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ARTICLE

# Short-term response to season of burn by amphibians and reptiles in a Florida longleaf pine – wiregrass sandhill

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**Abstract:** We investigated how herpetofauna respond to burning and burn season in longleaf pine (*Pinus palustris* Mill.) sandhills by contrasting preburn species richness, diversity, and evenness and captures of six reptile and six amphibian species to the first (Y+1) or second (Y+2) year after burn or between dormant-season burns (DSB) and growing-season burns (GSB). Responses to burning overall or burn season were inconsistent among species; several showed no response, whereas others responded positively or negatively. Most responses were evident only in Y+1. Reptile species richness, diversity, and evenness responses were not detected. Amphibian richness increased after burning overall; diversity and evenness decreased more in GSB than in DSB in Y+1. Southern toad (*Anaxyrus terrestris* (Bonnaterre, 1789)) captures increased and Florida crowned snake (*Tantilla relicta* Telford, 1966) captures decreased following burns overall in Y+1. Ground skink (*Scincella lateralis* (Say in James, 1823)) captures increased more in DSB than GSB in Y+1. Florida gopher frog (*Lithobates capito* (LeConte, 1855)) and southeastern five-lined skink (*Plestiodon inexpectatus*; Taylor, 1932) captures increased, and oak toad (*Anaxyrus quercicus* (Holbrook, 1840)) decreased more in GSB than DSB in Y+2. Responses were likely due to changes in aboveground activity affecting captures or (for amphibians especially) annual variability in captures unrelated to burns. Our results indicated that reptiles and amphibians of sandhills are resilient to short-term effects of burning overall and burn season.

*Key words:* amphibians, dormant-season burns, growing-season burns, longleaf pine – wiregrass sandhills, prescribed fire, reptiles, sandhills, season of burn.

**Résumé :** Nous avons étudié de quelle façon l'herpétofaune réagit au brûlage et à la saison durant laquelle a lieu le brûlage dans les communautés de pin des marais (*Pinus palustris* Mill.) établies sur des collines sableuses. Nous avons comparé l'uniformité, la diversité et la richesse en espèces ainsi que les captures de six espèces de reptiles et six espèces d'amphibiens avant un brûlage et un ou deux ans après le brûlage. Nous avons aussi comparé les effets du brûlage durant la période de dormance (BPD) et du brûlage durant la saison de croissance (BSC). Dans l'ensemble, les réactions au brûlage ou au moment où il a été effectué ont varié selon l'espèce; plusieurs n'ont eu aucune réaction et d'autres ont réagi soit positivement, soit négativement. La plupart des réactions étaient évidentes seulement après un an. Aucune réaction de l'uniformité, de la diversité et de la richesse en espèces de reptiles n'a été détectée. La richesse des amphibiens a généralement augmenté après un brûlage; après un an, l'uniformité et la diversité avaient davantage diminué avec le BSC qu'avec le BPD. Les captures du crapaud criard (*Anaxyrus terrestris* (Bonnaterre, 1789)) ont augmenté et celles de la couleuvre couronnée de Floride (*Tantilla relicta* Telford, 1966) ont diminué un an après l'ensemble des brûlages. Dans l'année qui a suivi, les captures du scinque brun mineur (*Scincella lateralis* (Say in James, 1823)) ont davantage augmenté après un BPD qu'après un BSC. Les captures de la grenouille des terriers (*Lithobates capito* (LeConte, 1855)) et du scinque pentaligne du sud-est (*Plestiodon inexpectatus* Taylor, 1932) ont augmenté et celles du crapaud des chênes (*Anaxyrus quercicus* (Holbrook, 1840)) ont davantage diminué deux ans après le brûlage à la suite d'un BSC qu'à la suite d'un BPD. Les réactions étaient probablement dues aux changements dans l'activité au-dessus du sol qui influençaient les captures, ou (surtout dans le cas des amphibiens) à la variation annuelle des captures non reliée au brûlage. Nos résultats indiquent que les reptiles et les amphibiens des collines sableuses sont en général résilients face aux effets à court terme du brûlage et du moment où est effectué le brûlage. [Traduit par la Rédaction]

*Mots-clés :* amphibiens, brûlage durant la période de dormance, brûlage durant la saison de croissance, communautés de pin des marais et d'aristide des pinèdes établies sur des collines sableuses, brûlage dirigé, reptiles, collines sableuses, saison durant laquelle le brûlage a lieu.

## 1. Introduction

Many reptile and amphibian species are endemic to the endangered longleaf pine (*Pinus palustris* Mill.) – wiregrass (*Aristida stricta* Michx.) sandhill ecosystem (Means and Grow 1985). Longleaf pine once occupied 38 million hectares within the southeastern US Coastal Plain landscape, from Virginia to Texas (Frost 1993). Today, only 4% remains (USDA Forest Service 2019) due to development and conversion to pine plantation or other uses (Noss et al. 1995; Brockway et al. 2015), with much of the remaining habitat degraded by fragmentation and fire exclusion (Means and Grow 1985). Populations of many reptile and amphibian species characteristic of sandhills have declined accordingly, including some

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species of conservation concern such as sand skinks (*Plestiodon reynoldsii* (Stejneger, 1910)), gopher frogs (*Lithobates capito* (LeConte, 1855)), and striped newts (*Nothophthalmus perstriatus* (Bishop, 1941)) (Florida Fish and Wildlife Conservation Commission 2016).

Historically, frequent, low-intensity, landscape-level fires (Tanner et al. 2018) curtailed hardwood encroachment (Greenberg and Simons 1999), thereby maintaining low-density, open-canopy, uneven-aged longleaf pine forests with scattered or clumped midstory oaks (*Quercus* spp.) and a nearly continuous groundcover dominated by wiregrass and diverse herbaceous plants (Myers, 1990; Glitzenstein et al. 2012). Historically, during dry periods, fires burned through ephemeral ponds, reducing organic buildup and tree or shrub encroachment (Kirkman et al. 1999). Fires were most common during the growing season, ignited by lightning strikes associated with late spring and summer thunderstorms (Myers, 1990) and by Native Americans and (later) European settlers (Huffman 2006). Changes in policy and attitudes towards prescribed fire led to widespread fire suppression beginning in the 1930s (Frost 1993).

