Burn regime matters: A review of the effects of prescribed fire on vertebrates in the longleaf pine ecosystem

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Review

Burn regime matters: A review of the effects of prescribed fire on vertebrates in the longleaf pine ecosystem

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ABSTRACT

A clear understanding of how management influences vertebrate biodiversity is critical for the conservation of rare ecosystems, such as the longleaf pine (*Pinus palustris*) ecosystem in the southeastern United States. We used scientific literature to assess how vertebrate use of the longleaf pine ecosystem (High or low) differed in response to high (1–3 years), moderate (>3–5 years), and low (>5 years) burn frequencies. For all species combined, we found that the number of high use (HU) species associated with moderately burned forests (n = 140) was 22% and 33% greater than in high (n = 115) and low burn (n = 105) frequency forests, respectively. This pattern was most clear for Aves and Reptilia. Specifically, the number of HU species associated with moderate burn frequencies (Aves – n = 69; Reptilia – n = 36) was 21% and 25% greater for Aves and 56 and 63% greater for Reptilia than high (Aves – n = 57; Reptilia – n = 23) and low burn frequencies (Aves – n = 55; Reptilia – n = 22), respectively. We found no difference in the number of HU species across burn frequencies for Amphibia or Mammalia. For species considered longleaf pine specialists, across all vertebrate taxa the number of HU species was associated with areas of high and moderate burn frequencies. We posit that moderate burn frequencies had the greatest number of HU species because of requirements for multiple habitat types, structural diversity, and habitat components that are reduced in, or not provided by, areas with high burn frequencies. If conservation of specific longleaf pine specialists that rely on habitat created by high fire frequencies (e.g. Red-cockaded woodpeckers) is the objective, we suggest managing with high burn frequencies at the local scale. Conversely, if management objectives include maximizing wildlife diversity, managers should use a more variable fire regime across the landscape, from annual to less frequent 5 year burn intervals, to maintain localized patches of oaks and increase the compositional and structural diversity within the system.

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1. Introduction

Across the globe, dominant ecosystems (e.g. estuarine and coastal [worldwide]; coastal sage scrub [California]; longleaf pine [southeastern United States]; Lotze et al., 2006; Noss et al., 1995) have declined in size and functionality due to anthropogenic impacts (Ellis et al., 2010; Hannah et al., 1994; Vitousek et al., 1997). One ecosystem that has been the subject of numerous conservation efforts is the longleaf pine (*Pinus palustris*; LLP) ecosystem. The LLP ecosystem has been described as bilayered with a diverse understory dominated by wiregrass (*Aristida beyrichiana* and *A. stricta*) or bluestem (*Schizachyrium* spp.), a sparse midstory of pyrophytic oaks, described in detail by Hiers et al. (2014), and a canopy of LLPs (Jose et al., 2006). The LLP ecosystem historically covered approximately 37,000,000 ha in the southeastern United States, but less than 3% remains (Frost, 1993). The ecosystem declined due to large-scale clearcutting of old-growth LLP forests prior to the 1930s, and the encroachment of mesic hardwoods and woody understory vegetation associated with fire suppression (Frost, 1993).

Similar to other imperiled ecosystems, management success within the LLP ecosystem has been determined by comparing metrics (e.g. plant and wildlife species richness) of the restored site to reference sites (e.g. Litt et al., 2001; Provencher et al., 2001; Steen et al., 2013a,b). Reference sites are often selected using accounts from travelers during the 1700–1800 s that describe an open, bilayered landscape with few oaks (e.g.; Brockway et al., 1998; Harper et al., 1997; Means, 1996; Myers, 1990). To mimic reference conditions, prescribed fire on 1–3 year burn intervals and herbicide and manual oak removal have been commonly used for restoration (Lewis and Harshbarger, 1976; Provencher et al., 2001). Yet, historical descriptions may be biased because travelers would have used the path of least resistance, leading to descriptions of uncharacteristically open landscapes (Landers et al., 2001). Additionally, fire likely would not have been spatially or temporally constant as the recommended 1–3 year burn interval suggests. Dendrochronology data indicate that average fire return intervals within longleaf pine ecosystems may have been from 2.2 to 6.7 years (Henderson, 2006; Huffman et al., 2004; Stambaugh et al., 2011), and ranging from 0.5 to 12 years (Stambaugh et al., 2011) prior to the implementation of fire suppression by settlers in the 1930s. These variable fire frequencies would have provided variation in vegetative structure and environmental conditions, including areas similar to LLP reference sites, and areas containing more hardwoods and increased structural diversity.

