219.51	159.19

### **Chapter 3: Fawn Population Vital Rates Across Two Ecoregions Using Passive Sampling** *Formatted for Journal of Wildlife Management*

#### **Abstract**

Recruitment is a fundamental population process that heavily influences ungulate population growth rates and therefore understanding the factors influencing recruitment is necessary for population management. White-tailed deer (*Odocoileus virginianus*, hereafter, deer) fawn survival rates can be particularly low in longleaf pine (*Pinus palustris*; hereafter, LLP) forests potentially due to fire-facilitated predation. Fire alters cover and forage resources in temporally dynamic ways, which could both positively and negatively influence deer survival, but little is known about how fire, a common land management tool in LLP ecosystems, influences fawn survival and recruitment. Therefore, we estimated the effects of fire, soil productivity, and predator activity on fawn population vital rates, within two remote-sensing camera trap arrays (i.e. North Array and South Array) comprised of 60 traps per array across two adjoining ecoregions in northeastern Florida. We identified fawns using their sport patterns and utilized a novel, non-invasive spatial capture-recapture technique to estimate vital rates. We evaluated activity of deer predators (i.e. coyote [*Canis latrans*], bobcat [*Lynx rufus*], and black bear [*Ursus americanus floridanus*]) based on detection rates and habitat characteristics. Although no spatial covariates affected fawn birth site density and survival, the number of births was greater in the North Array in 2018 (2017: 77.19, 95% CrI: 55 – 136; 2018: 54.93, 95% CrI: 48 – 66) compared to the South Array in 2018 (2017: 44.89, 95% CrI: 12 – 173; 2018: 13.63, 95% CrI: 11 – 22), but were not statistically different in 2017. In addition, the number of recruits was greater in the North Array (2017: 28.04, 95% CrI: 25 – 31; 2018: 37.56, 95% CrI: 35 – 41) than the South Array (2017: 5.71, 95% CrI: 5 – 9; 2018: 4.11, 95% CrI: 4 – 5) during both years. This suggests that the variation in environmental characteristics (e.g. soil productivity, land cover, and predator

activity) between, but not within arrays, likely drove differences in population vital rates. We report vastly different population performance over a small spatial scale, which emphasizes the importance of managers accounting for spatial variation within their management units as site characteristics likely lead to differences in population vital rates. Furthermore, we demonstrated a framework for estimating vital rates while incorporating spatial covariates and provided recommendations for improving future approaches utilizing this technique.

**KEY WORDS** fawn recruitment, prescribed burning, soil productivity, spatial capture recapture, white-tailed deer, *Odocoileus virginianus*.

## **Introduction**

Recruitment is a fundamental population process that heavily influences ungulate population growth rates and understanding the factors driving recruitment is vitally important for population management (Williams et al., 2002; USFWS, 2017). Recruitment is broadly defined as the introduction of new individuals into a population either through immigration or birth and survival to a defined age (Nichols and Pollock, 1990; Schaub et al. 2006). Although adult female survival is commonly considered the driver of ungulate population growth rate (Nelson and Peek, 1982; Escos et al. 1994; Walsh et al. 1995; Eberhardt, 2002), ungulate juvenile survival is lower and more variable (Gaillard et al. 1998), thus, understanding the factors influencing juvenile mortality is also important due to its variable response to density dependent factors and environmental stochasticity (Coughenour and Singer 1996; Unsworth et al. 1999; Raithel et al. 2007).

White-tailed deer (*Odocoileus virginianus*; hereafter deer) recruitment in parts of the Southeast has declined and high neonate depredation is thought to be an important causal agent (Epstein et al. 1985; Kilgo et al. 2010, 2012, 2014; Jackson and Ditchkoff, 2013; Chitwood et al. 2015a; Nelson et al. 2015). Predation is the greatest source of fawn mortality overall in much of North America, yet the variation in rates and sources of mortality across landscapes suggest fawn survival may be influenced by landscape characteristics (Gingery et al. 2018). For example, studies have demonstrated a link between fawn survival and land cover (Shuman et al. 2018) and landscape configuration (Gulsby et al. 2018). At a finer scale, concealment cover can influence fawn predation, with studies reporting both decreased (Grovenburg et al. 2012) and increased (White et al. 2010) predation risk. Structural impediments to escape may increase risk and result in avoiding areas with abundant downed woody debris (Lyon and Jensen, 1980; White et al. 2010). Alternatively, concealment cover can provide refuge to minimize detection of prey by predators (Cherry et al. 2017). Additionally, the spatial variation of nutritional resources can influence fawn recruitment, and landscape composition and configuration can influence resource availability and subsequently nutritional condition, pregnancy rates, litter sizes and fawn survival (Verme, 1969; Ozoga and Verme, 1982; Murphy and Coates, 1966; Langenau and Lerg, 1976).

Deer fawn survival rates can be particularly low in longleaf pine (*Pinus Palustris*; hereafter, LLP) forests potentially due to fire-facilitated predation (Nelson et al. 2015, Chitwood et al. 2015b). Only 3% of the historical range of the LLP ecosystem remains today and many species associated with the ecosystem are endangered, threatened, or in decline (Frost, 1993; Brockway et al. 2005). As such, restoration of the LLP ecosystems is of high priority, and prescribed burning is the primary land management tool used in restoration and maintenance of LLP

ecosystems (Landers et al. 1986). However, the effects of fire on deer, an important primary herbivore in the ecosystem that generate substantial revenue for conservation, is still largely understudied (Waller and Alverson, 1997; Southwick, 2009; USFWS, 2016, Cherry et al. 2016). Fire alters cover and forage resources in temporally dynamic ways, which could both positively and negatively influence deer survival. Fire temporarily decreases concealment cover by consuming vegetation, which can decrease fawn survival by decreasing concealment cover; but fire also improves the quality of forage (Christensen, 1977; Longhurst et al. 1979; Batmanian and Haridasan, 1985; Johnson et al. 1992, Van de Vijver et al. 1999), which is often associated with increased survival and population growth (Verme, 1962; Kunkel and Mech, 1994). However, fawn-rearing females, the demographic group targeted for habitat improvements aimed at increasing nutrition, often avoid recently burned areas and decrease foraging in recently burned stands (Lashley et al. 2015, Cherry et al. 2017). Nonetheless, the link between these behavioral responses and demographic rates has not been established

Despite the widespread use of fire to manage LLP ecosystems and the ecological and cultural importance of deer in these systems, little is known about how fire influences deer vital rates. Therefore, we utilized a novel, non-invasive spatial capture-recapture technique, (Chandler et al. 2018; hereafter, Fawn SCR) to examine fawn survival and recruitment in a LLP ecosystem in northern Florida. We developed a non-invasive study with two remote-sensing camera trap arrays to estimate the effects of fire, soil productivity, and predator activity on fawn population vital rates. The arrays occurred at the interface of a sand ridge soil formation that separates two distinct ecoregions, with arrays occurring on sites with substantially different soil productivity but managed under the same authority and guiding objectives (Figure 1). This provided the

opportunity to examine the effects of environmental factors on two sites that are similar in broad scale factors such as climate, weather, human disturbance, and fine scale factors, such as ownership and management prescriptions, but are different in soil productivity and floral communities. Using this framework, we tested the following predictions: recruitment would be greater at the high productivity site and vary with soil productivity within sites; fawn recruitment would be greater in more recently burned sites, due to the improved available forage; and fawn recruitment would be greater in areas with lower predator activity.