After decades of fire exclusion and consequent hardwood encroachment, forest managers and ecologists came to recognize that frequent burning was critical for reducing fuel loads for wildfire prevention and to restore and maintain the open canopy and groundcover structure required by the diverse, fire-adapted plant and animal species characteristic of the sandhills ecosystem. Initially, most forest managers burned during the dormant season (winter) due to drier fuels and to avoid nesting season for ground-nesting gamebirds such as Bobwhite Quail (*Colinus virginianus* (Linnaeus, 1758)) (Brennan et al. 1998). Subsequent research showed that growing-season (late spring–summer) burns promote flowering by wiregrass and several herbaceous species (Platt et al. 1988) and associated higher fire temperatures can more effectively top-kill hardwood trees (Robbins and Myers 1992). These findings led many forest managers to burn more during the growing season to better mimic the natural disturbance regime and potentially expedite ecosystem restoration (Brockway et al. 2015). Still, very little is known about how season of burning affects wildlife, especially reptile and amphibian species (Pilliod et al. 2003).

Direct, fire-related mortality of reptiles and amphibians is difficult to detect, and evidence is largely anecdotal (Russell et al. 1999). Anecdotal observations (Vogl 1973) or radio-tracking data (Humphries and Sisson 2012; Pitt et al. 2013) indicate that direct mortality is minimal due to avoidance behaviors such as burrowing in and under coarse woody material (Means and Campbell 1981; Pitt et al. 2013), burrowing underground (Pitt et al. 2013), finding refuge in existing refuges such as stumpholes (Humphries and Sisson 2012) or in burrows created by gopher tortoises (*Gopherus polyphemus* (Daudin, 1801)) (Lips 1991; Roznik et al. 2009) or small mammals, climbing trees, or moving into water (Humphries and Sisson 2012) or nearby unburned areas (Komarek 1969; Means and Campbell 1981). Although fire-related mortality is thought to be low, changes to forest structure (e.g., canopy and ground cover) resulting from either a long absence of fire or frequent burning in xeric sandhills or sand pine (*Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarg.) scrub can influence relative abundance of some species (Greenberg 2002).

Small, isolated, ephemeral ponds (henceforth termed ponds) are critical in sustaining the biological diversity of the xeric longleaf pine – wiregrass ecosystem by supporting semi-aquatic reptile and pond-breeding amphibian species (Moler and Franz 1987; Semlitsch and Bodie 1998). Many amphibian species depend completely or facultatively on temporary ponds for reproduction and inhabit surrounding sandhill uplands after metamorphosis for most of their adult lives (Moler and Franz 1987). Some reptile species within sandhills such as several turtle species and swamp snakes (*Seminatrix pygaea* (Cope, 1871)), use ponds as their primary habitat (Ashton and Ashton 1985); others are fully terrestrial but often include pond margins within their home ranges (Palmer 1995). Thus, the longleaf pine – wiregrass uplands surrounding ponds are the primary habitat for most sandhill herpetofauna and provide biological connectivity (Smith et al. 2018).

Because both reptiles (e.g., Palmer 1995) and amphibians (e.g., Wright 2002; Greenberg et al. 2017*a*) differ in seasonal periods of peak surface activity, season of burning could differentially affect mortality or capture rates of species. For example, dormant-season burns would impact winter-breeding amphibian species moving to or from breeding sites or those overwintering under leaf litter (Pilliod et al. 2003; Humphries and Sisson 2012), whereas growing-season burns would more likely impact summer-breeding adults and metamorphs emigrating from ponds. Short-term changes to forest structure or invertebrate prey abundance (Hardy 2003) after dormant- and (or) growing-season prescribed burns could also affect herpetofaunal abundance or alter activity patterns and detectability as reflected by capture rates (O'Donnell et al. 2015). Despite a general consensus that frequent fire in longleaf pine – wiregrass sandhills maintains a forest structure required to sustain diverse, abundant herpetofaunal communities over the long term (e.g., Greenberg 2002), there are very few studies that have addressed the immediate and short-term effects of prescribed burning or how season of burn affects community composition and relative abundance of different herpetofaunal species.

We used data from 24 years of continuous, concurrent trapping with drift fences surrounding the upland perimeter of seven ponds to compare short-term responses of reptile and amphibian communities (species richness, diversity, and evenness) and species (six reptile, six amphibian) to season of burning (dormant season versus growing season) in a xeric, longleaf pine – wiregrass ecosystem. We hypothesized that responses to prescribed burning overall (regardless of season) and to dormant-season or growing-season burns would be few and (or) transient given that herpetofaunal species in the longleaf pine – wiregrass ecosystem evolved with frequent fire.