Maintenance of biodiversity, including vertebrate diversity, is recognized as a central restoration objective (SER, 2004) because biodiversity loss has been linked to reduced ecosystem function and the alteration or elimination of ecosystem services (Cardinale et al., 2012). Nevertheless, few management plans specifically embrace biodiversity as a metric for evaluating success and instead focus on the needs of a few rare species (e.g. umbrella, flagship, and keystone species; Simberloff, 1998) and their responses to management (Landres et al., 1988). Practical and ecological limitations including limited budgets, the difficulty of determining the abundances and habitat requirements of a variety of species within an area, variability in spatial and temporal responses, and the possibility that management for one species may negatively influence another cause this discrepancy (Margules and Pressey, 2000). Although managing for surrogate species is done under the auspices of maximizing biodiversity, there is little research supporting these assumptions (Andelman and Fagan, 2000; Simberloff, 1998) and the use of surrogates to manage biodiversity is context dependent (Bichet et al., 2016; Jones et al., 2016; Nicholson et al., 2013; White et al., 2013).

LLP management goals often focus on single species that are rare and/or provide recreational opportunities (e.g. Red-cockaded woodpeckers and bobwhite quail, respectively). Yet, without quantification it is impossible to determine if management efforts guided by the requirements of surrogate species within an ecosystem actually benefit biodiversity, or if they have unintended consequences. Additionally, there is increasing recognition that management should focus on whole ecosystems rather than single, rare or imperiled species (Hallett et al., 2013; Jackson and Hobbs, 2009; Perring et al., 2015; Suding et al., 2015). Although rare species are, and should, be a conservation priority, the role of common species in shaping and increasing the resistance and resiliency of ecosystems cannot be ignored within the context of rapid global change and uncertainty (Gaston, 2011; Gaston and Fuller, 2008; Golladay et al., 2016; Jackson and Hobbs, 2009; Lindenmayer and Likens, 2011). Common species are often not considered within management goals because it is assumed that common species will remain common and they are typically considered less valuable, which is evidenced by the use of the words "weedy" and "trash" to describe them (Gaston, 2011). Yet, many common or once common species are in decline (e.g. Rusty blackbirds [*Euphagus carolinus*; Greenberg and Droege, 1999], spotted skunks [*Spirogale putorius*; Gompper and Hackett, 2005], several bird species in Europe [Inger et al., 2015; Krebs et al., 1999], regal fritillary butterflies [*Speyeria idalia*; Powell et al., 2007], several species of bumblebees [Cameron et al., 2011]) and some have gone extinct (e.g. Carolina parakeet [*Conoropsis carolinensis*] and passenger pigeon [*Ectopistes migratorius*; Gaston and Fuller, 2008]). Management that deemphasizes common species ignores the important roles that common species play (e.g. propagule dispersal, pollination, trophic interactions [Dickman and Steeves, 2004; Gaston, 2010; Goldingay et al., 1991; Gregory et al., 2005]) in shaping the environment that less common species rely on (Gaston, 2011).

It is clear that current LLP management promotes understory plant diversity similar to reference sites (Brockway et al., 1998, 2005; Brockway and Outcalt, 2000) and longleaf pine specialists, but the influence of these practices on vertebrate diversity are less clear. There have been numerous studies on the response of specific wildlife species to LLP restoration (e.g. Litt et al., 2001; Stratman and Pelton, 2007; Armitage and Ober, 2012). Still, there is no unified understanding of how LLP management may influence vertebrate diversity though prescribed fire influences vegetative structure and subsequently the food resources which wildlife rely on (e.g. soft mast; Hiers et al., 2014; Lashley et al., 2014). Consequently, the objective of our review was to determine if frequent prescribed fire (1–3 years) equates to a greater diversity of wildlife within the LLP ecosystem. Specifically, the goals of our research were to determine (1) if restoration to reference conditions utilizing frequent fire in LLP increases vertebrate diversity, (2) what fire return interval promotes the greatest vertebrate diversity, and (3) if restoration to reference conditions with frequent fire enhances the prevalence of specialized species.

