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# Response of reptile and amphibian communities to the reintroduction of fire in an oak/hickory forest



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## ABSTRACT

Fire can have diverse effects on ecosystems, including direct effects through injury and mortality and indirect effects through changes to available resources within the environment. Changes in vegetation structure such as a decrease in canopy cover or an increase in herbaceous cover from prescribed fire can increase availability of preferred microhabitats for some species while simultaneously reducing preferred conditions for others. We examined the responses of herpetofaunal communities to prescribed fires in an oak/hickory forest in western Kentucky. Prescribed fires were applied twice to a 1000-ha area one and four years prior to sampling, causing changes in vegetation structure. Herpetofaunal communities were sampled using drift fences, and vegetation attributes were sampled via transects in four burned and four unburned plots. Differences in reptile community structure correlated with variation in vegetation structure largely created by fires. Amphibian community structure differed on a yearly basis, indicating that sampled communities were likely influenced by environmental factors other than the burning. We found taxa-specific differences in abundances for Coluber constrictor, Diadophis punctatus, Sceloporus undulatus, Lithobates clamitans and snakes as a group, being more abundant in burned areas while Anaxyrus sp., Notophthalmus viridescens and Plethodon glutinosus were more abundant in unburned areas. Differences in amphibian taxa abundances may have been influenced by availability of aquatic breeding habitat and yearly weather variation. Our results suggest that the vegetation structure changes caused by prescribed fire can have indirect impacts on reptile abundances and community structure, while not significantly impacting amphibian communities.

# 1. Introduction

Fire is an important landscape disturbance, one that has shaped ecological communities across the world. Fires in eastern North America were historically started by both natural lightning strikes and Native Americans managing for game (Delcourt et al., 1998). Many ecosystems have evolved in response to recurring fire and other disturbances (e.g. grazing by large ungulates), and plant and animal communities have adapted to conditions resulting from periodic disturbances (Harper et al., 2016; Stambaugh et al., 2015). However, disturbance regimes have changed drastically over the past several centuries; the practice of fire suppression and the loss of large grazing ungulates have led to an alteration of North American vegetation communities from historically open pyrogenic ecosystems to closed mesophytic systems that are more resistant to burning (Nowacki and Abrams, 2008). This drastic change in vegetation structure has led to the loss of biodiversity within these formerly fire-dependent ecosystems; declines in disturbance-dependent biological communities have been documented across the eastern United States, including fire-dependent plants (Nowacki and Abrams, 2008; Vander Yacht et al., 2017), insects (Wood et al., 2011), birds (Hunter et al., 2001), amphibians (Gorman et al., 2009), and reptiles (Russell et al., 1999). As habitat loss and degradation, such as succession in historically open habitats, have been implicated in the global decline of reptile and amphibian populations (Alford and Richards, 1999; Gibbons et al., 2000), it is important to understand how land management decisions influence these communities (Gardner et al., 2007).

Recently, there has been increased concern over the loss of

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biological diversity in the historically oak-dominated systems in the interior southeastern United States (Noss, 2013), especially as pyrophobic maples (*Acer*) have begun to replace pyrophilic oaks (*Quercus*) as the dominant tree group (McShea et al., 2007; Stambaugh et al., 2015). Oak woodlands and savannas rank among the most imperiled ecosystems of the eastern United States, with less than 1% of their historic extent remaining (Davis et al., 2002). In the past several decades prescribed burning has been widely implemented as a management practice intended to restore vegetative communities with low canopy cover, promote oak regeneration, and limit the potential for catastrophic wildfires (McIver et al., 2013; Pyne et al., 1996; Schwilk et al., 2009). Understanding the impacts of prescribed burning on wildlife communities, especially in oak dominated hardwood systems, is crucial to help refine management techniques to meet conservation goals.

Key to understanding the impact of prescribed fires on biological communities is to consider historic fire regimes and the temporal response to applied fire. Coarse-scale modeling of fire return intervals suggest that fires occurred every 4-6 years in our study area (Guyette et al., 2012), and fire scar data from historic oak woodlands in Tennessee suggest a mean fire return interval of 2.2 years, though great variability existed throughout the landscape (Stambaugh et al., 2016). As interest in restoring these imperiled vegetative communities grows, it is becoming evident that initial management schemes may require more intensive and repeated disturbance regimes than previously thought, such as basal area reduction in addition to fire (Harper et al., 2016; Vander Yacht et al., 2017). Season of burn (growing vs. dormant) can be an important factor in vegetative response (Harper et al., 2016; Knapp et al., 2009), but it has been suggested that canopy reduction is likely a more important for herpetofaunal response (Greenberg et al., 2018).

Many studies have focused on herpetofaunal responses to a single application of a prescribed burn to areas previously fire-suppressed for more than a decade (Langford et al., 2007; Radke et al., 2008; Sutton et al., 2013). While these studies are certainly informative regarding the initial community responses to a burn, they provide little insight to potential long-term effects, both from a single fire or from recurring fire regimes, which have been suggested to cause lasting impacts on lizard and salamander abundances (Matthews et al., 2010). This study focused on the responses of reptile and amphibian communities to two largescale (1000-ha) prescribed fires in a formerly fire-suppressed oak/ hickory forest. The size of the fires potentially emulates how fires would have historically influenced the landscape. We examined the response of the herpetofaunal communities for six years after the fires to understand how changes in community composition and abundance would result from changes in vegetation structure over a meaningful time period for this vertebrate group.

# 2. Methods - Data collection

# 2.1. Study site

We conducted the study at Land Between the Lakes National Recreation Area (LBL) in southwestern Kentucky. LBL is a large (69,000 ha) inland peninsula located within the Highland Rim Section of the Interior Low Plateau Physiographic Province created by the construction of dams on the Cumberland and Tennessee rivers (Chester and Fralish, 2002). Originally managed by the Tennessee Valley Authority, LBL now falls under the jurisdiction of the US Forest Service. Topography is characterized as highly dissected with narrow ridge tops with elevations ranging from 115 m to 200 m. Soils are predominately Baxter-Hammack and Brandon-Saffell and are generally well-drained with gravelly silt-loam associations (Soil Survey Staff, Natural Resources Conservation Service, 2017). Oral histories of the area, historic pollen analyses, and the persistence of early-successional species (e.g. pinesnake [*Pituophis melanoleucus*], northern bobwhite [*Colinus*] *virginianus*]) suggest that prior to European settlement the ridgetops of LBL were dominated by oak-savanna and oak-woodlands (Franklin, 1994; Snyder et al., 2016). These conditions were maintained by the combination of fires set by Native Americans and grazing by large herbivores, but decades without fire and the loss of megafauna (elk, bison) have led to a dominant land cover of dense oak/hickory forest, resulting in declines of species associated with early successional vegetation (Franklin, 1994; Franklin et al., 1993).

# 2.2. Experimental design and treatments

We used the Franklin Creek Burn Unit, a 1000-ha area that received prescribed burns in April 2007 and September 2010 for sampling. Fires were set by dropping plastic incendiary spheres from a helicopter, a practice called aerial ignition. The spheres are filled with potassium permanganate and ignited by the injection of ethylene glycol. Ignition was started on ridge tops and spread into valleys with varying intensity and flame height, with rate of spread depending on topography and available fuel loads. We established four 64-ha ( $800 \times 800$  m) plots in both burned and unburned areas in 2010 and each plot was separated by a minimum of 200 m from the nearest neighboring plot, resulting in four plots within the burned area and four plots in unburned areas (Fig. 1). We considered plots to be independent in analyses because no recaptured animals were recorded in different sampling arrays.

#### 2.3. Herpetofauna sampling

We installed a 100-m drift fence in the center of each study plot in 2010. Fences were constructed of silt fencing, with four pitfall traps (19-L buckets) and six funnel-box traps located along the fence (Todd et al., 2007). Funnel traps located on the end of the fence had one funnel, while traps located in the center of the fence had two funnels. Pitfall traps were located halfway between funnel traps. We sampled in 2011, 2012, 2015, and 2016 between April and the end of September. Trapping duration varied between 3 and 30 days per month among years but was equivalent among sampling periods, and between burn and unburned units (effort summarized in Appendix 2).

We marked and identified each captured animal. We performed batch toe-clipping on amphibians and little brown skinks (*Scincella lateralis*) corresponding to year of capture; all other lizards received individual toe clips (Phillott et al., 2007). We clipped individual ventral scales on snakes (Brown and Parker, 1976) and inserted PIT tags (Biomark, model HTP9, Boise, ID) sub-dermally (for individuals with body size > 400 mm). We marked turtles with marginal scute notching (Cagle, 1939). We released all animals at the capture site.

#### 2.4. Vegetation structure and composition sampling

We used transects to quantify vegetation structure in both burned and unburned plots. Transect surveys were performed concurrently with herpetofaunal sampling during the spring and summer in 2011-2012 and 2015-2016. Transects were 100-m long, with starting point and direction determined by randomly selecting points on a grid of each study plot. We collected measurements at 20-m intervals along transects, for a total of six points per transect. We measured fifteen transects per plot in 2011-2012, three per plot in 2015 and eight in 2016. At each sample point, we measured percent canopy cover using a spherical crown densiometer, leaf litter depth, (  $\pm$  0.1 cm), distance to nearest overstory tree (OST, > 7.5 cm diameter breast height [DBH]), and distance to nearest understory tree (UST, woody stem < 7.5 cm DBH, but taller than breast height). A 7.5-cm DBH distinguished between OST and UST in previous reptile habitat use studies (Howey et al., 2016; Reinhert, 1984). We determined ground cover composition using a 1-m<sup>2</sup> frame (Daubenmire, 1959) to quantify percent cover of leaf litter, bare ground, woody plant, forb, vine, grass, coarse woody debris (CWD, > 5 cm diameter), rock, and moss.



Fig. 1. Map of study area in Land Between the Lakes National Recreation Area, Trigg County, KY. Drift fence locations are represented by a star symbol, burned areas by hashing, and study plots by squares.

#### 2.5. Data analysis

#### 2.5.1. Vegetation structure and composition

We tested our vegetation structure data for the assumption of homogenous multivariate dispersion using a permutation test (function *permutest* in package vegan) among site type and year (Anderson, 2006). We used a multivariate permutational analysis of variance (function *adonis* in package vegan [Oksanen et al., 2017] in program R [R Core Team, 2015]) to test for differences in overall vegetation structure (Anderson, 2001). Site type (burned vs. unburned), year, and a site by year interaction term were used as factors. Prior to multivariate analyses, ground cover characteristics accounting for less than 5% overall (e.g. moss, rock) were removed due to numerous zeros.