## 2. Methods

### 2.1. Study area

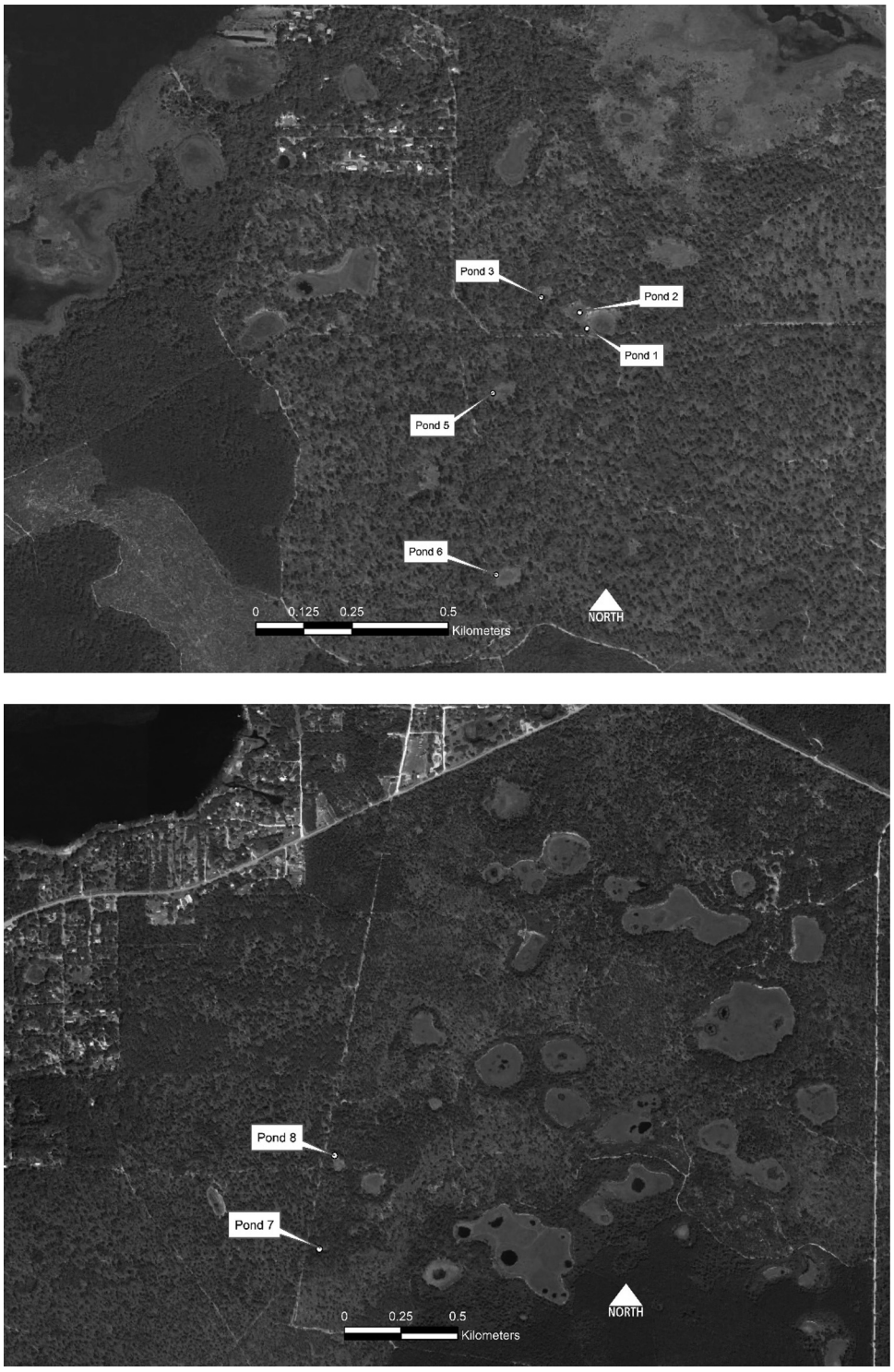
Our seven study ponds were a representative selection of small (0.10–0.35 ha), ephemeral, groundwater-driven sinkhole ponds, embedded within xeric longleaf pine – wiregrass uplands of the Floridan aquifer system region, Ocala National Forest, Marion County, Florida (Greenberg et al. 2015). Five study ponds (1, 2, 3, 5, 6) were all within about 0.7 km of one another; two (7, 8) were approximately 9.5 km south of the others (Fig. 1). The upland forest matrix surrounding study ponds was generally savanna-like sandhills with a wiregrass–forb ground cover and widely spaced longleaf pine trees. Hardwood and sand pine densities in the ecotones surrounding study ponds and the surrounding upland landscape were patchy and variable but generally greater surrounding ponds 1, 2, and 3 (Fig. 1).

We measured average weekly temperatures (February 1997 to December 2017) ranging from a minimum of –1.0 °C in January to a maximum of 41.1 °C in July and average annual precipitation (1995–2017) of 139.2 cm, with more than half occurring during late spring and summer (unpublished data). Heavy precipitation providing groundwater recharge was associated with thunderstorms and tropical systems in summer and fall and wet autumn, winter, or spring frontal systems (Winsberg 1990). Pond depths were generally highest in winter and lowest in summer due to rainfall patterns and groundwater recharge and reduced evapotranspiration in winter (Greenberg et al. 2017*a*).

### 2.2. Prescribed burns

Upland landscapes surrounding our study ponds were burned multiple times at <1- to 6-year intervals, by Ocala National Forest personnel, within the 24-year study period (1994–2017). Prior to

**Fig. 1.** Locations of study ponds in the Ocala National Forest, Marion County, Florida.






2003, prescribed burns were conducted primarily during the dormant season (January or February); subsequently, most were conducted during the growing season (May, June, or July). Prescribed burns typically did not burn into the ponds, as most contained water on burn dates and were surrounded by a naturally occurring ring of bare sand that functioned as a fire break. Prescribed burns were conducted at a landscape (Forest Service forest "compartment") level, with burn units ranging from 174 to 625 ha (431–1545 acres) in size. Burn dates were the same for several study ponds if they were located within the same burn unit. Generally, fires were ignited aerially, with igniting dot heads dropped at approximately 15 to 30 m intervals across the entire burn unit. Fire intensity was generally low, and all prescribed burns were relatively complete, with 75%–100% burned (D. Quisenberry, personal communication). For our study, we selected a subset of burns and ponds based on the following criteria: (*i*) burns were conducted within the dormant (January or February) or growing (May, June, or July) seasons; (*ii*) there were at least two years

(24 consecutive months) since a prior burn and at least one year (12 consecutive months; in most cases, two years, 24 months) before the next burn; this limited range of pre- and post-burn years was necessary to maintain consistency and comparability of burn effects among ponds due to the high frequency of prescribed burns and different numbers of years between burns among compartments; and (*iii*) traps were fully operational (e.g., minimal or no flooding) during all years used in the analyses. We did not measure burn effects on vegetation structure but illustrate immediate fire effects with before and after photographs at pond 6 (Fig. 2).

### 2.3. Amphibian and reptile sampling

We installed drift fences 7.6 m long and spaced 7.6 m apart around the terrestrial perimeter of each pond near the high-water line such that 50% of each pond was fenced, with fences and spaces equally distributed and encircling ponds. Pitfall traps (19 L buckets) were positioned inside and outside at each end of each fence (four per fence), and a double- or single-ended funnel trap (one of each per fence) was positioned at the midpoint of each fence on opposite sides to detect directional movement to and from ponds. Additionally, we placed a PVC pipe (5 cm in diameter; approximately 1.4 m in height) between each drift fence to attract treefrogs. We placed a sponge in each pitfall trap and moistened them as needed during trap checks. All traps were checked approximately three times weekly from 31 January 1994 through December 2017. We identified, sexed (when possible), and measured snout–vent length (SVL) of captured animals. All individuals were marked by pond number and year of capture by toe (anurans and lizards) or scale (snakes) clipping; exceptions were recent metamorphs of some anuran species that were too small to be toe-clipped. Because all ponds were sampled continuously and in proportion to basin size, we did not adjust for trap-nights.

### 2.4. Statistical analysis

Numerous prescribed burns occurred within our study area during our long-term study. Three dormant-season burns (DSB), each affecting three to five ponds (total of 11 pond burns used in analyses), and four growing-season burns (GSB), each affecting two to three ponds (total of nine pond burns used in analyses), met our selection criteria (Table 1). To achieve a reasonable degree of balance, we included one preburn and two postburn years (the first (Y+1) and second (Y+2) years after the burn date) in our analyses, except in two cases in which one of the postburn years was eliminated from analyses due to prolonged flooding of traps that compromised data (Table 1). A "burn year" included a full year (12 months) prior to (preburn) or after (Y+1 or Y+2) respective burn dates. All first-captured individuals and recaptures from prior years were included in capture totals for each pond and year; recaptures from the same year were omitted. We determined that the spatial arrangement of ponds was not relevant to our analyses, as interpond movement by amphibians was uncommon in our study (e.g., Greenberg and Tanner 2005*a*, 2005*b*) and unlikely to affect results.