### **Study Site**

We conducted our study on Camp Blanding Joint Training Center and Wildlife Management Area (hereafter, CB) in northeastern Florida, a 227 km<sup>2</sup> site that ranges from 15 - 74 m above sea level in elevation. Located in a subtropical climate with hot humid summers and mild winters, at CB the mean annual temperature was 20.5°C and the mean annual precipitation was 123.5 cm. Land use included military training, forest management, sand mining, and wildlife habitat maintenance and restoration. Prescribed burning on a 3- to 5-year burn interval dependent on forest stand composition was the primary forest management technique used for wildlife habitat restoration. There is considerable variation in site soil productivity across CB as a function of spanning the boundary of the two ecoregions, with the more productive Sea Islands Flatwoods to the north comprised of upland flatwoods with marshes, and swamps with poorly drained spodosol soils while the less productive Ridges and Uplands to the south comprised largely of xeric sandhills with soils that are thick, acidic, sandy and excessively to moderately drained (Omernik and Griffith, 2014; Figure. 1). The site was dominated by uneven-aged longleaf pine woodlands, planted pine plantations, and bottomland hardwood forests. Archery, gun, and dog-

accompanied hunting, as well as trapping and fishing were permitted within designated areas of CB (FWC, 2017). Florida Fish and Wildlife Conservation Commission and Florida Department of Military Affairs manage wildlife across the installation cooperatively.

## **Methods**

### **Field methods**

We designed a camera survey to investigate the effects of fire, soil productivity, and predator activity on variation in deer birth location and recruitment. We established unbaited camera arrays (i.e. North Array and South Array) on the northern and southern portions of CB. Each array consisted of 60 cameras placed on roads, trails, and habitat edges across a range of land cover and fire history conditions. Surveys were conducted 06 June – 10 October 2017 and 14 May – 11 September 2018 with cameras programmed with no delay between triggers. We separated cameras by approximately 500m to ensure individual fawns would be detected at multiple cameras. The area for each array was 33.21 km<sup>2</sup> for the North Array, and 35.93 km<sup>2</sup> for the South Array when lakes were included and 30.04 km<sup>2</sup> when lakes were removed. We visited cameras monthly to retrieve data, replace batteries, and clear vegetation.

### **Data Interpretation**

We interpreted images using MediaPro (Phase One, Melville, NY) software. We recorded the species captured in the image as well as the date, time, and location. For fawns, we identified individuals using their unique spot patterns (Figure 2). Fawn images from left and right flanks were combined when flanks were able to be joined by full visibility of one flank and partial visibility of the other in the same image or the images were less than five seconds apart and no

other fawns were detected within that individuals' detection bout. Partial identification occurred when unique spot patterns from the left and right flanks could not be linked, in which case images were excluded from analyses. Inclusion of partially identified fawns could result in biased vital rate estimates as unpaired left and right flank images potentially represent a single individual. For each grid in each year, we calculated the minimum known number of fawns by adding the number of uniquely identified fawns with the highest number of partially identified fawns (i.e. left or right flank). Detections of any individual occurring within 5 minutes of a previous detection of that animal at the same camera trap were omitted from analyses to attempt to not violate the conditional independence assumption. We derived this independent detection interval by visually inspecting histograms of the differences in time between consecutive detections of individual fawns at each camera at values ranging from 1 to 10 minutes. Detection times should be independent once fawn age and distance between activity centers and cameras have been accounted for (Chandler et al. 2018). Individual fawn birth dates, including a minimum and maximum birth date range, were estimated based on morphology at first detection by two experts with extensive experience in deer husbandry and bottle-rearing of captive fawns. Although our experts had extensive experience, some amount of error will always be associated with these estimates as there are morphological differences that could not be accounted for such as sex and litter size, which is why a birthdate range was used to allow to better estimate errors associated with the estimates. We identified fawn predators to species, which consisted of detections of American black bears (*Ursus americanus floridanus*), bobcats (*Felis rufus*), and coyotes (*Canis latrans*), which were again buffered by a 5 minute threshold derived by the same protocol.

## **Covariates**

To evaluate the effects of our covariates on fawn population vital rates, we generated shapefiles and raster layers representing predator activity, fire history, and soil productivity using ArcGIS 10.3 (Table 1; ESRI; Redlands, CA). We created a 30 x 30m raster where each cell represented the number of years since the last fire and developed a spatially explicit time-since-fire using CB fire history data. We developed a spatially explicit productivity metric using the United States Department of Agriculture Productivity Index (Schaetzl et al. 2012) to identify soil productivity at different soil classifications (Soil Survey Staff, 2017).

## **Predator Activity Covariate**

We generated shapefiles and raster layers representing land cover and soil productivity. We developed land cover covariates using vegetation data maintained by CB Natural Resources staff. We reclassified dominant vegetative cover types into seven major classes including, Hardwood forest, Mixed pine-hardwood forest, Pine forest, Open habitat, Shrub/scrub, Water, and Swamp (Table1). We developed predator activity surfaces from capture histories describing the predator detections in both arrays and years for coyote and the entire fawn predator guild (coyote, black bear, and bobcat). Whereas bobcats and black bears are known fawn predators, coyote activity was included independently because coyotes were believed to be the most important fawn predator in the LLP ecosystem (Nelson et al. 2015, Chitwood et al. 2015), were the most frequently detected fawn predator in our study, and were the only predator with images containing depredated fawns (n=14; North Array: 7, South Array: 7). We fit Poisson generalized linear models (GLMs) including camera-specific counts of detections as our response variable and distance to the reclassified land cover types and soil productivity as explanatory variables.

Because not all cameras were operational at all times due to battery depletion and camera failure, we included  $\log(\text{trap days})$  as an offset in our GLMs allowing for prediction of camera-specific predator detection rates as indices of predator activity (Table 2). We estimated predator activity for each year-array combination to accurately represent risk in that year and array. We used Akaike Information Criteria (AIC) to compare candidate models and identify the top model (Akaike, 1973). We then used the top models to predict predator- and year-specific activity surfaces across each array (Table 2). Predator activity surface values were scaled from 0 to 1 and were included as spatial covariates (i.e. 30 x 30m rasters) in our Fawn SCR models (Figure 2, 3).

### **Fawn SCR Analysis**

We estimated fawn births, recruitment, and the effects of time-since-fire, soil productivity, and predator activity on density of fawns in a Bayesian framework using Program R (R Core Team 2018). Our models were based on Chandler et al. (2018), which extends recent SCR advancements that allow for the estimation of survival and recruitment while accounting for individual variation in detection probability (Gardner et al. 2010, Royle et al. 2013). This hierarchical model utilizes a spatio-temporal point process model to estimate the number, times, and locations of births while simultaneously using a failure time approach to model survival to a given age (i.e. recruitment age). Activity centers derived in this model represent birth sites, as such, fawn density and fawn birth site density are used interchangeably to represent the number of birth sites estimated to be within the state-space. We incorporated expertly estimated birth date ranges into our survival model to account for the fact that fawns are rarely detected in the first weeks of life and to improve estimates of survival. Although Chandler et al. (2018) defined

recruitment at 180 days since birth, we used 70 days since birth as our threshold for recruitment. Chandler et al. (2018) analyzed fawn recruitment in a system with Florida panthers (*Puma concolor coryi*), which are efficient predator of deer of all ages. In the absence of such a predator, fawn survival studies in the Southeast have reported negligible depredation past 50 days of age (Kilgo et al. 2012, Chitwood et al. 2015, Shuman et al. 2017). If fawns were detected past recruitment age (i.e. 70 days since birth), they were considered recruited into the adult population. Survival was modeled in a failure time approach, with fawn lifetime as a random variable (Chandler et al. 2018). We modeled spatial variation in the density of birth locations using spatially referenced covariates. We used Bayesian methods for statistical inference and analysis was performed using a custom Gibbs sampler (Chandler et al. 2018). We fit eight *a priori* models and a null model to each site-year dataset separately. We ran one chain for 25,000 iterations discarding the first 2,000 as burn-in. Visual inspections of the trace plots was used to assess convergence along with Gelman-Rubin diagnostic statistics.