2. Methods

2.1. Data collection

There are approximately 733 terrestrial vertebrates within the coastal plain of the southeastern United States (Griep and Collins, 2013), but many are not associated with, or rarely inhabit, the LLP ecosystem. We used a cumulative species list of four classes of vertebrates (Aves, Mammalia, Amphibia, and Reptilia) found within the LLP ecosystem (Means, 2006; Appendix Table A) to delineate vertebrate LLP inhabitants from other species inhabiting the southeastern U.S., and to determine which species were specialists within the LLP ecosystem. We conducted a literature review and compiled a database of studies to determine each species response to fire frequency using the search engines Web of Science and Google Scholar. Initially, we used general search terms to locate literature on multiple species such as "longleaf pine prescribed fire wildlife" and variations of these search terms with the name of a specific taxonomic group included. Following initial searches, we completed species-specific searches to locate papers on each species within the longleaf pine ecosystem. We selected studies conducted in the LLP ecosystem, or geographically within the historic LLP ecosystem. When system specific studies were not available, we included studies conducted in similar southeastern pyrophytic pine forests (e.g. slash pine [*Pinus elliottii*], loblolly pine [*Pinus taeda*]). If studies within these systems were not located, we used species accounts to determine a species response to fire frequency.

2.2. Fire frequency

Fire return intervals from 1 to 3 years reduce the establishment of fire tolerant species (Engstrom et al., 2001; Ware et al., 1993), though some studies support burning on a 1–2 year interval to maintain LLP understory diversity (Glitzenstein et al., 2012). Additionally, Kirkman et al. (2004) found declines in plant species diversity after 4 on mesic sites. Based on these studies and historical information, land managers often burn on a 2–3 year fixed return interval (Hiers et al., 2014; Lashley et al., 2014), leading to increased understory plant diversity but little structural diversity for wildlife.

Consequently, we classified the LLP vegetation community, including flatwoods and sandhill communities, into 1 of 3 categories based on burn frequency including 1–3 years when there is a sparse understory and less fire tolerant species are present leading to little to no midstory vegetation and less structure (Category 1; [Engstrom et al., 2001; Lashley et al., 2014; Ware et al., 1993]), >3–5 years when a more pronounced midstory begins to form and a more continuous fuel accumulation is present to provide for fire-free refugia that may increase structural diversity for wildlife (Category 2; [Hiers et al., 2014; Lashley et al., 2014]), and >5 years when understory plant diversity decreases and stands begin conversion to a hammock stage with increasing time from fire (Category 3; [Varner et al., 2005]). Although some site level differences likely occur within burn categories, these are unlikely to influence our analysis due to the broad pattern examined within this study.

2.3. Measuring use

From the studies we assessed the intensity of use for each species as either high (HU) or low (LU) use for each of the 3 categories (Appendix Table A). We designated HU for the burn categories of the highest importance to each species, while LU included all other categories. When possible, categorization as HU or LU within each category was determined based on statistical analyses or comparisons of standard errors provided within the papers. If these data were not available, categorization was determined based on count data or descriptions of species preferences. A species was excluded from analysis if a classification could not be determined using published literature. In the event where the importance of burn regime varied seasonally, or provided a vital resource (food, shelter, etc.), each category that provided important resources was categorized as HU. If burn frequency was not stated, or the paper was a species account, we used additional criteria to determine burn frequency categories (Table 1). Few research studies have been completed on the response of specific wildlife to different fire regimes. Consequently, in the rare event that there were multiple research studies conducted on a particular species (Appendix Table A) we only used one study to classify a species. If there was one correlational study and a descriptive study, the correlational study was used to classify a species. If there was >1 correlational study within a category and they agreed, the species was classified based on each study. If two correlational studies did not agree, then the one with the more rigorous study design (e.g. greater sample sizes, random assignment of treatments) was used (occurred with <10% of classifications). If there were >2 correlational studies that did not agree, the species was classified as HU or LU within the category based on the greatest number of correlational papers that agreed (<5% of classifications).

2.4. Data analyses

To determine differences in the number of HU species between burn Categories 1 through 3, we fit a general linear model (GLM) with a binomial distribution. Most classifications of species within

Table 1
The criteria used to classify the longleaf pine vegetation community, including flatwoods and sandhill communities, within each literature source into 1 of 3 categories based upon burn frequency including category 1 (1–3 years), category 2 (>3–5 years), and category 3 (>5 years).