Response variables for analysis were species richness (number of species), Shannon–Weiner diversity index ($H'$), and evenness ($H'$ divided by the natural logarithm of species richness) of reptiles and amphibians (separately) and relative abundance of species that were sufficiently common for statistical analysis. We used a two-factor fixed-effects repeated-measures mixed model with season (DSB, GSB) and burn year (preburn, Y+1, and Y+2) and their interactions (SAS Institute Inc. 2011) for analysis of all response variables. Amphibian captures exhibited little year-to-year correlation, so for simplicity, we did not use repeated measures for amphibian species only; this helped to avoid nonconvergence problems that often occur with such complex models. The random component was burn within season. The repeated-measures factor was year, where the subject was defined as pond within burn within season. Several covariance matrices (variance components, autoregressive 1, and compound symmetry) were compared using the corrected Akaike information criterion (AICc). For reptiles, compound symmetry was usually best and was used for all reptile models. Examination of residuals revealed that reptile species captures exhibited a normal distribution; amphibian species captures generally exhibited a clumped distribution and, therefore, a negative binomial distribution was used. All commu-

**Fig. 2.** Photographs of pond 6 before the burn (9 June 2010; top), immediately after the burn (10 June 2010; middle), and one year after the burn (9 June 2011; bottom), Ocala National Forest, Marion County, Florida.

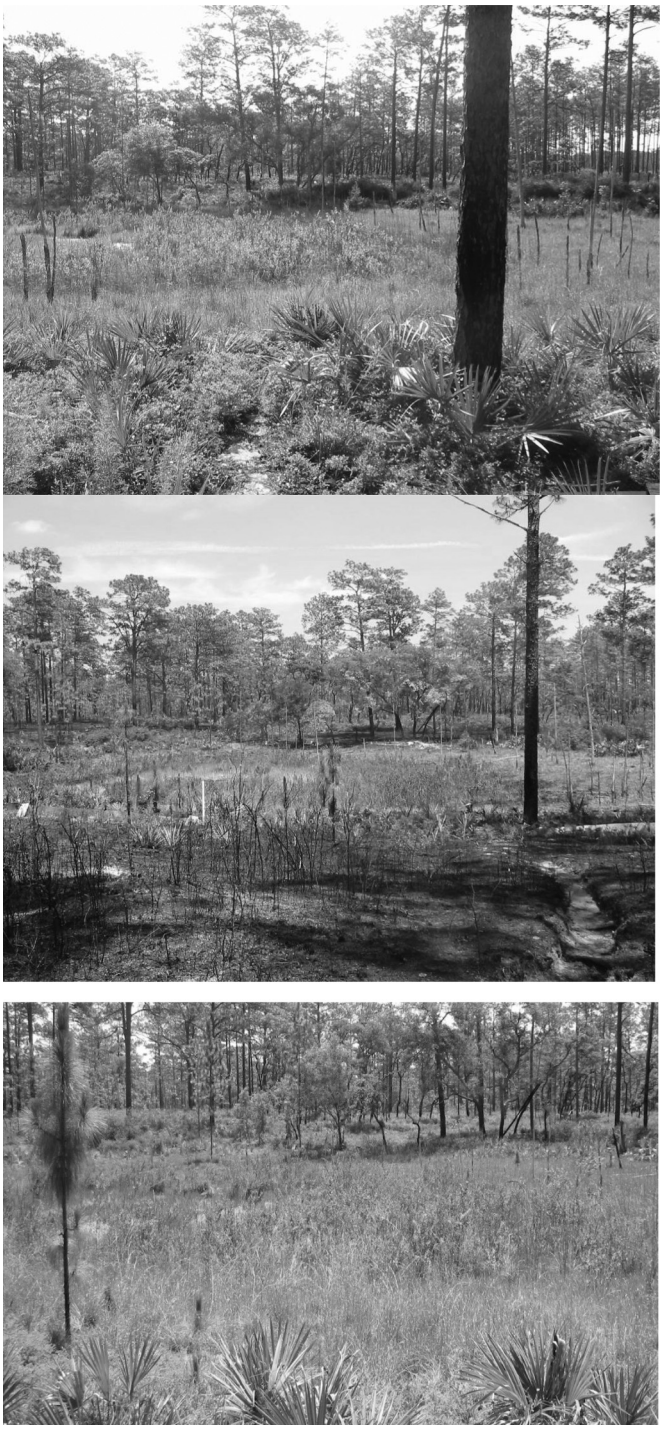


**Table 1.** Date and season of prescribed burns at each study pond used in data analyses and years (most included one year before burn and one and two years after burn (Y+1 and Y+2, respectively)) omitted from analyses due to prolonged flooding of traps that compromised capture data.

| Burn date | Season | Ponds | Burn-years omitted |
|---|---|---|---|
| 18 January 1996 | Dormant | 1, 2, 3 | |
| 13 January 1998 | Dormant | 1, 2, 3 | Y+1 |
| 26 February 2002 | Dormant | 1, 2, 3, 5, 6 | |
| 31 May 2010 | Growing | 7, 8 | |
| 9 June 2012 | Growing | 5, 6 | Y+2 |
| 22 June 2012 | Growing | 1, 2, 3 | |
| 26 July 2013 | Growing | 7, 8 | |

nity ($H'$, richness, and evenness) metrics for both reptiles and amphibians were analyzed using a normal distribution and repeated measures. We tried incorporating annual rainfall and pond hydroregime (mean depth, number of times dried per burn year, percent weeks with depth > 0 cm in week of burn) covariates, but they did not improve the models and thus were not included. We used PROC MIXED for all normality models and PROC GLIMMIX for negative binomial models (SAS Institute Inc. 2011).

Our primary interest was to determine how herpetofaunal communities and species responded to prescribed burns overall and if they responded differently to DSB and GSB. Because this was not a designed study with true controls or burns assigned to specific ponds and years, the effects of burn season and year are confounded and could not be evaluated. The mixed-model ANOVA provided the basic analysis for testing season of burn and year, but we mainly wanted to test specific hypotheses that would control for preburn levels of the variables that would provide higher statistical power. Therefore, we additionally developed and tested a priori contrasts specifically targeting our questions, using an approach similar to a before–after control–impact analysis (BACI; Smith 2002) that adjusted the effects of each burn to its preburn level for each pond used in the analysis (Table 1). The overall main effect of burns was tested by estimating contrasts between preburn and Y+1 and (separately) preburn and Y+2. Season of burn effects contrasts were tested under the null hypothesis that the change in each response variable from the preburn year to Y+1 or Y+2 (respectively) was the same for DSB and GSB (e.g., $H_0$: (Y+1 DSB – preburn DSB) = (Y+1 GSB – preburn GSB); similarly for Y+2).