#### 2.5.2. Reptile and amphibian community structure

Nonmetric multidimensional scaling (NMDS) was performed to discern the overall reptile and amphibian community responses to prescribed fire treatments. This approach measures community dissimilarity using ranks of dissimilarities to map differences between ecological communities across sampling years and treatments (Borcard et al., 2011). We used catch per unit effort (CPUE; total captures/total fence nights, not including recaptures) for each species in each plot and year to compare relative species abundances and grouping was defined by sampling year and treatment (e.g. burn 2011, unburned 2012). Including rare species in our analyses did not change the interpretation of the ordinations, and others have suggested that removing rare species from this type of analysis may have important site-level impacts (Cao et al., 2001). We conducted separate NMDS analyses for reptile and amphibian communities using the Bray-Curtis dissimilarity matrix in both 2 and 3 dimensions to find the optimal stress (Clarke and Warwick, 2001). Stress values denote the disagreement between the NMDS dimension ordination and the predicted values, ranging from 0 to 1, and are considered a typical representation of ecological community

dissimilarity when they fall between 0.1 and 0.2 (Clarke and Warwick, 2001; McCune and Grace, 2002). Nonmetric multidimensional scaling was performed in program R using function *metaMDS* in the package vegan. We compared differences between communities in a treatment within a year using 95% confidence interval ellipses (*ordiellipse* function in vegan); overlapping ellipses were interpreted as a lack of statistical difference (Bowman and Somers, 2005; Howey et al., 2016; Larrivée and Buddle, 2009). We used Spearman's rank correlations of habitat variables for the ordination using the *envfit* function in the vegan package to help visualize the gradient in vegetation structure between treatments (Oksanen, 2015). We considered vegetation correlations with a p-value < 0.05 significant; significance was determined by random permutations using the *envfit* function in package vegan.

#### 2.5.3. Species and vegetation structure comparisons

We used canonical correspondence analysis (CCA) to understand how individual species responded to differences in vegetation conditions. We examined the relationships between species abundances and vegetative structure using CCA; a method of direct gradient analysis that constrains species abundance data to a set of *a priori* environmental characteristics that are hypothesized to influence species distribution patterns (Ter Braak, 1987). Species abundances were standardized CPUE, as used in previous analysis, with rare species (< 14 captures) excluded. We included environmental variables in this analysis that were not highly correlated (Pearson's correlation of lower than 0.5), and used means of vegetation values for each plot within a year. We performed one CCA for reptiles and one for amphibians using package *vegan* (Oksanen et al., 2017) in program R version 3.2.3.

#### 2.5.4. Species abundance

We compared differences in species abundances in response to prescribed fire using a mixed-model analysis of variance. Only species that were captured in 4 or more plots during a year and had greater than 100 unique total captures were examined for differences in abundance across treatments. Higher-level taxonomic groups (e.g. Caudata, Serpentes) were also examined in the same framework using a generalized linear mixed-effects model with a negative binomial distribution using package lme4 (Bates et al., 2015) in R version 3.2.3. We used individual counts (by species) as the response variable with



(caption on next page)

**Fig. 2.** Nonmetric Multidimensional Scaling ordination relating differences in reptile community structure between burned (solid circles) and unburned sites (open circles). From top left: Convex polygons and 95% Confidence Interval Ellipses representing total burn (red) and unburned (blue) communities across all years and species optimums; vector overlays of vegetation characteristics significantly correlated with the ordination; and overlays of 95% CI ellipses for sites within each sampled year. Species codes: AGCO (*Agkistrodon contortrix*), CAAM (*Carphophis amoenus*), CECO (*Cemophora coccinea*), COCO (*Coluber constrictor*), CRHO (*Crotalus horridus*), DIPU (*Diadophis punctatus*), HEPL (*Heterodon platirinos*), LAEL (*Lampropeltis elapsoides*), LANI (*Lampropeltis nigra*), LATR (*Lampropeltis triangulum*), NEER (*Nerodia erythrogaster*), NERH (*Nerodia rhombifer*), NESI (*Nerodia sipedon*), OPAE (*Opheodrys aestivus*), PASP (*Pantherophis spiloides*), PLFA (*Plestiodon fasciatus*), PLIN (*Plestiodon laticeps*), SCLA (*Scincella lateralis*), SCUN (*Sceloporus undulatus*), STDE (*Storeria dekayi*), STOC (*Storeria occipitomaculata*), TACO (*Tantilla coronata*) THSI (*Thamnophis sirtalis*) VIVA (*Virginia valeriae*). Stress = 0.138. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

treatment (burn vs. unburned) and Year used as categorical predictors with plot as a random effect. Additionally, an offset command corresponding to the number of trap nights for each plot was used to account for differences in sampling effort. This approach is more appropriate for non-normal count data than applying a data transformation (O'Hara and Kotze, 2010). We obtained p-values for our categorical predictors using package *car* (Fox and Weisberg, 2011) in R version 3.2.3. We used the Benjamini-Hochberg method to adjust p-values of treatment and year effects to control the false discovery rate for the overall study at 0.05 (Benjamini and Hochberg, 1995; Waite and Campbell, 2006).

Due to differences in sampling effort among years and low recapture rates, we could not account for potential differences in detection among treatments and years. Detection rates are often difficult to meaningfully quantify for many cryptic and fossorial species using passive sampling techniques (Steen, 2010), and often have not been quantified in similar studies (Greenberg et al., 2017, 2016; Greenberg and Waldrop, 2008; Moorman et al., 2011; Perry et al., 2009; Steen et al., 2013). Our results may have been influenced by differences in detection; detection and movement has been shown to increase in time periods directly following fire for certain species (Driscoll et al., 2012; O'Donnell et al., 2016), thus our abundance differences may be more reflective of movement rates.

#### 3. Results

#### 3.1. Vegetation structure

Dispersion of vegetation structure characteristics differed between burned and unburned sites ( $F_{1,1917} = 89.80$ , p < 0.001, Permutest) and years ( $F_{3.1915} = 27.067$ , p < 0.001, Permutest), suggesting that structural heterogeneity changed due to burning and over time. We differences in vegetation structure between found sites  $(F_{1,1911} = 111.33, p < 0.001, ADONIS), year (F_{3,1911} = 117.70,$ p < 0.001, ADONIS) and the site by year interaction ( $F_{3,1917} = 14.30$ , p < 0.001, ADONIS). Increased canopy cover and leaf litter depth/ cover were associated with the unburned areas, while the burned areas had more grasses and forbs. Further distances to nearest overstory tree and understory tree (inverse measures of tree density) were associated with the burned areas, though this difference became less pronounced as time since fire increased. Woody coverage in burned units increased proportional to the time since the last fire. Differences in vegetation structure between burned and unburned areas persisted even after six years without a burn.

### 3.2. Herpetofaunal captures

A total of 2103 individuals of 27 reptile species and 6175 individuals representing 22 amphibian species were captured through 2237 trap nights between 2011 and 2012 and 2015–2016 (summarized in n Appendices 2 & 3). The most frequently captured species for each major taxonomic group were the North American Racer (*Coluber constrictor*, n = 128), the eastern fence lizard (*Sceloporus undulatus*, n = 484), the eastern box turtle (*Terrapene carolina*, n = 22), the Fowler's toad (*Anaxyrus fowleri*, n = 2038), and the eastern newt (*Notophthalmus viridescens*, n = 240). A total of 196 reptile captures and 189 amphibian captures were from recaptured individuals, with the majority of reptile recaptures belonging to two species (common fivelined skink [*Plestiodon fasciatus*], n = 64, and eastern fence lizards, n = 74), and almost every amphibian recapture was an *Anaxyrus* toad (n = 178 of 189).

#### 3.3. Community structure

Two NMDS ordinations were produced, one for squamate communities (Fig. 2) and one for amphibian communities (Fig. 3). For both groups, a three-dimensional solution best fit the data, with the reptile ordination having a final stress value of 0.138 and the amphibian ordination having a final stress value of 0.153. In the reptile ordination, most of the burn communities clustered on the left side of the ordination; most burn communities were more similar in composition to each other than the unburned communities (Fig. 2). Many snake species clustered around the burn communities in the ordinations, suggesting they contribute more to the community composition in burned areas. Interval ellipses with 95% confidence overlapped between burn and unburned treatments for all years except 2015; community structure had not significantly diverged between burned and unburned communities (Fig. 2). When significantly correlated vegetation structure variables were overlaid on the ordination (Fig. 2) grass, woody stems, and understory tree distance were correlated with the left side of the ordination, while litter coverage was correlated with the right side of the ordination, suggesting that these factors may be influencing community structure.

The amphibian NMDS ordination (Fig. 3) did not distinguish between burned and unburned communities, and 95% confidence intervals overlapped substantially between treatment within each year, while many years did not overlap with each other. Sites from 2015 to 2016 clustered on the right side of the ordination, while the other years clustered on the left, suggesting that amphibian community structure varied yearly.

#### 3.4. Species and vegetation structure comparisons

Reptile abundances were influenced by vegetation structure (Canonical correspondence analysis, F = 1.76 df = 8,23, p = 0.001; Fig. 4). Eastern fence lizard abundance was associated with burned vegetation characteristics such as overstory tree distance and woody growth, while little brown skinks and Dekay's brownsnake (*Storeria dekayi*) abundances increased along with unburned vegetation characteristics such as deeper litter depth and greater canopy cover. Abundances of the two *Plestiodon* skink species, copperhead (*Agkistrodon contortrix*), and common gartersnake (*Thamnophis sirtalis*) showed no strong relationship with any measured variable. Eastern wormsnake (*Carphophis amoenus*) abundances increased with higher coarse woody debris, while smooth earthsnake (*Virginia valeriae*) abundance increased as distance to nearest tree increased.

Relationships between amphibian abundances and vegetation characteristics (Fig. 5; F = 2.20, p = 0.015, df = 9,22) showed Cope's gray treefrog (*Hyla chrysoscelis*) and northern slimy salamander (*Plethodon glutinosus*) abundances increased with higher coarse woody debris. However, strong relationships were not observed between the majority of the amphibian species captured and the measured vegetation structure variables; *Anaxyrus* toads were in the middle of the

ordination, reflecting their generalist nature.

