FINAL PERFORMANCE REPORT

As Required by

THE ENDANGERED SPECIES PROGRAM

TEXAS

Grant No. TX E-114-R-1

Endangered and Threatened Species Conservation

Detection of fine scale outcomes from prescribed fire relevant to the endangered Houston toad (*Bufo houstonensis*) within the Lost Pines ecoregion of Texas

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8 November 2012

INTERIM PERFORMANCE REPORT

STATE: ____Texas_______________ **GRANT NUMBER:** ___TX E-114-R-1_

GRANT TITLE: Detection of fine scale outcomes from prescribed fire relevant to the endangered Houston toad (*Bufo houstonensis*) within the Lost Pines ecoregion of Texas

REPORTING PERIOD: ____1 Sep 09 to 28 Feb 13_

OBJECTIVE(S): To determine the fine scale effects of prescribed fire on Houston toad habitat selection and reproductive success over three years based on integrated study of terrestrial and aquatic systems.
Segment Objectives:

Task 1. Aug 2009-Aug 2011 (monthly). Hydroperiod monitoring.

Task 2. Mar-Apr (annually). Daily amphibian trapping using Y-shaped arrays.

Task 3. Mar-Apr (annually). Amphibian call surveys and Houston toad breeding activity and success monitoring.

Task 4. Aug-Sept (annually). Terrestrial habitat sampling.

Task 5. Sep-Nov (annually). Aquatic habitat sampling.

Task 6. Nov-Jan (annually under design see Figure 1). Prescribed burn.

Task 7. Nov-Jan (annually). Immediate post-burn aquatic habitat sampling.

Task 8. Nov-Jan (annually). Immediate post-burn terrestrial habitat sampling.

Task 9. July-Aug (annually). Analysis of outcomes, particularly short term results and effects.

Significant Deviations: None.

Summary Of Progress: See pdf file, attached.

Location: Bastrop County, Texas.

Cost: ___Costs were not available at time of this report.

Prepared by: _Craig Farquhar_____________ **Date:** _24 May 2013

Approved by: ______________________________ **Date**:_____24 May 2013_____
C. Craig Farquhar

2013 Final Report

Detection of the fine scale outcomes from prescribed fire relevant to the endangered Houston toad (*Bufo houstonensis*) within the Lost Pines Ecosystem of Texas

(E-114)

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I. EXECUTIVE SUMMARY

Historically fire was an important natural disturbance shaping the structure and composition of pine-dominated forests in the southern U.S. (Gilliam and Platt 1999, Knebel and Wentworth 2007, Hanberry et al. 2012). Longstanding fire suppression policies have resulted in structural and compositional changes, notably accumulation of heavy fuel loads and reduction in vegetation species diversity (Agee 1996, Shang et al. 2007, Crotteau et al. 2013). Fire suppression, coupled with climatic trends towards warmer and drier conditions, have resulted in an increase in high severity wildfires (Figure 1), particularly in the southern and western U.S. (Davis 2001, Miller et al. 2009), with this trend projected to continue into the next century (Moritz et al. 2012). The term fire severity refers to amount of organic matter lost through burning, as opposed to the related term fire intensity, which refers to the heat energy of fire (Keeley 2009). The current research scope has been enabled by prescribed fires, but also by our collection of data immediately prior to the Bastrop Complex Fire of 2011. As the fire was ongoing we adapted our research design to enabld to test the effects of that fire on Houston toads, their habitat, and the aquatic systems upon which they depend during the larval stages. We consider the project thus far to have provided information crucial to management of the Houston toad in the recovery from the Bastrop Complex Fire, but also to enable management decisions for the remaining occupied habitat patches.

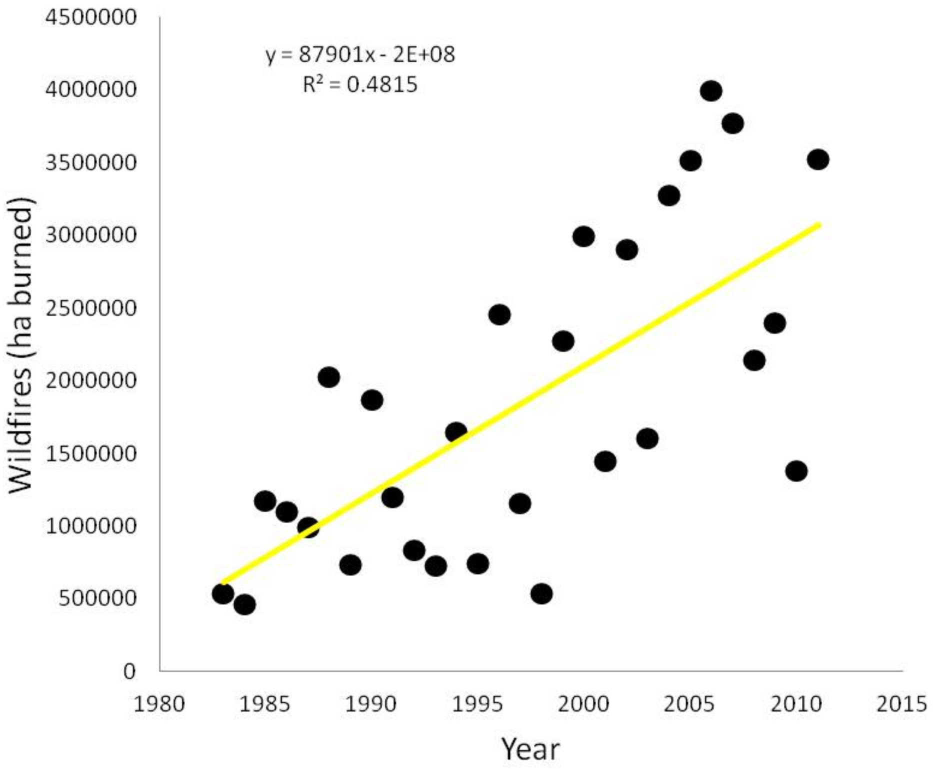

Figure 1. Number of ha burned through wildfires in the U.S. between 1983 and 2011 (National Interagency Fire Center 2013). Based on a least-squares linear regression, area burned increased by 87,901 ha annually over this time period.

Prescribed burning is currently one of the primary tools used for restoration of fire suppressed forests (Allen et al. 2002, Glasgow and Matlack 2007, Mitchell et al. 2009). Although site-specific goals of burning vary, overarching goals typically include reduction of heavy fuel loads (Fernandes and Botelho 2003, Shang et al. 2007, Webster and Halpern 2010), and mimicking ecosystem impacts of historically natural wildfires within a controlled setting (Moore et al. 1999, Vose 2000, Allen et al. 2002). Much research has been devoted to effects of burn season and frequency, particularly on vegetation (e.g., Cain et al. 1998, Sparks et al. 1998, Taylor 2000, Webster and Halpern 2010). Much less is known about effects of burn severity, given that prescribed burns are typically low to moderate severity fires. In contrast, high severity wildfires are unplanned, and thus wildfire research is by necessity a response to non-designed treatments, and opportunities for research are more limited. However, the need to improve our understanding of the influence of fire severity on ecosystem responses to fire is becoming an increasingly pressing need as the annual area burned in high severity fires in the U.S. continues to rise.

This project was originally funded with the goal of providing information relevant to the management of Houston toad habitat through prescribed fire, as well as to continue to enhance our understanding of Houston toad ecology. However, we have modified our research goals in response to the high severity Bastrop County Complex Fire, which occurred in September and October 2011. The fire burned 13,406 ha in the Lost Pines ecoregion, much of which was known occupied Houston toad habitat. This singular event could potentially have the most dramatic population-level impact since the extirpation of the species from Harris County. Thus, much of our Houston toad research in the coming years will be heavily management-oriented, with the primary objectives of documenting impacts to the species and its habitat, and providing information directly applicable to recovery efforts.

The spatial distribution of the wildfire on our primary study area, the 1,948 ha Griffith League Ranch (GLR), represents the best possible scenario for investigating impacts of the Bastrop County Complex Fire. New fire breaks were installed during the fire, which restricted the burn to 50.7% of the property. However, the fire breached the containment area on 4 October 2011, burning an additional 4.1% of the property. Over the past 2 years we used the GLR to assess initial impacts of the wildfire, and will continue utilizing the property to assess biotic and abiotic impacts in the coming years.

The relevant studies completed since initiation of this Section 6 grant are included in this report. Our primary goals were: 1) to increase our knowledge of fire impacts on amphibians and reptiles, collectively referred to as herpetofauna, the least studied major terrestrial vertebrate groups in relation to fire research; 2) to improve our understanding of fire severity as a factor influencing the response of ecosystem components to fire; and 3) to increase our understanding of the temporal and spatial ecology, and impacts of fire, on the invasive red imported fire ant (RIFA; *Solenopsis invicta*), a species which has been implicated in the decline of several herpetofaunal species, and for which almost no information exists concerning fire impacts. We accomplished this through the completion of 6 field-based studies. We used low and moderate severity prescribed fire to manipulate the habitat, and incorporated unplanned high severity wildfires into our study designs.

The herpetofaunal investigations indicated that direct mortality from fire was not significant, even for high severity wildfires. Further, survivorship of juvenile amphibians may have increased following a moderate severity summer prescribed fire, and the potential increase in survivorship could have been related to a reduction in arthropod predation. The high severity wildfire research indicated the post-wildfire landscape provided suitable habitat for herpetofauna ca. 6 months after the wildfire. In addition, movement-rates of Hurter's spadefoot toads (*Scaphiopus hurterii*) appeared to increase following the wildfire, and to our knowledge this was the first study that investigated the impacts of fire on amphibian movement-rates.

The study investigating the influence of fire severity on responses of ecosystem components to fire indicated that fire severity was an important factor, and the influence was related to magnitude, but not direction, of effects. For some components (e.g., pond nutrient levels) the magnitude effect was clear, whereas for others (e.g., species composition of understory vegetation) it was dichotomous in that no effect was apparent for low severity fire and a strong effect was apparent for high severity fire. An additional important finding was mortality of loblolly pine (*Pinus taeda*) trees was nearly 100% in the high severity wildfire zone, and subsequently loblolly pine tree recruitment was low. Thus, restoration of the Lost Pines will require significant active management through reseeding of loblolly pines, with the alternative being a shift to hardwood-dominated forest patches in the high severity wildfire zone.

The RIFA investigations indicated that peak annual RIFA activity coincides with the period when juvenile Houston toads are found at high densities around breeding ponds, and thus are particularly vulnerable to population-level impacts of predation. Further, there was a strong inverse relationship between RIFA captures and overstory canopy cover, and high severity fire appeared to positively affect RIFA through reduction in canopy cover. This is a concerning result given the substantial tree mortality across the high severity wildfire zone, and thus the potential for increases in RIFA abundance and distribution in the Lost Pines ecoregion.

The extension of the duration of this grant will enable the completion of several additional studies relevant to recovery and management initiatives in the Lost Pines ecoregion. These will include, an investigation of current Houston toad population dynamics on the GLR using data collected during the last several years, an investigation of fire and post-fire management impacts on environmental variables relevant to both Houston toad and loblolly pine survivorship, and an investigation of post-fire management impacts on the herpetofaunal community. The research supported or enabled by the Section 6 award (E-114) are listed in Table A.

Table A. Research completed to date since the initiation of this Traditional Section 6 Grant.

In Print:

Brown, D. J., T. M. Swannack, and M. R. J. Forstner. 2013. Predictive models for calling and movement activity of the endangered Houston toad. American Midland Naturalist 169(2):303-321.

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Jones, M. C., D. J. Brown, I. Mali, A. McKinney, and M. R. J. Forstner. 2012. Assessment of public knowledge and support for recovery of the endangered Houston toad in Bastrop County, Texas. Human Dimensions of Wildlife 17(3):220-224.

Vandewege, M. W., D. J. Brown, and M. R. J. Forstner. 2012. Head-start juvenile dispersal. *Bufo houstonensis*. Herpetological Review 43(1):117-118.

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Brown, D. J., J. T. Baccus, D. B. Means, and M. R. J. Forstner. 2011. Potential positive effects of fire on juvenile amphibians in a southern USA pine forest. Journal of Fish and Wildlife Management 2(2):135-145.

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In Press:

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Brown, D. J., M. C. Jones, J. Bell, and M. R. J. Forstner. In press. Feral hog damage to endangered Houston toad (*Bufo houstonensis*) habitat in the Lost Pines of Texas. Texas Journal of Science.

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Cain, M. D., T. B. Wigley, and D. J. Reed. 1998. Prescribed fire effects on structure in uneven-aged stands of loblolly and shortleaf pines. Wildlife Society Bulletin 26:209−218.

Crotteau, J. S., J. M. Varner, and M. W. Ritchie. 2013. Post-fire regeneration across a fire severity gradient in the southern Cascades. Forest Ecology and Management 287:103−112.

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Miller, J. D., H. D. Safford, M. Crimmins, and A. E. Thode. 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and Southern Cascade Mountains, California and Nevada, USA. Ecosystems 12:16−32.

Mitchell, S. R., M. E. Harmon, and K. E. B. O'Connell. 2009. Forest fuel reduction alters fire severity and long-term carbon storage in three Pacific Northwest ecosystems. Ecological Applications 19:643−655.

Moore, M. M., W. W. Covington, and P. Z. Fule. 1999. Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. Ecological Applications 9:1266−1277.

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II. POTENTIAL POSITIVE EFFECTS OF FIRE ON JUVENILE AMPHIBIANS IN A SOUTHERN USA MIXED PINE FOREST

Abstract

Prescribed fire is a common tool used to conserve and manage the integrity of forest ecosystems. We investigated short-term juvenile amphibian capture and body condition changes subsequent to fire (i.e., one prescribed burn and two wildfires) in a southern USA pine forest. We surveyed amphibians and predatory invertebrates before and after fires during summer 2010. We tested for treatment (i.e., control, wildfire, or prescribed burn) and status (i.e., pre-burn or post-burn) differences in: (1) genus-level captures of amphibians, (2) amphibian health (inferred through a body condition index), and (3) predatory invertebrate captures. *Bufo* and *Scaphiopus* captures increased in the prescribed burn treatment; whereas, no differences in *Gastrophryne* captures were observed. We did not detect a burn status effect on amphibian body condition. Predatory invertebrate captures were higher post-burn in control and wildfire treatments. Neither a moderate severity prescribed burn nor moderate severity wildfires negatively impacted short-term juvenile amphibian captures. Further, we speculate that *Bufo* and *Scaphiopus* survivorship may have been higher after the prescribed burn.

Keywords: amphibians; fire; forest; Houston toad; predators.

Introduction

Prescribed fire has increased as a primary tool for conservation and recovery of fire-maintained ecosystems (Agee 1996; Sparks et al. 1998; Kloor 2000; Pyne 2010). Prescribed fire is often used to decrease heavy fuel loads in historically fire-suppressed forests, in the prevention of catastrophic wildfires, and to stimulate the recovery of understory vegetation (Sweeney and Biswell 1961; Lovaas 1976; Cain et al. 1998; Ryu et al. 2006). Restoring understory vegetation in fire-suppressed forests may promote greater animal diversity and abundance (Moseley et al. 2003; Smucker et al. 2005; Benson et al. 2007). Fire also stimulates aquatic productivity through increased nutrient loads in streams and ponds (Gresswell 1999; Scrimgeour et al. 2001) and has been linked to mitigation of spruce beetle (*Dendroctonus rufipennis*) outbreaks (Bebi et al. 2003).

Scientific investigations of fire effects on wildlife have progressed slowly from game to non-game species over the last century. Amphibians are possibly the least-studied major vertebrate group in relation to fire research (Russell et al. 1999; Pilliod et al. 2003). The importance of amphibians to terrestrial and aquatic food webs (Burton and Likens 1975; Semlitsch et al. 1996; Walls and Williams 2001; Davic and Welsh 2004) accentuates their potential use as vertebrate bioindicators (Welsh and Ollivier 1998; Kerby et al. 2010) and inherent ecological value. There is a need to achieve a better understanding of changes in amphibian populations due to fire.

Historically, amphibians were assumed vulnerable to direct mortality from fire, largely due to limited mobility and direct mortality observations (Babbitt and Babbitt 1951). However, the majority of published research found no evidence that fire significantly affects short-term abundance of amphibian species (Ford et al. 1999; Ruthven et al. 2008). Grafe et al. (2002) suggested surface-aestivating anurans (i.e., frogs and toads) respond to auditory cues produced as a result of approaching fire by seeking burn-resistant refugia. Longer-term responses to fire-induced habitat changes are species and context specific (Moseley et al. 2003; Cummer and Painter 2007; Cano 2009; Rochester et al. 2010).

Prescribed burning during terrestrial post-metamorphic growth phases could potentially affect juvenile amphibian survivorship and health by reducing the quantity and quality of refugia by lessening litter, duff, and coarse woody debris (Tinker and Knight 2000; Matthews et al. 2010). Fire could impact juveniles both negatively and positively through invertebrate mortality. Moretti et al. (2006) and Vasconcelos et al. (2009) reported negative impacts on arthropod communities following fire, while Taber et al. (2008) and Greenberg et al. (2010) found little or no differences. Fire could negatively affect juvenile amphibians through a decline in their food base, but positively affect them through predator mortality (Toledo 2005). Predation probably plays a major role in survivorship of most amphibians at all life stages (Wells 2007). In addition to removal of predatory invertebrates, fire may also reduce predation by mesocarnivores. Jones et al. (2004) found raccoons (*Procyon lotor*) had higher preference for unburned compared to burned longleaf pine (*Pinus palustris*) stands, and Sunquist (1967) found raccoons reduced foraging activity in a Minnesota savannah following a prescribed burn.

The purposes of our study were to determine whether fire affected juvenile amphibian captures per unit effort (CPUE), and thus potentially juvenile amphibian survivorship, whether fire affected health (i.e., body condition) of individuals, and whether fire affected CPUE of potentially predatory invertebrates. To our knowledge this is the first quantitative study specifically addressing the short-term effects of fire explicitly on terrestrial juvenile amphibians.

Study Site

We conducted this study on the 1,948-ha Griffith League Ranch (GLR) in Bastrop County, Texas, USA. The GLR is located in the Lost Pines ecoregion, a 34,400-ha remnant patch of pine-dominated forest isolated from the East Texas Piney Woods ecoregion during the Pleistocene (Bryant 1977; Al-Rabab'ah and Williams 2004). The GLR is primarily a forested ranch with an overstory dominated by loblolly pine (*Pinus taeda*), post oak (*Quercus stellata*), blackjack oak (*Quercus marilandica*), and eastern red cedar (*Juniperus virginiana*), and an understory dominated by yaupon holly (*Ilex vomitoria*), American beautyberry (*Callicarpa americana*), and farkleberry (*Vaccinium arboreum*). The GLR contains three permanent ponds (i.e., ponds have not dried in at least 12 years), 10 semi-permanent ponds (i.e., ponds typically dry several times per decade), and dozens of ephemeral pools that hold water for days to months annually depending on rainfall. Prior to 2009, the study area had been fire suppressed for at least 60 years.

We documented 12 amphibian species on the GLR; 5 were included in this investigation (Figure 1): the coastal plain toad (*Bufo* [*Incilius*] *nebulifer*), the endangered Houston toad (*Bufo* [*Anaxyrus*] *houstonensis*), Hurter's spadefoot toad (*Scaphiopus hurterii*), the eastern narrowmouth toad (*Gastrophryne carolinensis*), and the Great Plains narrowmouth toad (*Gastrophryne olivacea*). These species typically breed in spring and early summer in this region, beginning in February for the Houston toad, and late March or early April for the remaining species (Forstner and Swannack 2004; Saenz et al. 2006; Brown et al. *In press*).