To estimate the effects of predation risk on fawn birth site density, we included site-year specific cumulative predator and coyote activity surfaces as spatial covariates in the density components of our hierarchical models. Eight *a priori* models were constructed representing all possible combinations of time-since-fire, soil productivity, coyote activity, and cumulative predator activity as predictors of fawn birth site density, or gamma ( $\gamma$ ) (Table 3). We estimated the effect of time-since-fire and fawn age on survival, or omega ( $\omega$ ), in all models. Additionally, because fawn mobility increases with age, we included fawn age as a predictor of sigma ( $\sigma$ ), the shape of the detection function. Lastly, we included survey day as a predictor of lambda ( $\lambda$ ), the probability of detection. We used total model deviance to compare model weights and identify

the top model from each candidate set (Table 3). Parameters were considered supported when their credible intervals did not overlap zero.

## Results

We identified a minimum of 80 and 67 fawns in the North Array for 2017 and 2018, respectively. Comparatively, a minimum of 32 and 20 fawns were identified in the South Array for 2017 and 2018, respectively (Table 4). Results are presented as follows: *year: parameter mean, CI/CrI: lower interval – upper interval*. Coyote detection rates in the North Array (2017: 4.67 detections per 100 camera days, CI: 4.66 – 4.68; 2018: 4.78 detections per 100 camera days, CI: 4.75 – 4.80) were lower than the South Array (2017: 8.98 detections per 100 camera days, CI: 8.54 – 8.56; 2018: 7.97 detections per 100 camera days, CI: 7.93 – 7.99). Fawn predator detection rates in the North Array (2017: 10.52 detections per 100 camera days, CI: 10.51 – 10.53; 2018: 12.07 detections per 100 camera days, CI: 11.99 – 12.15) were similar to the South Array (2017: 12.98 detections per 100 camera days, CI: 12.97 – 13.00; 2018: 10.95 detections per 100 camera days, CI: 10.91 – 10.98). Fawn detection rates in the North Array (2017: 1.22 detections per 1000 camera days, CI: 0.14 – 4.80; 2018: 1.34 detections per 1000 camera days, CI: 0.14 – 5.51) were similar to the South Array (2017: 0.70 detections per 1000 camera days, CI: 0.17 – 1.85; 2018: 0.59 detections per 1000 camera days, CI: 0.14 – 2.07). The number of traps sites at which individuals were detected, or spatial recaptures, was similar in the North Array (2017: 1.72 cameras per fawn, CI: 1.00 – 5.70; 2018: 1.28 cameras per fawn, CI: 1.00 – 2.00) compared to the South Array (2017: 2.22 cameras per fawn, CI: 1 – 4.80; 2018: 1.45 cameras per fawn, CI: 1.00 – 2.75) and were similar across years (Table 5). The mean fawn birth date estimated by our experts across years was 06 June, which was slightly later than the

literature estimated mean birth date of 21 May (Figure 4) derived by adding the length of average deer gestation (200 days; Verme, 1965) to the mean breeding date (02 November) on CB (Richter and Labisky, 1985). The number of fawns born were similar across years, but were higher in the North Array in 2018 (2017: 77.19, 95% CrI: 55 – 136; 2018: 54.93, 95% CrI: 48 – 66) compared to the South Array in 2018 (2017: 44.89, 95% CrI: 12 – 173; 2018: 13.63, 95% CrI: 11 – 22), but were not statistically different in 2017. However, the number of estimated fawn recruited was greater in the North Array (2017: 28.04, 95% CrI: 25 – 31; 2018: 37.56, 95% CrI: 35 – 41) compared to the South Array (2017: 5.71, 95% CrI: 5 – 9; 2018: 4.11, 95% CrI: 4 – 5) for both years. Our results indicate that the North Array hosted higher recruitment in both years, and more births in 2018, than the South Array (Table 6). Posterior mean birth dates were similar across both arrays, but varied across years (North 2017: 07 June; South 2017: 09 June; North 2018: 20 May; South 2018: 19 May), which was congruent with our expert estimate averaged across both years (06 June) and the reported peak fawning dates (21 May). Top models predicting fawn density and survival varied by array and year (Table 5). However, none of the variables in any models were informative parameters and we did not detect any effects of spatial covariates in our models.

## **Discussion**

We examined fawn birth and recruitment in two ecoregions in Florida and provided spatially explicit estimates of the density of birth locations and recruits (fawns surviving >70 days). Fawn recruitment was greater on the higher productivity site (i.e. North Array) than the low productivity site (i.e. South Array), however, within arrays soil productivity did not have a demonstrable effect. In fact, we observed differences between sites, but did not observe any effects of covariates on spatial variation in density or survival within arrays. We did not find

support for our prediction that more frequent and recent fire would improve deer recruitment, nor did we find support for our prediction that predator activity would reduce density or survival of fawns. The variation in time-since-fire, soil productivity, and predator activity may have not been large enough to influence birth site density and survival within arrays or they may not influence birth site density and recruitment. However, variation in these and other characteristics may have driven differences seen between arrays.

The known minimum number of individual fawns, recruitment, and during one year, density of birth locations was greater in the North site than the South site. Variation in soil productivity, land cover type, predator communities between arrays likely influenced population vital rates. Although we did not explicitly test the factors influencing our parameters between arrays, we hypothesize that the variation in coyote activity rates as well as soil productivity and its subsequent effects (i.e. forage availability, concealment cover, and land cover type) likely drove the differences we saw between sites. Attributes of the North Array not only produced more fawns (i.e. births), meaning the attributes likely better met dam nutritional demands, but it also sustained a greater number of fawns that reached recruitment age, meaning they also likely better protected fawns from risks after birth (e.g. predation and starvation). For example, we detected more coyotes in the South Array than in the North Array which may be influencing fawn depredations between the two sites, as areas with greater coyote activity likely have more fawn-predator encounters. Furthermore, we saw smaller differences in the fawn predator guild detections across both grids, connecting only the differences in coyote activity to the differences we saw in fawn population vital rates across grids and not the fawn predator guild as a whole. This further suggests that coyotes are the most important fawn predator in this system as

previously studies have shown (Nelson et al. 2015, Chitwood et al. 2015). We recorded vastly different recruitment rates at sites in close proximity, suggesting population vital rates can vary at small spatial scales, which is similar to the varied recruitment rates that Gulsby et al. (2015) found between two sites 8 km apart.