#### 3.5. Species abundance

Several species and species group abundances differed between site type (burn vs. unburned; summarized as CPUE for ease of comparison in Figs. 6 and 7) after correcting for family-wise error rate. Abundances were higher in burned sites for all snake species combined (p = 0.003), North American racer (p = 0.01), ring-necked snakes (p < 0.01), eastern fence lizard (p = 0.04) and green frog (*Lithobates clamitans*, p = 0.02), and were approaching significance for all reptiles combined (p = 0.08). Abundances were lower in burn sites for amphibians overall

(p = 0.03), overall anurans (p = 0.04), *Anaxyrus* toads (p = 0.02), eastern newt (p < 0.001), and northern slimy salamanders (p = 0.03), and was approaching significance for. No treatment effect was observed for lizards overall (p = 0.5), common five-lined skink (p = 0.48), broad-headed skink (*Plestiodon laticeps*, p = 0.71), little brown skink (p = 0.1), Cope's gray treefrog (p = 0.72), eastern narrow-mouthed toad (p = 0.67) southern leopard frog (*Lithobates sphenocephalus*, p = 0.1), or salamanders overall (p = 0.1). Year effects were observed for every species and species group examined (summarized in Table 1); this was likely due to differences in sampling effort and weather among years.



**Fig. 3.** Nonmetric Dimensional Scaling ordination relating differences in community structure of amphibian species between burned (solid circles) and unburned sites (open circles). From top left: overlay of convex polygon and 95% Confidence Interval Ellipses containing all sites for all years within a burn treatment (red lines) and unburned treatments (blue lines); species optimum for the ordination; and overlays of 95% CI ellipses for burn (red 95% CI ellipses) and unburned sites (blue 95% CI ellipses) for 2011 (solid), 2012 (dotted); 2015 (dashed), and 2016 (dash + dot). No differences in community structure between treatment were seen within any year, but year-to-year differences were evident. Species Codes: AMMA (*Ambystoma* maculatum), AMOP (*Ambystoma* opacum), AMTE (*Ambystoma* texanum), ANSP (*Anaxyrus americanus/Anaxyrus fowleri*), EUCI (*Eurycea cirrgera*), EULO (*Eurycea longicauda*), EULU (*Eurycea lucifuga*), GACA (*Gastrophryne carolinensis*), HYCH (*Hyla chrysoscelis*), HYCI (*Hyla cinerea*), LICA (*Lithobates catesbeianus*), LICL (*Lithobates clamitans*), LISP (*Lithobates sphenocephalus*), NOVI (*Notopthalmus viridescens*), PLDO (*Plethodon dorsalis*), PLGL (*Plethodon glutinosus*), PSCR (*Pseudacris crucifer*), PSFE (*Pseudacris feriarum*). Stress = 0.153. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



Fig. 4. CCA biplot relating relationships between reptile species to measured vegetation characteristics. Species codes are the same as for previous ordinations. Species codes: AGCO (Agkistrodon contortrix), CAAM (Carphophis amoenus), COCO (Coluber constrictor), DIPU (Diadophis punctatus), HEPL (Heterodon platirinos), LANI (Lampropeltis nigra), LATR (Lampropeltis triangulum), PLFA (Plestiodon fasciatus), PLLA (Plestiodon laticeps), SCLA (Scincella lateralis), SCUN (Sceloporus undulatus), STOC (Storeria occipitomaculata), THSI (Thamnophis sirtalis) VIVA (Virginia valeriae).



Fig. 5. CCA biplot relating relationships between amphibian species to measured vegetation characteristics. Species codes are the same as for previous ordinations. Species Codes: AMMA (*Ambystoma maculatum*), AMOP (*Ambystoma opacum*), ANSP (*Anaxyrus americanus/Anaxyrus fowleri*), EULO (*Eurycea longicauda*), GACA (*Gastrophryne carolinensis*), HYCH (*Hyla chrysoscelis*), LICL (*Lithobates clamitans*), LISP (*Lithobates sphenocephalus*), NOVI (*Notopthalmus viridescens*), PLGL (*Plethodon glutinosus*).

# 4. Discussion

Our results indicate that prescribed fire created a gradient of available vegetation structure, inducing a response by reptile communities, while not appreciably impacting overall amphibian community structure. Responses to changes in vegetation structure were generally taxa-specific, with positive effects seen for some lizard and snake species, while some amphibians showed moderately higher abundances in unburned sites, although this is likely due to location of productive breeding areas in relation to sampling arrays. Our sites had been fire suppressed for several decades—reptile communities were likely impacted by this suppression and would likely continue to respond if vegetation structure continues to change with a the return of a historic fire regime.

Prescribed fires can be important in shaping reptile community structure. Several studies examining the short-term effects of burning have shown only minor herpetofaunal community responses (Greenberg and Waldrop, 2008; Litt et al., 2001; Matthews et al., 2010). When these same systems were studied throughout long-term (> 10 years) repeated application of prescribed fire, delayed speciesspecific responses became apparent (Greenberg et al., 2017) and reptile communities became indistinguishable with those present in sites used as a reference condition (Steen et al., 2013). Differences we found in reptile community structure may become more pronounced following repeated prescribed fires over time, as vegetation structure in hardwood forests does not typically respond drastically to the application of one or two fires (Franklin et al., 2003; Schwilk et al., 2009). Perry et al. (2009 and 2012) examined the differences in herpetofaunal community structure between restored fire-maintained pine-woodlands and unrestored controls and found that differences in vegetation structure and time since burn influenced herpetofaunal abundances, with many species being more abundant in burned woodlands compared to fire suppressed controls. Our results suggest that the differences in reptile community structure we observed are likely to become more pronounced if burning continues at LBL.

We saw a positive trend in overall squamate abundances in prescribed burn sites, but no trend in overall lizard abundances, obscuring the species-specific impacts that changes in vegetation structure may yield. Although other studies have reported higher lizard abundances in frequently disturbed areas (Greenberg and Waldrop, 2008; Langford et al., 2007; McLeod and Gates, 1998; Mushinsky, 1985; Perry et al., 2009), species-specific responses may not reflect differences in



Fig. 6. Comparisons of relative abundances (animals captured/number of "fence nights [FN]") of commonly captured reptile species in burned and unburned areas. Fires were applied in 2007 and 2010 prior to sampling. Bars are means of catch-per-unit-effort of each treatment within a year, and error bars are standard error. Single asterisks indicate species for which a significant year effect was found using GLM analysis, double asterisks indicate both a significant year and site type (burned vs. unburned) effect.



Fig. 7. Comparisons of relative abundances (animals captured/number of "fence nights [FN]") for commonly captured amphibian species in burned and unburned areas. Fires were applied in 2007 and 2010 prior to sampling. Bars are means of catch-per-unit-effort at each sampling array, error bars are standard error. Single asterisks indicate species for which a significant year effect was found using GLM analysis, double asterisks indicate both a significant year and site type (burned vs. unburned) effect.

#### Table 1

Total individual captures (not including recaptures) and results (corrected p-values) of generalized linear mixed models comparing site type and year on the abundances of commonly captured reptile and amphibian species at Land Between the Lakes National Recreation Area, Trigg County, Kentucky, USA, 2011–2012 and 2015–2016.

	Total Captures	Site Type (burned vs. unburned)	Year
Reptilia, Reptiles	1907	0.08	< 0.001
Serpentes, Snakes	557	0.003	< 0.001
Coluber constrictor, North American Racer	128	0.01	< 0.01
Diadophis punctatus, Ring-necked Snake	118	< 0.01	< 0.01
Lacertilia, Lizards	1329	0.51	< 0.001
Plestiodon fasciatus, Common Five-lined skink	379	0.48	< 0.001
Plestiodon laticeps, Broad-headed Skink	144	0.71	< 0.001
Scincella lateralis, Little Brown Skink	365	0.1	< 0.001
Sceloporus undulatus, Eastern Fence Lizard	410	0.04	< 0.001
Amphibia, Amphibians	5986	0.03	< 0.001
Anurans, Frogs and Toads	5384	0.04	< 0.001
Anaxyrus sp., American/Fowler's Toads	4438	0.02	< 0.001
Gastrophryne carolinensis, Eastern Narrow-mouthed Toad	229	0.67	< 0.001
Hyla chrysoscelis, Cope's Grey Treefrog	125	0.72	< 0.001
Lithobates clamitans, Green Frog	289	< 0.01	0.02
Lithobates sphenocephalus, Southern Leopard Frog	110	0.1	0.01
Caudata, Salamanders	602	0.1	< 0.001
Notophthalmus viridescens, Eastern Newt	238	< 0.001	< 0.001
Plethodon glutinosus, Northern Slimy Salamander	108	0.03	0.04

abundances of higher taxonomic groupings. We found higher abundances of the eastern fence lizard in burned sites, but no differences in abundances of the three other most commonly occurring lizard species (common five-lined skink, broad-headed skink, and little brown skink). Lizards associated with open-canopy environments with higher environmental temperatures, such as eastern fence lizards and the sixlined racerunner (Aspidoscelis sexlineata), are often in greater abundance in areas receiving intensive management practices such as prescribed fire and tree thinning (Matthews et al., 2010; Mushinsky, 1985; Perry et al., 2009; Ruthven et al., 2008; Steen et al., 2013; Sutton et al., 2013). Our examination of the relationship of abundances of eastern fence lizards and vegetation characteristics indicates a preference for landscapes with features maintained by frequent disturbances (reduced tree density, increased woody and herbaceous growth), similar to findings of other studies (Perry et al., 2009; Sutton et al., 2013), perhaps reflecting enhanced thermoregulatory opportunities or an increase in preferred prey items.

Our results indicate that prescribed fire may have a negative impact on abundances of the little brown skink, a leaf litter specialist, due to reduction in leaf litter and canopy cover. Others have suggested that this species may have reduced abundance in frequently burned areas (Steen et al., 2013; Wilgers and Horne, 2006), though the impacts may be short lived (Sutton et al., 2013), or have a positive influence on abundances (Perry et al., 2009); this species likely has a wide range of tolerance for vegetation structure over its wide distribution. We found no impacts of two prescribed fires on the two species of commonly captured *Plestiodon* skinks, likely reflecting the generalist nature of these species. Findings of other studies (Cantrell et al., 2013; Greenberg et al., 2016; Matthews et al., 2010; Perry et al., 2009; Sutton et al., 2013) suggest that abundance and recruitment of *Plestiodon* may benefit from disturbances to eastern forests, potentially through the creation of a more heterogeneous thermal environment.