## 3. Results

### 3.1. Mixed-model ANOVA

Total captures and results from the overall two-factor fixed-effects repeated-measures model are shown in Table 2. Among the six amphibian species tested, a season of burn effect was detected only for oak toads (*Anaxyrus quercicus* (Holbrook, 1840)). A year effect was detected for southern toads (*Anaxyrus terrestris* (Bonnaterre, 1789)), oak toads, narrowmouth toads (*Gastrophryne carolinensis* (Holbrook, 1835)), and Florida gopher frogs (*Lithobates capito*); a season × year interaction effect was detected only for Florida gopher frogs. A season of burn and year effect was detected for amphibian species richness. A season of burn and season × year interaction effect was detected for amphibian diversity. A year and season × year interaction effect was detected for amphibian evenness.

Among the six reptile species tested, a season of burn, year, and season × year interaction was detected only for ground skinks (*Scincella lateralis* (Say, in James, 1823)). Southeastern five-lined skinks (*Plestiodon inexpectatus* (Taylor, 1932)) exhibited a season × year interaction effect. There were no significant main effects or interactions for reptile species richness, diversity, or evenness. Further analysis was not focused on all multiple comparisons within a significant main effect but on the two types of a priori contrasts defined in the statistical section. The mixed-model ANOVA provided the basic analysis for testing season of burn and year and was needed for testing the more important specific hypotheses via contrasts that controlled for preburn levels of the variables.

### 3.2. Overall burn contrasts

The overall effect of burning (averaged over season of burn and ignoring any possible interaction effects) on herpetofauna, based on the contrasts between the preburn year and each postburn year (Y+1 and Y+2) was most evident in Y+1, and responses varied among herpetofaunal species (Table 3; Fig. 3). Among amphibians, southern toad and oak toad captures increased in Y+1 compared with preburn year (Fig. 3). Florida gopher frog captures increased during Y+2 relative to preburn, which was due to a Y+2 increase in GSB but little change in DSB (Fig. 3) and reflects the season × year interaction seen in the ANOVA (Table 2). Capture rates of pinewoods treefrogs (*Hyla femoralis* Daudin, 1800), narrowmouth toads, and southern leopard frogs (*Lithobates sphenocephalus* (Cope, 1886)) did not change from preburn to either postburn year. Total amphibian species richness increased during Y+1 compared with the preburn year. Evenness decreased during Y+1 (only) due mainly to decreased evenness in GSB, with little change in DSB (Fig. 4); again, this reflects the season × year interaction effect in the ANOVA (Table 2). Among reptiles, ground skink captures increased in Y+1 compared with preburn year, which was due to a substantial Y+1 increase in DSB, with little change in GSB (Fig. 3), reflecting the season × year interaction seen in the ANOVA (Table 2). Florida crowned snake (*Tantilla relicta* Telford, 1966) captures decreased during Y+1 compared with preburn year; no differences were detected for Y+2 (Fig. 3). Six-lined racerunners (*Cnemidophorus sexlineatus* (Linnaeus, 1766)), southeastern five-lined skinks, mole skinks, and swamp snakes showed no response to burns overall in either postburn year. Reptile species richness, diversity, and evenness did not differ before and after burning.

### 3.3. Season of burn contrasts

Contrasts comparing amphibian species responses to season of burn indicated that oak toad captures decreased more in GSB than in DSB in Y+2 relative to preburn levels, whereas Florida gopher frogs increased more in GSB than in DSB in Y+2 relative to preburn levels (Table 3; Fig. 3). Postburn captures of southern toads, narrowmouth toads, pinewoods treefrogs, and southern leopard frogs did not differ between DSB and GSB relative to their preburn levels. Amphibian species diversity and evenness decreased more in GSB than in DSB in Y+1 relative to preburn levels; in Y+2, no differences in species richness, diversity, and evenness were detected between DSB and GSB relative to preburn levels (Table 3; Fig. 4). Among reptile species, ground skink captures increased from preburn levels more in DSB than in GSB in Y+1 (Table 3; Fig. 3), whereas southeastern five-lined skinks captures increased from preburn levels more in GSB than in DSB in Y+2. Postburn captures of six-lined racerunners, mole skinks (*Plestiodon egregius* Baird, 1959), swamp snakes, Florida crowned snakes (Fig. 3), or reptile species richness, diversity, and evenness (Fig. 4) did not differ between DSB and GSB relative to their preburn levels (Table 3).

## 4. Discussion

Our results indicated that growing- and dormant-season burns overall had few and transient short-term effects on herpetofaunal communities and tested species. Half of the 12 species examined did not show a response to burning overall or season of burn, and most responses were seen only during Y+1. Reptile species richness, diversity, and evenness were unaffected by season of burn or burning overall. Amphibian species richness, diversity, and even-

**Table 2.** Total number of captures (first captures and recaptures from prior years) for tested amphibian and reptile species and results of mixed-model ANOVA comparing treatment (season of burn) ($P_{trt}$), year (one year before burn and two years after burn) ($P_{yr}$), and treatment × year ($P_{trt\times yr}$) effects on reptile and amphibian captures and species richness, Shannon's diversity ($H'$), and evenness, Ocala National Forest, Marion County, Florida.