Within arrays, we found no support for our prediction that fawn recruitment would be greater in areas with lower predator activity. This was surprising given predators can have a strong effect on fawn survival and recruitment in LLP ecosystems (Chitwood et al. 2015, Nelson et al. 2015, Conner et al. 2016). This may be due to the spatial variation in predators not accurately representing the spatial variation in risk. For example, predator activity can interact with vegetation structure to determine prey susceptibility (Kauffman et al. 2007). Alternatively, spatial variation in predator activity may not be a key factor driving fawn recruitment.

We also did not find support for our prediction that areas with more recent fire would have greater fawn recruitment. Our variable, time-since-fire at the annual scale may not have captured the variability in fire conditions in this frequently burned landscape. Behavioral studies have shown responses in habitat selection and foraging behavior to time-since-fire in LLP ecosystems (Lashley et al. 2015, Cherry et al. 2017). However, population vital rates may not respond to fire attributes at such a fine scale, but instead respond to improved forest health that results from repeated fire. For example, in California black-tailed deer (*Odocoileus hemionus*) fawn survival was significantly influenced by the habitat characteristics, but not fire (Klinger et al. 1989).

A limitation of our study was our inability to identify drivers of spatial variation in recruitment. This stems from low sample sizes, which is driven by two limitations revealed in our study. First, the area being sampled must be large enough to include an adequate number of fawns for the desired statistical power. This can be a challenge in low density areas as evidenced by larger error estimates in the low-density South Array. The number of births across the North Array and South Array were significantly different in 2018, but not 2017. This was likely the result of low sample size in the South for 2017 ( $n=9$ ), which resulted in large credible intervals. Second, low sample size can stem from the inability to link capture histories of the left and right flanks. This likely degrades the richness of capture histories for individuals with a portion of the detections discarded and potentially excludes entire individuals. One solution to this issue would be to follow a commonly noted approach in camera trap studies (Augustine et al. 2018) by including the left or right capture histories, which contained more data, and exclude capture histories from the other flank, although there is some bias associated with that as well. Future studies should attempt to reconcile this issue by deploying paired cameras at each trap site to detect both flanks simultaneously or by incorporating spatial partial identity models, which probabilistically resolves uncertainty of partially identified fawns using location and time of capture (Augustine et al. 2018).

We found a substantial difference in fawn recruitment at a small spatial scale on a frequently burned site at the interface of two unique ecoregions. We used a novel, non-invasive technique to provide spatially explicit estimates of fawn birth site density and fawn recruitment for four site-years and demonstrate considerable differences in quality of deer habitat between two adjacent sites. These results are relevant to local managers and provide support for unit-specific,

deer management on CB. With this technique we demonstrated the framework for estimating vital rates to compare across two sites while incorporating spatial covariates and provided recommendations for improving future approaches utilizing this technique.

### **Management Implications**

The differences in birth site densities and recruitment rates between the North and South Arrays support the use of unique harvest goals within compartments of CB (i.e. North compartment 80.48 km<sup>2</sup> and South compartment 38.55 km<sup>2</sup>). If fawn recruitment varies across a management unit and harvest goals are uniform, then the magnitude of the effect of harvest on deer population abundance and growth rate would be greater in areas of lower birth and recruitment rates.

Quantifying the differences in fawn density and utilizing spatially explicit estimates allows managers to more accurately match doe harvest to differences in fawn densities so that effects of harvest are uniform across the site. Understanding factors influencing population vital rates across a site is fundamental to proscribing harvest quotas that account for the variation in local limits within a managed area. This study found differences in fawn birth and recruitment within two distinct ecoregions utilizing a novel spatial capture-recapture model, which suggests managers need to quantify differences in fawn population vital rates across their managed area to better prescribe harvest quotas based on the variation of limitations across management units.

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## Tables

**Table 3. 1** Descriptions of spatial covariates included in (a) Poisson generalized linear models (GLMs) to estimate detection rates and predict predator activity surfaces for inclusion in (b) spatially-explicit capture-recapture (SCR) models used to estimate fawn births, density, survival, recruitment, and the effects of habitat, predator activity, and soil productivity on fawn survival and recruitment.

<b>Model</b>	<b>Name</b>	<b>Description</b>
<i>Predator GLM (a)</i>		
	<i>Soil Productivity</i>	United States Department of Agriculture measure of soil productivity based on soil taxonomic information ranging from 0 (least productive) to 19 (most productive). Our sites productivity had a range of 2 to 6.11 across the on the different scales.
	<i>Land Cover Type</i>	Distance (m) to nearest cover type (deciduous forest, mixed pine-hardwood forest, pine forest, open habitat, shrub/scrub, and swamp) from each site. Distance calculated using the 30m resolution reclassified land cover rasters in GIS.
<i>Fawn SCR Model (b)</i>		
	<i>Time-Since-Fire</i>	Number of growing seasons since the last burn at the location of the camera.
	<i>Soil Productivity</i>	United States Department of Agriculture measure of soil productivity based on soil taxonomic information ranging from 0 (least productive) to 19 (most productive). Our sites productivity had a range of 2 to 6.11 across the on the different scales.
	<i>Land Cover Type</i>	Distance (m) to nearest cover type (deciduous forest, mixed pine-hardwood forest, pine forest, open habitat, shrub/scrubland, and swamp) from each site. Distance calculated using the 30m resolution reclassified land cover raster in GIS.
	<i>Predator Activity</i>	Daily predator (American black bear + coyote + bobcat) detections by site predicted by best generalized linear model. Model was predicted across the 30m resolution reclassified land cover rasters.
	<i>Coyote Activity</i>	Daily coyote detections by site predicted by best generalized linear model. Model was predicted across the 30m resolution reclassified land cover rasters.

**Table 3. 2** Top Poisson generalized linear models for estimating detection rates of coyote alone and cumulative predators (i.e. coyote, black bear, bobcat) from camera trap data collected 06 June – 10 October 2017 and 14 May – 11 September 2018 in two 60-camera arrays (North and South) on Camp Blanding Joint Military Center, Starke, FL.

<b>Year</b>	<b>Array</b>	<b>Species</b>	<b>Model</b>
2017			
	<i>North</i>	<i>Coyote</i>	open + shrub + decid + pine + swamp + soil productivity
		<i>Predators</i>	soil productivity + swamp + shrub + decid + open
	<i>South</i>	<i>Coyote</i>	soil productivity + swamp + water + decid + shrub + open
		<i>Predators</i>	soil productivity + swamp + water + pine + decid + shrub
2018			
	<i>North</i>	<i>Coyote</i>	swamp + decid + shrub
		<i>Predators</i>	soil productivity + pine + decid + mixed + shrub
	<i>South</i>	<i>Coyote</i>	soil productivity + decid + mixed + shrub + open
		<i>Predators</i>	soil productivity + swamp + pine + decid + mixed + shrub

pine = distance to pine forest, decid = distance to deciduous forest, open = distance to open habitat, swamp = distance to swamps, shrub = distance to shrub/scrubland, mixed = distance to mixed pine-hardwood forest, water = distance to water, soil productivity = United States soil productivity index.

**Table 3. 3** Model deviance table for spatial capture-recapture models estimating fawn abundance, density, detectability, and survival from 06 June – 10 October 2017 and 14 May- 11 September 2018 across two, 60-trap arrays (North and South) on Camp Blanding Joint Military Center, Starke, FL.