Species-specific responses drove the differences that we observed in overall snake abundances. Our most commonly captured snake, the North American racer, was found in higher abundances in burned plots. The racer is an active foraging diurnal species and tends to use habitat features (new plant growth, low canopy cover) associated with edge and burned habitats (Carfagno and Weatherhead, 2006; Howey et al., 2016; Plummer and Congdon, 1994). Forest disturbance through prescribed fire or basal area reduction (vegetative thinning) is generally believed to have a positive or neutral impact on racers, with studies either showing increased abundance in managed areas (Cantrell et al., 2013; Sutton et al., 2013), or no impact of fire overall (Perry et al., 2009). Caution should be taken in interpreting differences in relative abundances of racers, as differences in habitat use (Howev et al., 2016) and time since burn (Cavitt, 2000; Perry et al., 2012) may influence the observed abundances of this animal when monitored through passive sampling. We found associations between other commonly captured large-bodied colubrids (eastern black kingsnake [Lampropeltis nigra], eastern milksnake [Lampropeltis triangulum], and eastern hog-nosed snake [Heterodon platirhinos]) and open vegetation structure (understory tree distance, herbaceous growth; Fig. 4), supporting other findings that these species are associated with more open vegetation structure (Perry et al., 2009; Sutton et al., 2013). Conversely, we found no strong vegetation association for eastern copperheads and common gartersnake, though the position of these species in the NMDS suggests they use cooler microhabitats with more canopy and litter cover (Cantrell et al., 2013; Perry et al., 2009).

Our finding of higher ring-necked snake abundance in burned areas is unusual in that no previous studies found a similar response for this species, though other studies in eastern hardwood systems typically did not capture enough individuals to conduct statistical analysis of abundances (Greenberg et al., 2016; Matthews et al., 2010; Sutton et al., 2013). A study in the tallgrass prairie of Kansas found that ring-necked snakes were most abundant in long-term unburned areas (Wilgers and Horne, 2006), and the species was found to disappear from areas burned frequently in the Florida sandhills (Steen et al., 2013). Cantrell et al. (2013) found ring-necked snakes to be associated with vegetation structures more common in disturbed areas (herbaceous cover), corroborating associations we found in a similar oak-dominated system. Small bodied litter-dwelling snakes are often negatively associated with frequent fire (Steen et al., 2013; Wilgers and Horne, 2006), and heavy disturbances (Todd and Andrews, 2008). We observed no strong patterns in relative abundances of other small snake species, although Dekay's brownsnake and red-bellied snake were associated with litter depth, eastern wormsnake associated with coarse woody debris, and smooth earthsnake associated with less understory. Small snake species can provide important ecosystem functions as links in food webs (Ernst and Ernst, 2003; Willson and Winne, 2016) and future studies should seek to better understand the ecology of this often overlooked group, especially with respect to forest management.

Overall amphibian, anuran, and salamander abundances showed trends of higher abundance in unburned areas than burned areas, and many of these responses were likely not due to prescribed fire, but rather due to the proximity of breeding wetlands in relation to our sampling arrays. Both Anaxyrus species and eastern newts have a fully terrestrial life stage and are known to be common in frequently disturbed and xeric habitats (Dodd Jr., 2013; Petranka, 1998) and studies have shown positive or neutral short-term responses of these species to fire and other open-habitat management (Cantrell et al., 2013; Greenberg et al., 2016; Matthews et al., 2010; Perry et al., 2009; Sutton et al., 2013). As we saw no strong relationship between these species and any measured vegetation characteristics, the differences we observed in Anaxyrus and eastern newts among treatments and years were likely due to differences in breeding locations and year-to-year breeding success, as annual abundances of these species can vary widely (Semlitsch et al., 1996). Although all of our arrays were established near intermittent streams, differing hydroperiods in these streams and other temporary wetlands nearby likely influenced the amphibian communities both across treatments and years. Higher abundances of

green frogs in burned areas was likely driven by the presence of permanent artificial ponds close to sampling arrays in burn units, though this species has been shown to tolerate clearcuts (Patrick et al., 2006). Sutton et al. (2013) suggested that location and varying hydroperiods of breeding sites was likely related to amphibian captures in upland areas, and it has been demonstrated that stochastic weather events can heavily influence amphibian movement patterns (Todd and Winne, 2006). Due to the variability of rainfall throughout sampling, and the potential that rain events far removed from sampling periods likely influenced breeding success of amphibians (e.g. drought conditions during April 2012 and heavy rains in spring 2015 likely influenced hydroperiod of amphibian breeding wetlands), we could not account for weather effects through our statistical models. Changes in vegetative structure may alter the permeability of areas to amphibian movements, potentially influencing capture rates (Graeter et al., 2008; Popescu and Hunter Jr., 2011). Some of our aquatic-breeding amphibian abundance estimates may have been biased by these factors-our sampling was limited to spring and summer and likely missed some amphibian migrations to and from breeding ponds. We observed no changes in abundances of other aquatic-breeding amphibian species in response to the application of fire, suggesting that there are only modest impacts of low-intensity prescribed fire on the preferred microhabitats of these species.

Often utilized as indicators of forest health, Plethodontid salamanders have received considerable attention with respect to potential negative impacts of land management schemes that create open vegetation structure, such as prescribed fire, due to loss of preferred cool and moist microhabitats (Homyack and Haas, 2009; Karraker and Welsh, 2006; Knapp et al., 2003; O'Donnell et al., 2015). We saw a trend of decreasing abundances five and six years after the last fire in northern slimy salamander in burned sites. Plethodon salamander populations are often of concern with respect to prescribed fire because of their fully terrestrial life cycle (Feder, 1983; Petranka, 1998). Treatments intended to restore more open canopy ecosystems often show no short-term decline of Plethodontid salamanders (Cantrell et al., 2013; Ford et al., 2010; Greenberg and Waldrop, 2008; Raybuck et al., 2015), but studies examining long-term impacts of management techniques have demonstrated that it may take several years for population declines to become apparent, especially when fires are repeated (Greenberg et al., 2016; Homyack and Haas, 2009; Matthews et al., 2010). Complicating our understanding of these responses is that changes to microhabitat structure can alter patterns of Plethodon surface activity, and therefore alter detectability-Plethodon albagula (a similar large-bodied Plethodontid) was found to be less surface active yet travel farther distances in areas recently burned (O'Donnell et al., 2016). This change in activity may account for the higher relative abundances we observed of northern slimy salamander in the two years following the burn when compared to five and six years post-burn, reflecting a potentially impacted population.

# 5. Conclusion

Our results provide insight into potential impacts of restoring historic vegetation structural conditions on reptile and amphibian communities. The gradient in vegetative characteristics we observed appears to be influencing the community structure of reptiles, while not appreciably impacting community structure of amphibians. Reptile community shifts were driven by taxa-specific responses to changes in vegetative structure, aligning with taxa-specific microhabitat preferences created by application of prescribed fire. As habitat degradation due to lack of disturbance regimes has been implicated in reptile and amphibian declines, understanding these responses is important when planning and implementing land management practices to preserve the historic biodiversity of the hardwood systems of the Southeastern United States.

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## **Conflict of interest**

None.

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Appendix 1.	. Total mean and stand	ard deviation for	vegetative structure	characteristics measured	ed in burned and	unburned plo	ots across
sampling yea	rs.						