Tier	Component	Category 1	Category 2	Category 3
1	Burn interval	1–3 years	>3–5 years	>5 years
2	Dominant canopy	Longleaf (<5 m^2/ha oak, may be greater if management newly implemented)	Longleaf (<10 m^2/ha oak)	Longleaf/oak or oak (>10 m^2/ha oak, highly variable dependent on fire interval, etc.)
3	Midstory cover	Absent to minimal (<10%, $\leqslant$0.2 m^2/ha)	Present (10–$\leqslant$25%, >0.2–$\leqslant$1 m^2/ha)	Present (>25%, >1 m^2/ha)
4	Understory cover	High (Largely grasses, minimal woody) Grasses: Wiregrass and/or bluestem dominant Woody/other: See cat. 2 species. Less cover comprised of woody/other	High (Grasses and woody) Grasses: Wiregrass and/or bluestem dominant Woody/other: Oak saplings, saw palmetto, gallberry, vaccinium, and vines (Smilax)	Sparse
5	Terminology	• Pine savanna • Bilayered • Two-layered forest • Open midstory • Study site – (e.g. Joseph W. Jones Ecological Research Center) • No (lacking) vertical structure • Fire-intense • Frequent burns (fire) • Reference site	• Peak soft mast • Moderate burn frequency • Three layered • Midstory present • Moderate burn cycle • Vertical structure	• Unburned • Fire suppressed • Often the control • Thick litter layer

a category were made from one descriptive or research study (>95%). Consequently, we did not account for publication bias or effect sizes within these analyses. We included occupancy (HU = 1; LU = 0) as our dependent variable and the burn Category (1, 2, or 3) as our independent variable. We fit the models for all species combined and separately for LLP specialists and each vertebrate class. We used Program R Version 2.15.3 (R Development Core Team, 2005) for all statistical analyses. We considered an $\alpha \leqslant 0.05$ to indicate statistical significance.

3. Results

We collected sufficient data to consider the use of burn frequency categories for 177 vertebrates (Aves [n = 82]; Reptilia [n = 45], Amphibia [n = 25], Mammalia [n = 25]). We classified 31 species as LLP specialists (Appendix Table A). For all species combined, we found that the number of high use (HU) species in Category 2 (n = 140) was 22% and 33% greater than in Categories 1 (n = 115, 95% CI: $-1.22 \leqslant \beta \leqslant -0.25$) and 3 (n = 105, 95% CI: $-1.46 \leqslant \beta \leqslant -0.50$), respectively (Fig. 1, Table 2). This pattern was clear for Aves and Reptilia. Specifically, the number of HU species associated with moderate burn frequencies (Aves – n = 69; Reptilia – n = 36) was 21% and 25% greater for Aves and 56 and 63% greater for Reptilia than the number of HU species within category 1 (Aves – n = 57, 95% CI: $-1.60 \leqslant \beta \leqslant -0.09$; Reptilia – n = 23, 95% CI: $-2.51 \leqslant \beta \leqslant -0.49$) and 3 (Aves – n = 55, 95% CI: $-1.71 \leqslant \beta \leqslant -0.21$; Reptilia – n = 22, 95% CI: $-2.60 \leqslant \beta \leqslant -0.58$; Fig. 1, Table 2), respectively. We found no difference in the number of HU species across categories for Amphibia or Mammalia (Fig. 1,

Table 2
The beta ($\hat{\beta}$) coefficients, standard errors (SE), t-statistic (t), and P-values associated with general linear models fit to assess the difference in the number of species categorized as high use in three categories associated with burn frequency: category 1 (1–3 years), category 2 (>3–5 years), and category 3 (>5 years). Items in **bold** indicate a significant difference ($\alpha \leqslant 0.05$).