<b>Year</b>	<b>Array</b>	<b>Model</b>	<b>Deviance</b>
<i>2017</i>			
	<i>North</i>	$\gamma(\text{TSF} + \text{Soil Prod} + \text{Coyote}),\omega(\text{TSF})$	19521.61
		Global model	19568.67
		$\gamma(\text{TSF}),\omega(\text{TSF})$	19568.11
		$\gamma(\text{TSF} + \text{Pred} + \text{Coyote}),\omega(\text{TSF})$	19577.76
		$\gamma(\text{TSF} + \text{Soil Prod}),\omega(\text{TSF})$	19587.54
		$\gamma(\text{TSF} + \text{Soil Prod} + \text{Pred}),\omega(\text{TSF})$	19603.84
		$\gamma(\text{TSF} + \text{Coyote}),\omega(\text{TSF})$	19604.47
		NULL Model	19722.97
		$\gamma(\text{TSF} + \text{Pred}),\omega(\text{TSF})$	20051.89
	<i>South</i>	Global model	13271.65
		$\gamma(\text{TSF} + \text{Soil Prod} + \text{Pred}),\omega(\text{TSF})$	13496.32
		$\gamma(\text{TSF} + \text{Soil Prod}),\omega(\text{TSF})$	13651.31
		$\gamma(\text{TSF} + \text{Pred}),\omega(\text{TSF})$	13666.41
		$\gamma(\text{TSF} + \text{Soil Prod} + \text{Coyote}),\omega(\text{TSF})$	13982.48
		NULL Model	15745.71
		$\gamma(\text{TSF}),\omega(\text{TSF})$	16710.32
		$\gamma(\text{TSF} + \text{Pred} + \text{Coyote}),\omega(\text{TSF})$	2.70E+28
		$\gamma(\text{TSF} + \text{Coyote}),\omega(\text{TSF})$	3.17E+33
<i>2018</i>			
	<i>North</i>	$\gamma(\text{TSF} + \text{Soil Prod} + \text{Pred}),\omega(\text{TSF})$	30078.76
		$\gamma(\text{TSF} + \text{Soil Prod}),\omega(\text{TSF})$	30116.11
		$\gamma(\text{TSF} + \text{Pred}),\omega(\text{TSF})$	30173.09
		$\gamma(\text{TSF} + \text{Pred} + \text{Coyote}),\omega(\text{TSF})$	30177.38
		$\gamma(\text{TSF} + \text{Coyote}),\omega(\text{TSF})$	30181.20
		$\gamma(\text{TSF} + \text{Soil Prod} + \text{Coyote}),\omega(\text{TSF})$	30194.72
		Global model	30234.40
		$\gamma(\text{TSF}),\omega(\text{TSF})$	30486.57
		NULL Model	30572.57
	<i>South</i>	$\gamma(\text{TSF}),\omega(\text{TSF})$	7128.35
		$\gamma(\text{TSF} + \text{Soil Prod} + \text{Coyote}),\omega(\text{TSF})$	15739.31
		$\gamma(\text{TSF} + \text{Pred} + \text{Coyote}),\omega(\text{TSF})$	15784.48
		$\gamma(\text{TSF} + \text{Soil Prod} + \text{Pred}),\omega(\text{TSF})$	15930.15
		$\gamma(\text{TSF} + \text{Coyote}),\omega(\text{TSF})$	16331.87
		$\gamma(\text{TSF} + \text{Soil Prod}),\omega(\text{TSF})$	16394.17
		Global model	16488.67
		$\gamma(\text{TSF} + \text{Pred}),\omega(\text{TSF})$	16566.46
		NULL Model	16640.18

\*All models included:  $\lambda$  (survey day),  $\sigma$  (fawn age),  $\omega$  (fawn age),

Gamma =  $\gamma$ , Omega =  $\omega$ , Sigma =  $\sigma$ , Lambda =  $\lambda$

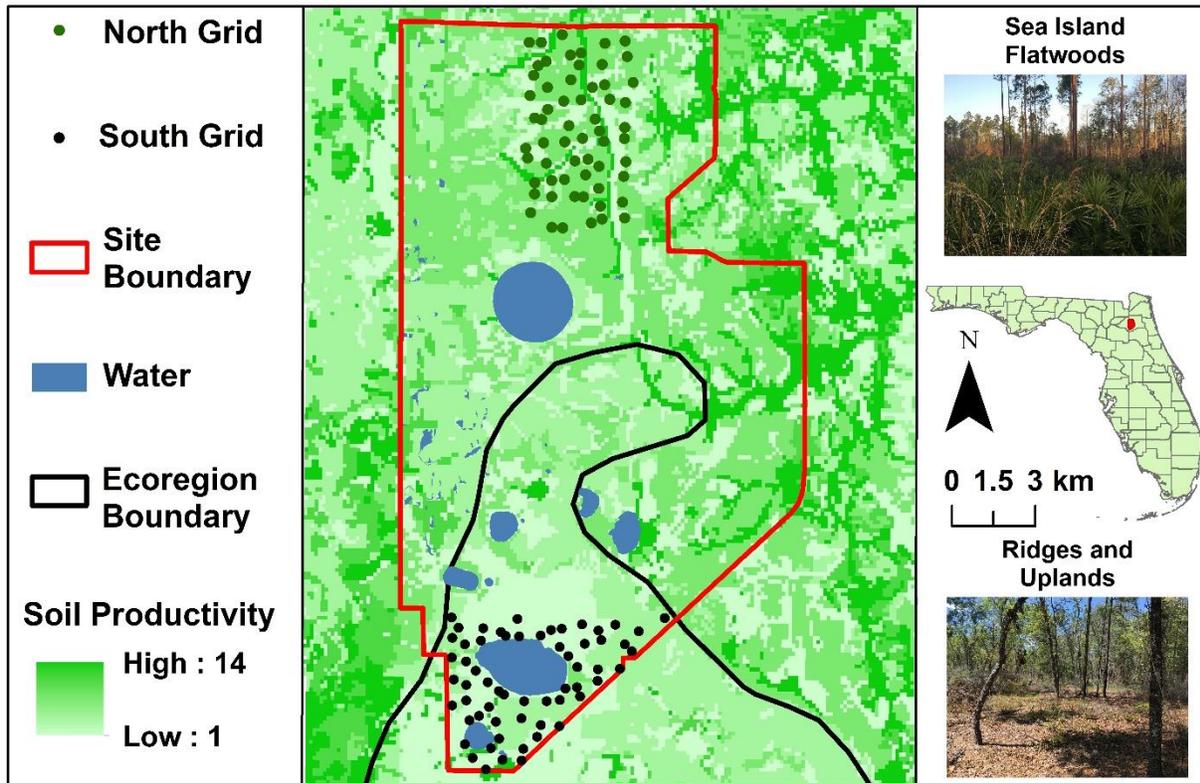
**Table 3. 4** Number of uniquely identified white-tailed deer fawns and independent predator detections from camera surveys conducted 06 June – 10 October 2017 and 14 May- 11 September 2018 to two 60-camera arrays (North and South) on Camp Blanding Joint Military Center, Starke, FL. Left and right flank represent fawns that were only able to be identified by one side, and the minimum total is the greatest possible number of unique fawns detected.