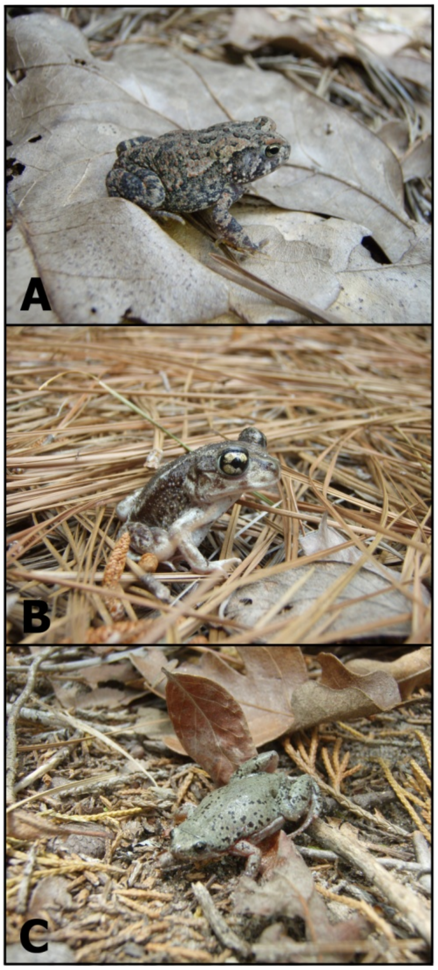

Figure 1. Genera included in our investigation on short-term impacts of fire on juvenile amphibians on the Griffith League Ranch (GLR), Bastrop County, Texas, USA in summer 2010: *Bufo* **(A)**, *Scaphiopus* **(B)**, and *Gastrophryne* **(C)**. Individuals shown are the Houston toad *B. houstonensis*, Hurter's spadefoot toad *S. hurterii*, and the Great Plains narrowmouth toad *G. olivacea*, respectively.

Metamorphosis usually occurs 15 to 50 days after eggs hatch, with a shorter time to metamorphosis for *Scaphiopus* and longer time to metamorphosis for *Bufo* (Wright and Wright 1949; Hillis et al. 1984). Pond-breeding anurans typically aggregate near pond edges for several weeks to months after metamorphosis and then disperse into the surrounding terrestrial landscape

(Arnold and Wassersug 1978; Greuter 2004). Studies have shown directional preferences in initial movement away from ponds (deMaynadier and Hunter 1999; Vasconcelos and Calhoun 2004), after which point movement appears to be essentially random outside of the microhabitat scale (Semlitsch 2008). Juvenile movements and foraging activities occur throughout summer months (June to September), with daily activity patterns likely heavily influenced by weather conditions (Roe and Grayson 2008; Child et al. 2009).

Methods

The primary goal of the GLR prescribed fire management policy is to reduce the depth of litter and duff layers accumulated over the past one-half century. This reduces the probability of a catastrophic wildfire and mimics the type of prescribed burns currently conducted throughout the Lost Pines ecoregion. We conducted a moderate severity prescribed burn on a 262-ha burn unit on 7 August 2010. Two moderate severity wildfires occurred on the GLR on 21 August 2010, burning 153 ha and 36 ha, respectively. Burn breaks were installed during the wildfires due to the intensity of the burns and the risk of the fires spreading beyond the boundaries of the GLR.

We assessed initial burn effects on habitat using vegetation plots (20 m by 50 m) established in 2008 by random placement within forested habitat. We surveyed vegetation plots between 10 and 29 days following the burns using National Park Service (2003) fire monitoring guidelines. Four vegetation plots were burned during the prescribed burn and one vegetation plot was burned during the wildfire. We assessed burn severity to substrate and vegetation within each plot using four 15 m transect lines, each consisting of four points spaced 5 m apart. We assigned points a burn severity ranking from 1 (heavily burned) to 4 (scorched) using a qualitative visual assessment (National Park Service 2003). In addition, we estimated char height and recorded status (i.e., alive or dead) for all overstory trees (i.e., diameter at breast height > 15 cm) within vegetation plots.

Sampling design

We used 18 Y-shaped and eight linear arrays for trapping amphibians and invertebrates. Y-shaped arrays consisted of three 15 m arms of flashing with a 19 L center bucket and a 19 L bucket at each arm terminus. Seven linear arrays consisted of a 15 m arm with a 19 L bucket at each end, and a double-throated funnel trap in the center of the array on each side of the flashing. One linear array consisted of a 121 m arm with a 19 L bucket at each end and a 19 L bucket near the center of the trap. We equipped pitfall traps with flotation devices to mitigate mortality during bucket flooding, and both pitfall and funnel traps with wet sponges to provide a moist environment for amphibians. We also equipped pitfall traps with predator exclusion devices (Ferguson and Forstner 2006).

The sampling design consisted of six sets of arrays with each set containing three Y-shaped arrays spread along drainages and between ponds, and one linear array adjacent to, and parallel with, a pond. The two remaining linear arrays were used to monitor amphibian movement between forest and grassland habitat, and activity at an additional pond, respectively. We did not create this sampling design explicitly for this experiment, but rather as part of long-term investigations on amphibian activity, movement, treatment response (e.g., prescribed fire), and habitat use (Swannack et al. 2009). To determine if the sampling design was suitable for detecting juvenile amphibians (arrays were located up to 618 m from breeding ponds) we regressed numbers of juvenile captures of three genera (*Bufo*, *Gastrophryne*, *Scaphiopus*) against array distance from breeding pond. These analyses showed that captures for all 3 genera spanned the distribution of array distance from source ponds; captures were positively associated with distances from breeding pond, and slopes were similar between sampling periods. Therefore, we included all 26 arrays in this study.

We trapped amphibians and invertebrates for seven days between 17 July 2010 and 24 July 2010 (i.e., 21 to 27 days prior to the prescribed burn), and seven days between 5 September 2010 and 12 September 2010 (i.e., 29 to 35 days after the prescribed burn, and 15 to 21 days after the wildfires). The September sampling period was unusually wet due to a heavy rain event caused by Tropical Storm Hermine. We checked traps and processed amphibians daily. We toe-clipped amphibians using an individual numbering system (Martof 1953), recorded snout-vent length (SVL) and head width to the nearest 0.1 mm using digital calipers (Control Company, Friendswood, Texas), and weight to the nearest 0.1 g using spring scales (Pesola, Baar, Switzerland). We collected invertebrates from all pitfall traps on the last day of each sampling period (i.e., we allowed pitfall traps to accumulate invertebrates for 7 days) and euthanized them by freezing. Handling permits were provided by Texas Parks and Wildlife Department (SPR-0102-191) and U.S. Fish and Wildlife Service (TE 039544-0). Trapping and handling methods were approved by the Texas State University-San Marcos Institutional Animal Care and Use Committee (Protocol No. 0810_0208_11).

A 1-m fire break was cleared around arrays in the prescribed burn unit, and we ensured that the burn carried to those breaks and spread throughout the adjacent habitat. Thus, the prescribed fire treatment included all four arrays within the treatment area. The wildfires occurred adjacent to two of the array sets. The distance from wildfire perimeters to these arrays ranged from 0 m to 280 m, with a mean distance of 94 m. Terrestrial juvenile anuran movement patterns are not well-studied (Wells 2007), and thus it is difficult to define the appropriate cutoff distance for wildfire influence on array captures during our study period. Smith and Green (2006) reported that most recaptured juvenile and adult Fowler's toads (*Bufo* [*Anaxyrus*] *fowleri*; *n* = 1326) were within 100 m of the location of initial capture over the course of two month sampling periods. Semlitsch (2008) suggested that long distance dispersal of most amphibian species is probably broken up into discrete events over multiple years due to low stamina in juveniles and a positive relationship between body size and locomotor capacity.

Because our preliminary regression analyses did not indicate that we were capturing juveniles actively dispersing from breeding ponds in the first sampling period (i.e., slopes were similar between sampling periods), we assumed that most individuals remained in the vicinity of their initial capture for the duration of the study. We considered captures at arrays >100 m from wildfire perimeters unlikely to be significantly affected by the wildfires, and we included these arrays as controls. The wildfire treatment included seven arrays, and the mean distance from wildfire perimeters to wildfire treatment arrays was 52 m (Figure 2). The prescribed fire treatment contained four arrays, with distance to unburned habitat ranging from 96 m to 209 m. The control treatment included 15 arrays, with distance to burned habitat ranging from 190 m to 1,295 m.

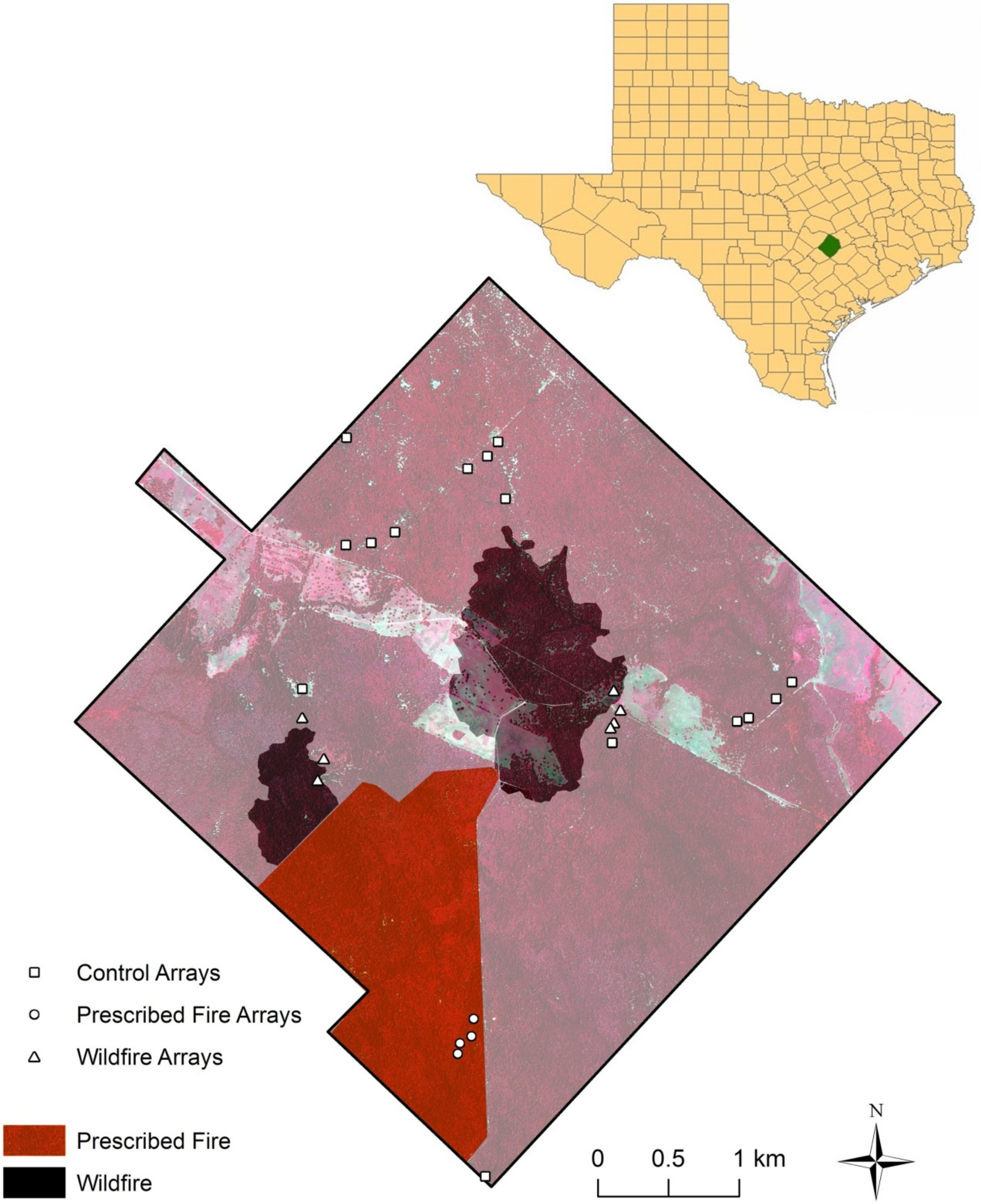

Figure 2. Aerial image of the Griffith League Ranch (GLR), Bastrop County, Texas, USA. Overlain on the image are the boundaries of the prescribed burn (7 August 2010) and wildfires (21 August 2010), and the arrays used to determine if number of amphibians captured, amphibian body condition, and number of predatory invertebrates captured differed among

treatments and sampling periods. The prescribed fire unit was 262 ha, and the wildfires burned 153 ha and 36 ha, respectively. The control, wildfire, and prescribed burn treatments contained 15, 7, and 4 arrays, respectively.

Statistical analyses

To increase sample sizes for amphibian capture comparisons we grouped captures by genus using a traditional classification system (Dixon 2000): *Bufo* (*B. nebulifer* and *B. houstonensis*), *Scaphiopus* (*S. hurterii*), and *Gastrophryne* (*G. carolinensis* and *G. olivacea*). We did not analyze the other genera present in our study area, *Acris*, *Ambystoma*, *Hyla*, and *Rana* (*Lithobates*), due to low total captures (i.e., <15 individuals per genus) of these taxa. Based on SVL values reported in Wright and Wright (1949), we captured 55 adults and removed these individuals from the data set.

For the three genera investigated, we used the total numbers of unique juveniles captured at each array within each sampling period as the response variable. We analyzed these data using mixed effects models, which allow for unbalanced designs (Zuur et al. 2009). We designated treatment (i.e., control, wildfire, or prescribed fire) and status (i.e., pre-burn or post-burn) as fixed effects and array as a random effect. We assessed assumptions of normality and homoscedasticity using residual plots. When we found significant differences, we determined which means were different using contrast comparisons (Maindonald and Braun 2003). We performed these analyses with the program R (R Version 2.10.1, www.r-project.org) using the nlme (Pinheiro et al. 2009) and contrast (Kuhn et al. 2010) packages.

We used body condition indices (BCI) to determine if health of individuals was affected by fire (Reading and Clarke 1995). For each genus within each sampling period, we regressed body length (SVL) on weight and used residuals as our response variable (Schulte-Hostedde et al. 2005). Positive and negative residuals indicate above and below average body condition, respectively. We removed 33 individuals from the data set because SVL or weight was not recorded, as well as recaptures within sampling periods. We linearized data for all three genera using the $\log_{10}$ transformation (Fowler et al. 1998). We analyzed these data using generalized least squares (gls) models, with treatment and status as predictors (Zuur et al. 2009). When we found significant differences, we determined which means were different using contrast comparisons (Maindonald and Braun 2003). We performed these analyses with the program R (R Version 2.10.1, www.r-project.org) using the nlme (Pinheiro et al. 2009) and contrast (Kuhn et al. 2010) packages.

Several larger invertebrates in our study system are likely to exert substantial predation pressure on terrestrial juvenile amphibians, including members of the class Arachnida (orders Scorpiones [i.e., scorpions] and Araneae [i.e., spiders]), and beetles in the family Carabidae (Toledo 2005). Although ants are also known to prey upon juvenile amphibians, we did not include ant captures because they can crawl into and out of pitfall traps, and thus, we could not accurately detect their captures with this sampling design. However, individuals are probably most vulnerable to ant predation when they first leave the water (Freed and Neitman 1988; Toledo 2005). Thus, for the predatory invertebrate analysis we used the total number of scorpions (*Centruroides vittatus*; Taber and Fleenor 2003), ground-dwelling spiders (primarily wolf spiders), and carabid beetles captured at each array within each sampling period as the response variable. We analyzed these data using identical statistical methods as for amphibian captures.

Results

The live fuel moisture during the prescribed burn was ca. 130%, with temperature, relative humidity, and wind speed estimates of 32.4 °C, 56.5%, and 1.6 kph, respectively, taken during the burn. Fire passed through 27 of the 64 substrate burn severity points during the prescribed burn, 13 of which contained vegetation. The mean severity ranking for substrate and vegetation was 3.5 and 3.7, respectively. Of the 164 overstory trees, 73 were charred, with a mean char height of 0.4 m. Four of the 141 overstory trees that were alive prior to the burn were killed. Temperature, relative humidity, and wind speed estimates taken during the wildfire were 37.6 °C, 32.4%, and 3.2 kph, respectively, with wind gusts up to 12.9 kph. Fire passed through all sixteen substrate burn severity points during the wildfires, 10 of which contained vegetation. The mean severity ranking for substrate and vegetation was 2.5 and 2.2, respectively. Of the 37 overstory trees, 33 were charred, with a mean char height of 2.8 m. Ten of the 30 overstory trees that were alive prior to the burn were killed.

We captured 210 *Bufo*, *Scaphiopus*, and *Gastrophryne* pre-burn, and 217 *Bufo*, *Scaphiopus*, and *Gastrophryne* post-burn. Individual species results are shown in Table 1. We recaptured two individuals in both sampling periods, and recaptured nine individuals within sampling periods. We found a significant treatment and treatment-status interaction effect for *Bufo*, and a treatment-status interaction effect for *Scaphiopus* (Table 2). Contrast comparisons showed that pre-burn and post-burn captures differed in the prescribed fire treatment for *Bufo* ($t_{44} = -3.03$, $P = 0.004$) and *Scaphiopus* ($t_{44} = -3.87$, $P < 0.001$), with no differences detected for the control or wildfire treatments (Figure 3).

Table 1. Number of pre-burn (trapped 17 July 2010 to 24 July 2010) and post-burn (trapped 5 September 2010 to 12 September 2010) captures in three treatments: control, wildfire, and prescribed fire, for juvenile amphibians on the Griffith League Ranch (GLR), Bastrop County, Texas, USA.

Species	Control[a]		Wildfire[b]		Prescribed fire[c]	
	Pre-burn	Post-burn	Pre-burn	Post-burn	Pre-burn	Post-burn
Bufo houstonensis	3	0	1	0	1	0
Bufo nebulifer	57	51	7	20	3	52
Bufo spp.[d]	8	0	5	0	9	0
Gastrophryne carolinensis	14	4	0	2	5	3
Gastrophryne olivacea	27	17	12	9	4	3
Scaphiopus hurterii	38	31	4	8	2	17

[a] Control treatment captures included 15 arrays.

[b] Wildfire treatment captures included 7 arrays.

[c] Prescribed fire treatment captures included 4 arrays.

[d] Young individuals lacked interspecific morphological trait differences.

Table 2. Results from a mixed effects model analysis with treatment (i.e., control, wildfire, or prescribed fire) and status (i.e., pre-burn or post-burn) as fixed effects and array as a random effect, used to determine if number of captures differed among treatments and sampling periods for three amphibian genera on the Griffith League Ranch (GLR), Bastrop County, Texas, USA.

Genus	Source of Variation	df	*F*	*P*
Bufo	Treatment	2,23	5.03	0.015
	Status	1,23	0.61	0.444
	Treatment*Status	2,23	4.97	0.016
Scaphiopus	Treatment	2,23	0.85	0.439
	Status	1,23	1.48	0.236
	Treatment*Status	2,23	7.51	0.003
Gastrophryne	Treatment	2,23	0.12	0.889
	Status	1,23	2.70	0.114
	Treatment*Status	2,23	0.42	0.662

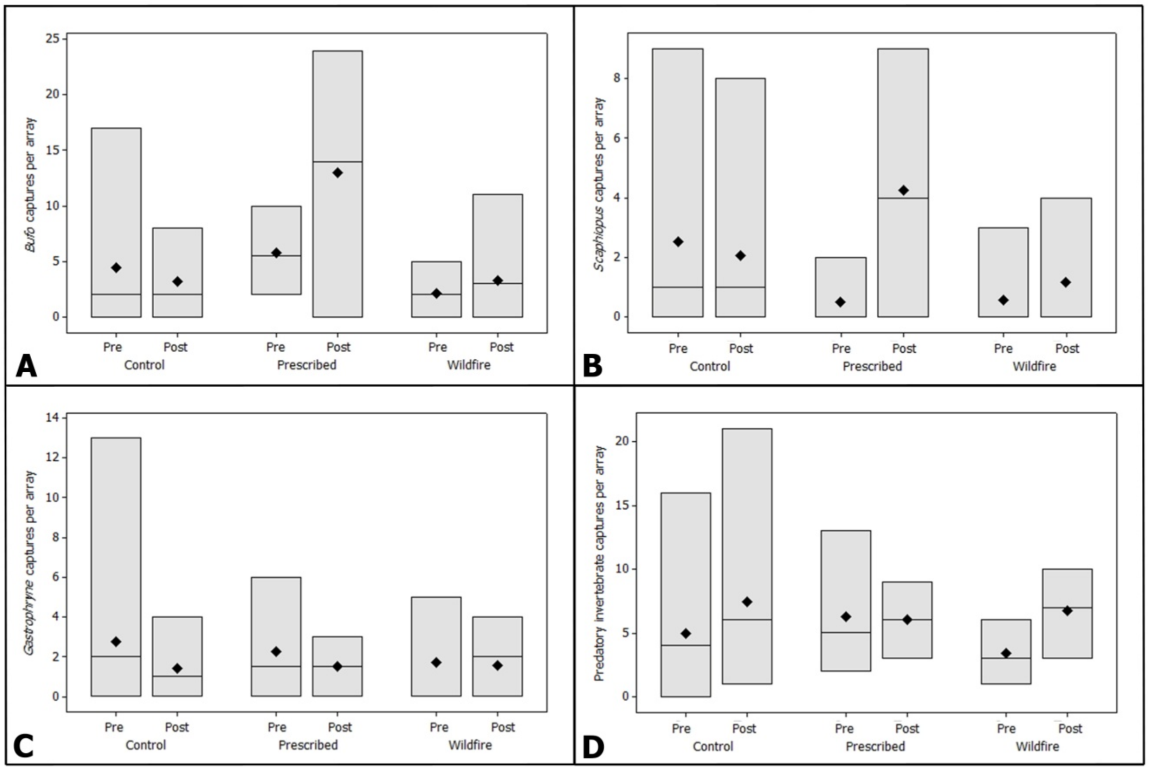

Figure 3. Number of pre-burn (trapped 17 July 2010 to 24 July 2010) and post-burn (trapped 5 September 2010 to 12 September 2010) captures at arrays in three treatments: control (n = 15), prescribed fire (n = 4), and wildfire (n = 7), for three amphibian genera: *Bufo* (A), *Scaphiopus* (B), and *Gastrophryne* (C), and predatory invertebrates (D) on the Griffith League Ranch (GLR), Bastrop County, Texas, USA. Boxes enclose the range, diamonds show the mean, and horizontal bars delineate the median number of captures at arrays within each treatment and sampling period.