Categories	$\hat{\beta}$	SE	t	P-value
Combined				
1 v. 2	0.74	0.25	2.98	**0.0029**
1 v. 3	−0.25	0.22	−1.11	0.2690
2 v. 3	−0.98	0.24	−4.02	**<0.0001**
Specialists				
1 v. 2	−1.18	0.73	−1.61	0.1082
1 v. 3	−2.98	0.72	−4.14	**0.00**
2 v. 3	−1.80	0.56	−3.20	**0.0014**
Amphibia				
1 v. 2	0	0.60	0	1
1 v. 3	−0.51	0.59	−0.87	0.3836
2 v. 3	−0.51	0.59	−0.87	0.3836
Aves				
1 v. 2	0.85	0.39	2.19	**0.0286**
1 v. 3	−0.11	0.34	−0.34	0.7372
2 v. 3	−0.96	0.38	−2.50	**0.0124**
Mammalia				
1 v. 2	0	0.63	0	1
1 v. 3	−0.70	0.60	−1.17	0.2420
2 v. 3	−0.70	0.60	−1.17	0.2420
Reptilia				
1 v. 2	1.50	0.51	2.92	**0.0036**
1 v. 3	−0.09	0.43	−0.22	0.8291
2 v. 3	−1.59	0.51	−3.10	**0.0020**

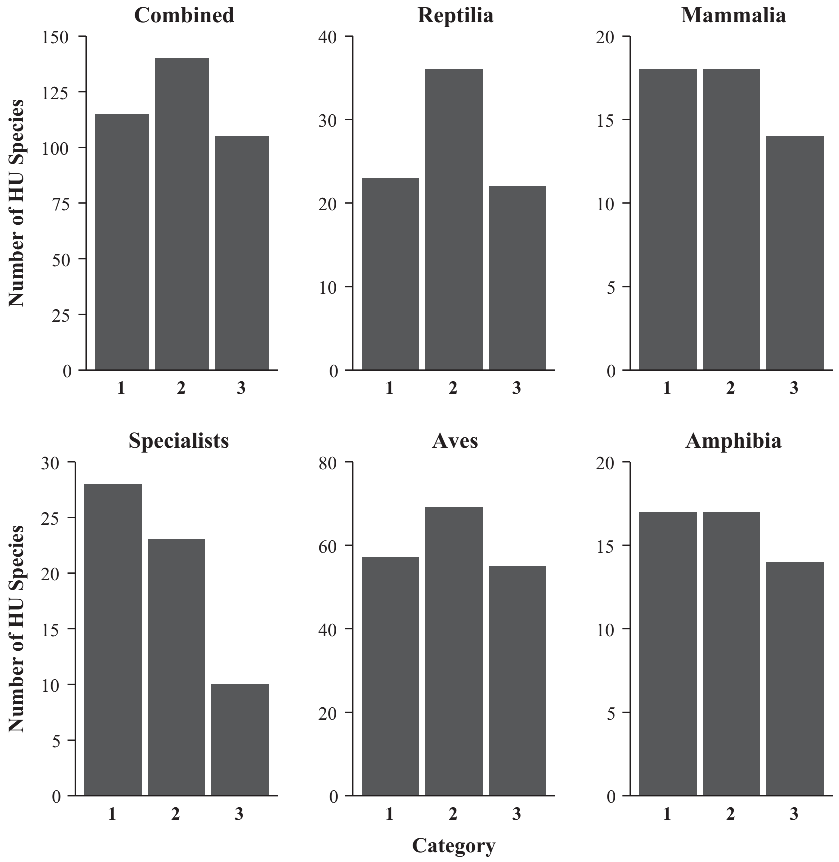

Fig. 1. The number of wildlife species categorized as high use (HU) in longleaf pine ecosystems managed with high (Category 1), moderate (Category 2), and low (Category 3) frequency burns for all taxonomic classes combined (n = 177), Reptilia (n = 45), Mammalia (n = 25), longleaf pine specialists (n = 31), Aves (n = 82), and Amphibia (n = 25).

Table 2). For the longleaf pine specialists (Appendix Table A), we found that there was no difference in the number of HU species in Category 1 (n = 28) and Category 2 (n = 23; Fig. 1, Table 2). Compared to Category 3, the number of HU species was 180% and 130% greater in Category 1 (n = 10, 95% CI: $-4.38 \leqslant \beta \leqslant -1.57$) and 2 (95% CI: $-2.90 \leqslant \beta \leqslant -0.70$), respectively (Fig. 1, Table 2).