		<b>2017</b>		<b>2018</b>	
		<b>North</b>	<b>South</b>	<b>North</b>	<b>South</b>
<i>Fawns</i>					
	<i>Both Flanks</i>	48	9	47	11
	<i>Left Flank</i>	27	19	20	10
	<i>Right Flank</i>	32	23	20	9
	<i>Minimum total</i>	80	32	67	20
<i>Predators</i>					
	<i>Bobcats</i>	114	131	170	181
	<i>Coyotes</i>	362	448	350	530
	<i>Bear</i>	283	98	378	122
	<i>Total</i>	759	677	898	833

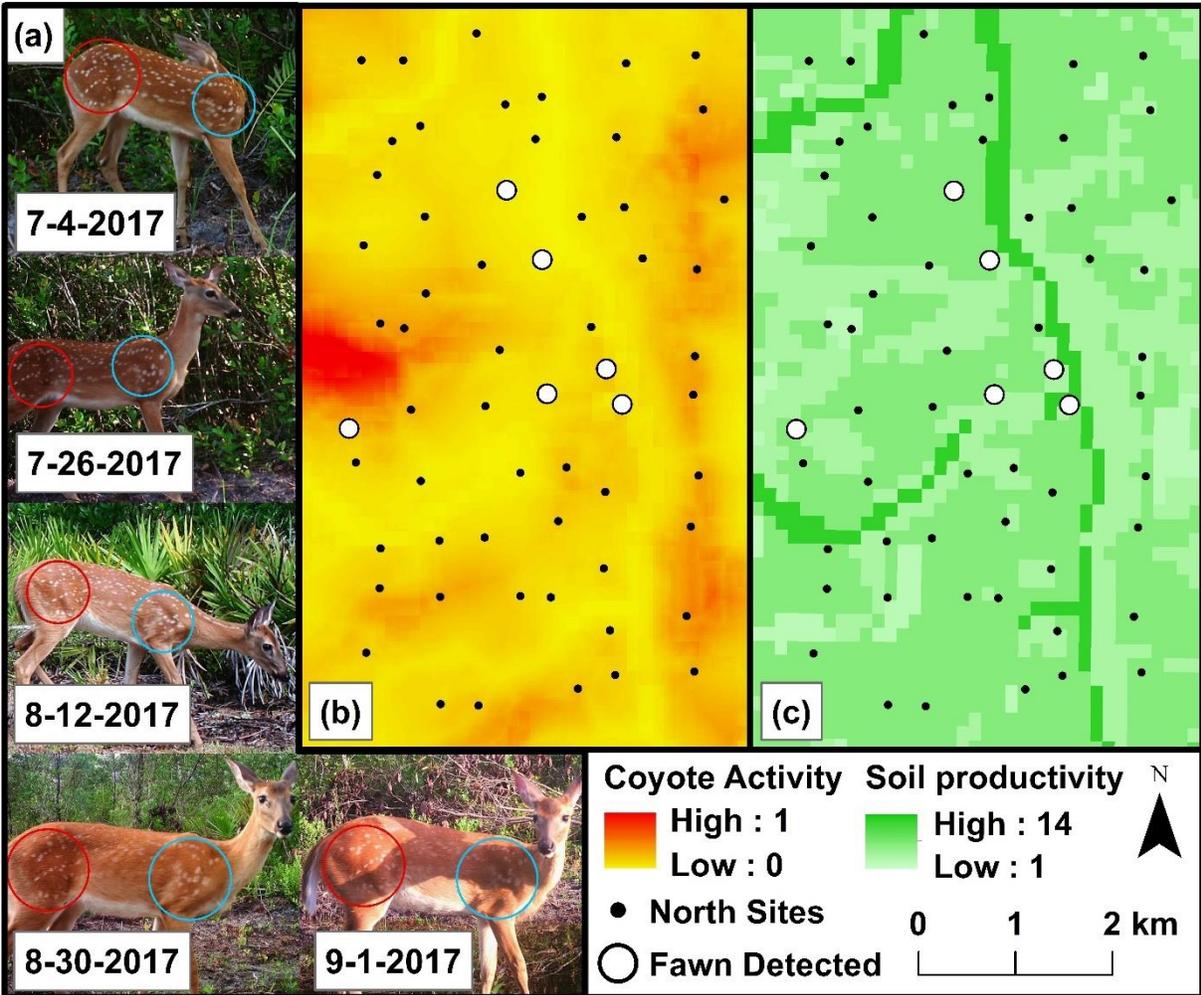
**Table 3. 5** Mean, standard deviations, 2.5% and 95% credible intervals for estimations from the posterior distributions from parameters of the fawn SCR model from white-tailed deer and predator camera surveys conducted 06 June – 10 October 2017 and 14 May- 11 September 2018 at 120 camera traps divided in to two, 60-camera arrays (North and South) on Camp Blanding Joint Military Center, Starke, FL.

<b>Parameter</b>	<b>Array</b>	<b>Mean</b>	<b>SD</b>	<b>2.5%CrI</b>	<b>97.5%CrI</b>
<i>Mean birth date</i>					
	<i>North</i>	6/7/2017	3.08	6/2/2017	6/13/2017
	<i>North</i>	5/20/2018	3.24	5/13/2018	5/25/2018
	<i>South</i>	6/9/2017	7.13	5/27/2017	6/23/2017
	<i>South</i>	5/19/2018	8.05	4/27/2018	6/1/2018
<i>Birth Date Variance</i>					
	<i>North</i>	20.57	2.52	16.50	26.09
	<i>North</i>	20.56	2.52	16.47	26.08
	<i>South</i>	17.13	5.93	8.45	28.85
	<i>South</i>	18.39	6.17	11.16	36.49
<i>Births</i>					
	<i>North</i>	77.19	20.61	55.00	136.00
	<i>North</i>	54.93	4.56	48.00	66.00
	<i>South</i>	44.89	38.86	12.00	173.00
	<i>South</i>	13.63	3.04	11.00	22.00
<i>Recruits</i>					
	<i>North</i>	28.04	1.53	25.00	31.00
	<i>North</i>	37.56	1.67	35.00	41.00
	<i>South</i>	5.71	1.12	5.00	9.00
	<i>South</i>	4.11	0.32	4.00	5.00
<i>TSF on Birth Site Density</i>					
	<i>North</i>	-0.37	0.49	-1.35	0.58
	<i>North</i>	0.25	0.24	-0.11	0.57
	<i>South</i>	-2.71	3.02	-8.34	0.96
	<i>South</i>	-0.14	0.57	-1.31	0.55
<i>Soil Productivity on Birth</i>					
	<i>North</i>	0.05	0.32	-0.71	0.58
	<i>North</i>	0.14	0.16	-0.20	0.41
	<i>South</i>	-2.70	2.31	-7.80	0.71
	<i>South</i>	NA	NA	NA	NA
<i>Coyote on Birth Site</i>					
	<i>North</i>	-0.06	0.24	-0.57	0.39
	<i>North</i>	NA	NA	NA	NA
	<i>South</i>	0.42	1.13	-1.55	2.59
	<i>South</i>	NA	NA	NA	NA
<i>All Predators on Birth</i>					
	<i>North</i>	NA	NA	NA	NA
	<i>North</i>	-0.37	NA	-0.95	0.09
	<i>South</i>	-2.30	1.53	-4.68	0.72
	<i>South</i>	NA	NA	NA	NA