| | | ANOVA results | | |
|---|---|---|---|---|
| Species and community-level metrics | Total | $P_{trt}$ | $P_{yr}$ | $P_{trt\times yr}$ |
| **Amphibians** | | | | |
| Southern toad (*Anaxyrus terrestris*) | 2280 | 0.8475 | **0.0161** | 0.6587 |
| Oak toad (*Anaxyrus quercicus*) | 2273 | **0.0357** | **0.0005** | 0.1668 |
| Narrowmouth toad (*Gastrophryne carolinensis*) | 3584 | 0.3668 | **0.0348** | 0.4154 |
| Pinewoods treefrog (*Hyla femoralis*) | 2152 | 0.1846 | 0.9198 | 0.9623 |
| Florida gopher frog (*Lithobates capito*) | 444 | 0.9735 | **0.0284** | **0.0030** |
| Southern leopard frog (*Lithobates sphenocephalus*) | 578 | 0.2046 | 0.5505 | 0.4506 |
| Amphibian species richness | — | **0.0015** | **0.0231** | 0.8303 |
| Amphibian species diversity | — | **0.0279** | 0.0794 | **0.0004** |
| Amphibian species evenness | — | 0.1641 | **0.0089** | **0.0008** |
| **Reptiles** | | | | |
| Six-lined racerunner (*Cnemidophorus sexlineatus*) | 1449 | 0.5255 | 0.1886 | 0.2236 |
| Mole skink (*Plestiodon egregious*) | 126 | 0.7459 | 0.3340 | 0.4938 |
| Southeastern five-lined skink (*Plestiodon inexpectatus*) | 676 | 0.1143 | 0.8197 | **0.0353** |
| Ground skink (*Scincella lateralis*) | 752 | **0.0283** | **0.0038** | **0.0088** |
| Swamp snake (*Seminatrix pygaea*) | 375 | 0.0541 | 0.8896 | 0.7999 |
| Florida crowned snake (*Tantilla relicta*) | 485 | 0.4747 | 0.0765 | 0.4061 |
| Reptile species richness | — | 0.2576 | 0.5334 | 0.5093 |
| Reptile diversity | — | 0.3378 | 0.9155 | 0.3847 |
| Reptile evenness | — | 0.6108 | 0.7095 | 0.2802 |

**Note:** Boldface $P$ values indicate statistical significance ($P < 0.05$).

**Table 3.** Contrasts for overall burn effects[a] (preburn versus one year after burn (Y+1) and preburn versus two years after burn (Y+2)) and contrasts for season of burn effects (dormant- and growing-season burns)[b] of total amphibian and reptile captures (first captures and recaptures from prior years), species richness, diversity ($H'$), evenness during Y+1 and Y+2 compared with preburn.

| | Overall burn contrasts | | Season of burn contrasts | |
|---|---|---|---|---|
| Species and community-level metrics | $P$ value preburn: Y+1 | $P$ value preburn: Y+2 | $P$ value preburn: Y+1 | $P$ value preburn: Y+2 |
| **Amphibians** | | | | |
| Oak toad (*Anaxyrus quercicus*) | **0.0078** | 0.7825 | 0.5616 | **0.0431** |
| Southern toad (*Anaxyrus terrestris*) | **0.0034** | 0.2371 | 0.3975 | 0.9211 |
| Narrowmouth toad (*Gastrophryne carolinensis*) | 0.2395 | 0.1104 | 0.2031 | 0.7946 |
| Pinewoods treefrog (*Hyla femoralis*) | 0.8271 | 0.6857 | 0.8427 | 0.9356 |
| Florida gopher frog (*Lithobates capito*) | 0.6309 | **0.0335** | 0.7791 | **0.0036** |
| Southern leopard frog (*Lithobates sphenocephalus*) | 0.3876 | 0.8546 | 0.9867 | 0.2694 |
| Amphibian species richness | **0.0084** | 0.5625 | 0.9093 | 0.5610 |
| Amphibian species diversity | 0.1074 | 0.4638 | **<0.0001** | 0.0872 |
| Amphibian species evenness | **0.0091** | 0.7101 | **0.0002** | 0.1934 |
| **Reptiles** | | | | |
| Six-line racerunner (*Cnemidophorus sexlineatus*) | 0.1640 | 0.0941 | 0.1640 | 0.7588 |
| Mole skink (*Plestiodon egregious*) | 0.4546 | 0.1423 | 0.2760 | 0.3682 |
| Southeastern five-lined skink (*Plestiodon inexpectatus*) | 0.5379 | 0.8595 | 0.5108 | **0.0120** |
| Ground skink (*Scincella lateralis*) | **0.0065** | 0.5032 | **0.0051** | 0.9292 |
| Swamp snake (*Seminatrix pygaea*) | 0.7467 | 0.8617 | 0.5076 | 0.7531 |
| Florida crowned snake (*Tantilla relicta*) | **0.0494** | 0.8832 | 0.8461 | 0.2716 |
| Reptile species richness | 0.2616 | 0.9483 | 0.5894 | 0.3578 |
| Reptile species diversity | 0.9622 | 0.7713 | 0.1704 | 0.5969 |
| Reptile species evenness | 0.5691 | 0.7114 | 0.1715 | 0.9534 |

**Note:** Boldface $P$ values indicate statistical significance ($P < 0.05$).

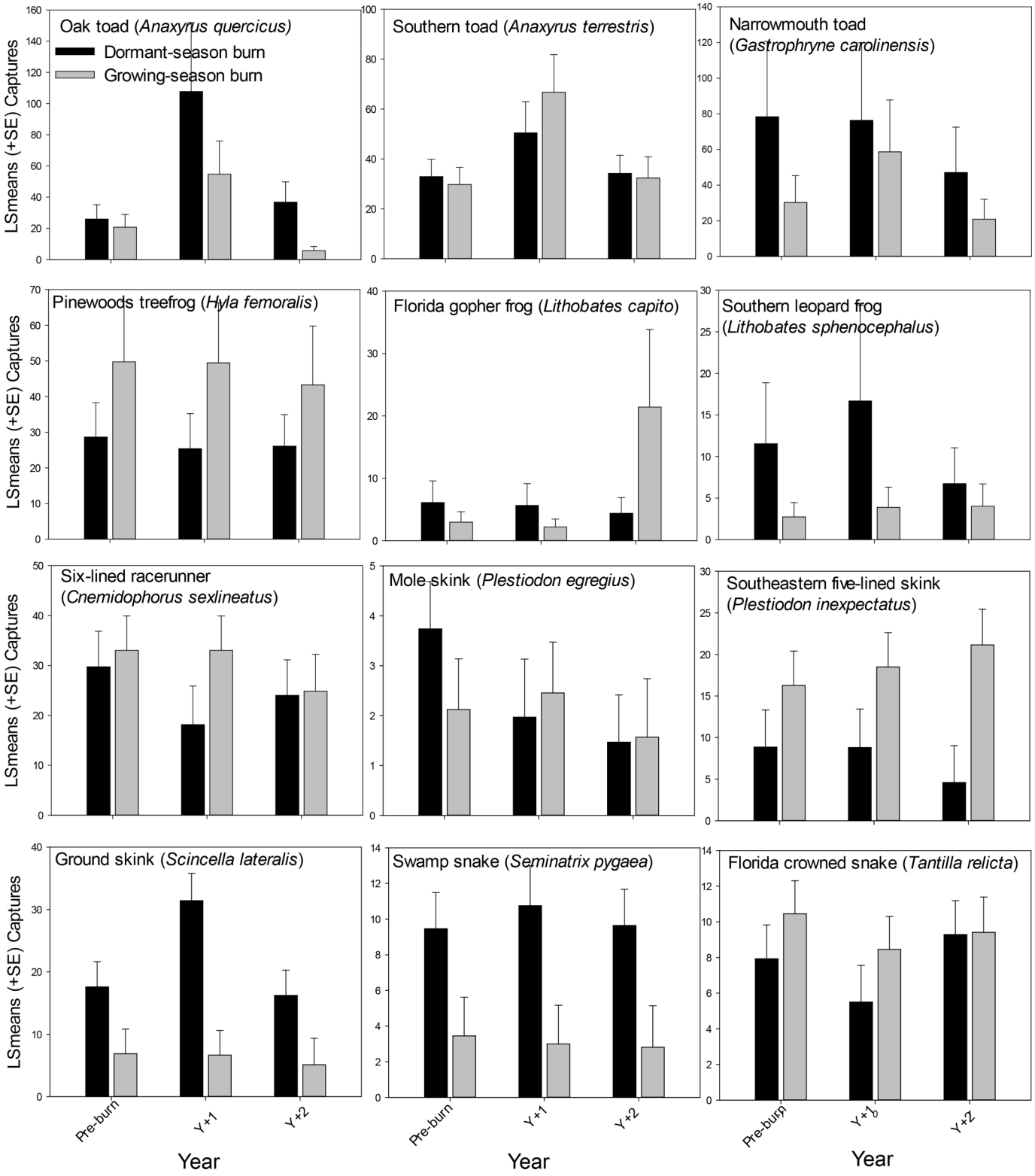
[a]Overall burn contrasts are defined as Y+1 minus preburn and Y+2 minus preburn.