For body condition comparisons we found a treatment effect for *Bufo*, and no significant differences for *Scaphiopus* or *Gastrophryne* (Table 3). For *Bufo*, the contrast comparisons showed body condition in the prescribed burn treatment differed from both the control (t_{212} = -2.98, P = 0.003) and wildfire (t_{212} = -3.59, P < 0.001) treatments. In both pre-burn and post-burn samples, *Bufo* in the control and wildfire treatments had a greater than average mean BCI score, and *Bufo* in the prescribed burn treatment had a lower than average mean BCI score.

Table 3. Results from a generalized least squares analysis with treatment (i.e., control, wildfire, or prescribed fire) and status (i.e., pre-burn or post-burn) as factors, used to determine if body condition differed between treatments and sampling periods for 3 amphibian genera on the Griffith League Ranch (GLR), Bastrop County, Texas, USA.

Genus	Source of Variation	df	*F*	*P*
Bufo	Treatment	2,212	7.71	<0.001
	Status	1,212	0.40	0.528
	Treatment*Status	2,212	1.64	0.196
Scaphiopus	Treatment	2,86	0.01	0.994
	Status	1,86	0.00	0.996
	Treatment*Status	2,86	0.03	0.967
Gastrophryne	Treatment	2,80	0.48	0.621
	Status	1,80	0.00	0.998
	Treatment*Status	2,80	0.66	0.517

We captured 123 predatory invertebrates pre-burn, and 182 predatory invertebrates post-burn. We found a status effect for predatory invertebrate captures ($F_{1,23} = 6.91$, $P = 0.015$). Treatment ($F_{2,23} = 0.18$, $P = 0.836$) and treatment-status interaction ($F_{2,23} = 0.86$, $P = 0.438$) effects were not significant.

Discussion

We found that neither the prescribed fire nor the wildfires negatively impacted juvenile captures or body condition for the three amphibian genera investigated. Indeed, *Bufo* and *Scaphiopus* captures were higher post-burn in the prescribed fire treatment. The fact that we captured substantially more *Bufo* and *Scaphiopus* post-burn in the prescribed fire unit warrants the following potential explanations: 1) the statistical increase in individuals was purely a function of weather-influenced activity; 2) new individuals entered the prescribed fire unit after the first sampling period, either through tadpole metamorphosis or dispersal into the unit; 3) capture rates were higher in the prescribed fire unit after the burn (presumably as a function of increased mobility and hence pitfall encounters by these species); or 4) survivorship was higher in the prescribed fire unit.

Weather is often strongly tied to amphibian population trends and activity patterns (Hillis et al. 1984; Pechmann and Wilbur 1994; Wells 2007) and undoubtedly influenced the number of captures within each sampling period. Here Tropical Storm Hermine resulted in substantial rains (8.1 cm) across the study area during the September sampling period. However, if weather were the only explanatory factor, we would expect to see the fire treatment results mirrored in the control treatment results. This appeared to be the case for *Gastrophryne* but not for *Bufo* or *Scaphiopus* with respect to the prescribed fire treatment. Thus, as discussed below, it appears additional factors influenced numbers of post-burn captures for at least the two latter species.

Another potential explanation is that the numbers of individuals increased in the prescribed fire unit after the first sampling period either through recruitment (i.e., tadpole metamorphosis) or dispersal into the unit. If recruitment were a major factor, we would expect SVL to be similar in the second sampling period (i.e., a mix of new small juveniles plus larger juveniles present during the first sampling period). Based on mean (± 1 SD) SVL between sampling periods in the prescribed fire unit (*Bufo* pre-burn: 20.26 mm ± 8.16, *Bufo* post-burn: 38.11 mm ± 6.40; *Scaphiopus* pre-burn: 20.30 mm ± 1.41, *Scaphiopus* post-burn: 29.91 mm ± 4.67), it is unlikely that recruitment can explain the results.

Although we cannot rule out the possible influence of dispersal into the prescribed fire unit, the nearest potential source pond outside of the sampling area was 900 m away. Further, only 1 of the 11 recaptures was found at a trap different from where it was first captured. Two individuals were captured in both sampling periods, and both of them were recaptured at the same trap. Finally, the mean BCI score in the prescribed fire treatment was significantly lower than control and wildfire treatments, but similar between sampling periods (*Bufo* pre-burn: -0.03 ± 0.07, *Bufo* post-burn: -0.01 ± 0.03; *Scaphiopus* pre-burn: 0.01 ± 0.06, *Scaphiopus* post-burn: 0.00 ± 0.04). These data, coupled with the regression analyses indicate that long distance dispersal was not prevalent during our study period.

The reduction in vegetative cover and litter depth in the prescribed fire treatment could have increased juvenile amphibian movement rates, and thus capture rates. Chelgren et al. (2011) found that detection probability for terrestrial salamanders was higher in burned than unburned plots. However, their sampling design consisted of randomized searching under substrates (i.e., active sampling) and thus did not address movement rates. The prescribed burn left much of the live vegetation unconsumed, and although the upper litter layer was consumed, there were no obvious changes that would have greatly increased mobility potential.

We hypothesize the most likely explanation for increased *Bufo* and *Scaphiopus* captures following the prescribed burn was increased survivorship coupled with increased activity levels as a consequence of Tropical Storm Hermine. Further, based on the BCI results, if this hypothesis is correct, it was more likely due to reduced predation pressure following the burn, relative to the other treatments, rather than an increase in food resources. Although we did not find statistical support for a treatment difference in predatory invertebrate captures, the significant post-burn increase was driven by increased captures in the control and wildfire treatments (see Figure 2). Further, mesopredators may have dispersed out of the prescribed-burn unit during or following the burn. Jones et al. (2004) found raccoons selected for non-burned longleaf pine (*Pinus palustris*) forest, presumably because fire inhibited production of soft mast. However, we did not monitor vertebrate predators, and thus, have no hard evidence to support or refute this scenario.

The results of our study agree with observations by Means and Campbell (1982) and Grafe et al. (2002) that amphibians do not appear to be particularly vulnerable to direct mortality from fire. In contrast to *Bufo* and *Scaphiopus*, there were no noticeable treatment differences for *Gastrophryne*. However, species and genera-specific results are common in the amphibian fire literature (cf. Moseley et al. 2003; Hossack and Corn 2007). With these trend-based data, it is not possible to discern whether fire had no short-term influence on *Gastrophryne* captures or a balance between negative (e.g., direct mortality) and positive (e.g., above hypotheses) capture influences.

In conclusion, the most important finding of our study was that fire did not appear to negatively impact short-term terrestrial juvenile amphibian survivorship or health. Further, we found intriguing evidence that in some cases fire might benefit amphibians not only through longer-term habitat changes (Means and Moler 1979; Hossack and Corn 2007), but also through short-term changes such as reduction in predator pressure, increased mobility potential, and increased food resources. However, we note that our interpretations were based on the assumption that seven day sampling periods were sufficient to accurately reflect differences among arrays for captures and body condition of amphibians. Further, we were unable to conduct multiple prescribed burns during the study period, and thus our ability to infer causation is limited. We encourage future research examining effects of fire on amphibian predators and predator-prey interactions. In addition to increasing causative understanding, this knowledge would help to elucidate the influence of burn season on amphibians and their community-level interactions, which influence both short-term and long-term outcomes of habitat restoration efforts.

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III. IMPACTS OF A HIGH SEVERITY WILDFIRE ON ABUNDANCE, MOVEMENT, AND DIVERSITY OF HERPETOFAUNA IN THE LOST PINES ECOREGION OF TEXAS

Abstract.—In September and October 2011, a high severity wildfire burned 39% of the 34,400-ha Lost Pines ecoregion in Bastrop County, Texas, USA. We assessed impacts of the wildfire on abundance, movement, and diversity of herpetofauna using drift fence array trap data collected prior to and after the wildfire, and anuran call survey data collected after the fire, on the 1,948-ha Griffith League Ranch. Based on *N*-mixture model analyses, abundance and movement of Six-lined Race Runners (*Cnemidophorus* [*Aspidoscelis*] *sexlineatus*) and Southern Prairie Lizards (*Sceloporus consobrinus*) were not significantly impacted by the wildfire shortly after its occurrence. A capture-recapture analysis indicated that movement rates were higher in the wildfire zone for Hurter's Spadefoot Toads (*Scaphiopus hurterii*) the following spring. Trap data indicated that the herpetofaunal species composition was not impacted by the wildfire shortly after the fire or subsequently, during the following spring. However, the anuran call survey data indicated that anuran species richness was higher in the wildfire zone. Collectively, it seems the wildfire had minimal negative impacts on abundance and diversity of herpetofauna in the short-term, a positive result for conservation in this ecoregion. In addition, our study indicated that investigations focused on fire impacts to ground-dwelling wildlife should consider detection probability when drawing inferences concerning abundances, particularly when differences in ground structure are apparent.

Key Words.—abundance; detection; diversity; fire; forest; herpetofauna; movement

INTRODUCTION

Pine-dominated forests throughout much of the U.S. are fire-maintained systems (Hartnett and Krofta 1989; Agee 1996; Schulte and Mladenoff 2005). In the absence of fire, flooding, and other disturbances, these forests progress towards a climax state dominated by hardwood trees (Gilliam and Platt 1999; Knebel and Wentworth 2007). Fire suppression over the last century altered the structure and composition of historically pine-dominated forests throughout the U.S. (Taylor 2000; Stephens and Ruth 2005; Nowacki and Abrams 2008). One issue associated with fire suppression is a consequent increase in fuel loads, which creates an environment conducive to high-severity fires (Davis 2001; Allen et al. 2002; Collins et al. 2010). Use of prescribed fire for reducing fuel loads and managing forest structure increased dramatically over the last half century. However, much of the U.S. forests remain severely fire-suppressed, and the frequency and severity of wildfires continues to increase in many regions (Houghton et al. 2000; Shang et al. 2007; Littell et al. 2009; Miller et al. 2009).

The Lost Pines ecoregion in Bastrop County, Texas, USA, is a 34,400-ha remnant patch of pine-dominated forest thought to have become finally isolated from the East Texas Piney Woods ecoregion between 10,000 and 14,000 y ago (Bryant 1977; Al-Rabah'ah and Williams 2004). The Lost Pines was extensively logged in the 1800s and early 1900s (Moore 1977). Fire suppression was implemented throughout the ecoregion since the early to mid-1900s, causing heavy fuel loads to accumulate. On 4 September 2011 a high-severity wildfire (i.e., the Bastrop County Complex Fire) began in the Lost Pines. The fire was unstoppable due to extreme drought conditions in central Texas coupled with wind gusts in excess of 58 kph resulting from the passage of Tropical Storm Lee. The fire after 18 d was 95% contained, and the total burned area encompassed 13,406 ha. The wildfire breached a fire break on 11 October 2011, burning another 125-ha.

Management and conservation initiatives in the Lost Pines largely focus on promoting healthy non-game wildlife populations, particularly the federally endangered Houston Toad (*Bufo* [*Anaxyrus*] *houstonensis*). Most previous research indicate that direct mortality during fires is minimal (e.g., Cunningham et al. 2002; Fenner and Bull 2007; Radke et al. 2008; Ruthven et al. 2008), but the impacts of fire on herpetofauna remains severely understudied (Russell et al. 1999; Pilliod et al. 2003). However, few previous studies assessed high-severity forest fires, and thus there is little information available to gauge direct mortality of such wildfires to herpetofauna. The immediate concern from governmental agencies and landowners was the possibility of substantial direct mortality because of the catastrophic nature of the Bastrop County Complex Fire (Lost Pines Recovery Team 2011). In addition to direct mortality, another topic currently of interest to both managers and researchers is how herpetofaunal species detection probabilities are affected by fire. This is relevant given that fire can significantly modify ground structure, potentially influencing activity and visibility of species (Hossack and Corn 2007; Chelgren et al. 2011).

We have recently studied the use of prescribed fire for managing Houston Toad populations and other herpetofauna in the Lost Pines (Brown et al. 2011). As part of this research, we surveyed herpetofauna on our primary study property in July 2011, 6 weeks prior to a wildfire. Here, we use these pre-burn data to investigate the possibility of significant direct herpetofaunal mortality during the Bastrop County Complex Fire. We also assessed movement of herpetofaunal species shortly after the fire, as well as the following spring, and determined whether species composition differed between burned and non-burned habitat in all three sampling periods. Finally, we use anuran call survey data collected in spring 2012 to determine whether species richness of calling anurans differed between burned and non-burned habitat. Collectively, these analyses provided useful insights into the short-term impacts of high-severity wildfires in a forest ecosystem, and the influence of detection on monitoring herpetofauna.

MATERIALS AND METHODS

***Study site*.—**We conducted this study on the 1,948-ha Griffith League Ranch (GLR), which primarily was forested with an overstory dominated by Loblolly Pine (*Pinus taeda*), Eastern Red Cedar (*Juniperus virginiana*), and Post Oak (*Quercus stellata*), and an understory dominated by Yaupon Holly (*Ilex vomitoria*), American Beautyberry (*Callicarpa Americana*), and Farkleberry (*Vaccinium arboreum*). The GLR contains three permanent ponds (i.e., ponds had not dried in at least 12 y), 10 semi-permanent ponds (i.e., ponds that typically dried several times per decade), and dozens of ephemeral pools that held water for days to months annually, depending on rainfall. Fire had been suppressed for at least 60 years prior to 2009 on the GLR, but since 2009 both prescribed burns and wildfires occurred on the study area. We conducted three low-severity prescribed burns between November 2009 and August 2010, burning ca. 378 ha. Two medium- to high-severity wildfires occurred on the GLR on 21 August 2010, which together burned 189 ha. The high-severity wildfire on 4 September 2011 burned 987 ha, followed by a second wildfire on 4 October 2011, which burned an additional 80.5 ha (Fig. 3.1). Because of their intensity, and thus their potential to dramatically impact the forest ecosystem, burn breaks were installed during all fires to minimize their spread.

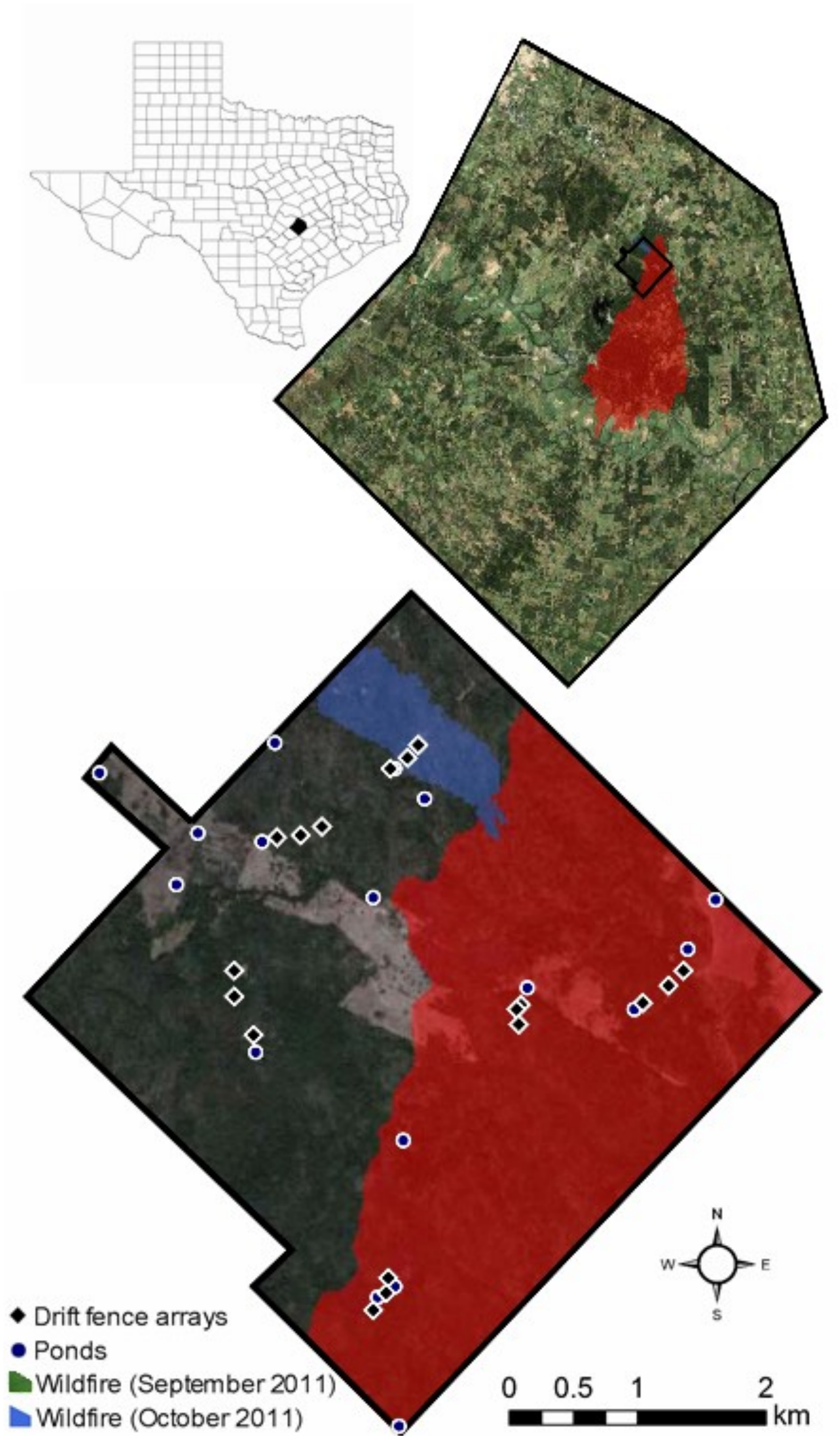

FIGURE 3.1. Aerial image of the Griffith League Ranch (GLR), Bastrop County, Texas, and its location with respect to a 13,406 ha wildfire that occurred in the Lost Pines ecoregion in

September 2011, with a breach of the fire break resulting in an additional 125 ha burned in October 2011. Overlain on the image are the wildfires, drift fence arrays and ponds used to study the abundance, movement, and diversity of herpetofauna following the wildfires. The September 2011 wildfire burned 987 ha (50.7%) of the GLR, and the October 2011 wildfire burned 80.5 ha (4.1%) of the GLR.

***Fire severity*.—**We assessed fire severity for the Bastrop County Complex Fire using vegetation plots (20 m by 50 m) randomly placed within forested habitat in 2008, and surveyed vegetation plots between 32-66 d after the wildfire using National Park Service (2003) fire-monitoring guidelines. Of the 31 vegetation plots on the GLR, 15 burned during the wildfire. We assessed burn severity to substrate within each plot using four 15 m transect lines, each consisting of four points spaced 5 m apart. We assigned points a burn severity ranking from one (heavily burned) to five (unburned). In addition, we estimated char height and recorded status (alive or dead) for all overstory trees (i.e., diameter at breast height > 15 cm) within vegetation plots.