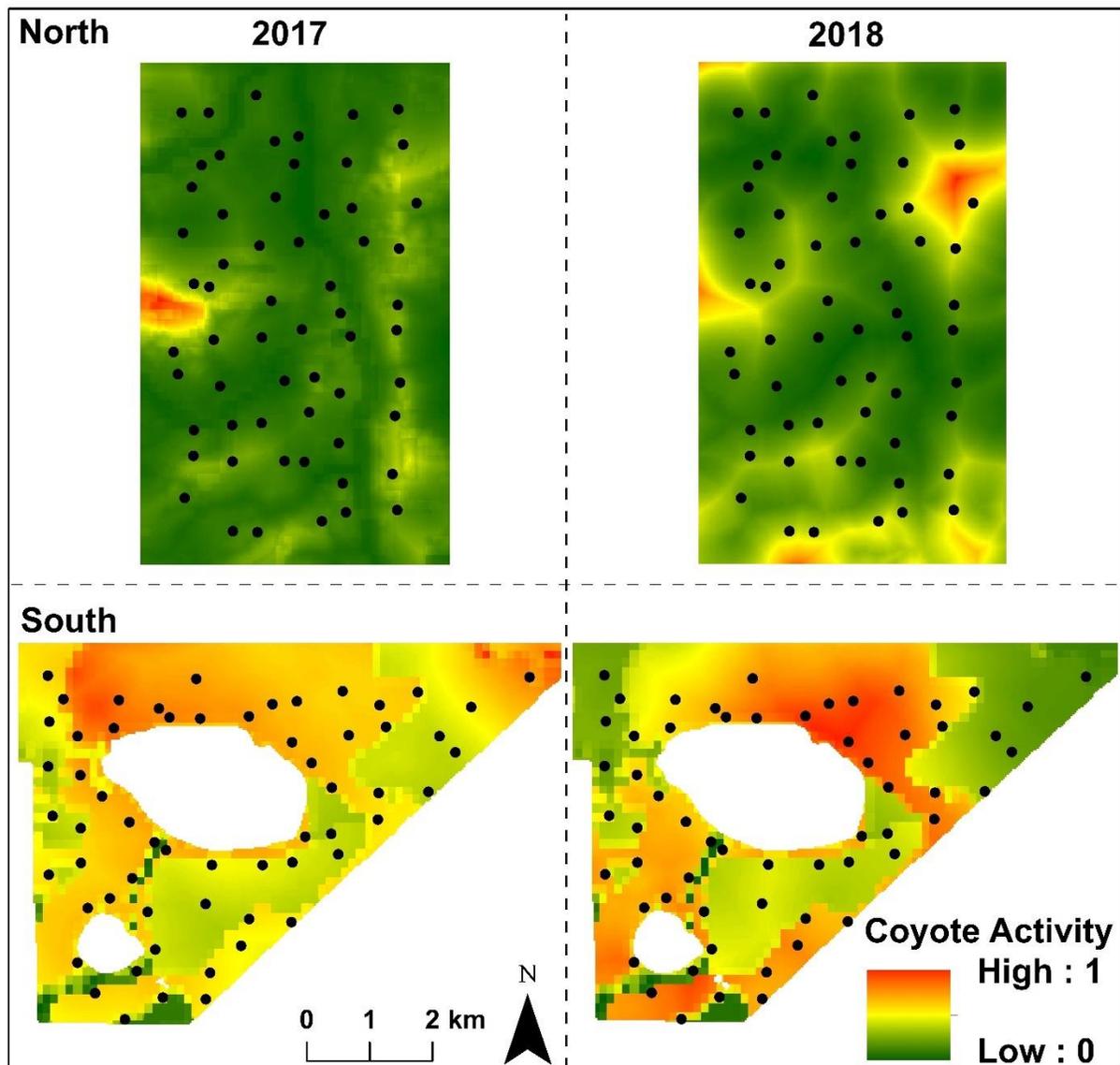
## Figures



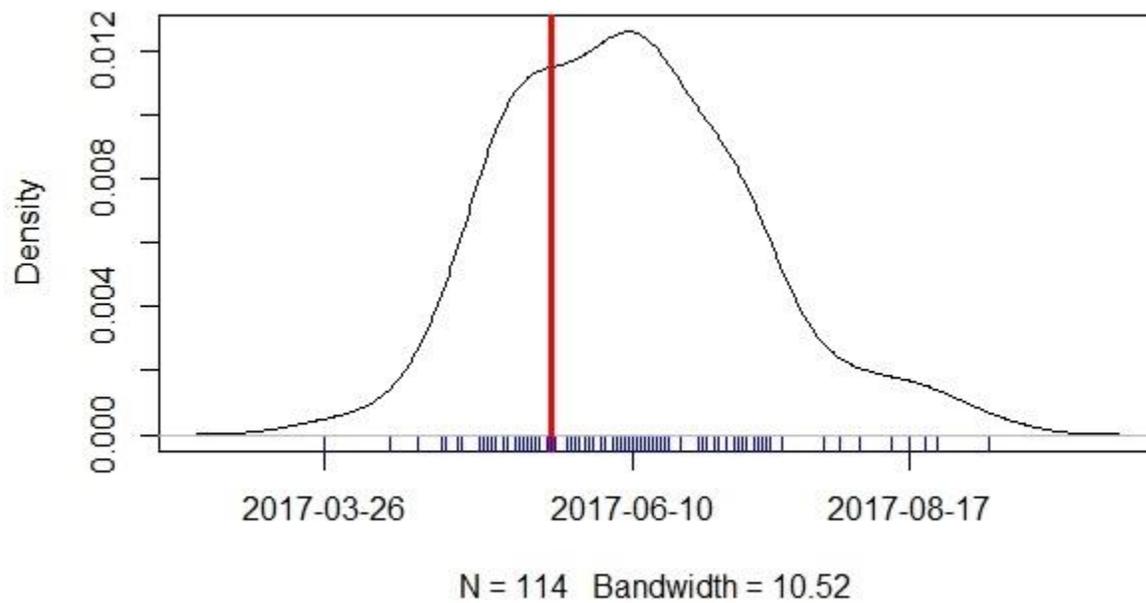
**Figure 3. 1** Camera trap locations (n=120) for white-tailed deer and predator surveys conducted 06 June – 10 October 2017 and 14 May – 11 September 2018. Cameras were deployed in two, 60-trap arrays (North and South) on Camp Blanding Joint Military Center, Starke, FL, with two representative images of the distinct ecoregions.