	2011		2012		2015		2016		Total
Vegetation Characteristic	Burn	Unburned	Burn	Unburned	Burn	Unburned	Burn	Unburned	
Canopy (%) OSTDst (m) USTDst (m) CWD (%) Forb (%) Grass (%) Litter (%) Moss (%) Rock (%) Vine (%) Bare (%)	$\begin{array}{c} 0.78 \ \pm \ 0.12 \\ 2.69 \ \pm \ 2.09 \\ 3.51 \ \pm \ 3.14 \\ 0.16 \ \pm \ 0.08 \\ 0.06 \ \pm \ 0.07 \\ 0.09 \ \pm \ 0.10 \\ 0.42 \ \pm \ 0.17 \\ 0.02 \ \pm \ 0.07 \\ 0.02 \ \pm \ 0.07 \\ 0.02 \ \pm \ 0.09 \\ 0.06 \ \pm \ 0.10 \\ 0.06 \ \pm \ 0.10 \end{array}$	$\begin{array}{c} 0.89 \ \pm \ 0.06 \\ 2.27 \ \pm \ 1.32 \\ 1.48 \ \pm \ 0.90 \\ 0.17 \ \pm \ 0.09 \\ 0.04 \ \pm \ 0.06 \\ 0.03 \ \pm \ 0.05 \\ 0.54 \ \pm \ 0.19 \\ 0.04 \ \pm \ 0.08 \\ 0.01 \ \pm \ 0.03 \\ 0.04 \ \pm \ 0.03 \\ 0.04 \ \pm \ 0.08 \\ 0.05 \ \pm \ 0.09 \end{array}$	$\begin{array}{c} 0.79 \ \pm \ 0.19 \\ 3.94 \ \pm \ 2.78 \\ 3.35 \ \pm \ 2.19 \\ 0.10 \ \pm \ 0.11 \\ 0.04 \ \pm \ 0.08 \\ 0.66 \ \pm \ 0.20 \\ 0.01 \ \pm \ 0.20 \\ 0.01 \ \pm \ 0.07 \\ 0.01 \ \pm \ 0.04 \\ 0.04 \ \pm \ 0.04 \\ 0.04 \ \pm \ 0.01 \end{array}$	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	$\begin{array}{c} 0.76 \ \pm \ 0.16 \\ 2.94 \ \pm \ 1.31 \\ 1.76 \ \pm \ 1.08 \\ 0.03 \ \pm \ 0.03 \\ 0.03 \ \pm \ 0.04 \\ 0.04 \ \pm \ 0.08 \\ 0.82 \ \pm \ 0.15 \\ 0.02 \ \pm \ 0.10 \\ 0.01 \ \pm \ 0.02 \\ 0.00 \ \pm \ 0.01 \\ 0.02 \ \pm \ 0.01 \end{array}$	$\begin{array}{c} 0.85 \ \pm \ 0.08 \\ 2.51 \ \pm \ 1.40 \\ 1.67 \ \pm \ 1.14 \\ 0.02 \ \pm \ 0.02 \\ 0.01 \ \pm \ 0.02 \\ 0.01 \ \pm \ 0.02 \\ 0.01 \ \pm \ 0.01 \\ 0.01 \ \pm \ 0.08 \\ 0.01 \ \pm \ 0.05 \\ 0.00 \ \pm \ 0.00 \\ 0.01 \ \pm \ 0.00 \\ 0.01 \ \pm \ 0.02 \end{array}$	$\begin{array}{c} 0.84 \ \pm \ 0.17 \\ 3.12 \ \pm \ 2.12 \\ 1.84 \ \pm \ 1.67 \\ 0.07 \ \pm \ 0.08 \\ 0.07 \ \pm \ 0.14 \\ 0.08 \ \pm \ 0.12 \\ 0.55 \ \pm \ 0.23 \\ 0.00 \ \pm \ 0.01 \\ 0.00 \ \pm \ 0.01 \\ 0.00 \ \pm \ 0.01 \\ 0.03 \ \pm \ 0.09 \\ 0.01 \ \pm \ 0.04 \end{array}$	$\begin{array}{c} 0.95 \ \pm \ 0.03 \\ 2.18 \ \pm \ 1.16 \\ 1.95 \ \pm \ 1.28 \\ 0.07 \ \pm \ 0.09 \\ 0.01 \ \pm \ 0.03 \\ 0.02 \ \pm \ 0.06 \\ 0.67 \ \pm \ 0.21 \\ 0.02 \ \pm \ 0.09 \\ 0.01 \ \pm \ 0.02 \\ 0.06 \ \pm \ 0.14 \\ 0.02 \ \pm \ 0.05 \end{array}$	$\begin{array}{c} 0.85 \ \pm \ 0.11 \\ 2.66 \ \pm \ 1.58 \\ 2.26 \ \pm \ 1.67 \\ 0.08 \ \pm \ 0.07 \\ 0.03 \ \pm \ 0.06 \\ 0.04 \ \pm \ 0.07 \\ 0.64 \ \pm \ 0.19 \\ 0.02 \ \pm \ 0.06 \\ 0.01 \ \pm \ 0.05 \\ 0.04 \ \pm \ 0.08 \\ 0.05 \ \pm \ 0.10 \end{array}$
Woody (%) LtrDpth(cm)	$0.06 \pm 0.10$ $0.10 \pm 0.08$ $1.59 \pm 0.81$	$0.05 \pm 0.09$ $0.09 \pm 0.09$ $2.02 \pm 0.90$	$0.04 \pm 0.11$ $0.14 \pm 0.15$ $3.48 \pm 1.74$	$0.04 \pm 0.11$ $0.09 \pm 0.11$ $4.18 \pm 1.99$	$0.02 \pm 0.08$ $0.03 \pm 0.02$ $2.71 \pm 1.49$	$0.00 \pm 0.02$ $0.02 \pm 0.03$ $3.10 \pm 1.05$	$0.01 \pm 0.04$ $0.18 \pm 0.18$ $2.82 \pm 1.00$	$0.02 \pm 0.05$ $0.12 \pm 0.13$ $3.21 \pm 1.12$	$0.05 \pm 0.10$ $0.08 \pm 0.08$ $2.80 \pm 1.30$

Appendix 2. . Total reptile captures in drift fence arrays at land between the Lakes National Recreation Area, Trigg Co. Kentucky, USA. 2010, 2013, and 2014 were not used in any analysis. Numbers in parentheses represent recaptures. Total fence nights (FN) are indicated below year. Species with an \* were observed outside of standardized sampling and not used in analyses. Total captures only include years used in analyses.

	2010 [164 FN]	2011 [685 FN]	2012 [400 FN]	2013 [58 FN]	2014 [176 FN]	2015 [352 FN]	2016 [800 FN]	Total [2237 FN]
	111	111	INJ	111]	111	111	110]	111
Reptilia, Reptiles	229(15)	706(19)	540(11)	56(3)	68(7)	142(16)	715(150)	2103(196)
Squamata, Squamates	228(14)	701(19)	531(10)	53(3)	65(7)	138(16)	710(149)	2080(194)
Serpentes, Snakes	67(3)	201(3)	154(5)	13(0)	17(1)	41(2)	175(4)	571(14)
Agkistrodon contortrix, Eastern copperhead	5(0)	38(0)	17(0)	2(0)	1(0)	4(0)	12(0)	71(0)
<i>Carphophis amoenus</i> , Common Wormsnake	12(1)	14(0)	6(0)	6(0)	0	8(0)	9(1)	37(1)
Cemophora coccinea, Scarletsnake	0	2(0)	0	0	0	0	0	2(0)
Coluber constrictor, North American	7(0)	40(1)	45(1)	1(0)	4(0)	9(1)	39(2)	133(5)
Racer								
Crotalus horridus, Timber Rattlesnake	1(0)	4(0)	1(0)	0	0	0	0	5(0)
Diadophis punctatus, Ring-necked Snake	29(2)	40(1)	35(0)	0	5(0)	7(0)	38(0)	120(2)
Heterodon platirhinos, Eastern Hog- nosed Snake	2(0)	7(0)	8(2)	0	0	3(0)	9(0)	27(2)
Lampropeltis elapsoides, Scarlet Kingsnake	0	1(0)	1(0)	0	0	0	2(0)	4(0)
Lampropeltis nigra, Black Kingsnake	1(0)	8(1)	3(1)	0	1(0)	3(1)	6(0)	20(3)
Lampropeltis triangulum, Eastern Milksnake	1(0)	12(0)	8(0)	1(0)	1(0)	1(0)	4(0)	25(0)

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	Nerodia erythrogaster, Plain-bellied	0	1(0)	1(0)	0	*	*	1(0)	3(0)
		0	1(0)	1(0)	0	0	0	0	0(0)
	Werodia rhombifer, Diamond-backed Watersnake	0	1(0)	1(0)	0	0	0	0	2(0)
	Nerodia sipedon, Common Watersnake	0	1(0)	2(1)	0	0	0	0	3(1)
	Opheodrys aestivus, Rough Greensnake	0	*	*	0	0	0	1(0)	1(0)
	Pantherophis spiloides, Gray Ratsnake	1(0)	3(0)	1(0)	0	0	*	*	4(0)
	Storeria dekayi, Dekay's Brownsnake	3(0)	1(0)	6(0)	0	0	0	4(0)	11(0)
	Storeria occipitomaculata, Red-bellied	3(0)	11(0)	5(0)	0	2(1)	2(0)	27(0)	45(0)
	Slicke	0	0	0	0	0	*	2(0)	2(0)
	Snake	0	0	0	0	0		3(0)	3(0)
	Thamnophis sirtalis, Common	1(0)	16(0)	9(0)	3(0)	2(0)	3(0)	13(1)	41(1)
	Gartersnake								
	Virginia valeriae, Smooth Earthsnake	1(0)	1(0)	5(0)	0	1(0)	1(0)	7(0)	14(0)
La	certilia, Lizards	161(11)	500(16)	377(5)	40(3)	48(6)	97(14)	535(1 4 5)	1509(180)
La	<b>certilia, Lizards</b> Aspidoscelis sexlineata, Six-lined	161(11) 0	500(16) 0	377(5) 0	40(3) 0	48(6) 0	97(14) 0	535(1 4 5) *	1509(180) *
La	<b>certilia, Lizards</b> A <i>spidoscelis sexlineata</i> , Six-lined Racerunner	161(11) 0	500(16) 0	377(5) 0	40(3) 0	48(6) 0	97(14) 0	535(1 4 5) *	1509(180) *
La	<b>certilia, Lizards</b> Aspidoscelis sexlineata, Six-lined Racerunner Plestiodon fasciatus, Common Five-lined skink	161(11) 0 39(1)	500(16) 0 173(6)	377(5) 0 91(3)	40(3) 0 6(0)	48(6) 0 9(1)	97(14) 0 41(10)	535(1 4 5) * 138(55)	1509(1 8 0) * 443(64)
La	<b>certilia, Lizards</b> Aspidoscelis sexlineata, Six-lined Racerunner Plestiodon fasciatus, Common Five-lined skink Plestiodon inexpectatus, Southeastern	161(11) 0 39(1) 0	500(16) 0 173(6) 0	377(5) 0 91(3) 0	40(3) 0 6(0)	48(6) 0 9(1) 0	97(14) 0 41(10) 0	535(1 4 5) * 138(55) 1(0)	1509(1 8 0) * 443(64) 1(0)
La	<b>certilia, Lizards</b> Aspidoscelis sexlineata, Six-lined Racerunner Plestiodon fasciatus, Common Five-lined skink Plestiodon inexpectatus, Southeastern Five-lined Skink	161(11) 0 39(1) 0	500(16) 0 173(6) 0	377(5) 0 91(3) 0	40(3) 0 6(0) 0	48(6) 0 9(1) 0	97(14) 0 41(10) 0	535(1 4 5) * 138(55) 1(0)	1509(1 8 0) * 443(64) 1(0)
La	<b>certilia, Lizards</b> Aspidoscelis sexlineata, Six-lined Racerunner Plestiodon fasciatus, Common Five-lined skink Plestiodon inexpectatus, Southeastern Five-lined Skink Plestiodon laticeps, Broad-headed Skink	161(11) 0 39(1) 0 26(5)	500(16) 0 173(6) 0 79(6)	377(5) 0 91(3) 0 33(0)	40(3) 0 6(0) 0 7(1)	48(6) 0 9(1) 0 2(0)	97(14) 0 41(10) 0 9(0)	535(1 4 5) * 138(55) 1(0) 44(15)	1509(1 8 0) * 443(64) 1(0) 165(21)
La	certilia, Lizards Aspidoscelis sexlineata, Six-lined Racerunner Plestiodon fasciatus, Common Five-lined skink Plestiodon inexpectatus, Southeastern Five-lined Skink Plestiodon laticeps, Broad-headed Skink Scincella lateralis, Little Brown Skink	161(11) 0 39(1) 0 26(5) 40(1)	500(16) 0 173(6) 0 79(6) 85(1)	377(5) 0 91(3) 0 33(0) 119(1)	40(3) 0 6(0) 0 7(1) 5(0)	48(6) 0 9(1) 0 2(0) 27(2)	97(14) 0 41(10) 0 9(0) 22(0)	535(1 4 5) * 138(55) 1(0) 44(15) 190(9)	1509(1 8 0) * 443(64) 1(0) 165(21) 376(11)
La	certilia, Lizards Aspidoscelis sexlineata, Six-lined Racerunner Plestiodon fasciatus, Common Five-lined skink Plestiodon inexpectatus, Southeastern Five-lined Skink Plestiodon laticeps, Broad-headed Skink Scincella lateralis, Little Brown Skink Sceloporus undulatus, Eastern Fence Lizard	161(11) 0 39(1) 0 26(5) 40(1) 56(4)	500(16) 0 173(6) 0 79(6) 85(1) 163(3)	377(5) 0 91(3) 0 33(0) 119(1) 134(1)	40(3) 0 6(0) 0 7(1) 5(0) 22(2)	48(6) 0 9(1) 0 2(0) 27(2) 10(3)	97(14) 0 41(10) 0 9(0) 22(0) 25(4)	535(1 4 5) * 138(55) 1(0) 44(15) 190(9) 162(66)	1509(1 8 0) * 443(64) 1(0) 165(21) 376(11) 484(74)
La	certilia, Lizards Aspidoscelis sexlineata, Six-lined Racerunner Plestiodon fasciatus, Common Five-lined skink Plestiodon inexpectatus, Southeastern Five-lined Skink Plestiodon laticeps, Broad-headed Skink Scincella lateralis, Little Brown Skink Sceloporus undulatus, Eastern Fence Lizard studines, Turtles	161(11) 0 39(1) 0 26(5) 40(1) 56(4) 1(1)	500(16) 0 173(6) 0 79(6) 85(1) 163(3) 5(0)	377(5) 0 91(3) 0 33(0) 119(1) 134(1) 9(1)	40(3) 0 6(0) 0 7(1) 5(0) 22(2) 3(0)	48(6) 0 9(1) 0 2(0) 27(2) 10(3) 3(0)	97(14) 0 41(10) 0 9(0) 22(0) 25(4) 4(0)	535(1 4 5) * 138(55) 1(0) 44(15) 190(9) 162(66) 5(1)	1509(1 8 0) * 443(64) 1(0) 165(21) 376(11) 484(74) 23(2)
La	certilia, Lizards Aspidoscelis sexlineata, Six-lined Racerunner Plestiodon fasciatus, Common Five-lined skink Plestiodon inexpectatus, Southeastern Five-lined Skink Plestiodon laticeps, Broad-headed Skink Scincella lateralis, Little Brown Skink Sceloporus undulatus, Eastern Fence Lizard studines, Turtles Sternotherus odoratus, Eastern Musk Turtle	161(11) 0 39(1) 0 26(5) 40(1) 56(4) 1(1) 0	500(16) 0 173(6) 0 79(6) 85(1) 163(3) 5(0) 0	377(5) 0 91(3) 0 33(0) 119(1) 134(1) 9(1) 1(0)	40(3) 0 6(0) 0 7(1) 5(0) 22(2) 3(0) 0	48(6) 0 9(1) 0 2(0) 27(2) 10(3) 3(0) 0	97(14) 0 41(10) 0 9(0) 22(0) 25(4) 4(0) 0	535(1 4 5) * 138(55) 1(0) 44(15) 190(9) 162(66) 5(1) 0	1509(1 8 0) * 443(64) 1(0) 165(21) 376(11) 484(74) 23(2) 1(0)
La	certilia, Lizards Aspidoscelis sexlineata, Six-lined Racerunner Plestiodon fasciatus, Common Five-lined skink Plestiodon inexpectatus, Southeastern Five-lined Skink Plestiodon laticeps, Broad-headed Skink Scincella lateralis, Little Brown Skink Sceloporus undulatus, Eastern Fence Lizard studines, Turtles Sternotherus odoratus, Eastern Musk Turtle Terrapene carolina, Eastern Box Turtle	161(11) 0 39(1) 0 26(5) 40(1) 56(4) 1(1) 0 1(1)	500(16) 0 173(6) 0 79(6) 85(1) 163(3) 5(0) 0 5(0)	377(5) 0 91(3) 0 33(0) 119(1) 134(1) 9(1) 1(0) 8(1)	40(3) 0 6(0) 0 7(1) 5(0) 22(2) 3(0) 0 3(0)	48(6) 0 9(1) 0 2(0) 27(2) 10(3) 3(0) 0 3(0)	97(14) 0 41(10) 0 9(0) 22(0) 25(4) 4(0) 0 4(0)	535(1 4 5) * 138(55) 1(0) 44(15) 190(9) 162(66) 5(1) 0 5(1)	1509(1 8 0) * 443(64) 1(0) 165(21) 376(11) 484(74) 23(2) 1(0) 22(2)