[b]Season of burn contrasts are defined as (dormant season: Y+1 minus preburn) minus (growing season: Y+1 minus preburn) and (dormant season: Y+2 minus preburn) minus (growing season: Y+2 minus preburn).

ness differed before and after burning or between growing- and dormant-season burns during Y+1. Reptile and (especially) amphibian populations (e.g., Greenberg et al. 2018) are influenced by multiple biotic and edaphic factors, making it difficult to determine whether responses to burning or burn season were biologically meaningful.

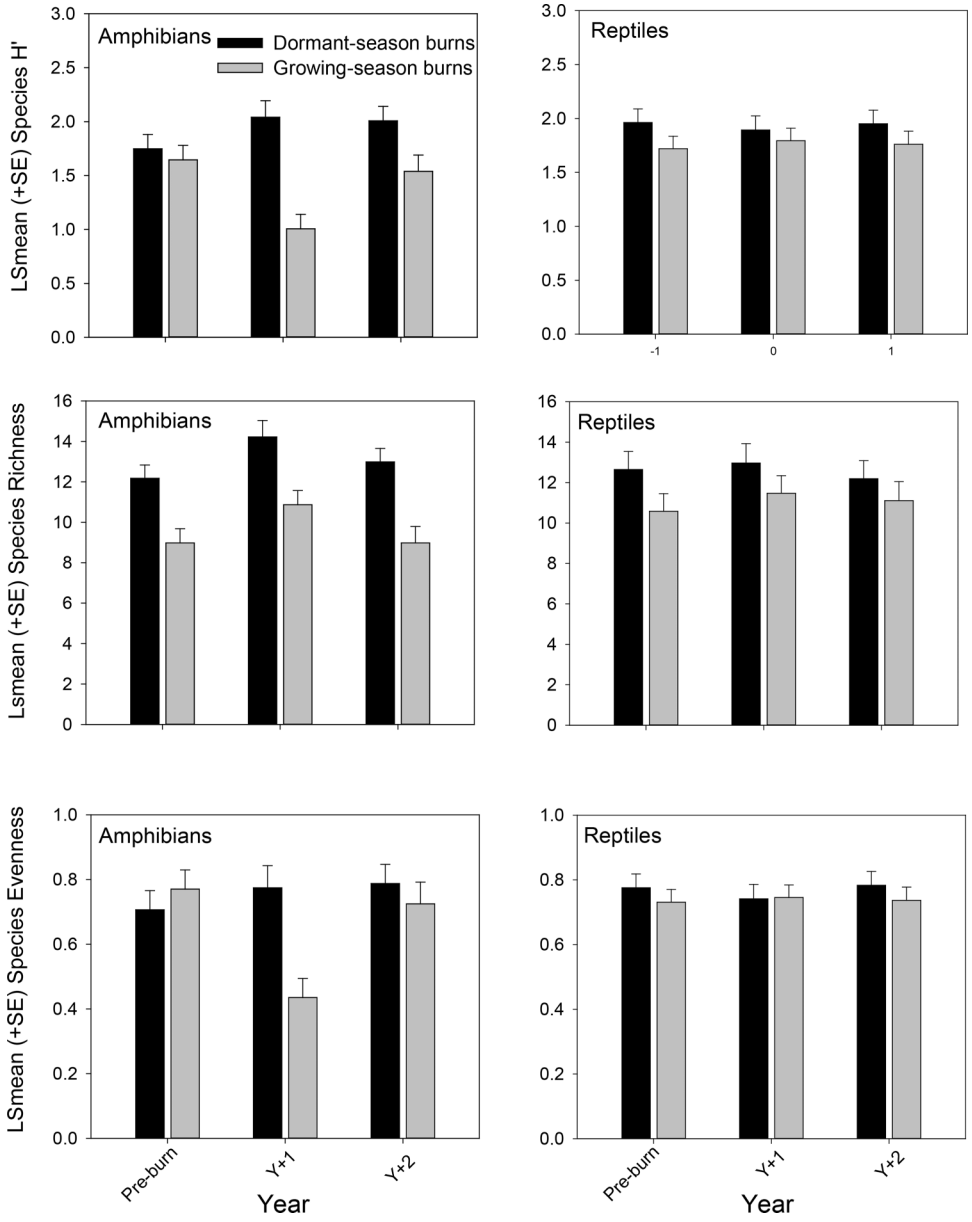
We observed little to no evidence of direct, fire-related mortality and thus suggest that species responses were most likely due to

**Fig. 3.** Least squares (LS) mean (+SE) captures of six amphibian and six reptile species per pond, one year before the burn (preburn) and one (Y+1) and two (Y+2) years after dormant- and growing-season burns, Ocala National Forest, Marion County, Florida.