***Herpetofaunal sampling*.—**We used 18 Y-shaped and six linear drift fence arrays to trap herpetofauna. The linear drift fence arrays were located adjacent to, and parallel with, ponds to maximize amphibian captures, whereas the Y-shaped arrays were located up to 600 m from the nearest pond. The aboveground height of the drift fence array flashing was at least 18 cm, with the flashing buried ca. 10 cm belowground. We buried flashing ca. Y-shaped arrays consisted of three 15 m arms with a 19 L center bucket and a 19 L bucket at each arm terminus. Linear arrays consisted of a 15 m arm with a 19 L bucket at each end, and a double-throated funnel trap in the center of the array on each side of the flashing. We equipped pitfall traps with flotation devices to mitigate mortality during bucket flooding, and both pitfall and funnel traps had wet sponges to provide a moist environment. We also equipped pitfall traps with predator exclusion devices (Ferguson and Forstner 2006). Most traps within the burned area were destroyed by the fire, so we rebuilt them in their exact pre-burn locations. The burn breaks installed on the ranch during the September 2011 wildfire fortuitously resulted in a balanced sampling design for the first post-wildfire sampling period, with 12 traps (nine Y-shaped arrays and three linear arrays) located in burned and control areas, respectively. The October 2011 wildfire burned the habitat surrounding two additional arrays, resulting in 14 traps (11 Y-shaped arrays and three linear arrays) located in burned areas, and 10 traps (seven Y-shaped arrays and three linear arrays) located in control areas, for the second post-wildfire sampling period.

We trapped herpetofauna for 7 d between 16-23 July 2011 (hereinafter pre-burn), 7 d between 25 September-2 October 2011 (hereinafter post-burn 1st), and 72 d between 19 February-30 April 2012 (hereinafter post-burn 2nd). We checked traps and processed herpetofaunal captures daily, estimated snout-vent length and tail length to the nearest 0.1 mm using digital calipers (Control Company, Friendswood, Texas, USA) or dial calipers (Wiha, Monticello, Minnesota, USA), and estimated weight to the nearest 0.1 g using spring scales (Pesola, Baar, Switzerland). We marked amphibians and lizards using toe clips (Ferner 2007), with amphibians marked individually and lizards cohort-marked.

We obtained sufficient captures of two lizard species, the Southern Prairie Lizard (*Sceloporus consobrinus*) and the Six-lined Race Runner (*Cnemidophorus* [*Aspidoscelis*] *sexlineatus*), to assess immediate wildfire impacts on abundance and detection probability. We obtained sufficient Hurter's Spadefoot Toad (*Scaphiopus hurterii*) captures and recaptures during the post-burn 2nd sampling period to determine if detection probabilities, and thus movement rates, differed between the control and wildfire habitats using a capture-recapture analysis. Finally, we determined if herpetofaunal species composition differed between the control and wildfire habitats during all three sampling periods.

In addition to sampling herpetofauna using traps, we also completed 24 anuran call surveys between 31 January-16 May 2012 following the protocol of Jackson et al. (2006). On each survey night we surveyed all ponds holding water (*n* = 15-19). We began surveys at dusk and surveyed each pond once per survey night for 5 min. We recorded the number of individuals heard calling for all detected species, unless the number of individuals calling was too large to count accurately (typically > 10 individuals). We used these data to determine if species richness of calling anurans (i.e., anurans engaged in breeding activity) differed between the unburned and burned locations. Thus, we assumed that a sufficient number of call surveys were completed to ensure that if a species was present at a pond it would have been detected at least once. We believe this was likely given previous work on call survey detection probabilities on the GLR (i.e., Jackson et al. 2006), and our knowledge of anuran calling activity on the GLR based on 11 years of call survey monitoring prior to this study.

***Statistical analyses*.—**We used a *N*-mixture modeling approach to estimate herpetofaunal abundance and detection probability (*P*) prior to and shortly after the wildfire (Dail and Madsen 2011). This approach uses both spatial and temporal replication of count data to jointly estimate abundance and *P* (Royle 2004). Thus, it accounts for observed numbers being a product of both ecological and observational processes. We used the open population *N*-mixture model (i.e., pcountOpen) developed by Dail and Madsen (2011), using the software package unmarked (version 0.9-8) in program R (version 2.14.2; Fiske and Chandler 2011). We assumed our statistical populations were closed within survey periods, but open between survey periods. We used the ‘constant’ population dynamics model in pcountOpen (i.e., apparent survival and recruitment were not explicitly linked in the model). In addition, we included habitat (control or wildfire) and time (pre-burn or post-burn) as covariates in estimations of *P*. We used Wald tests to assess the significance of the two covariates and their interaction ($\alpha = 0.05$). We determined the most appropriate distributions for our data sets (i.e., Poisson, zero-inflated Poisson, or negative binomial) by comparing the goodness-of-fit of each distribution using the ‘parboot’ function (Fiske and Chandler. 2012. Overview of Unmarked: An R package for the Analysis of Data from Unmarked Animals. Available from http://cran.r-project.org/web/ packages/unmarked/vignettes/unmarked.pdf [Accessed 1 September 2012]). We used a zero-inflated Poisson distribution for the Six-lined Race Runner analysis ($P = 0.29$), and a negative binomial distribution for the Southern Prairie Lizard analysis ($P = 0.31$).

Our data sets were not robust enough to achieve convergence when including habitat, time, and their interaction as covariates in estimations of apparent survival. Thus, to assess the short-term effect of the wildfire on abundance, we used the trap and time-specific estimated abundances as our count data in an additional analysis. We determined if habitat, time, and their interaction were significant predictors of Six-lined Race Runner and Southern Prairie Lizard abundance using generalized linear models with Poisson distributions (Zuur et al. 2009). We assessed assumptions of normality and homoscedasticity using residual plots. These analyses were conducted using program R (version 2.14.2).

We conducted a capture-recapture analysis to determine if apparent survival and *P* (and thus movement rates) of Hurter’s Spadefoot Toads differed between burned and non-burned habitat during the post-burn 2nd sampling period. Hurter’s Spadefoot Toads are explosive breeders (Wells 1977), and thus not all individuals emerged (i.e., entered the statistical population) simultaneously. Thus, we analyzed these capture-recapture data using a Cormack-Jolly-Seber model structure, which assumes the population is open (Cormack 1964, Jolly 1965, Seber 1965), and which allowed us to estimate both apparent survival and P. We specified four groups in the analysis: adult males, adult females, unburned habitat, and burned habitat. Through preliminary analyses we determined data were too sparse to accommodate time effects on either apparent survival or P. Therefore, time was not considered as a possible constraint in subsequent analyses. Consequently, the analysis assumed apparent survival and P to be constant across the duration of the post-burn 2nd sampling period. The constraints we considered assessed whether apparent survival and P did not vary between each sex nor across burned and unburned habitats (denoted *constant*), varied between each sex (*sex*), varied across burned and unburned habitats (*habitat*), or varied between each sex as well as across habitats (*sex* x *habitat*). Model selection was based on AIC, corrected for small sample size (AIC_C), and AIC_C weights (i.e., the most parsimonious model had the smallest AIC_C and the largest AIC_C weight; Burnham and Anderson 1998). We conducted model averaging to estimate parameters in the event that models were competing (≤ 2 AIC_C unit deviance in the highest ranking models). We conducted this analysis using program MARK (White and Burnham 1999).

To assess if herpetofaunal species composition differed between burned and non-burned habitat, we used an ecological distance approach (Clarke 1993). We performed Analysis of Similarity (ANOSIM) tests, using the Kulczynski ecological distance equation (Kindt and Coe 2005), for the pre-burn, post-burn 1st, and post-burn 2nd sampling periods. We included habitat as a predictor in the analyses to determine if sites were more similar within than between burned and unburned areas. For this statistical test, the computed test statistic (R) ranges from -1 to 1, with values near 0 indicating differences in species composition between burned and unburned habitats were small. We used a permutation test (*n* = 1,000) to assess the significance of *R* (α = 0.05). For the post-burn 2nd sampling period, we did not include terrestrial juvenile anurans that metamorphosed during the sampling period in the analysis. We assumed individuals did not disperse between burned and unburned habitats within each sampling period, which was supported by our recapture data. We conducted these analyses using the software package BiodiversityR (version 1.6) in program R (version 2.14.2).

To determine if species richness of calling anurans differed between unburned and burned areas we used a species accumulation curve approach. This approach was appropriate because species richness estimates are affected by sample size (Kindt and Coe 2005), and the number of surveyed ponds in each habitat type was not identical (*n* = 9 [burned]; *n* = 10 [non-burned]). We calculated the average pooled species richness (± SD) at each pond, within each habitat, for each sample size (i.e., 1 to 10 ponds surveyed), and assessed differences graphically using species accumulation curves. We conducted this analysis using the software package BiodiversityR (version 1.6) in program R (version 2.14.2).

RESULTS

***Fire severity*.—**Fire passed through 231 of the 240 substrate burn severity points during the September 2011 wildfire. The mean burn severity ranking for each plot ranged from 1−4.3, and the mean burn severity ranking among plots was 1.7 (Fig. 3.2). Of the 478 overstory trees that were alive in plots before the wildfire, 235 were killed during the fire (49.2% mortality). Seventy of these trees were not detected following the burn and were likely completely consumed by fire (i.e., 63.8% of overstory trees were either unaccounted for or dead). Mean estimated char height for all overstory trees was 7.3 m.

FIGURE 3.2. Terrestrial habitat around a drift fence array on the Griffith League Ranch (GLR), Bastrop County, Texas, USA, before (A) and after (B) a high severity wildfire on 4 September 2011. Nearly all of the understory vegetation, litter, duff, and coarse woody debris were consumed in most of the burned area, with substantial overstory tree mortality.

***Herpetofaunal impacts*.—**We captured 13, 9, and 18 herpetofaunal species during the pre-burn, post-burn 1st, and post-burn 2nd sampling periods, respectively. We captured 205 unique individuals during the pre-burn sampling period, 131 unique individuals during the post-burn 1st sampling period, and 7,153 unique individuals during the post-burn 2nd sampling period, of which 5,455 were recently metamorphosed Hurter's Spadefoot Toads (Table 3.1).

TABLE 3.1. Number of unique pre-burn (trapped 16 July 2011 to 23 July 2011), post-burn 1st (trapped 25 September 2011 to 2 October 2011), and post-burn 2nd (trapped 19 February 2012 to 30 April 2012) herpetofaunal captures on the Griffith League Ranch (GLR), Bastrop County, Texas, USA, using 24 drift fence arrays. The post-burn 1st sample included 12 arrays located in non-burned (Control) habitat, and 12 arrays located in burned (Wildfire) habitat. The post-burn 2nd sample included 10 arrays located in non-burned habitat, and 14 arrays located in burned habitat. The relative abundance of Hurter's Spadefoot Toads (*Scaphopus hurterii*) in the wildfire habitat (post-burn 2nd) is biased low due to erosion issues following heavy rainfall events, which caused most of the wildfire habitat pitfall traps to completely fill with sand. Captured juvenile amphibians that entered the terrestrial landscape during the post-burn 2nd sampling period are shown in parentheses.

Species	Control			Wildfire[a]		
	Pre-burn	Post-burn 1st	Post-burn 2nd	Pre-burn	Post-burn 1st	Post-burn 2nd
Amphibians						
Acris crepitans (Blanchard's Cricket Frog)	1	0	0	0	0	0
Ambystoma tigrinum (Tiger Salamander)	0	0	0	0	0	59
Bufo [*Incilius*] *nebulifer* (Coastal Plain Toad)	7	0	12 (1)	3	2	25 (4)

Gastrophryne carolinensis (Eastern Narrow-mouthed Toad)	1	0	2	2	2	4
Gastrophryne olivacea (Western Narrow-mouthed Toad)	5	4	14	3	10	11
Hyla cinerea (Green Tree Frog)	0	0	0	1	0	0
Hyla versicolor (Gray Tree Frog)	0	0	0	0	0	4
Pseudacris streckeri (Strecker's Chorus Frog)	0	0	0	0	0	0 (13)
Rana [*Lithobates*] *catesbeiana* (American Bullfrog)	0	0	0	0	0	2
Rana [*Lithobates*] *sphenocephala* (Southern Leopard Frog)	1	0	2	2	0	10
Scaphiopus hurterii (Hurter's Spadefoot Toad)	0	0	468 (85)	0	0	939 (5,370)
Lizards						
Scincella lateralis (Little Brown Skink)	3	1	3	2	1	5
Cnemidophorus [*Aspidoscelis*] *sexlineatus* (Six-lined Race Runner)	18	12	14	27	18	25
Sceloporus consobrinus (Southern Prairie Lizard)	77	45	42	48	33	30
Snakes						
Agkistrodon contortrix (Broad-banded	1	0	0	0	0	0

Copperhead)						
Heterodon platirhinos (Eastern Hog-nosed Snake)	0	1	1	0	0	0
Leptotyphlops [*Rena*] *dulcis* (Texas Threadsnake)	0	0	0	0	0	1
Micrurus tener (Texas Coralsnake)	0	0	0	1	0	1
Nerodia erythrogaster (Plain-bellied Watersnake)	0	0	0	0	0	2
Storeria dekayi (Texas Brownsnake)	0	0	0	0	0	1
Tantilla gracilis (Flat-headed Snake)	1	0	1	0	1	2
Thamnophis proximus (Ribbon Snake)	0	0	0	1	1	0

[a]Wildfires occurred on 4 September 2011 and 4 October 2011, burning 987 ha (50.7%), and 80.5 ha (4.1%) of the study area, respectively.

***Lizard abundance and detection*.—**We captured 45 and 97 unique Six-lined Racerunners and Southern Prairie Lizards during the pre-burn sampling period, respectively, and 30 and 31 unique Six-lined Racerunners and Southern Prairie Lizards during the post-burn 1st sampling period, respectively. We recaptured 1 Six-lined Racerunner and 7 Southern Prairie Lizards that were marked during the pre-burn sampling period. Cumulative estimated abundance of Six-lined Racerunners was 25.5 individuals in the control habitat and 25.4 individuals in the wildfire habitat during the pre-burn sampling period, and 69.4 individuals in the control habitat and 68.3 individuals in the wildfire habitat during the post-burn 1st sampling period. For Six-lined

Racerunners, we did not find a significant habitat-time interaction for abundance (*Z* = 0.03, df = 44, *P* = 0.977), and abundance did not differ by habitat (*Z* = -0.10, df = 44, *P* = 0.924). However, abundance differed by time (*Z* = -4.32, df = 44, *P* < 0.001). Cumulative estimated abundance of Southern Prairie Lizards was 299.6 individuals in the control habitat and 306.1 individuals in the wildfire habitat during the pre-burn sampling period, and 33.8 individuals in the control habitat and 36.6 individuals in the wildfire habitat during the post-burn 1st sampling period. For Southern Prairie Lizards, we did not find a significant habitat-time interaction for abundance (*Z* = -0.23, df = 44, *P* = 0.819), and abundance did not differ by habitat (*Z* = 0.33, df = 44, *P* = 0.741). However, abundance differed by time (*Z* = 12.02, df = 44, *P* < 0.001).

For Six-lined Race Runners, we did not find a significant habitat-time interaction for *P* (*Z* = -0.24, *P* = 0.808), and *P* did not differ by habitat (*Z* = 1.63, *P* = 0.103), or time (*Z* = -1.46, *P* = 0.145). Estimated detection probabilities were higher post-burn in both habitats, and were higher in the wildfire habitat than the control habitat (Fig. 3.3a). For Southern Prairie Lizards, we did not find a significant habitat-time interaction for *P* (*Z* = -1.20, *P* = 0.231), and *P* did not differ by time (*Z* = 1.19, *P* = 0.233). However, *P* differed by habitat (*Z* = -2.76, *P* = 0.006). Estimated detection probabilities were higher pre-burn in both habitats, and were higher in the control habitat than the wildfire habitat (Fig. 3.3b).

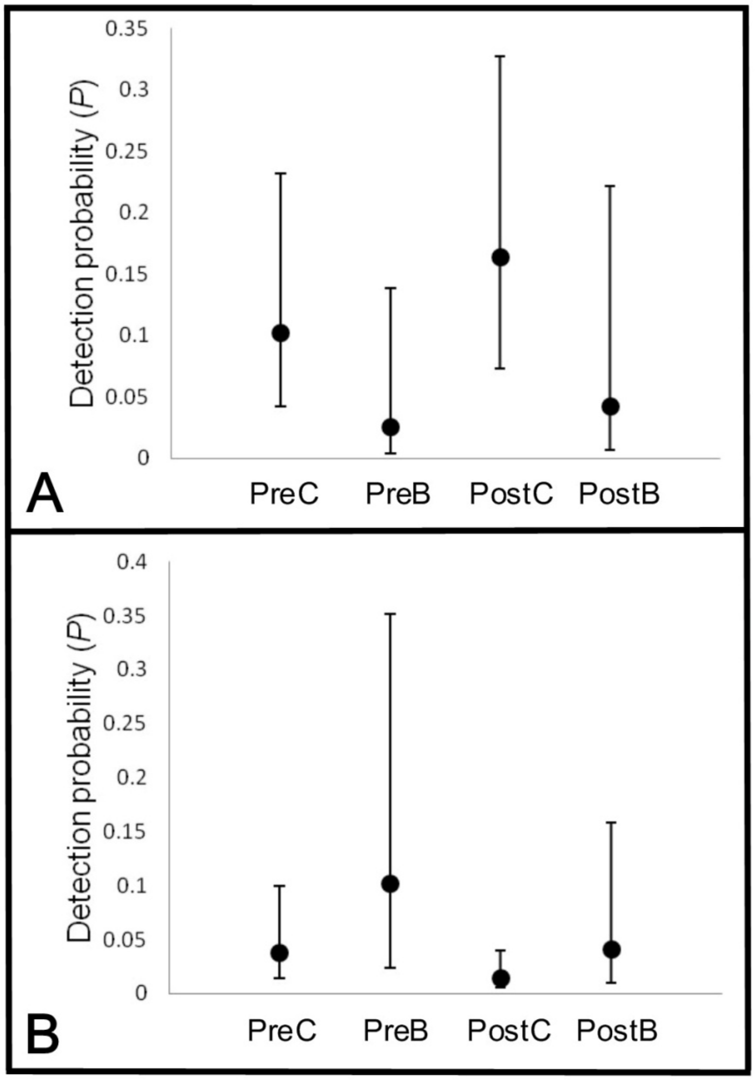

FIGURE 3.3. Estimated detection probabilities for Six-lined Race Runners (A) and Southern Prairie Lizards (B), before (Pre) and after (Post) high severity wildfire in control (C) and burn (B) habitats on the Griffith League Ranch (GLR), Bastrop County, Texas, USA. Parameter estimates are shown with 95% confidence intervals. The wildfire did not appear to alter detection probabilities for these species in the short-term, which were sampled using drift fence arrays.

Hurter's Spadefoot Toad detection.—We captured 1349 unique adult Hurter's Spadefoot Toads, 123 of which were recaptured at least once. The highest ranked model included no covariate for apparent survival, and habitat as the covariate for *P* (AIC_C weight = 0.17). However, there was little support for this model over the second highest ranked model (ΔAIC_C = 0.09), which included habitat as a covariate for apparent survival, and no covariate for *P* (AIC_C weight = 0.17), or additional models that included sex as a covariate (Table 3.2). Despite the lack of strong support for a single model, results were consistent, with both apparent survival and *P* for both males and females being higher in the burned than in the unburned habitat (Fig. 3.4).

TABLE 3.2. Model selection results from a capture-recapture analysis used to determine if apparent survival (*S*) and detection probability (*P*) varied by sex and between non-burned and burned habitat for adult Hurter's Spadefoot Toads (*Scaphiopus hurterii*) on Griffith League Ranch (GLR), Bastrop County, Texas, USA, during spring 2012. We sampled the population using 24 drift fence arrays, 14 of which were located in burned habitat. We used a Cormack-Jolly-Seber model structure, which assumes the population was open, and did not include time effects on estimates of *S* and *P*. Model selection was based on Akaike Information Criterion, corrected for small sample size (AIC_C). We used 1,349 unique individuals (742 male and 607 female) in the capture-recapture analysis.