Appendix 3. . Total amphibian captures at land between the Lakes National Recreation Area, Kentucky, USA. 2010, 2013, and 2014 were not used in any analysis. Numbers in parentheses represent recaptures. Total fence nights (FN) are indicated below year. Total captures only include years used in analyses.

	2010 [164 FN]	2011 [685 FN]	2012 [400 FN]	2013 [58 FN]	2014 [176 FN]	2015 [352 FN]	2016 [800 FN]	Total [2237) FN]
Amphibia, Amphibians	538(18)	1059(3)	515(0)	188(8)	207(10)	1852(33)	2749(153)	6175(189)
Anurans, Frogs and Toads	502(18)	925(3)	439(0)	186(8)	152(10)	1802(32)	2405(152)	5571(187)
Acris crepitans, Northern Cricket Frog	1(0)	2(0)	5(0)	3(0)	1(0)	1(0)	3(0)	11(0)
Anaxyrus americanus, American Toad	334(11)	397(0)	133(0)	96(4)	106(7)	287(10)	960(56)	1777(66)
Anaxyrus fowleri, Fowler's Toad	60(6)	300(1)	223(0)	46(4)	31(3)	900(3)	740(93)	2038(97)
Anaxyrus spp., Unknown toads	0	1(0)	2(0)	13(0)	1(0)	499(15)	299(0)	801(15)
Gastrophyne carolinensis, Eastern	13(0)	27(0)	7(0)	11(0)	6(0)	17(0)	179(1)	230(1)
Narrow-mouthed Toad								
Hyla chrysoscelis, Cope's Grey Treefrog	16(0)	68(0)	31(0)	1(0)	0	3(0)	24(1)	126(1)
Hyla cinerea, Green Treefrog	1(0)	6(0)	9(0)	1(0)	0	0	0	15(0)
Lithobates catesbeianus, American Bullfrog	0	0	1(0)	1(0)	1(0)	3(1)	11(0)	15(1)
Lithobates clamitans, Green Frog	35(0)	67(2)	22(0)	3(0)	0	63(3)	143(1)	295(6)
Lithobates sphenocephalus, Southern Leopard Frog	42(1)	45(0)	3(0)	8(0)	5(0)	28(0)	33(0)	110(0)
Pseudacris crucifer, Spring Peeper	0	8(0)	0	0	1(0)	1(0)	1(0)	10(0)
Pseudacris feriarum, Upland Chorus Frog	0	4(0)	3(0)	3(0)	0	0	11(0)	18(0)
Scaphiopus holbrookii, Eastern Spadefoot	0	0	0	0	0	0	1(0)	1(0)
Caudata, Salamanders	36(0)	134(0)	76(0)	2(0)	55(0)	50(1)	344(1)	604(2)
Ambystoma maculatum, Spotted Salamander	0	14(0)	7(0)	1(0)	45(0)	6(0)	27(0)	54(0)
Ambystoma opacum, Marbled Salamander	5(0)	31(0)	43(0)	1(0)	3(0)	2(0)	38(1)	114(1)
Ambystoma texanum, Small-mouthed Salamander	0	4(0)	0	0	0	0	0	4(0)

<i>Eurycea cirrigera</i> , Southern Two-lined Salamander	0	0	0	0	0	0	1(0)	1(0)
<i>Eurycea longicauda</i> , Long-tailed Salamander	6(0)	15(0)	2(0)	0	0	3(0)	36(1)	56(1)
Eurycea lucifuga, Cave Salamander	0	1(0)	0	0	1(0)	0(0)	1(0)	2(0)
Notophthalmus viridescens, Eastern Newt	5(0)	15(0)	4(0)	0	1(0)	36(1)	185(1)	240(2)
<i>Plethodon dorsalis</i> , Northern Zigzag Salamander	0	21(0)	0	0	0	0	0	21(0)
<i>Plethodon glutinosis</i> , Northern Slimy Salamander	20(0)	33(0)	19(0)	0	5(0)	3(0)	53(0)	108(0)
Pseudotriton ruber, Red Salamander	0	0	1(0)	0	0	0	3(0)	4(0)