changes in surface activity affecting capture rates or (for amphibians in particular) annual variability in capture rates unrelated to burns (Greenberg et al. 2018). Although postburn wiregrass and herbaceous groundcover recovery is rapid (within a year or less) in longleaf pine –wiregrass savanna (e.g., Langford et al. 2007), possible differences in the timing of burning and groundcover recovery between dormant- and growing-season burns could affect species differently based on their annual periods of peak activity. However, it seems unlikely that responses observed only during Y+2 would be directly associated with changes to vegetation structure. Possibly, a delayed response could be associated with longer term changes in prey availability that differed between dormant-

**Fig. 4.** Least squares (LS) mean (+SE) amphibian and reptile species diversity ($H'$), richness, and evenness per pond, one year before the burn (preburn) and one (Y+1) and two (Y+2) years after dormant- and growing-season burns, Ocala National Forest, Marion County, Florida.




and growing-season burns (Hardy 2003). We were unable to determine if herpetofauna used ponds as refugia during burns (e.g., Humphries and Sisson 2012) or if our results might have changed had ponds been dry and fires burned through them within our study period.

Although some amphibian community metrics and species showed a short-term response to season of burn, we emphasize that these results should be interpreted cautiously. Trapping adjacent to ponds may potentially confound detection of fire effects on amphibian populations with other factors affecting breeding and recruitment. Ponds function as a "magnet" for many pond-breeding amphibian species during their respective breeding seasons, although many spend most of their lives in the surrounding uplands. In contrast, ponds are not critical in the life history of most terrestrial reptiles and thus capture rates near ponds are likely to better reflect their response to burns and structural changes within the surrounding upland matrix.

Pond-breeding amphibian populations are highly variable (Greenberg et al. 2018) relative to reptiles that lay eggs on land (personal observations), as breeding effort and juvenile recruitment are heavily influenced by weather and hydroregime characteristics such as the timing, depth, and duration of water in ponds. Further, amphibian species differ in their life history requirements such as breeding seasons and rates of aquatic larval development within ponds (Greenberg et al. 2017*a*, 2017*b*); thus, their responses might also be expected to differ. Juvenile recruitment is also influenced by seemingly stochastic underwater dynamics of competition and predation on amphibian eggs and larvae, often resulting in highly variable recruitment among seemingly similar ponds, even within years (Greenberg et al. 2017*b*). Thus, capture rates and community-level metrics such as diversity and evenness are likely to vary dramatically among years independently of burns, particularly for amphibians.

Responses to burning did not seem to correspond among some species with similar habits. For example, six-lined racerunners,

southeastern five-lined skinks, and ground skinks are nonfossorial (Ashton and Ashton, 1985), yet differed in their responses. Six-lined racerunners showed no response to burning, ground skink captures increased in the first year after dormant-season burns compared with growing-season burns, and southeastern five-lined skink captures increased during the second year after growing-season burns compared with dormant-season burns. Mole skinks and Florida crowned snakes showed no response to season of burning, as might be expected given their semi-fossorial habits. Swamp snake captures also showed no response to burning, likely because they generally do not inhabit the upland matrix surrounding ponds (Ashton and Ashton 1985). Similarly, amphibian responses did not appear to correspond among species with similar breeding habits. For example, oak toad captures decreased during the second year after growing-season burns compared with dormant-season burns, but other summer-breeding species (Greenberg et al. 2017*a*), including pinewoods treefrogs, southern toads, and narrowmouth toads, showed no response to growing- or dormant-season burns. Similarly, Florida gopher frogs and southern leopard frogs breed throughout most of the year, with juveniles emigrating ponds during late spring and summer (Greenberg et al. 2017*a*); yet Florida gopher frog captures increased after growing-season burns compared with dormant-season burns during Y+2, whereas southern leopard frog captures did not.

Results are inconsistent among the few studies addressing short-term effects of burning or season of burn in xeric, pine-dominated forests and conditions analogous to those within our study area. Hardy (2003) reported no differences in amphibian or reptile species richness or abundance between dormant- and growing-season burns at ephemeral ponds within an upland sandhills matrix. Schurbon and Fauth (2003) reported that prescribed burns decreased amphibian species richness at temporary ponds for two years, primarily because salamanders (including several *Ambystoma* spp. that did not occur at our study ponds) rarely used recently burned sites. In contrast, Langford et al. (2007) reported a greater abundance of herpetofauna in recently burned Mississippi pine savanna, but no difference in species diversity between burned and unburned uplands. Noss and Rothermal (2015) reported higher tadpole survival in recently burned ponds than ponds burned more than 3 years earlier Brown et al. (2011) reported no short-term negative effects of low-intensity growing-season prescribed burns or high-severity wildfires on juvenile amphibian captures and increased postburn captures of two amphibian genera. We suggest that inconsistencies among studies, including ours, are due to variable among-year populations unrelated to burning, particularly for pond-breeding amphibians.

Several studies indicate that longer term changes to canopy cover or groundcover of wiregrass and herbaceous plants, leaf litter, or bare ground in xeric longleaf pine or sand pine forests resulting from either fire exclusion or frequent burning can influence relative abundance of some species. For example, Florida scrub lizards (*Sceloporus woodi* Stejneger, 1918), sand skinks, six-lined racerunners, mole skinks, and Florida crowned snakes are more abundant in recently disturbed sand pine scrub with low canopy cover and a high proportion of bare sand compared with mature, forested sand pine scrub (Campbell and Christman 1982; Means and Campbell 1981; Mushinsky 1985; Greenberg et al. 1994; Greenberg 2002; Button et al. 2019), whereas southeastern five-lined skinks are more abundant in sites that were not recently burned, with greater leaf litter accumulation (Mushinsky 1992; Greenberg et al. 1994). Densities of gopher tortoises and their burrows, used as refugia by many herpetofaunal species (Jackson and Milstrey 1989; Lips 1991), are greater in open, regularly burned sandhills with abundant groundcover (Diemer 1986). In contrast, Litt et al. (2001) and Meshaka and Layne (2002) reported few differences in the diversity or abundance of herpetofaunal species between long-unburned and frequently burned Florida sandhills. Our study compared only short-term herpetofaunal responses to frequently burned sandhills and was not designed to compare responses between long-unburned and regularly burned sandhills.

Our study showed that individual reptile and amphibian species responded differently to burning overall or season of burn; responses ranged from none to positive or negative. Further, most responses were seen only in Y+1. Our study illustrated that prescribed burning overall and season of burn are unlikely to adversely affect reptile or amphibian communities or species in the short term, and most responses are short-lived.

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