Model	AIC_C	ΔAIC_C	AIC_C weight	Parameters
S(.) *P*(treatment)	1537.8	0.00	0.17	3
S(treatment) *P*(.)	1537.9	0.09	0.17	3
S(sex) *P*(treatment)	1538.3	0.47	0.14	4
S(treatment) *P*(sex)	1538.5	0.67	0.12	4
S(treatment) *P*(treatment)	1539.0	1.22	0.09	4
S(sex x treatment) *P*(.)	1540.0	2.23	0.06	5

S(.) *P*(sex x treatment)	1540.4	2.65	0.05	5
S(sex x treatment) *P*(treatment)	1541.1	3.31	0.03	6
S(.) *P*(.)	1541.2	3.42	0.03	2
S(sex) *P*(.)	1541.6	3.78	0.03	3
S(treatment) *P*(sex x treatment)	1541.6	3.85	0.03	6
S(.) *P*(sex)	1541.7	3.88	0.02	3
S(sex x treatment) *P*(sex)	1541.7	3.94	0.02	6
S(sex) *P*(sex x treatment)	1542.1	4.30	0.02	6
S(sex) *P*(sex)	1543.4	5.57	0.01	4
S(sex x treatment) *P*(sex x treatment)	1543.8	6.02	0.01	8

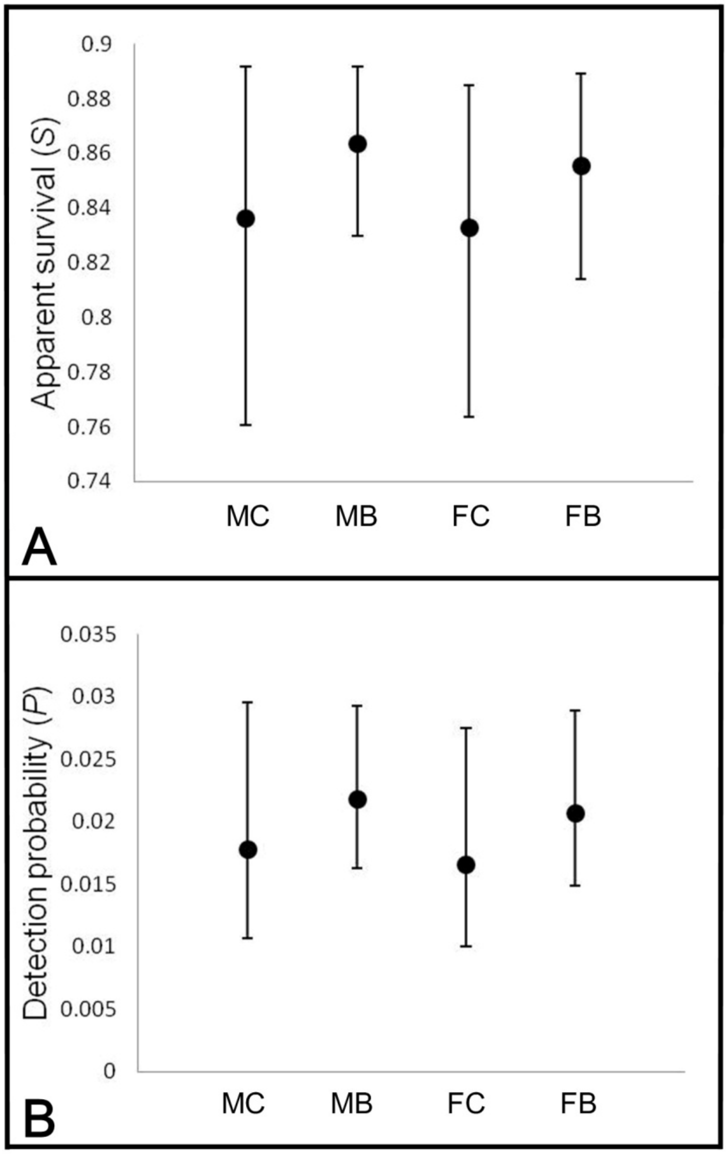

FIGURE 3.4. Adult male (M) and female (F) Hurter's Spadefoot Toad (*Scaphiopus hurterii*) apparent survival (*S*; A) and detection probability (*P*; B) estimates in non-burned (C) and burned (B) habitat during spring 2012 on Griffith League Ranch (GLR), Bastrop County, Texas, USA. Parameter estimates represent model-averaged results from competing models (see Table 2), and are shown with 95% confidence intervals. Estimates of both *S* and *P* were higher for both males and females in burned compared to non-burned habitat. However, support for an optimal model was low.

***Herpetofaunal species composition*.**—We found no difference in herpetofaunal species composition between unburned and burned habitat during the pre-burn (R = -0.020, P = 0.56), post-burn 1st (R = 0.021, P = 0.32), or post-burn 2nd sampling periods (R = -0.073, P = 0.90). During the pre-burn sampling period we detected 10 herpetofaunal species in unburned habitat and 10 species in burned habitat; 7 species were captured in both habitat types. During the post-burn 1st sampling period we detected 4 species in unburned habitat and 8 species in burned habitat; 4 species were captured in both habitat types. During the post-burn 2nd sampling period we detected 10 species in unburned habitat and 17 species in burned habitat; 9 species were captured in both habitat types. During the post-burn 1st sampling period, all species captured in unburned habitat were also captured in burned habitat. During the post-burn 2nd sampling period, the only species captured in unburned habitat that was not captured in burned habitat was the Eastern Hog-nosed Snake (*Heterodon platirhinos*), which was represented by only one individual.

***Species richness of calling anurans*.**—We found that total species richness of calling anurans was equal between ponds in unburned and burned habitat (10 total species detected). However, the species accumulation curves indicated that species richness of calling anurans was higher at ponds in burned habitat when at least eight ponds were surveyed (i.e., SD did not overlap; Fig. 3.5).

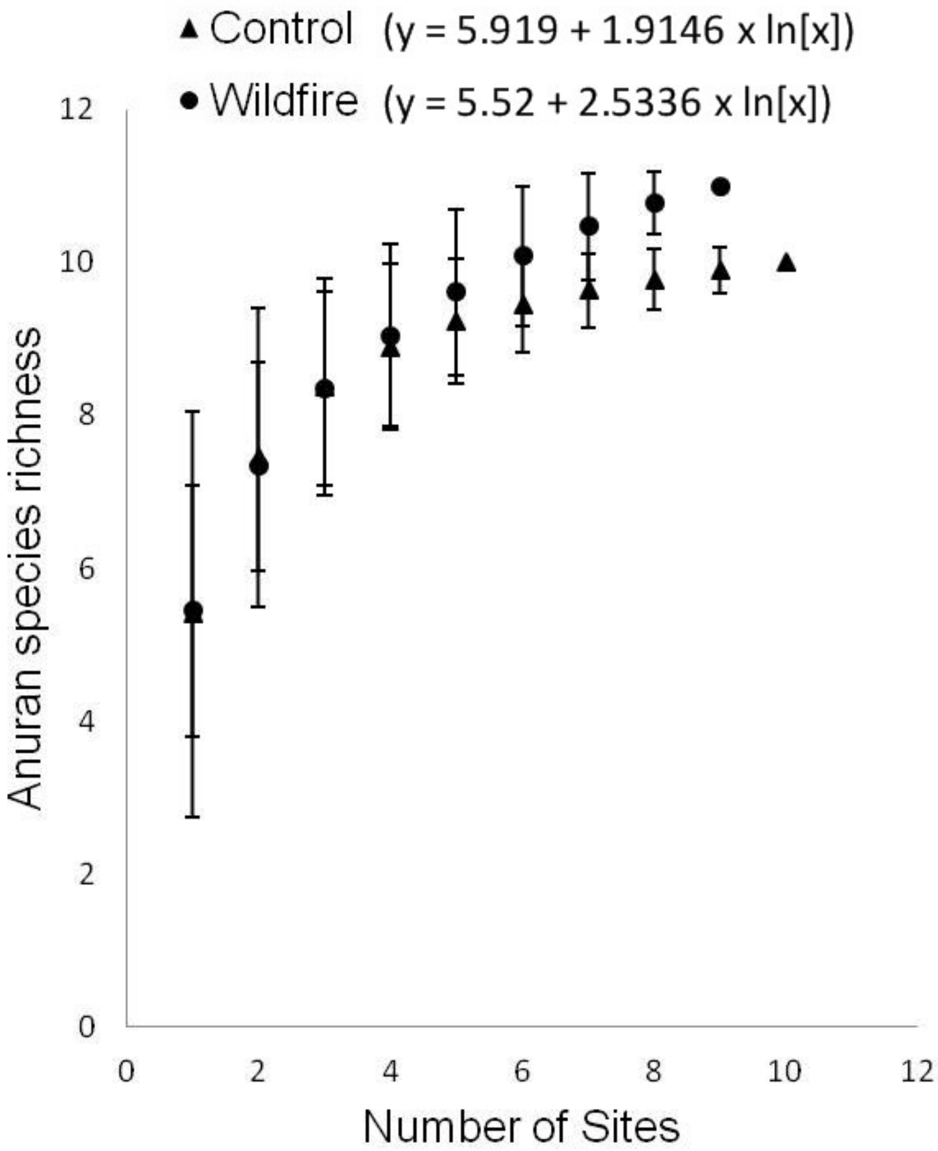

FIGURE 3.5. Species accumulation curves for calling anurans at ponds located within non-burned (wildfire; *n* = 9) and burned (control; *n* = 10) habitat on the Griffith League Ranch (GLR), Bastrop County, Texas, USA. We completed 24 anuran call surveys between 31 January 2012 and 16 May 2012. We surveyed all ponds holding water on each survey night (*n* = 15 to 19).

DISCUSSION

Our results agree with most previous studies, which concluded mortality from fire was minimal for amphibians and reptiles (e.g., Cunningham et al. 2002; Fenner and Bull 2007; Greenberg and Waldrop 2008; Radke et al. 2008; Brown et al. 2011; Milanovich et al. 2011). Observational studies during prescribed burns documented lizards escaping fire by burrowing under the soil and climbing trees (Bishop and Murrie 2004; Beane 2006), and Grafe et al. (2002) suggested that surface-aestivating anurans respond to auditory cues of approaching fire by seeking burn-resistant refugia. Most individuals that survived this wildfire were likely underground, given that crowning (i.e., fire in the tree canopy) was prevalent. For herpetofauna that were active at the time of the wildfire, with the possible exception of the terrestrial Three-toed Box Turtle (*Terrapene carolina triunguis*) and any dispersing semi-aquatic turtles, rapid burrowing under the soil was probably not difficult given the predominance of deep sandy soils in the Lost Pines ecoregion (Baker et al. 1979). While surveying and searching within the burn zone, we did find several Red-eared Slider (*Trachemys scripta elegans*) turtle shell fragments, and a partial Three-toed Box Turtle plastron, but cannot be certain those turtles died from the wildfire.

Our results indicated that detection probability (*P*) of two lizard species was not affected by the wildfire in the short-term. This gives some credence to results from previous studies using drift fence sampling that did not model *P* when assessing responses of lizards to fire, which as far as we are aware, includes all but one previous study (Driscoll et al. 2012). However, we note that Driscoll et al. (2012) found evidence that the detection probability model they used, which included a daily detection/non-detection framework (as opposed to individual-based detection probabilities used here), did not capture what were likely differences in activity levels between burned and unburned areas. We also note that our *P* estimates lacked precision, as indicated by broad confidence intervals (see Fig. 3). Alternately, we obtained some evidence that *P* for Hurter's Spadefoot Toad was higher in the burned than in the unburned habitat. Chelgren et al. (2011) concluded that a wildfire positively influenced detection probabilities for five salamander species sampled using active searches. As far as we are aware, ours is the first study to indicate this phenomenon for amphibians using drift fences, which suggests that movement rates can increase after fires. However, we cannot conclude from these data what factors changed following fire that resulted in our observations, and thus we do not know if this was a general fire effect or a habitat-specific effect. An additional observation during the post-burn 2nd sampling period on adult Tiger Salamanders (*Ambystoma tigrinum*) is worth noting. Between spring 2008 and summer 2011 we trapped for 387 days, including 56 to 89 days each year between February and April, using 4 drift fence arrays located near a GLR pond within what would become the high-severity wildfire zone (Pond 9), and captured two Tiger Salamanders. During the 72 days of trapping in spring 2012, we captured 57 unique individuals near Pond 9. These data indicate that either movement rates or movement distances increased dramatically for Tiger Salamanders following the wildfire, or alternately some other factor led to a seemingly dramatic increase in detection for this species after the wildfire.

The evidence for higher anuran species richness at ponds in the wildfire habitat indicated that anurans were not only present in burned habitat, but used it for reproduction. Thus, despite the dramatic habitat changes, the post-fire landscape was not perceived by anurans to be unsuitable habitat. This result agrees with previous studies that addressed impacts of a single wildfire on amphibian habitat use (Kirkland et al. 1996; Cummer and Painter 2007; Guscio et al. 2007; Hossack and Corn 2007). Our results indicated that pond occupancy within burned habitat may have increased after wildfire, and we intend to assess this possibility across the Lost Pines ecoregion in the coming years. As discussed earlier, the reduced vegetation and ground structural complexity could have increased movement rates, and thus potentially dispersal distances. In addition, we hypothesize that anuran calls traveled further in the burned habitat because of reduced vegetation, which could assist with pond colonization by breeding anurans. Hossack and Corn (2007) found that pond occupancy by Boreal Toads (*Bufo* [*Anaxyrus*] *boreas*) increased dramatically following a wildfire in Montana. If the endangered Houston Toad responds similarly in the Lost Pines, this could be viewed as a positive effect of wildfire. During spring 2012 anuran call surveys throughout the Lost Pines ecoregion, we detected Houston Toads at ponds in both unburned and burned habitat, including several ponds within the burn zone where we had not detected them during call surveys over the last decade. However, we note that because this species has critically low numbers (Duarte et al. 2011), and Houston Toad breeding success at a given pond increases exponentially with number of calling males (Gaston et al. 2010), increased occupancy in suboptimal habitat (e.g., ponds located within residential areas or similar small forest fragments) may actually expedite the extirpation of this species from the Lost Pines.

The limited mortality inferred from our analyses is a positive result for management of the endangered Houston Toad and other threatened herpetofauna (i.e., Texas Horned Lizard *Phrynosoma cornutum* and Timber Rattlesnake) found in the Lost Pines (Brown et al., in press). Despite the positive immediate wildfire effects on herpetofauna found in this study, indirect effects (e.g., prey reduction, litter and coarse woody debris removal, overstory tree thinning, water quality impacts) are still a major concern. In our opinion, the most critical impact of the wildfire was overstory tree loss. Both the endangered Houston Toad and threatened Timber Rattlesnake prefer heavily canopied environments (U.S. Fish and Wildlife Service 1984; Brown

1993). The estimated loss of 63.8% of overstory trees on the GLR was similar to an overall projection from the Texas Forest Service for the entire burned area (78%; Lost Pines Recovery Team 2011), and it will take decades for these areas to return to mature forest.

Although most of the remaining wild Houston Toads are currently in the Lost Pines ecoregion (Brown 1971, 1975), it would be valuable to focus some future recovery efforts (e.g., headstarting, Vandewege et al. 2012) on other geographically disjunct populations to prevent against extinction in the wild, given the unknown trajectory of the Lost Pines population. This latter point is supported by previous studies emphasizing that probability of extinction in the Lost Pines will likely increase dramatically with a catastrophic wildfire (Seal 1994), or lack of multiple viable populations (Hatfield et al. 2004).

In conclusion, this study adds to the growing literature indicating high severity fires are not inherently detrimental to amphibians and reptiles, even in the immediate and short-term. Further, the wildfire could increase herpetofaunal diversity in the coming decades due to habitat diversification (e.g., the creation of large patches of early-succession forest habitat). We intend to continue monitoring herpetofauna in the Lost Pines to document population and community trends in relation to natural forest recovery and active restoration initiatives.

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IV. COMPARISON OF LOW, MODERATE, AND HIGH SEVERITY FIRE IMPACTS TO AQUATIC AND TERRESTRIAL ECOSYSTEM COMPONENTS OF A SOUTHERN USA MIXED PINE FOREST

ABSTRACT

Historically fire was an important natural disturbance shaping the structure and composition of pine-dominated forests in the southern United States. Longstanding fire suppression policies have resulted in structural and compositional changes, notably accumulation of heavy fuel loads and reduction in vegetation species diversity. Primary goals of forest management through prescribed burning include fuel load reduction and mimicking ecosystem impacts of historically natural wildfires. In addition to the influences of fire frequency and season, the influence of fire severity on ecosystem responses is currently of interest. In this study we assessed the impacts of low, moderate, and high severity fires to several aquatic and terrestrial ecosystem components of a southern U.S. mixed pine forest using a before-after, control-impact (BACI) approach. The ecosystem components we assessed were water quality, species composition of aquatic arthropods (wildfire impacts only), forest structure characteristics, species composition of understory vegetation, and species composition of ground-dwelling arthropods. We found that fire severity was an important factor influencing the response of the ecosystem components we assessed. Fire at all severity levels increased aquatic nutrient levels and productivity, but the magnitude of effects increased with severity. Low and moderate severity fires had weak effects on forest structure characteristics, species composition of understory vegetation, and species composition of ground-dwelling arthropods. In contrast, high severity fires dramatically reduced fine and large fuel loads, increased diversity and cover of understory vegetation, and influenced species composition of ground-dwelling arthropods. However, we did not detect a fire response for aquatic arthropods. Our results contribute to the growing evidence that fire severity is a primary factor influencing responses of ecosystems to fire.

Keywords:
Arthropods
Forest
Prescribed fire
Vegetation
Water chemistry
Wildfire

Highlights:

1. The magnitude of fire effects on water quality increased with increasing fire severity.
2. Low and moderate severity fires had weak effects on forest structure characteristics and species composition of understory vegetation, whereas high severity fires dramatically reduced fine and large fuel loads and increased tree mortality and diversity and cover of understory vegetation.
3. Low and moderate severity fires had no detectable effects on species composition of ground-dwelling arthropods, whereas high severity fires influenced species composition.

1. Introduction

Climatic trends towards warmer and drier conditions, coupled with longstanding broad-scale fire suppression, have resulted in an increase in high severity wildfires in the southern and western United States (Davis, 2001; Miller *et al.*, 2009), with this trend projected to continue into the next century (Moritz *et al.*, 2012). These wildfires are prevalent in pine-dominated forests (Miller *et al.*, 2009), which are naturally fire-maintained systems (Hartnett and Krofta, 1989; Schulte and Mladenoff, 2005). In the absence of fire these forests typically progress towards a climax state dominated by hardwood trees (Gilliam and Platt, 1999; Knebel and Wentworth, 2007; Hanberry *et al.*, 2012). Further, suppression-induced increase in fuel loads often creates environments conducive to abnormally high severity wildfires (Davis, 2001; Allen *et al.*, 2002; Collins *et al.*, 2010). Thus, integration and maintenance of fire management is necessary for restoration and sustainability of healthy pine forests (Agee, 1996). Although the use of prescribed fire for reducing fuel loads and managing forest communities has increased dramatically over the last half century, much of the U.S. remains severely fire-suppressed (Houghton *et al.*, 2000; Shang *et al.*, 2007; Gebert and Black, 2012).

In addition to reducing fuel loads, a common goal of prescribed burning is to mimic ecosystem impacts of historically natural wildfires within a controlled setting (Vose, 2000). Thus, increasing our knowledge of similarities and differences between prescribed fire and wildfire, with respect to ecosystem impacts, is of interest to both ecologists and land managers (Schwilk *et al.*, 2006; Glasgow and Matlack, 2007; Arkle and Pilliod, 2010). This question has resulted in much research being devoted to effects of burn season and frequency, particularly on vegetation (e.g., Cain *et al.*, 1998; Sparks *et al.*, 1998; Taylor, 2000; Webster and Halpern, 2010). Much less is known about effects of burn severity, given that prescribed burns are typically low to moderate severity fires. In contrast, high severity wildfires are unplanned, and thus wildfire research is by necessity a response to non-designed treatments, and opportunities for research are more limited.

Previous research suggests there are consistencies with regards to fire impacts on nutrients in both terrestrial and aquatic environments. In the short-term, fire often increases soil nitrogen (N) and phosphorus (P) availability through conversion of organic to inorganic forms, with fire severity positively related to nutrient increases (Wan *et al.*, 2001; Certini, 2005). Similarly, N and P in both still and flowing waters typically increases after fire (Battle and Golladay, 2003; Earl and Blinn, 2003). In both terrestrial and aquatic environments, nutrient availability tends to decrease to background levels over a period of weeks to a few years (Wan *et al.*, 2001; Earl and Blinn, 2003; Spencer *et al.*, 2003). However, in some cases fire can impact nutrient levels for decades (McEachern *et al.*, 2000; Duran *et al.*, 2010).