# References

- Alford, R.A., Richards, S.J., 1999. Global amphibian declines: a problem in applied ecology. Annu. Rev. Ecol. Syst. 30, 133–165. http://dx.doi.org/10.1146/annurev. ecolsys.30.1.133.
- Anderson, M.J., 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62, 245–253. http://dx.doi.org/10.1111/j.1541-0420.2005.00440.x.
- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral. Ecol. 26, 32–46. http://dx.doi.org/10.1111/j.1442-9993.2001. tb00081.x.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Statisical Softw. 67, 1–48.
- Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple controlling the false discovery rate: a practical and powerful approach to multiple testing. J. R. Stat. Soc. 57, 289–300. http://dx.doi. org/10.2307/2346101.
- Borcard, D., Gillet, F., Legendre, P., 2011. Numerical Ecology with R, Springer. New York, NY. https://doi.org/10.1017/CBO9781107415324.004.
- Bowman, M.F., Somers, K.M., 2005. Considerations when using the reference condition approach for bioassessment of freshwater ecosystems. Water Qual. Res. J. Canada 40, 347–360. http://dx.doi.org/10.1111/j.1365-2427.2004.01295.x.
- Brown, W.S., Parker, W.S., 1976. A ventral scale clipping system for permanently marking snakes (Reptilia, Serpentes). J. Herpetol. 10, 247–249. http://dx.doi.org/10.2307/ 1562986.
- Cagle, F.R., 1939. A system of marking turtles for future identification. Copeia 1939, 170–173. http://dx.doi.org/10.2307/1436818.
- Cantrell, A.W., Wang, Y., Schweitzer, C.J., Greenberg, C.H., 2013. Short term response of herpetofauna to oak regeneration treatments on the mid-Cumberland Plateau of southern Tennessee. For. Ecol. Manage. 295, 239–247. http://dx.doi.org/10.1016/j. foreco.2013.01.027.
- Cao, Y., Larsen, D.P., Thorne, R.S.-J., 2001. Rare species in multivariate analysis for bioassessment: some considerations. J. North Am. Benthol. Soc. 20, 144–153. http:// dx.doi.org/10.2307/1468195.
- Carfagno, G.L.F., Weatherhead, P.J., 2006. Intraspecific and interspecific variation in use of forest-edge habitat by snakes. Can. J. Zool. 84, 1440–1452. http://dx.doi.org/10. 1139/z06-124.
- Cavitt, J.F., 2000. Fire and a tallgrass prairie reptile community: effects on relative abundance and seasonal activity. J. Herpetol. 34, 12–20. http://dx.doi.org/10.2307/ 1565233.
- Chester, E.W., Fralish, J.S., 2002. Land Between the Lakes, Kentucky and Tennessee: four decades of Tennessee Valley Authority Stewardship. Austin Peay State University, Clarksville, TN.
- Clarke, K.R., Warwick, R.M., 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition, second ed. PRIMER-E. Plymouth, UK. Daubenmire, R., 1959. A canopy-coverage method of vegetational analysis. Northwest Sci. 33, 43.
- Davis, J.E., McRae, C., Estep, B.L., Barden, L.S., Matthews, J.F., 2002. Vascular flora of piedmont prairies: evidence from several prairie remnants. Castanea 67, 1–12. http://dx.doi.org/10.2307/4034311.
- Delcourt, P.A., Delcourt, H.R., Ison, C.R., Sharp, W.E., Gremillion, J., 1998. Prehistoric human use of fire, the eastern agricultural complex, and Appalachian oak-chestnut forests: paleoecology of Cliff Palace Pond. Kentucky. Am. Antiq. 63, 263–278. http:// dx.doi.org/10.1525/aa.1961.63.5.02a00100.
- Dodd Jr., C.K., 2013. Frogs of the United States and Canada: Volumes 1 and 2. Johns Hopkins University Press, Baltimore, MD.
- Driscoll, D.A., Smith, A.L., Blight, S., Maindonald, J., 2012. Reptile responses to fire and the risk of post-disturbance sampling bias. Biodivers. Conserv. 21, 1607–1625. http://dx.doi.org/10.1007/s10531-012-0267-5.
- Ernst, C.H., Ernst, E.M., 2003. Snakes of the United States and Canada. Smithsonian Institution Press, Washington D.C.
- Feder, M.E., 1983. Integrating the ecology and physiology of Plethodontid salamanders. Herpetologica 39, 291–310.
- Ford, W.M., Rodrigue, J.L., Rowan, E.L., Castleberry, S.B., Schuler, T.M., 2010. Woodland salamander response to two prescribed fires in the central Appalachians. For. Ecol. Manage. 260, 1003–1009. http://dx.doi.org/10.1016/j.foreco.2010.06.022.

Fox, J., Weisberg, S., 2011. An  $\{R\}$  companion to Applied Regression, Second Edition. Franklin, S.B., 1994. Late Pleistocene and Holocene vegetation history of Land Between the Lakes, Kentucky and Tennessee. Trans. Kentucky Acad. Sci. 55, 6-19.

- Franklin, S.B., Robertson, P.A., Fralish, J.S., 2003. Prescribed burning effects on upland < i > Quercus < i/ > forest structure and function. For. Ecol. Manage. 184, 315–335. http://dx.doi.org/10.1016/S0378-1127(03)00153-1.
- Franklin, S.B., Robertson, P.A., Fralish, J.S., Kettler, S.M., 1993. Overstory vegetation and successional trends of Land Between The Lakes. USA. Veg. Sci. 4, 509–520. http://dx. doi.org/10.2307/3236078.
- Gardner, T.A., Barlow, J., Peres, C.A., 2007. Paradox, presumption and pitfalls in conservation biology: the importance of habitat change for amphibians and reptiles. Biol. Conserv. 138, 166–179. http://dx.doi.org/10.1016/j.biocon.2007.04.017.
- Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.a., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S., Winne, C.T., 2000. The global decline of reptiles, déjà vu amphibians. Bioscience 50, 653–666.
- Gorman, T.A., Haas, C.A., Bishop, D.C., 2009. Factors related to occupancy of breeding wetlands by flatwoods salamander larvae. Wetlands 29, 323–329. http://dx.doi.org/ 10.1672/08-155.1.
- Graeter, G.J., Rothermel, B.B., Gibbons, J.W., 2008. Habitat selection and movement of pond-breeding amphibians in experimentally fragmented pine forests. J. Wildl. Manage. 72, 473–482. http://dx.doi.org/10.2193/2006-330.
- Greenberg, C.H., Moorman, C.E., Matthews-Snoberger, C.E., Waldrop, T.A., Simon, D., Heh, A., Hagan, D., 2017. Long-term herpetofaunal response to repeated fuel reduction treatments. J. Wildl. Manage. 1–13. http://dx.doi.org/10.1002/jwmg.21402.
- Greenberg, C.H., Moorman, C.E., Raybuck, A.L., Sundol, C., Keyser, T.L., Bush, J., Simon, D.M., Warburton, G.S., 2016. Reptile and amphibian response to oak regeneration treatments in productive southern Appalachian hardwood forest. For. Ecol. Manage. 377, 139–149. http://dx.doi.org/10.1016/j.foreco.2016.06.023.
- Greenberg, C.H., Seiboldt, T., Keyser, T.L., McNab, W.H., Scott, P., Bush, J., Moorman, C.E., 2018. Reptile and amphibian response to season of burn in an upland hardwood forest. For. Ecol. Manage. 409, 808–816. http://dx.doi.org/10.1016/j.foreco.2017. 12.016.
- Greenberg, C.H., Waldrop, T.A., 2008. Short-term response of reptiles and amphibians to prescribed fire and mechanical fuel reduction in a southern Appalachian upland hardwood forest. For. Ecol. Manage. 255, 2883–2893. http://dx.doi.org/10.1016/j. foreco.2008.01.064.
- Guyette, R.P., Stambaugh, M.C., Dey, D.C., Muzika, R.M., 2012. Predicting fire frequency with chemistry and climate. Ecosystems 15, 322–335. http://dx.doi.org/10.1007/ s10021-011-9512-0.
- Harper, C.A., Ford, W.M., Lashley, M.A., Moorman, C.E., Stambaugh, M.C., 2016. Fire effects on wildlife in the Central Hardwoods and Appalachian regions. USA. Fire Ecol. 12, 127–159. http://dx.doi.org/10.4996/fireecology.1202127.
- Homyack, J.A., Haas, C.A., 2009. Long-term effects of experimental forest harvesting on abundance and reproductive demography of terrestrial salamanders. Biol. Conserv. 142, 110–121. http://dx.doi.org/10.1016/j.biocon.2008.10.003.
- Howey, C.A.F., Dickinson, M.B., Roosenburg, W.M., 2016. Effects of a landscape disturbance on the habitat use and behavior of the black racer. Copeia 104, 853–863. http://dx.doi.org/10.1643/CE-15-373.

Hunter, W.C., Buehler, D., Canterbury, R., Confer, J., Hamel, P., 2001. Conservation of disturbance-dependent birds in eastern North America. Wildl. Soc. Bull. 29, 440–455.

- Karraker, N.E., Welsh, H.H., 2006. Long-term impacts of even-aged timber management on abundance and body condition of terrestrial amphibians in Northwestern California. Biol. Conserv. 131, 132–140. http://dx.doi.org/10.1016/j.biocon.2006. 02.013.
- Knapp, E.E., Estes, B.L., Skinner, C.N., 2009. Ecological effects of prescribed fire season: a literature review and synthesis for managers. Gen. Tech. Rep. no. PSW-GTR-224 1–80.
- Knapp, S.M., Haas, C.A., Harpole, D.N., Kirkpatrick, R.L., 2003. Initial effects of clearcutting and alternative silvicultural practices on terrestrial salamander abundance. Conserv. Biol. 17, 752–762. http://dx.doi.org/10.1046/j.1523-1739.2003.02061.x.
- Langford, G.J., Borden, J.A., Major, C.S., Nelson, D.H., 2007. Effects of prescribed fire on the herpetofauna of a southern Mississippi pine savanna. Herpetol. Conserv. Biol. 2, 135–143.
- Larrivée, M., Buddle, C.M., 2009. Diversity of canopy and understorey spiders in northtemperate hardwood forests. Agric. For. Entomol. 11, 225–237. http://dx.doi.org/10. 1111/j.1461-9563.2008.00421.x.
- Litt, A.R., Provencher, L., Tanner, G.W., Franz, R., 2001. Herpetofaunal responses to restoration treatments of longleaf pine sandhills in Florida. Restor. Ecol. 9, 462–474. http://dx.doi.org/10.1046/j.1526-100X.2001.94015.x.
- Matthews, C.E., Moorman, C.E., Greenberg, C.H., Waldrop, T.A., 2010. Response of

reptiles and amphibians to repeated fuel reduction treatments. J. Wildl. Manage. 74, 1301–1310. http://dx.doi.org/10.2193/2008-513.

McCune, B., Grace, J.R., 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon.

McIver, J.D., Stephens, S.L., Agee, J.K., Barbour, J., Boerner, R.E.J., Edminster, C.B., Erickson, K.L., Farris, K.L., Fettig, C.J., Fiedler, C.E., Haase, S., Hart, S.C., Keeley, J.E., Knapp, E.E., Lehmkuhl, J.F., Moghaddas, J.J., Otrosina, W., Outcalt, K.W., Schwilk, D.W., Skinner, C.N., Waldrop, T.A., Weatherspoon, C.P., Yaussy, D.A., Youngblood, A., Zack, S., 2013. Ecological effects of alternative fuel-reduction treatments: highlights of the National Fire and Fire Surrogate Study (FFS). Int. J. Wildl. Fire 22, 63–82. http://dx.doi.org/10.1071/WF11130.

McLeod, R.F., Gates, J.E., 1998. Response of herpetofaunal communities to forest cutting and burning at Chesapeake Farms. Maryland. Am. Midl. Nat. 139, 164–177. http:// dx.doi.org/10.1674/0003-0031.

McShea, W.J., Healy, W.M., Devers, P., Fearer, T., Koch, F.H., Stauffer, D., Waldon, J., 2007. Forestry matters: decline of oaks will impact wildlife in hardwood forests. J. Wildl. Manage. 71, 1717–1728. http://dx.doi.org/10.2193/2006-169.