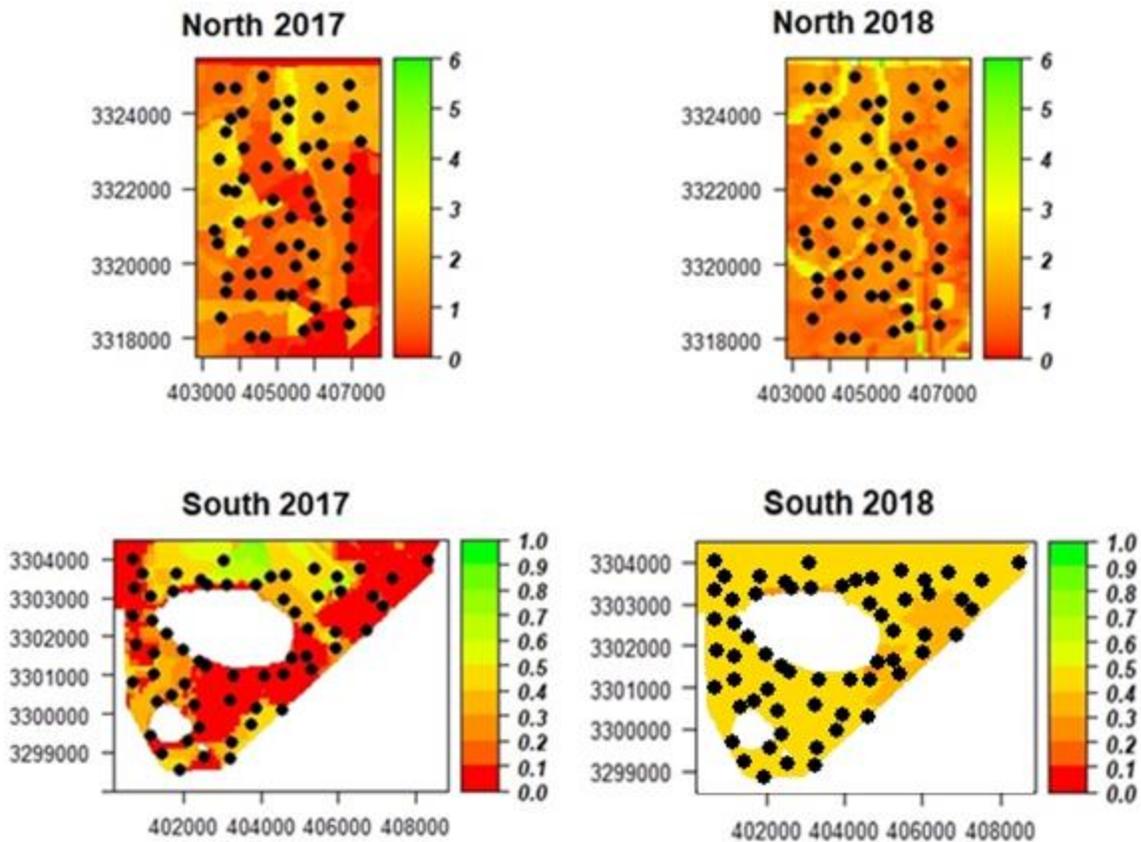
**Figure 3. 2** Example of images of a uniquely identified fawn (a) with detection locations in respect to coyote activity(c), scaled from 0 to 1, and soil productivity (c) from the North Array of the white-tailed deer and predator camera surveys conducted 06 June – 10 October 2017 on Camp Blanding Joint Military Center, Starke, FL. We identified fawns by their unique spot pattern. The fawn’s unique spot pattern is indicated within the red and blue ovals.



**Figure 3. 3** Coyote activity surfaces for North Array 2017 (a), 2018 (b) and South Array 2017 (c), 2018 (d) predicted from the top Poisson generalized linear models of predator detection rates during camera surveys conducted 06 June – 10 October 2017 and 14 May- 11 September 2018 at 120 camera traps on Camp Blanding Joint Military Center, Starke, FL. Activity estimates were scaled from 0 to 1 for each year and array. White spaces denote lakes and locations off-base which were not analyzed. Estimates were made and scaled for each year-array individually and should not be compared across but rather just within year-arrays.



**Figure 3. 4** Estimates of individual birth dates (blue ticks below the x-axis) by an expert for the 114 uniquely identified fawns, and the birth date distribution from the white-tailed deer camera surveys conducted 06 June – 10 October 2017 and 14 May- 11 September 2018 at 120 camera traps divided in to two, 60-camera arrays (North and South) on Camp Blanding Joint Military Center, Starke, FL. The vertical red line is an independent estimate of the mean birthdate derived by adding 200 days of gestation to the mean breeding date of does on Camp Blanding from 1978 to 1981 (Richter and Labisky, 1985).



**Figure 3. 5** Fawn density surfaces (per km<sup>2</sup>) predicted from spatially explicit capture-recapture models during camera surveys conducted 06 June – 10 October 2017 and 14 May- 11 September 2018 at 120 camera traps divided in to two, 60-camera arrays (North and South) on Camp Blanding Joint Military Center, Starke, FL. Black dots denote camera locations. Coordinates are in meters projected in the WGS 1984 UTM Zone 17N coordinate system.

## Overall Discussion

This study aimed to understand how fire, and environmental characteristics influenced wildlife communities in a pyric landscape. We used data collected from Camp Blanding Joint Training Center and Wildlife Management Area to understand how fire influences relative abundances of mammalian predators, occupancy and species richness of avian species, guilds and communities, and vital rates of white-tailed deer (*Odocoileus virginianus*) fawns.

Our results indicated that mammalian predator space use, and avian species richness were altered by fire and land cover. Mammalian predator space use was altered by fire conditions and land cover, which supports a predator management strategy that utilizes management tools commonly used in restoration and conservation of the LLP ecosystem to indirectly alter predator distributions, which has the potential to positively affect the management of important species within this ecosystem. Mammalian mesocarnivores historically common throughout the southeastern United States were rarely detected, suggesting more research is needed to identify the cause of the potential decline in mesocarnivores in the Southeastern United States.

Avian species richness at the community level was positively influenced by pyrodiversity, the heterogeneity of post fire conditions. The diversity of conditions in areas with greater pyrodiversity likely provided greater numbers of ecological niche spaces. This supports and further extends the ‘pyrodiversity begets biodiversity’ hypothesis for avian species to smaller spatial scales that are more applicable to management decisions occurring on more local scales. Avian species richness at the cavity nesting guild level was negatively influenced by increasing time-since-fire. Our results and characterization of pyrodiversity suggests that managers can promote avian community diversity by reducing the size of burn units to create areas with multiple adjacent burn units, with unique fire histories and a mosaic of post-fire conditions.

Combining our results from the first and second chapter illuminates how fire could be used to not only as a potential predator management strategy, but also as a means to promote avian species diversity all under the same management prescription of frequent small fires which are in close proximity.

Lastly, we examined fawn birth and recruitment in two ecoregions in Florida and provided spatially explicit estimates of the density of birth locations and recruits. Fawn recruitment was greater on the higher productivity site (i.e. North Array) than the low productivity site (i.e. South Array), however, within arrays soil productivity did not have a demonstrable effect. In fact, we observed differences between sites, but did not observe any effects of covariates on spatial variation in density or survival within arrays. Although we did not explicitly test the factors influencing our parameters between arrays, we hypothesize that the variation in coyote activity rates as well as soil productivity and its subsequent effects (i.e. forage availability, concealment cover, and land cover type) likely drove the differences we saw between sites. We used a novel, non-invasive technique to provide spatially explicit estimates of fawn birth site density and fawn recruitment for four site-years and demonstrate considerable differences in quality of deer habitat between two adjacent sites. These results are relevant to local managers and provide support for unit-specific, deer management on CB. With this technique, we demonstrated the framework for estimating vital rates to compare across two sites while incorporating spatial covariates and provided recommendations for improving future approaches utilizing this technique. In conclusion, understanding the influence of fire in a frequently burned landscape allows us to better inform management of predators and avian communities using prescribed burns and hardwood removal, and the differences in deer

populations between areas allowed us to better inform managers on harvest quotas so that the magnitude of the effect of harvest can better match the population vital rates of each area.