Fire can directly impact biotic communities through both heat-induced mortality (animals and plants) and heat-induced reproduction (plants; Gauthier *et al.*, 1996; Schwilk *et al.*, 2006; Engstrom, 2010). Fire can indirectly impact biotic communities through alteration of nutrient availability (Lewis, 1974; Gilliam, 1988; Battle and Golladay, 2003), structural habitat modification (e.g., removal or addition of debris; Sweeney and Biswell, 1961; Tinker and Knight, 2000; Hall *et al.*, 2006), and alteration of interspecific and intraspecific interactions, as a result of other direct and indirect impacts. Thus, fire effects on biotic ecosystem components are inherently complex and difficult to extrapolate to other ecosystems. Further, the impacts of high severity fires are typically not short-lived, but rather a fire can influence a given ecosystem for decades to centuries (Hall *et al.*, 2006; Lecomte *et al.*, 2006; Webster and Halpern, 2010).

Fire can influence plant community composition primarily through direct impacts on mortality and reproduction (Gauthier *et al.*, 1996; Simmons *et al.*, 2007), changes in nutrient availability (Wan *et al.*, 2001), and alteration of ground structure (e.g., removal of leaf litter), which influences space and light availability (Sweeney and Biswell, 1961; Tinker and Knight, 2000; Hall *et al.*, 2006). Because all of these factors are affected by fire severity, we would expect higher severity fires to have a greater impact on plant communities than lower severity fires in fire-suppressed forest ecosystems, where probability of tree survival is heavily influenced by fire intensity (Oosting, 1944; Safford *et al.*, 2012; Thies and Westlind, 2012), and understory plant growth is largely limited by dense litter and duff layers (Hodgkins, 1958; Glasgow and Matlack, 2007; Wayman and North, 2007).

Compared to nutrient and vegetation impacts, effects of fire on animal taxa are much more variable and unpredictable, likely due to more complex trophic interactions and their ability to adapt to habitat changes through both movement and behavioral responses (Geluso and Bragg, 1986; Jones *et al.*, 2004; Engstrom, 2010). Animal-based studies often detect minimal or no effects of prescribed fire (Ford *et al.*, 1999; Greenberg and Waldrop, 2008; Dickson *et al.*, 2009; Greenberg *et al.*, 2010). However, studies assessing impacts of fire severity on animals have found that severity is an important factor affecting population and community dynamics. Smucker *et al.* (2005) reported that several bird species responded positively to low severity fire and negatively to high severity fire in the same study area, and Roberts *et al.* (2008) found equivalent results for small mammals. Alternately, through a meta-analysis on bird and small mammal responses to fire severity, Fontaine and Kennedy (2012) concluded that fire severity did not impact species response direction, but response magnitude increased with fire severity. Further, response direction varied, which is a common result for fire effects studies on animal taxa (e.g., ground beetles in black pine (*Pinus nigra*) forests, Rodrigo *et al.*, 2008; lizards in a tropical savanna, Trainor and Woinarski, 1994).

The ensemble of previous fire research suggests that fire severity is an important, and potentially driving, factor in determining fire impacts to essentially all fire-affected ecosystem components (Knapp *et al.*, 2009). Thus, to improve our understanding of the potential of fire for ecosystem management, and to better understand the role of fire severity, there is a need to quantify the impacts of fire severity within ecosystems. In this study we used water quality, aquatic arthropod (wildfire impacts only), vegetation, and ground-dwelling arthropod data collected prior to and following low severity winter prescribed burns, moderate severity summer prescribed burns, moderate severity summer wildfires, and high severity summer wildfires to compare and contrast effects of fire severity on several ecosystem components within a mixed pine forest in the southern USA.

In addition to our basic interest concerning fire severity effects, we also have an applied interest specific to our study area, the Lost Pines ecoregion of Texas. This ecoregion is the last remaining stronghold for the federally endangered Houston toad (*Bufo* [*Anaxyrus*] *houstonensis*), and populations have been declining within the ecoregion for decades, to the point now where the species is at high risk of extinction in the wild (Gaston *et al.*, 2010; Duarte *et al.*, 2011; Brown *et al.*, 2013). Thus, we are interested in fire as a habitat restoration tool in this ecoregion, with particular interest in potential and realized effects on this endangered species (Brown *et al.*, 2011; Brown *et al.*, 2012). To this end, we included a discussion of results of this study with respect to potential impacts on the Houston toad.

2. Methods

2.1. Study area

This study was conducted in the Lost Pines ecoregion in Bastrop County, Texas, USA. The Lost Pines is a 34,400-ha remnant patch of pine-dominated forest that is thought to have been isolated from the East Texas Piney Woods ecoregion between 10,000 and 14,000 years ago (Bryant, 1977), with the pines of the area beginning to diverge up to 30,000 years ago (Al-Rabah'ah and Williams, 2004). The Lost Pines was extensively logged in the 1800s and early 1900s (Moore, 1977). Since the early to mid-1900s broad-scale fire suppression has been implemented throughout the ecoregion, resulting in the accumulation of heavy fuel loads.

The study area for this project was the 1,948-ha Griffith League Ranch (GLR). The GLR is primarily a forested ranch with an overstory dominated by loblolly pine (*Pinus taeda*), post oak (*Quercus stellata*), and eastern red cedar (*Juniperus virginiana*), and a pre-burn understory dominated by yaupon holly (*Ilex vomitoria*), American beautyberry (*Callicarpa Americana*), and farkleberry (*Vaccinium arboreum*). The property is underlain by deep sandy soils of the Patilo-Demona-Silstid Association (Baker *et al.*, 1979). The GLR contains 3 permanent ponds (i.e., ponds have not dried in at least 12 years), 10 semi-permanent ponds (i.e., ponds typically dry several times per decade), and dozens of ephemeral pools that hold water for days to months annually depending on rainfall.

2.2. Fires

2.2.1. Prescribed burns

We conducted prescribed burns on the GLR on 13 November 2009, 10 January 2010, and 7 August 2010, with the prescribed burn areas encompassing ca. 21 ha, 95 ha, and 262 ha, respectively. The habitat management goal of the prescribed burns was fuel load reduction, and burn intensities were low to reduce the potential for the fires to spread beyond the designated burn units, and to reduce the probability of crowning (i.e., aerial fire in the forest canopy).

2.2.2. Wildfires

Two moderate severity wildfires occurred on the GLR on 21 August 2010, which burned 36 ha and 153 ha, respectively. These fires were likely started from embers in the 7 August 2010 prescribed burn unit that were wind-thrown. Burn breaks were installed during the fires to restrict their spread. On 4 September 2011 a high severity wildfire began from multiple initial fire outbreaks across the Lost Pines. The fire was unstoppable due to wind gusts in excess of 58 kph resulting from the passage of tropical storm Lee, coupled with extreme drought conditions in central Texas (Lost Pines Recovery Team, 2011). After 18 days the fire was 95% contained, with the total burn area encompassing 13,406 ha. A fire break was installed on the GLR during the burn, restricting the fire on the property to 987 ha. On 11 October 2011 the wildfire breached a fire break on the GLR, burning an additional 125 ha (Figure 4.1).

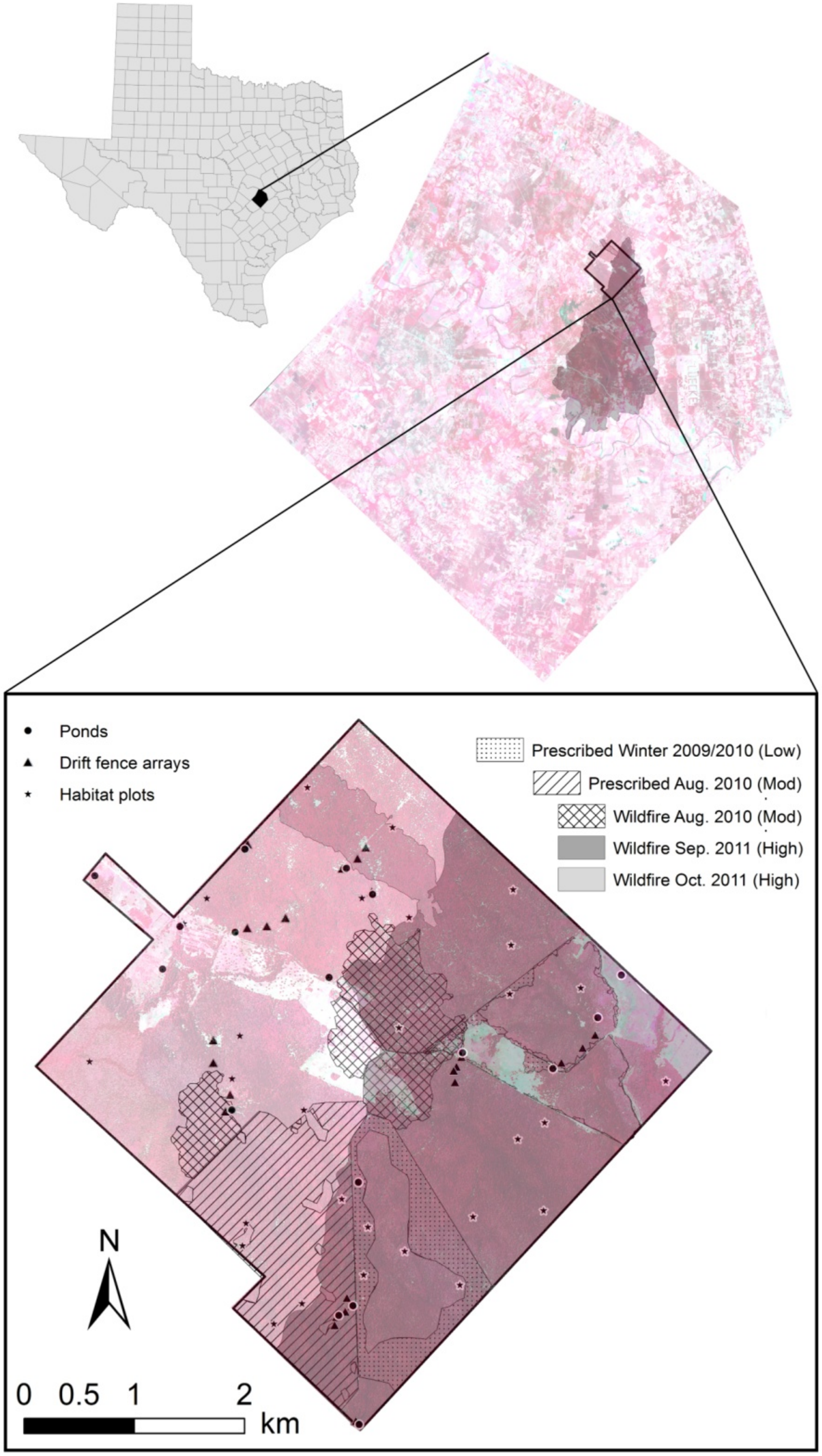
Ponds
Drift fence arrays
Habitat plots
Prescribed Winter 2009/2010 (Low)
Prescribed Aug. 2010 (Mod)
Wildfire Aug. 2010 (Mod)
Wildfire Sep. 2011 (High)
Wildfire Oct. 2011 (High)
N
0 0.5 1 2
km

Figure 4.1. Aerial image of the Griffith League Ranch (GLR), Bastrop County, Texas, USA, and its location with respect to a 13,406 ha wildfire that occurred in the Lost Pines ecoregion in September 2011, with a breach of the fire break resulting in an additional 125 ha burned in October 2011. Overlain on the image are the locations of all fires included in this study, and the locations of the ponds, terrestrial habitat plots, and drift fence arrays used for this study assessing the impacts of fire severity on aquatic and terrestrial ecosystem components.

2.3. Data collection

2.3.1. Water quality

We assessed water quality opportunistically at 16 ponds on the GLR between 17 April 2009 and 4 February 2012, with sampling frequency highest shortly before and following fires to capture immediate impacts. We sampled the study area a total of 32 times, with each pond sampled between 3 and 25 times (median = 15). Days between sampling ranged from 2 to 150 (mean = 33). Whether or not a given pond was sampled usually depended on whether or not the pond held water at the time of sampling. However, a subset of 5 ponds were sampled monthly in 2009 for an independent study (Gaertner et al. 2012), and ponds located in burned units were sampled more frequently immediately following burns. We sampled water within 1 m of pond edges using 1 L Nalgene® collection bottles. Within 24 hours of collection we estimated pH using a SympHony 5B70P pH meter, filtered pond water through Gelman A/E glass-fiber filters (1 µm pore size), and preserved water samples with 85% sulfuric acid. We extracted chlorophyll *a* (Chl-*a*) from filters with acetone, and analyzed Chl-*a* using a Turner Designs Trilogy fluorometer. We quantified total suspended solids (TSS) in the water column by drying precombusted and pre-weighed filters at 60 °C for 48 to 72 hours, re-weighing them, and combusting the filters at 550 °C for four hours (Heiri *et al.*, 2001). We obtained filter mass using a Mettler Tolido MX5 microbalance.

We used a Varian Cary 50 Ultraviolet-Visible light spectrophotometer for the remaining water quality analyses. We measured soluble reactive phosphorus (SRP) and total phosphorus (TP) using the molybdenum blue method (Wetzel and Likens, 2000). To estimate TP we digested unfiltered samples with potassium persulfate then quantified SRP. We measured nitrate (NO_3^-) and total nitrogen (TN) using second-derivative UV spectroscopy (Crumpton *et al.*, 1992). To estimate TN we digested unfiltered samples with alkaline potassium persulfate then quantified NO_3^-. We analyzed ammonium (NH_4^+) using the phenol-hypochlorite method (Wetzel and Likens, 2000). For all water quality analyses we collected two water samples per pond, and used the average of the replicates for this study.

In addition to measuring water quality variables, we also estimated pond area between August 2008 and March 2010, and percent canopy cover around each pond between August 2008 and February 2010, and during all post September 2011 wildfire sampling events, for use as covariables in water quality analyses. For small ponds we recorded perimeter lengths using a long tape and estimated area using area formulas for geometric shapes. For larger ponds we walked the perimeter of the pond and tracked our movements using a handheld GPS unit (Garmin GPSMAP 60). We then estimated area using a Geographic Information System (Esri ArcGIS 9.3). We estimated percent canopy cover around each pond using a spherical densiometer at two to six randomly selected points at the pond edge, with higher numbers of estimation points corresponding to larger ponds. We then averaged the estimates at each pond per sampling date. To obtain estimates for the water quality sampling dates when we did not estimate pond size or percent canopy cover, we regressed each variable against pond depth, which was recorded during each sampling event, and used pond depth to estimate the covariable values.

The terrestrial habitat surrounding 4 ponds was burned during the November 2009 and January 2010 prescribed fires, 2 ponds during the August 2010 prescribed fire, 2 ponds during the August 2010 wildfires (including 1 previous burn pond), and 7 ponds during the September 2011 wildfire (including 6 previous burn ponds). The remaining 8 ponds served as controls in this study. However, we note that these ponds were not necessarily completely free of fire impacts, as volatized nitrogen could have been deposited in control ponds through smoke deposition (Earl and Blinn, 2003).

2.3.2. Aquatic arthropods

Unfortunately sampling of aquatic arthropods was initiated after the low and moderate severity fires and most of the sampled ponds were not part of those burn treatments, and thus we were only able to assess impacts of the high severity fire. We sampled aquatic arthropods seasonally, collecting 7 samples at 8 ponds between August 2010 and January 2013 using a standard dip net (900 micron netting). The data set included 4 control ponds and 4 wildfire ponds, and 3 pre-burn and 4 post-burn samples. For each sampling period at each pond we sampled three points ca. 1 m from the perimeter, maintaining approximately even spacing between points, and performed 3 dip net sweeps per point. We stored samples in plastic collection tubes containing 95% ethanol. For this study we identified insects to family, with the exception of Ephemeroptera (mayflies) and Odonata (dragonflies and damselflies) identified to order, and we identified other arthropods to class or order. Further, we removed larval forms from the data set with the exception of Chironomidae (non-biting midges), Culicidae (mosquitos), Ephemeroptera, Odonata, and Trichoptera (caddisflies), for which all captures were larvae. The resulting data set contained 26 aquatic arthropod groups.

2.3.3. Vegetation

We used National Park Service (2003) fire monitoring guidelines to assess fire severity and impacts of the fires on forest structure characteristics and species composition of understory vegetation. We randomly placed thirty-one 20 m x 50 m plots in forested habitat, 29 of which were used in this study. The remaining 2 plots were abandoned after fire breaks were accidentally installed within them during wildfires. Only 1 plot was burned in the 2010 moderate severity wildfires, and this plot was used only in fire severity analyses. In addition, because no plots were burned in the November 2009 low severity prescribed fire, we installed 1 temporary plot adjacent to a permanent plot to assess fire severity. Two plots were burned during the January 2010 low severity prescribed fire, 4 plots during the August 2010 moderate severity prescribed fire, 1 plot during the August 2010 moderate severity wildfire, and 17 plots during the September and October 2011 high severity wildfires (including 4 plots that had been burned previously).

We surveyed vegetation plots throughout summer and fall of 2008, 2009, 2010, and 2012, and assessed fire severity at all plots within 66 days of a fire. In addition, we surveyed burned plots in 2011 to assess tree mortality from the low and moderate severity fires. For this study, we quantified the following variables in all plots: percent canopy cover, overstory (DBH ≥ 15 cm) and pole-sized (DBH ≥ 2.5 cm and < 15 cm) tree mortality by species, seedling tree (DBH < 2.5 cm) abundance, understory vegetation species cover, shrub and herbaceous vegetation abundance, litter and duff depth, and fuel abundance (1 hour, 10 hour, 100 hour, and 1000 hour). We identified shrubs, vines, and forbs to species or genus. We identified the 2 most common grasses in the study area to genus (i.e., *Dicanthelium* and *Eragrostis*), with the remaining grasses grouped into the family Poaceae for analyses. To assess fire severity to substrate within each burned plot we used four 15 m transect lines, each consisting of 4 points spaced 5 m apart. We assigned points a burn severity ranking from 0 (unburned) to 4 (heavily burned). Overstory canopy cover is not included in the National Park Service (2003) fire monitoring guidelines, but is of interest in our study area. We estimated percent canopy cover using a spherical densiometer at the 4 corners and center of each plot, then computed the mean of those 5 estimates for our plot estimate each survey year.

2.3.4. Ground-dwelling arthropods

We sampled ground-dwelling arthropods 24 times between 8 March 2009 and 21 April 2012 using 18 Y-shaped and 7 linear drift fence arrays. Y-shaped arrays consisted of three 15 m arms with a 19 L center bucket and a 19 L bucket at each arm terminus. Linear arrays consisted of a 15 m arm with a 19 L bucket at each end. We sampled at least once in spring, summer, and fall annually during the sampling period, with additional sampling events occurring during the spring months and following the burns. For each sampling event we allowed pitfall traps to collect arthropods for 7 days prior to collection. We euthanized arthropods through freezing, sorted arthropod captures by drift fence array, and identified insects to family and other arthropods to order. For this study we did not include larvae with the exception of Myrmeleontidae (antlions), and we removed captures of primarily flying arthropods (i.e., Diptera [flies], Cicadidae [cicadas], Aculeata [wasps], Lepidoptera [moths], and Odonata [dragonflies]).

We also did not include Formicidae (ant) captures due to their ability to easily crawl into and out of pitfall traps. The resulting data set contained 49 ground-dwelling arthropod groups.

The terrestrial habitat surrounding 4 drift fence arrays was burned during the November 2009 low severity prescribed fire, 4 drift fence arrays during the August 2010 moderate severity prescribed fire, and 14 drift fence arrays during the September and October 2011 high severity wildfires (including all 8 drift fence arrays that had burned previously). The remaining 10 drift fence arrays served as controls in this study.

2.4. Data analyses

2.4.1. Water quality

We assessed impacts of the fires to pond water quality using Principal Response Curves (PRC), an extension of Redundancy Analysis (RDA; Van den Brink and Ter Braak, 1999). This multivariate analysis method is designed to assess treatment effects over time, and allows both an overall community response and specific response variables to be assessed through comparisons to control sites (Lepš and Šmilauer, 2003). The significance of treatment-time interactions is assessed using Monte Carlo permutation tests, where sites are randomized within, but not across sampling periods (p-values in the results represent permutation tests for the first canonical axis).