4. Discussion

Within the LLP ecosystem we found that managing for reference conditions would likely not maximize the total number of vertebrate species. Instead, moderate burn frequencies (>3–5 years) would be more likely to create the highest diversity of fauna in restored LLP. These findings do not align with restoration goals of 1–3 year burn intervals, which are commonly implemented during LLP restoration (Hiers et al., 2014; Lashley et al., 2014; Palik et al., 2002). We posit that moderate burn frequencies were used more intensely by more species because many terrestrial vertebrates require a variety of environmental conditions and resources to meet their life requisites (Law and Dickman, 1998; Roth, 1976; e.g. eastern diamondback rattlesnake (*Crotalus adamanteus*), Louisiana pine snake (*Pituophis ruthveni*) [Hoss et al., 2010; Steen et al., 2007, 2013b] and wild turkey (*Meleagris gallopavo*) [Exum et al., 1987; Sisson et al., 1990]). Additionally, many species require specific environmental conditions, such as a moist litter layer (e.g. scarlet snake (*Cemophora coccinea*), Florida crowned snake (*Tantilla relicta*), and red-bellied snake (*Storeria occipitomaculata*) [Jensen et al., 2008]) and mast for food (e.g. Sherman's Fox Squirrel [Kaprowski, 1994], White-tailed deer [Smith, 1991], and many bird species [Snow and Snow, 1988]), that are absent or reduced in areas with frequent fire. Utilizing a 1–3 year burn interval within the LLP ecosystem can lead to a homogenous landscape that is not likely to provide a variety of environmental conditions, structure, and resources. Still, we cannot disregard potential significant spatial variability at smaller scales within the habitat matrix of each study. This variability may have influenced use of habitat by vertebrates and would not have been detected within the studies used for our analyses.

Currently, hardwood reduction using high burn frequencies is commonly implemented in the restoration of LLP forests (Brockway et al., 2005). The reduction of hardwoods concurrent with frequent fires likely decreases structural diversity of LLP forests. Decreased structural diversity may reduce wildlife diversity by providing fewer niches for species to exploit (Habitat heterogeneity hypothesis; Lack, 1969; MacArthur and Wilson, 1967; Simpson, 1949; Tews et al., 2004). We found several avian species (e.g. Hooded warbler [*Setophaga citrina*], yellow-billed cuckoo [*Coccyzus americanus*; Conner et al., 1999; Engstrom et al., 1984], northern parula [*Setophaga Americana*; Engstrom et al., 1984], hermit thrush [*Catharus guttatus*; Conner et al., 1999; Provencher et al., 2002]) were less likely to be present on sites with high burn frequencies with the corresponding reduction in midstory cover. Most studies show a positive relationship between avian diversity and structural diversity (MacArthur and MacArthur, 1961; Tews et al., 2004). Specifically, the vertical distribution of vegetation, rather than vegetative species composition, may increase avian guild diversity by allowing for the vertical partitioning of resources (Poulsen, 2002). Structural vegetation diversity is also important to Reptilia (Pianka, 1967; Reinert, 2001), and the lack of structural diversity within the LLP ecosystem may negatively influence several species (e.g. rough green snake [*Opheodrys aestivus*; Goldsmith, 1984; Jensen et al., 2008], green anole [*Anolis carolinensis*; Irschick et al., 2005; Jensen et al., 2008], eastern diamondback rattlesnake [Waldron et al., 2008], and broadhead skink [*Eumeces laticeps*; Jensen et al., 2008]).

Numerous LLP specialists utilize areas of moderate burn frequency (e.g. eastern diamondback rattlesnake, gopher tortoise [*Gopherus polyphemus*], and northern bobwhite quail [*Colinus virginianus*]; Appendix Table A). For instance, eastern diamondback rattlesnakes (*Crotalus adamanteus*) and Louisiana pine snakes (*Pituophis ruthveni*) are both considered longleaf pine specialists (Means, 2006). Nevertheless, the diamondback rattlesnake and pine snake are also positively correlated with mixed hardwood-pine forests and utilize longleaf pine landscapes interspersed with hardwoods and/or with adjacent stands of mixed hardwood-pine forest (Hoss et al., 2010; Steen et al., 2007, 2013b). Large-bodied snakes play an important role in ecosystems as top predators and can influence prey populations both directly via consumption and indirectly via altering prey behaviors (e.g. Bouskila, 1995; Kotler et al., 1993; Patten and Bolger, 2003). These indirect effects may have profound effects on ecosystems by altering seed dispersal, nutrient cycling, and other processes (Chapin et al., 1997). Alternatively, gopher tortoises are a species that require an open landscape characteristic of sites maintained with frequent burns (Tuberville et al., 2007; Wilson et al., 1997). However, Aresco and Guyer (1999) suggest that areas will remain suitable for gopher tortoises 5–7 years following a burn and Landers and Speaker (1980) indicate a burn interval of 2–4 years is preferable. Consequently, though management for gopher tortoises is important due to their role as a keystone species (Eisenberg, 1983), management with a combination of frequent and less frequent (up to 5 years) fire would not conflict with preserving gopher tortoise populations.