Moorman, C.E., Russell, K.R., Greenberg, C.H., 2011. Reptile and amphibian response to hardwood forest management, in: Sustaining Young Forest Communities: Ecology and Management of Early Successional Habitats in the Central Hardwood Region, USA. Managing Forest Ecosystems. pp. 1–20. https://doi.org/10.1007/978-94-007-1620-9\_11.

Mushinsky, H.R., 1985. Fire and the Florida sandhill herpetofaunal community: with special attention to responses of *Cnemidophorus sexlineatus*. Herpetologica 41, 333–342.

Noss, R.F., 2013. Forgotten Grasslands of the South. Island Press, Washington D.C. Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and "mesophication" of forests in the eastern United States. Bioscience 58, 123–138.

O'Donnell, K.M., Thompson, F.R., Semlitsch, R.D., 2016. Prescribed fire alters surface activity and movement behavior of a terrestrial salamander. J. Zool. 298, 303–309. http://dx.doi.org/10.1111/jzo.12316.

O'Donnell, K.M., Thompson, F.R., Semlitsch, R.D., 2015. Prescribed fire and timber harvest effects on terrestrial salamander abundance, detectability, and microhabitat use. J. Wildl. Manage. 79, 766–775. http://dx.doi.org/10.1002/jwmg.884.

O'Hara, R.B., Kotze, D.J., 2010. Do not log-transform count data. Methods Ecol. Evol. 1, 118–122. http://dx.doi.org/10.1111/j.2041-210X.2010.00021.x.

Oksanen, J.F., 2015. Multivariate analysis of ecological communities in R: vegan tutorial. R Doc. http://dx.doi.org/10.1016/0169-5347(88)90124-3.

- Oksanen, J.F., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2017. Vegan: Community Ecology Package. < https://cran.r-project.org/package = vegan > .
- Patrick, D.A., Hunter, M.L., Calhoun, A.J.K., 2006. Effects of experimental forestry treatments on a Maine amphibian community. For. Ecol. Manage. 234, 323–332. http://dx.doi.org/10.1016/j.foreco.2006.07.015.Perry, R.W., Craig Rudolph, D., Thill, R.E., 2012. Effects of short-rotation controlled
- Perry, R.W., Craig Rudolph, D., Thill, R.E., 2012. Effects of short-rotation controlled burning on amphibians and reptiles in pine woodlands. For. Ecol. Manage. 271, 124–131. http://dx.doi.org/10.1016/j.foreco.2012.02.004.

Perry, R.W., Rudolph, D.C., Thill, R.E., 2009. Reptile and amphibian responses to restoration of fire-maintained pine woodlands. Restor. Ecol. 17, 917–927. http://dx. doi.org/10.1111/j.1526-100X.2009.00521.x.

Petranka, J.W., 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington D.C.

- Phillott, A.D., Skerratt, L.F., McDonald, K.R., Lemckert, F.L., Hines, H.B., Clarke, J.M., Alford, R.A., Speare, R., 2007. Toe-clipping as an acceptable method of identifying individual anurans in mark recapture studies. Herpetol. Rev. 38, 305–308.
- Plummer, M.V., Congdon, J.D., 1994. Radiotelemetric study of activity and movements of racers (*Coluber constrictor*) associated with a Carolina Bay in South-Carolina. Copeia 1994, 20–26. http://dx.doi.org/10.2307/1446666.
- Popescu, V.D., Hunter Jr., M.L., 2011. Clear-cutting affects habitat connectivity for a forest amphibian by decreasing permeability to juvenile movements. Ecol. Appl. 21, 1283–1295.
- Pyne, S.J., Andrews, P.L., Laven, R.D., 1996. Introduction to wildland fire, second ed. John Wiley & Sons Inc, New York, NY.

R Core Team, 2015. R: A Language and Environment for Statistical Computing.

Radke, N., Wester, D., Perry, G., Rideout-Hanzak, S., 2008. Short-term effects of prescribed fire on lizards in mesquite-ashe juniper vegetation in central Texas. Appl. Herpetol. 5, 281–292. http://dx.doi.org/10.1163/157075408785911039.

Raybuck, A.L., Moorman, C.E., Fritts, S.R., Greenberg, C.H., Deperno, C.S., Simon, D.M., Warburton, G.S., 2015. Do silvicultural practices to restore oaks affect salamanders in the short term? Wildlife Biol. 21, 186–194. http://dx.doi.org/10.2981/wlb.00076. Reinhert, H.K., 1984. Habitat separation between sympatric snake populations. Ecology 65, 478–486.

- Russell, K.R., Lear, D.H. Van, Guynn, D.C., 1999. Prescribed fire effects on herpetofauna: review and management implications. Wildl. Soc. Bull. 27, 374–384.
- Ruthven, D.C., Kazmaier, R.T., Janis, M.W., 2008. Short-term response of herpetofauna to various burning regimes in the south Texas Plains. Southwest. Nat. 53, 480–487. http://dx.doi.org/10.1894/WL-17.1.
- Schwilk, D.W., Keeley, J.E., Knapp, E.E., McIver, J., Bailey, J.D., Fettig, C.J., Fiedler, C.E., Harrod, R.J., Moghaddas, J.J., Outcalt, K.W., Skinner, C.N., Stephens, S.L., Waldrop, T.A., Yaussy, D.A., Youngblood, A., 2009. The national fire and fire surrogate study: effects of fuel reduction methods on forest vegetation structure and fuels. Ecol. Appl. 19, 285–304. http://dx.doi.org/10.1890/07-1747.1.
- Semlitsch, R.D., Scott, D.E., Pechmann, J.H.K., Gibbons, J.W., 1996. Structure and dynamics of an amphibian community: evidence from a 16-year study of a natural pond, in: Cody, M.L., Smallwood, J.A. (Eds.), Long-Term Studies of Vertebrate Communities. Academic Press, San Diego, pp. 217–248. https://doi.org/10.1016/ B978-012178075-3/50010-6.

Snyder, D.H., Scott, A.F., Zimmerer, E.J., Frymire, D.F., 2016. Amphibians and reptiles of Land Between the Lakes. University Press of Kentucky, Lexington.

- Soil Survey Staff, Natural Resources Conservation Service, U.S.D. of A., 2017. Web Soil Survey [WWW Document]. Web Soil Surv, URL https://websoilsurvey.sc.egov.usda.gov/App/HomePage.htm (accessed 11.11.17).
- Stambaugh, M.C., Guyette, R.P., Marschall, J.P., Dey, D.C., 2016. Scale dependence of oak woodland historical fire intervals: contrasting the barrens of Tennessee and cross timbers of Oklahoma. USA. Fire Ecol. 12, 65–84. http://dx.doi.org/10.4996/ fireecology.1202065.
- Stambaugh, M.C., Varner, J.M., Noss, R.F., Dey, D.C., Christensen, N.L., Baldwin, R.F., Guyette, R.P., Hanberry, B.B., Harper, C.A., Lindblom, S.G., Waldrop, T.A., 2015. Clarifying the role of fire in the deciduous forests of eastern North America: Reply to Matlack. Conserv. Biol. 29, 942–946. http://dx.doi.org/10.1111/cobi.12473.
- Steen, D.A., 2010. Snakes in the grass: secretive natural histories defy both conventional and progressive statistics. Herpetol. Conserv. Biol. 5, 183–188.
- Steen, D.A., Smith, L.L., Conner, L.M., Litt, A.R., Provencher, L., Hiers, J.K., Pokswinksi, S., Guyer, C., 2013. Reptile assemblage response to restoration of fire-suppressed longleaf pine sandhills. Ecol. Appl. 23, 148–158. http://dx.doi.org/10.1890/12-0197.1.

Sutton, W.B., Wang, Y., Schweitzer, C.J., 2013. Amphibian and reptile responses to thinning and prescribed burning in mixed pine-hardwood forests of northwestern Alabama. USA. For. Ecol. Manage. 295, 213–227. http://dx.doi.org/10.1016/j. foreco.2012.12.047.

Ter Braak, C.J.F., 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. Vegetatio 69, 69–77. http://dx.doi.org/10.1007/ BF00038688.

Todd, B.D., Andrews, K.M., 2008. Response of a reptile guild to forest harvesting. Conserv. Biol. 22, 753–761. http://dx.doi.org/10.1111/j.1523-1739.2008.00916.x.

Todd, B.D., Winne, C.T., 2006. Ontogenetic and interspecific variation in timing of movement and responses to climatic factors during migrations by pond-breeding amphibians. Can. J. Zool. 84, 715–722. http://dx.doi.org/10.1139/z06-054.

Todd, B.D., Winne, C.T., Willson, J.D., Gibbons, J.W., 2007. Getting the drift: examining the effects of timing, trap type and taxon on herpetofaunal drift fence surveys. Am. Midl. Nat. 158, 292–305. http://dx.doi.org/10.1674/0003-0031(2007) 158[292:GTDETE]2.0.CO;2.

Vander Yacht, A.L., Barrioz, S.A., Keyser, P.D., Harper, C.A., Buckley, D.S., Buehler, D.A., Applegate, R.D., 2017. Vegetation response to canopy disturbance and season of burn during oak woodland and savanna restoration in Tennessee. For. Ecol. Manage. 390, 187–202. http://dx.doi.org/10.1016/j.foreco.2017.01.029.

Waite, T.A., Campbell, L.G., 2006. Controlling the false discovery rate and increasing statistical power in ecological studies. Ecoscience 13, 439–442. http://dx.doi.org/10. 2980/1195-6860(2006) 13.

- Wilgers, D.J., Horne, E.A., 2006. Effects of different burn regimes on tallgrass prairie herpetofaunal species diversity and community composition in the Flint Hills, Kansas. J. Herpetol. 40, 73–84. http://dx.doi.org/10.1670/162-05A.1.
- Willson, J.D., Winne, C.T., 2016. Evaluating the functional importance of secretive species: a case study of aquatic snake predators in isolated wetlands. J. Zool. 298, 266–273. http://dx.doi.org/10.1111/jzo.12311.
- Wood, E.M., Pidgeon, A.M., Gratton, C., Wilder, T.T., 2011. Effects of oak barrens habitat management for Karner blue butterfly (*Lycaeides samuelis*) on the avian community. Biol. Conserv. 144, 3117–3126. http://dx.doi.org/10.1016/j.biocon.2011.10.010.