Of the 16 ponds monitored, 8 were subjected to fire, with 6 subjected to multiples fires. Because the fires occurred at different times, we conducted 3 separate analyses, assessing impacts of low (i.e., winter 2010 and 2011 prescribed burns), moderate (i.e., summer 2010 prescribed burn and wildfires), and high (i.e., summer 2011 wildfires) severity fire. To minimize the influence of fires not included in a given analysis, we removed ponds from the data set (i.e., sampling periods) after they were burned in another fire. Ponds that were burned multiple times re-entered the data set after the fire of interest. Thus, the pre-burn samples were truly pre-burn in all analyses. In addition, for the low and moderate severity fire analyses, we did not include any sampling events after the 2011 wildfires, given that all but 1 of those ponds re-burned in those wildfires.

For all 3 analyses we included sampling period, pond depth, and canopy cover at the pond edge as covariates. Including sampling period allowed us to test for a treatment-time interaction. The data set included several missing values (i.e., 20 of 2710 observations), and we estimated those values using the mean for a given variable and pond across all samples. We centered and standardized the response data because variables were measured on different scales (i.e., response variables had a zero average and unit variance). In addition, we log transformed the response data so that percentage rather than absolute changes in captures were analyzed. We performed these analyses using the program CANOCO (version 4.5).

2.4.2. Aquatic arthropods

We assessed wildfire impacts on both total captures and species composition of aquatic arthropods. To assess wildfire impacts on total captures we used generalized least squares analyses, with the capture data transformed using the arcsinh (i.e., inverse hyperbolic sine) transformation to satisfy assumptions of normality and homoscedasticity (Fowler *et al.*, 1998). We accounted for non-independence in our repeated measures data using a continuous autoregressive term (corCAR1) nested within each pond (i.e., time series; Zuur *et al*., 2009). We then tested for an interaction between treatment (control or fire) and burn status (pre-burn or post-burn).

To assess impacts of the high severity wildfire on species composition we used redundancy analysis (RDA), again because our gradient lengths were short (< 4) and our predictors were categorical (Lepš and Šmilauer, 2003). To assess whether or not the wildfire impacted species composition we tested for a treatment-burn status interaction using a Monte Carlo permutation test (p-value in the results represents a permutation test for the first canonical axis). We included ponds as covariates. By including ponds as covariates we subtracted the average captures and assessed only capture changes within each pond (Lepš and Šmilauer, 2003). We log transformed the response data so that percentage rather than absolute changes in captures were analyzed. We performed this analysis using the program CANOCO (version 4.5).

2.4.3. Vegetation

We summarized differences in burn severity with respect to substrate and tree mortality using a visual descriptive statistics approach. We calculated the mean, median, and range of fire severity ranks in the low, moderate, and high severity fire vegetation plots. Further, we categorized the high severity plots by whether they were controls prior to the 2011 wildfire, or had been burned in the prior winter or summer fires. This allowed us to assess whether or not prior burning reduced severity of the 2011 wildfires. To compare impacts on tree mortality, we separated trees into 3 genus-level groups: pine (loblolly pine), oak (post oak, blackjack oak [*Quercus marilandica*], and water oak [*Quercus nigra*]), and cedar (eastern red cedar), and plotted the proportion of overstory and pole-sized trees that died within 1 year following the fires for each group.

To assess impacts of the fires to forest structure characteristics and species composition of understory vegetation, we used redundancy analyses (RDA), which is an extension of principal components analysis (PCA) to include explanatory variables. We chose RDA over canonical correspondence analysis (CCA) because our gradient lengths were short (< 4) and our predictors were categorical (Lepš and Šmilauer, 2003). For forest structure characteristics, we included 12 response variables: 1 hour fuel (0 to 0.64 cm), 10 hour fuel (0.65 to 2.54 cm), 100 hour fuel (2.55 to 7.62 cm), 1000 hour fuel (> 7.62 cm), litter depth, duff depth, overstory canopy cover, understory species cover, vegetation species richness, cedar seedling abundance, oak seedling abundance, and pine seedling abundance. Our understory species cover metric was the number of points along a transect line (i.e., 166 total points, with points located every 0.3 m along a 50 m transect) intersected by vegetation. Our species richness metric included all vegetation groups (see section 2.3.2) encountered from the tree, shrub and vine, and herbaceous vegetation sub-plots, and the understory species cover transect.

To assess whether or not the fires impacted forest structure characteristics and understory community composition, we tested for treatment-burn status interactions using a Monte Carlo permutation test (p-values in the results represent permutation tests for the first canonical axis). We included vegetation plots and cumulative precipitation between January and May (i.e., prior to initiation of sampling) for each sample year as covariates. By including plots as covariates, we subtracted the average response variable values and assessed only changes in response variable values within each plot (Lepš and Šmilauer, 2003).

For the forest structure characteristics analyses, we centered and standardized the response data because variables were measured on different scales (i.e., response variables had a zero average and unit variance). In addition, we log transformed the response data so that percentage rather than absolute changes in captures were analyzed. For the understory species composition analyses, we centered and log transformed the response data. We removed 10 shrub and 41 herbaceous vegetation records because we were unable to identify the plants. In addition, we removed dead individuals and species with less than 5 total observations (shrubs: $n = 5$; forbs: $n = 23$), resulting in 28 vegetation groups. We performed additional univariate analyses on species that appeared to display strong response in the high severity wildfire analysis, including yaupon holly, flowering spurge (*Euphorbia corollata*), pokeweed (*Phytolacca americana*), horseweed (*Conyza canadensis*), sedges (*Cyperus* spp.), and panic grasses (*Dicanthelium* spp.). For these analyses we used a generalized least squares approach, with the capture data transformed using the arcsinh (i.e., inverse hyperbolic sine) transformation to satisfy assumptions of normality and homoscedasticity (Fowler *et al.*, 1998). We included cumulative precipitation between January and May (i.e., prior to initiation of sampling) for each sample year as covariate, and accounted for non-independence in our repeated measures data using a continuous autoregressive term (corCAR1) nested within each plot (i.e., time series; Zuur *et al.*, 2009). We then tested for an interaction between treatment (control or fire) and burn status (pre-burn or post-burn).

The winter prescribed burn data sets included two pre-burn sampling years (2008 and 2009) and one post-burn sampling year (2010), with 2 treatment plots and 26 control plots. The summer prescribed burn data sets included 3 pre-burn sampling years (2008 to 2010) and 1 post-burn sampling year (2012). In addition, plots burned in the remaining fires were removed, as they did not represent true controls, resulting in 3 treatment plots and 9 control plots. The high severity wildfire data set included 3 pre-burn sampling years (2008 to 2010) and 1 post-burn sampling year (2012). For the wildfire analyses, we separated plots into 3 categories, those that were controls prior to the wildfire (*n* = 13), those that were within the low severity winter prescribed burn zone (*n* = 2), and those that were within the moderate severity summer prescribed burn zone (*n* = 1). Three summer prescribed burn plots were not re-burned in the wildfire and were removed from this data set, and the remaining 9 plots were used as controls. We performed these analyses using the program CANOCO (version 4.5).

2.4.4. Ground-dwelling arthropods

We assessed impacts of the fires on both total captures and species composition of ground-dwelling arthropods. In addition, we performed univariate analyses for species groups that appeared to show a response through the wildfire species composition analysis. These groups included Araneae (spiders), Carabidae (ground beetles), Curculionidae (snout beetles), Diplopoda (millipedes), Gryllacrididae (raspy crickets), Scarabaeidae (scarab beetles), and Scorpiones (scorpions). To assess fire impacts on total captures and individual species groups we used generalized least squares analyses, with the capture data transformed using the arcsinh (i.e., inverse hyperbolic sine) transformation to satisfy assumptions of normality and homoscedasticity (Fowler *et al.*, 1998). For all analyses we included cumulative precipitation during the sampling event and sampling season as covariates, and accounted for non-independence in our repeated measures data using a continuous autoregressive term (corCAR1) nested within each array (i.e., time series; Zuur *et al.*, 2009). We then tested for an interaction between treatment (control or fire) and burn status (pre-burn or post-burn). The winter and summer prescribed burn analyses included all sampling periods prior to the September 2011 wildfire, and each analysis excluded the arrays within the burn zone of the other fire, as those arrays were not true controls. For the wildfire analysis, we separated arrays into 3 categories, those that were controls prior to the wildfire, those that were within the low severity winter prescribed burn zone, and those that were within the moderate severity summer prescribed burn zone. Because the same response data were used in multiple analyses for the total capture analyses, we adjusted the level considered significant from the standard $\alpha = 0.05$ using the Bonferroni correction (i.e., $\alpha = 0.017$). We performed these analyses using the program R (version 2.14).

To assess impacts of the fires to species composition, we used redundancy analysis (RDA), again because our gradient lengths were short (< 4) and our predictors were categorical (Lepš and Šmilauer, 2003). To assess whether or not the fires impacted species composition, we tested for treatment-burn status interactions using a Monte Carlo permutation test (p-values in the results represent permutation tests for the first canonical axis). We included cumulative precipitation during each sampling event, sampling season, and arrays as covariates. By including arrays as covariates, we subtracted the average captures and assessed only capture changes within each array (Lepš and Šmilauer, 2003). We log transformed the response data so that percentage rather than absolute changes in captures were analyzed. As with the total abundance analyses, the winter and summer prescribed burn data sets included all sampling periods prior to the September 2011 wildfire, and each analysis excluded the arrays within the burn zone of the other fire; whereas, for the wildfire analysis we separated arrays into 3 categories, those that were controls prior to the wildfire, those that were within the low severity winter prescribed burn zone, and those that were within the moderate severity summer prescribed burn zone. We performed these analyses using the program CANOCO (version 4.5).

3. Results

3.1. Water quality

The PRC analyses indicated a significant treatment-time interaction for the low-severity, winter-fire ponds (*F*-ratio = 11.95; *P* = 0.032) and the high-severity, summer-fire ponds (*F*-ratio = 9.76; *P* = 0.024), but not for the moderate-severity, summer-fire ponds (*F*-ratio = 7.03; *P* = 0.60), with the first axis explaining 5%, 5%, and 4% of the variance, respectively. The PRC diagrams indicated increased pond nutrient levels in all burns, with corresponding increases in chl-*a* concentrations (Figure 4.2). Impacts on pH and DOC were variable, with pH decreasing following summer fires, but increasing slightly after winter fires, and DOC increasing following the low and moderate severity fires, but decreasing after the high severity fire.

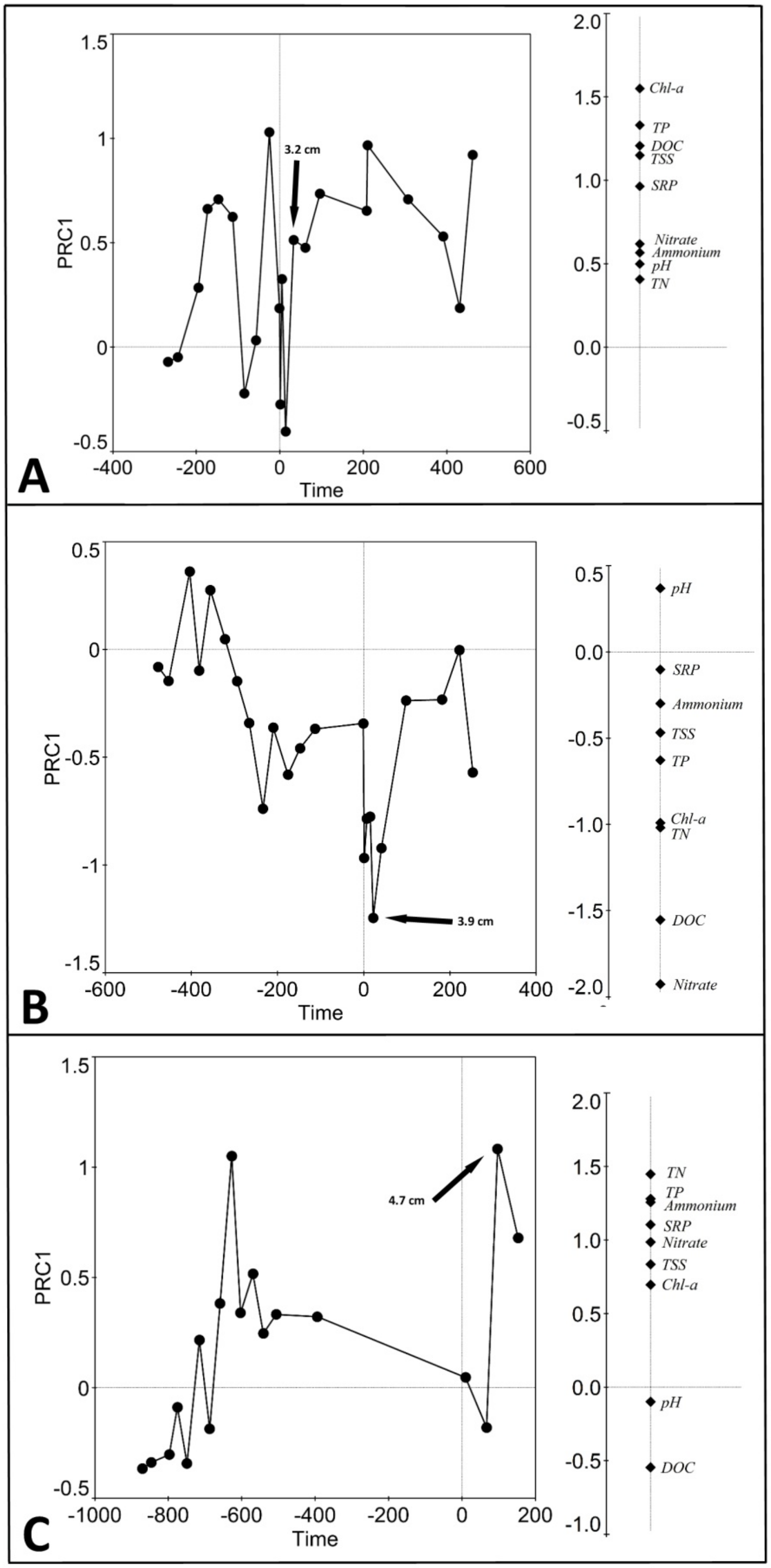
A
PRC1
Time
3.2 cm
Chl-a
TP
DOC
TSS
SRP
Nitrate
Ammonium
pH
TN
B
PRC1
Time
3.9 cm
pH
SRP
Ammonium
TSS
TP
Chl-a
TN
DOC
Nitrate
C
PRC1
Time
4.7 cm
TN
TP
Ammonium
SRP
Nitrate
TSS
Chl-a
pH
DOC

Figure 4.2. Results from Principal Response Curve (PRC) analyses used to assess the impacts of low (A), moderate (B), and high (C) severity fires on pond water quality on the Griffith League Ranch (GLR), Bastrop County, Texas, USA. Arrows indicate the first post-fire sampling event following significant precipitation (cm). Number of days before and after fires shown on the X-axes, and PRC scores shown on the left Y-axes. The right Y-axes allow the estimation of percentage differences between treatments for individual variables at any point in time. This is accomplished through the following equation: $\text{Difference } \% = 100 \times e(PRC1\ score\ at\ time\ point\ [left\ Y-axis] \times variable\ score\ [right\ Y-axis])$
The magnitude of impacts increased with fire severity, but water quality began to return to baseline levels within 200 days for all burn severities.

For most variables, the magnitude of difference between control and burn ponds was higher after the high severity fire compared to the low and moderate severity fires. For example, at the post-burn time point of greatest difference, TP was ca. 450% higher at high severity fire ponds relative to control ponds, compared to 350% and 200% higher at low and moderate severity burn ponds, respectively. Likewise, TN was ca. 500% higher at high severity fire ponds relative to control ponds, compared to 150% and 350% at low and moderate severity burn ponds, respectively. All analyses indicated the fires had little impact on pond water quality until a precipitation event.

Pre-burn and post-burn temporal variability was high for all 3 analyses, making it difficult to assess the length of time required for the water quality to return to baseline levels at burn ponds. The magnitude of difference between control and burn ponds began to decrease within 119, 41, and 97 days for the low, moderate, and high severity fires, respectively, indicating fire impacts were lessening. If we assume effects are essentially non-existent when the 0 point on the PRC axis is crossed, this occurred ca. 200 days following the moderate severity fires, whereas ponds subjected to low and high severity fires never reached this point (but note we stopped sampling 153 days after the high severity fire).

3.2. Aquatic arthropods

We did not detect a high severity wildfire impact on total captures of aquatic arthropods ($F_{1,52} = 0.71$, $P = 0.404$). The RDA analysis indicated that high severity wildfire had no impact on species composition of aquatic arthropods (F-ratio = 0.58, $P = 0.949$), with 3.2% of the variation explained by the model. A visual assessment of the species-environment biplot confirmed the statistical test, with all aquatic arthropod groups located either near the origin or at near right angles to the treatment x burn status predictor.

3.3. Vegetation

3.3.1. Fire severity

The range of fire severity ranks to substrate ranged from 0.5 to 1.44 for the low severity winter fires, 0.5 and 2.5 for the moderate severity summer fires, and 1.68 to 4 for the high severity summer fires when plots were controls prior to the fires (Figure 4.3). Our plots indicated that severity of the 2011 wildfires was not reduced in the low severity winter burn zone, but was dramatically reduced in the moderate severity summer burn zone (Figure 4.4).

Figure 4.3. Examples of vegetation plots following low (A), moderate (B), and high (C) severity fires (left panels), and ca. 1 year following the fires (right panel), on the Griffith League Ranch (GLR), Bastrop County, Texas, USA. Low and moderate severity fires did not significantly impact forest structure characteristics or species composition of understory vegetation, whereas high severity fires reduced overstory canopy cover, litter and duff depth, and the amount of fuel in all fuel classes, and increased diversity and cover of understory vegetation.

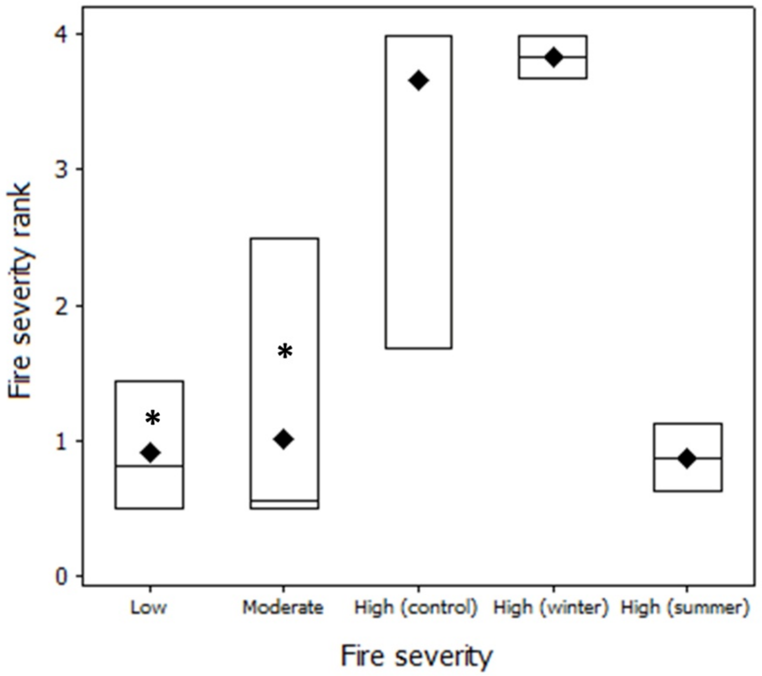

Figure 4.4. Visual descriptive statistics displaying fire severity to substrate on the Griffith League Ranch (GLR), Bastrop County, Texas, USA for low, moderate, and high severity fires. We assessed fire severity using four 15 m transect lines, each consisting of 4 points spaced 5 m apart, and assigned points a burn severity ranking from 0 (unburned) to 4 (heavily burned). We used the mean severity ranking of the 4 transects in this analysis. The high severity summer fires included 3 categories: 1) plots that were controls prior to the wildfire [High (control)], 2) plots that were part of the prior winter low severity fires [High (winter)], and 3) plots that were part of the prior summer moderate severity fires [High (summer)]. Boxes enclose the range, diamonds show the mean, and horizontal bars delineate the median fire severity rank for each category. Stars in the low and moderate severity categories denote the mean severity rank when unburned points were removed. Fire severity rank increased with fire severity, and prior moderate severity fires reduced substrate burn severity from the high severity fires.