Although we found no difference in the number of LLP specialists intensively using high and moderate burn frequencies, high burn frequencies would likely be most effective for restoring habitat for LLP specialists as eight species (Eastern spadefoot [*Scaphiopus holbrookii*]; Flatwoods salamander [*Ambystoma cingulatum*]; Oak toad [*Anaxyrus quercicus*]; Ornate chorus frog [*Pseudacris ornata*]; Bachman's sparrow [*Aimophila aestivalis*]; Brown-headed nuthatch [*Sitta pusilla*]; Eastern indigo snake [*Drymarchon couperi*]; Red-cockaded woodpecker [*Picoides borealis*]) were either excluded from or rarely use areas with moderate burn frequencies. Three of these eight species, the flatwoods salamander, eastern indigo snake, and red-cockaded woodpecker, are federally listed as threatened or endangered (USFWS, 2014). The dominance of fire-prone pine forests in the southeastern coastal plain over the last 5000 years (Watts, 1971) may have led to adaptations within these species (LLP specialists) that optimized their fitness in the presence of high burn regimes. Still, habitat heterogeneity is considered a precursor for biodiversity (Baumberger et al., 2012; Simberloff, 1998) and the homogenous application of fire within the LLP ecosystem leads to a homogenous landscape (Lashley et al., 2014). There is growing evidence, including our findings, that variability in fire return intervals are important to maintaining diversity within the LLP ecosystem (Hiers et al., 2000, 2014; Schurbon and Fauth, 2003). There is also increasing support for managing whole ecosystems instead of single species (Hallett et al., 2013; Jackson and Hobbs, 2009; Perring et al., 2015; Suding et al., 2015). Additionally, the homogenous application of fires does not account for historical variation in fire and may positively influence LLP specialists to the detriment of other non-focal species (Bean, 2009; Doremus, 1997; Franklin, 1993).

Although our study is scale independent, scale is particularly important to species with large home ranges and species that need different components of the LLP systems. Consequently, if restoration of LLP specialists is the stated objective, the ecology and scale of response of the target species should be considered to determine if it needs to be managed exclusively with high burn frequencies. For instance, maintenance of species such as red-cockaded woodpeckers (*Picoides borealis*) minimally requires 80 ha of frequently burnt longleaf pine habitat per cluster at a local scale rather than large-scale implementation of high frequency burns across the LLP landscape (USFWS, 2003). Given current rates of biodiversity loss and global change and the positive relationship between biodiversity and ecosystem resiliency (Butchart et al., 2010; Cardinale et al., 2012; Chapin et al., 2000; Isbell et al., 2015; Oliver et al., 2015), managers may want to manage habitat for red-cockaded woodpecker clusters with frequent burns (1–3 years), while incorporating variability in fire return intervals (1–5 years) into management of the surrounding matrix to maximize diversity.

When conservation objectives prioritize maximizing vertebrate diversity, we suggest managers diversify their methods. Although we recognize the simplicity associated with current management techniques (e.g. constant application of fire on short return intervals), we propose that managers should implement long-term (>25 years) adaptive management plans at the landscape scale to promote habitat diversity. Rather than using constant temporal application of fire across the landscape, plans should mimic average burn frequencies over time (2.2 years; Stambaugh et al., 2011) while recognizing that ecosystems are dynamic by varying the individual burn intervals from 1 to 5 years (Hiers et al., 2014; Lashley et al., 2014). Longer fire return intervals (>3 years) should not be applied across broad spatial scales consecutively and sites that are more productive may require a lower range of fire return intervals to reduce the potential for the rapid encroachment of hardwoods. Productivity in the longleaf pine ecosystem can be quantified via measures of ground cover biomass (Kirkman et al., 2001). Although this management strategy may be more complex, it would provide the most benefit to vertebrates by maintaining localized patches of oaks and increasing compositional and structural diversity (Lashley et al., 2014; Hiers et al., 2014).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.07.039.

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