Both overstory and pole-sized tree mortality was substantially greater in the high severity fire plots compared to the low and moderate severity fire plots (Figure 4.5). Similar to substrate impacts, our plots indicated that tree mortality following the high severity summer fires was not reduced in the low severity winter burn zone, but was dramatically reduced in the moderate severity summer burn zone, with the possible exception of overstory cedar trees. For all of the fires, pine tree mortality was greater than either oak or cedar tree mortality.

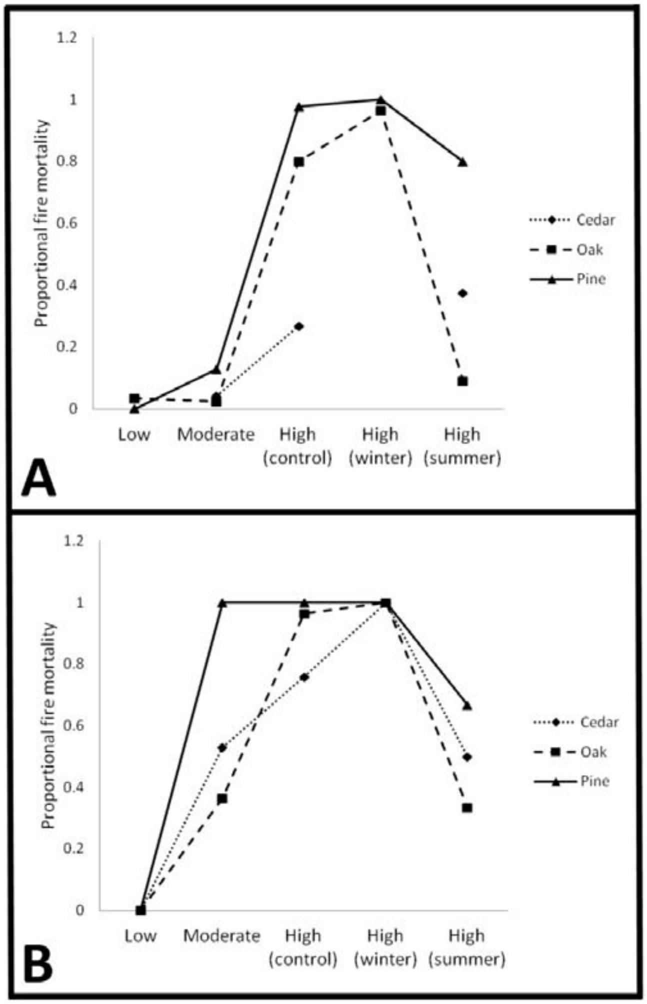

Figure 4.5. Overstory (A) and pole-sized (B) tree mortality on the Griffith League Ranch (GLR), Bastrop County, Texas, USA following low, moderate, and high severity fires. The high severity summer fires included 3 categories: 1) plots that were controls prior to the wildfire [High (control)], 2) plots that were part of the prior winter low intensity fires [High (winter)], and 3) plots that were part of the prior summer moderate intensity fires [High (summer)]. We separated trees into 3 genus-level groups: pine (loblolly pine), oak (post oak, blackjack oak [*Quercus marilandica*], and water oak [*Quercus nigra*]), and cedar (eastern red cedar), and plotted the proportion of overstory and pole-sized trees that died within 1 year following the fires for each group. Tree mortality increased with fire severity, and prior moderate severity fires reduced tree mortality caused by the high severity fires. Note there were no overstory cedar trees in the low severity winter plots.

3.3.2. Forest structure characteristics and understory species composition

The RDA analyses indicated the low severity winter fires had no significant impact on forest structure characteristics (*F*-ratio = 1.50, *P* = 0.133) or understory species composition (*F*-ratio = 1.83, *P* = 0.145), the moderate severity summer fires had no significant impact on forest structure characteristics (*F*-ratio = 1.67, *P* = 0.102) or understory species composition (*F*-ratio = 2.27, *P* = 0.082), and the high severity summer fires did impact forest structure characteristics (*F*-ratio = 32.76, *P* = 0.002) and understory species composition (*F*-ratio = 12.64, *P* = 0.002). The amount of total variation explained by the high severity fire models was 18.1% and 9.6% for forest structure characteristics and species composition of understory vegetation, respectively.

Visual assessment through biplots was congruent with the permutation tests (Figure 4.6). No variables appeared strongly associated with the low and moderate severity fires, as indicated by the direction and length of response arrows. For plots that were controls prior to the high severity wildfires, overstory canopy cover, litter depth, duff depth, and amount of fuel in all fuel classes was reduced ca. 1 year after the fire, whereas species richness and understory vegetation cover was higher ca. one year after the fire. In addition, for the vegetation species with a clear response to the wildfire, all responses were positive with the exception of yaupon holly. The univariate analyses supported the apparent positive responses of pokeweed ($F_{1,95} = 87.61$, $P < 0.001$), panic grasses ($F_{1,95} = 5.51$, $P = 0.021$), and sedges ($F_{1,95} = 33.59$, $P < 0.001$), and the apparent negative response of yaupon holly ($F_{1,95} = 45.31$, $P < 0.001$), to high severity wildfire. The wildfire analyses indicated that prior fires influenced the outcome for understory species composition. Abundance of flowering spurge ($F_{1,95} = 3.81$, $P = 0.054$) appeared to be positively associated with plots previously burned with low severity winter fires, whereas abundance of horseweed ($F_{1,95} = 3.23$, $P = 0.075$) appeared to be negatively associated with these plots. Plots previously burned with moderate severity summer fires indicated the opposite associations ($F_{1,95} = 3.42$, $P = 0.068$ and $F_{1,95} = 27.97$, $P < 0.001$, respectively).

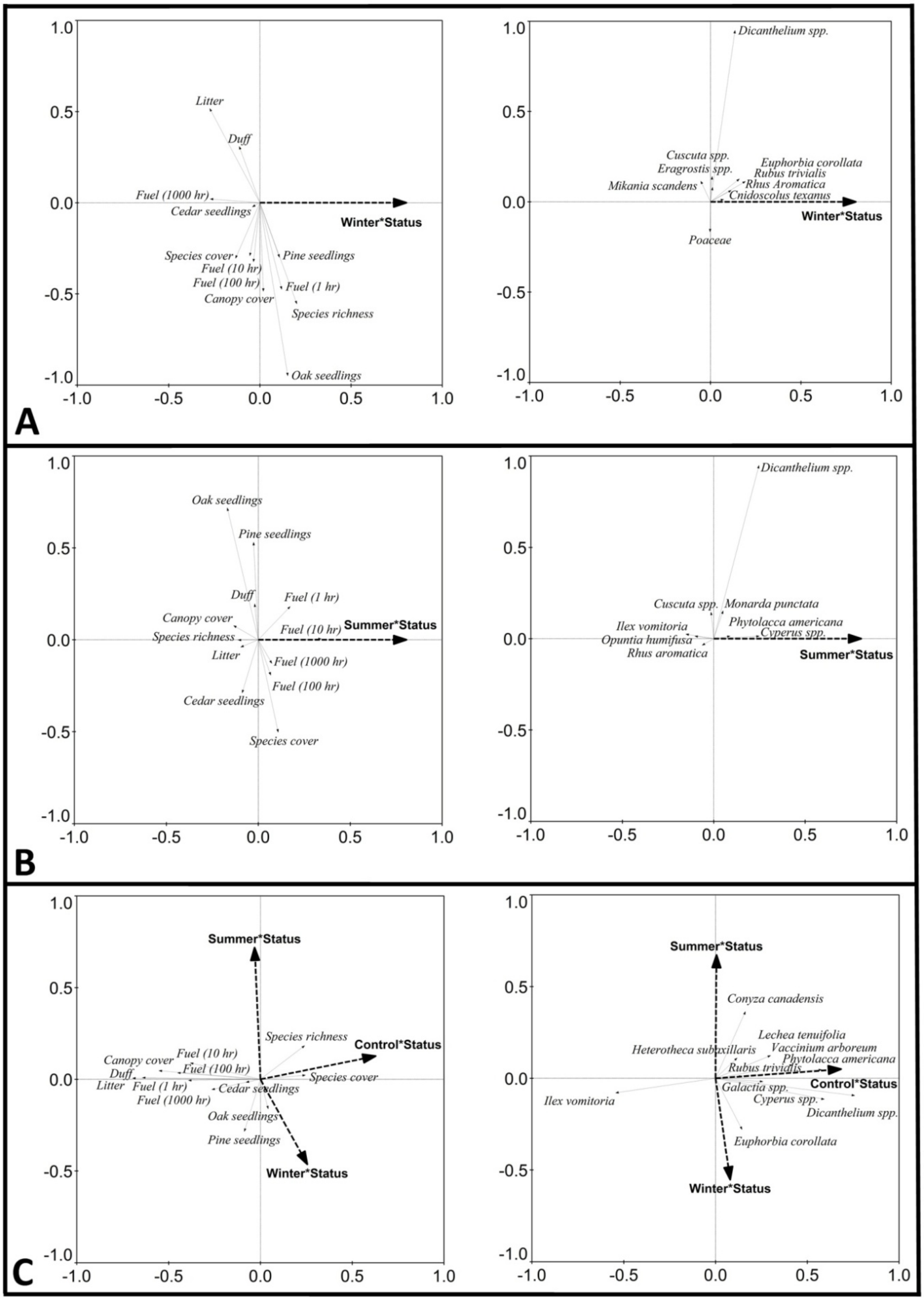
A
Litter
Duff
Fuel (1000 hr)
Cedar seedlings
Winter*Status
Species cover
Fuel (10 hr)
Fuel (100 hr)
Canopy cover
Pine seedlings
Fuel (1 hr)
Species richness
Oak seedlings
Dicanthelium spp.
Cuscuta spp.
Eragrostis spp.
Mikania scandens
Euphorbia corollata
Rubus trivialis
Rhus Aromatica
Cnidoscolus texanus
Poaceae
B
Oak seedlings
Pine seedlings
Duff
Fuel (1 hr)
Canopy cover
Fuel (10 hr)
Summer*Status
Species richness
Litter
Fuel (1000 hr)
Fuel (100 hr)
Cedar seedlings
Species cover
Cuscuta spp.
Monarda punctata
Ilex vomitoria
Phytolacca americana
Cyperus spp.
Opuntia humifusa
Rhus aromatica
C
Species richness
Control*Status
Canopy cover
Fuel (10 hr)
Fuel (100 hr)
Duff
Litter
Fuel (1 hr)
Fuel (1000 hr)
Cedar seedlings
Oak seedlings
Pine seedlings
Conyza canadensis
Lechea tenuifolia
Heterotheca subaxillaris
Vaccinium arboreum
Phytolacca americana
Rubus trivialis
Ilex vomitoria
Galactia spp.
Cyperus spp.
Dicanthelium spp.
Euphorbia corollata
1.0
0.5
0.0
-0.5
-1.0

Figure 4.6. Results from Redundancy Analyses (RDA) used to assess the impacts of low severity winter fires (A), moderate severity summer fires (B), and high severity summer fires (C) on forest structure characteristics (left biplot) and species composition of understory vegetation (right biplot) on the Griffith League Ranch (GLR), Bastrop County, Texas, USA. The high severity summer fires included 3 categories: 1) plots that were controls prior to the wildfire, 2) plots that were part of the prior winter low intensity fires, and 3) plots that were part of the prior summer moderate intensity fires. Dashed lines represent treatment-burn status interactions and solid lines represent response variable associations with those interactions. Of the 28 vegetation groups included in the analyses, only the 8 to 11 showing the greatest interaction response were included for ease of interpretation. The analyses indicated that low and moderate severity fires had weak effects on forest structure characteristics and species composition of understory vegetation. In contrast, high severity fires dramatically reduced fine and large fuel loads and increased diversity and cover of understory vegetation.

3.4. Ground-dwelling arthropods

We found no significant effect of fire on total abundance of ground-dwelling arthropods for all fire severities, as indicated by no significant treatment-burn status interaction effects. However, the models indicated fewer total arthropods in burned areas following all fires (i.e., interaction coefficients were negative; Table 4.1). The RDA analyses indicated the low-severity winter prescribed burn had no impact on species composition (*F*-ratio = 3.74, *P* = 0.110); whereas, the moderate-severity summer prescribed burn (*F*-ratio = 5.15, *P* = 0.024) and high-severity wildfires (*F*-ratio = 16.99, *P* = 0.002) did affect species composition. However, the amount of total variation explained by the low, moderate, and high severity models was low;

0.8%, 1.0%, and 2.9%, respectively. Visual assessment through biplots indicated that most arthropod groups had little or no response to fires (Figure 4.7). The univariate analyses indicated several groups responded to fire. For areas that were controls prior to the high-severity wildfire, Curculionidae ($F_{1,594} = 44.29$, $P < 0.001$) and Gryllacrididae ($F_{1,594} = 6.10$, $P = 0.014$) responded positively, and Araneae responded negatively ($F_{1,594} = 6.56$, $P = 0.011$). The apparent positive response of Scarabaeidae to areas burned in both the summer prescribed fire and the high-severity wildfire was trending towards significance ($F_{1,594} = 3.17$, $P = 0.076$). Although the RDA biplot indicated that Diplopoda responded negatively to fire in general, that response was not strongly associated with a particular category and was not found to be significant for areas that were controls prior to the wildfire ($F_{1,594} = 0.54$, $P = 0.464$), or areas that were part of the prior summer prescribed burn ($F_{1,594} = 1.32$, $P = 0.252$). Although Carabidae and Scorpiones appeared to show a moderate positive and negative response in areas that were controls prior to the wildfire, respectively, neither relationship was supported statistically ($F_{1,594} = 0.01$, $P = 0.943$ and $F_{1,594} = 1.42$, $P = 0.233$, respectively).

Table 4.1. Results of generalized least squares analyses used to assess if low severity winter prescribed burn, moderate severity summer prescribed burn, and high severity summer wildfires impacted total captures of ground-dwelling arthropods on the Griffith League Ranch (GLR), Bastrop County, Texas, USA, with sampling season and cumulative precipitation during the sampling period included as covariates. We sampled arthropods using 24 drift fence arrays with pitfall traps 24 times between 8 March 2009 and 21 April 2012. The low severity winter prescribed burn, moderate severity summer prescribed burn, and high severity wildfire occurred on 13 November 2009, 7 August 2010, and 4 September 2011, respectively. The high severity

summer fires included 3 categories: 1) plots that were controls prior to the wildfire (control), 2) plots that were part of the prior winter low intensity fires (winter), and 3) plots that were part of the prior summer moderate intensity fires (summer). The lack of significant treatment-burn status interaction effects indicated the fires did not significantly impact total abundance of ground-dwelling arthropods. However, the models indicated fewer total arthropods in burned areas following all of the fires (i.e., negative interaction coefficients).

Fire	Coefficient (±SE)	F-value	df	*P*
Prescribed (winter)				
Season	0.192 (0.07)	6.26	1,393	0.013
Precipitation	0.003 (0.002)	1.85	1,393	0.175
Treatment	0.426 (0.44)	2.28	1,393	0.132
Status	-0.081 (0.21)	1.60	1,393	0.207
Treatment*status	-0.807 (0.46)	3.06	1,393	0.081
Prescribed (summer)				
Season	0.114 (0.07)	3.07	1,393	0.080
Precipitation	0.004 (0.00)	5.52	1,393	0.019
Treatment	0.447 (0.28)	2.44	1,393	0.119
Status	0.228 (0.19)	1.14	1,393	0.286
Treatment*status	-0.206 (0.41)	0.26	1,393	0.613
Wildfire				
Season	0.101 (0.05)	2.87	1,590	0.091
Precipitation	0.007 (0.00)	16.15	1,590	< 0.001
Treatment (winter)	-0.154 (0.23)	2.45	1,590	0.118
Treatment (summer)	0.529 (0.23)	2.01	1,590	0.156
Treatment (control)	0.368 (0.19)	2.55	1,590	0.111
Status	-0.109 (0.23)	7.65	1,590	0.006
Treatment*status (winter)	-0.148 (0.42)	0.00	1,590	0.944
Treatment*status (summer)	-0.914 (0.42)	3.66	1,590	0.056
Treatment*status (control)	-0.427 (0.35)	1.48	1,590	0.224

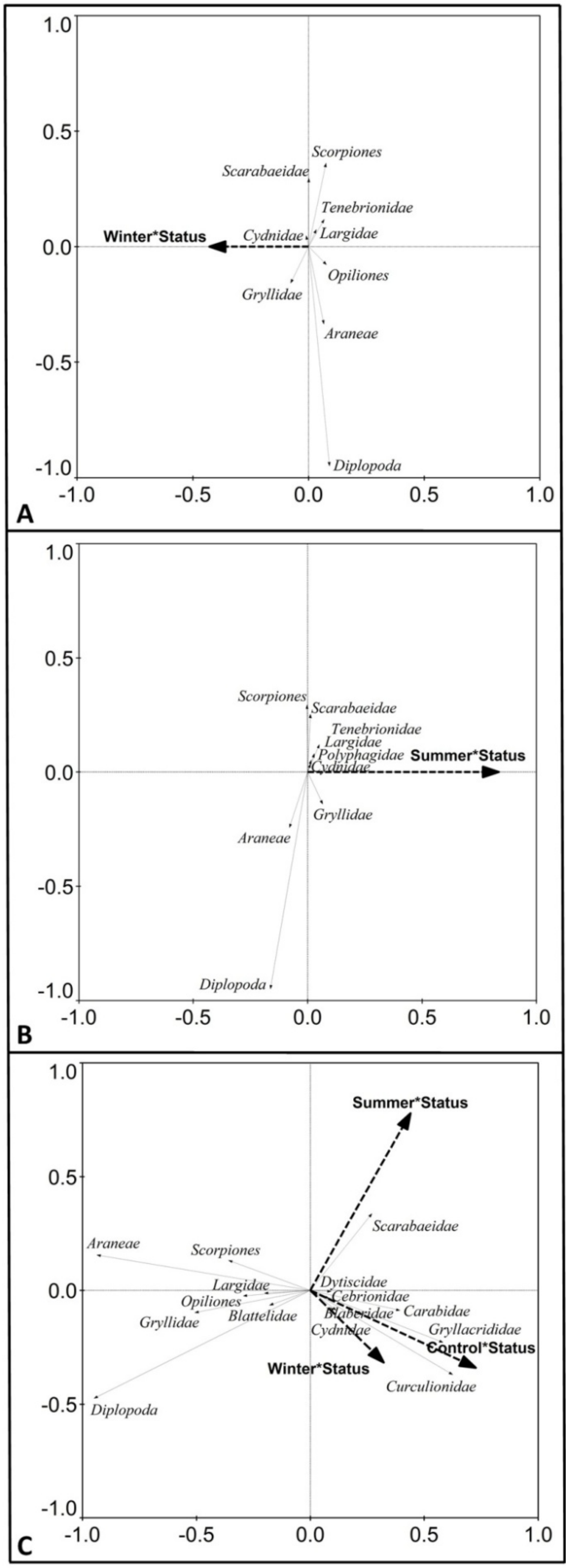
A
1.0
0.5
0.0
-0.5
-1.0
-1.0
-0.5
0.0
0.5
1.0
Scorpiones
Scarabaeidae
Tenebrionidae
Winter*Status
Cydnidae
Largidae
Opiliones
Gryllidae
Araneae
Diplopoda
B
1.0
0.5
0.0
-0.5
-1.0
-1.0
-0.5
0.0
0.5
1.0
Scorpiones
Scarabaeidae
Tenebrionidae
Largidae
Polyphagidae
Summer*Status
Cydnidae
Gryllidae
Araneae
Diplopoda
C
1.0
0.5
0.0
-0.5
-1.0
-1.0
-0.5
0.0
0.5
1.0
Summer*Status
Scarabaeidae
Araneae
Scorpiones
Dytiscidae
Largidae
Cebrionidae
Opiliones
Carabidae
Blaberidae
Gryllidae
Blattelidae
Cydnidae
Gryllacrididae
Control*Status
Winter*Status
Curculionidae
Diplopoda

Figure 4.7. Results from Redundancy Analyses (RDA) used to assess the impacts of a low severity winter fires (A), moderate severity summer fires (B), and high severity summer fires (C) on ground-dwelling arthropods in the Lost Pines ecoregion of Texas, USA. We sampled arthropods using drift fence arrays with pitfall traps. The high severity summer fires included 3 categories: 1) traps that were controls prior to the wildfire, 2) traps that were part of the prior winter prescribed burn, and 3) traps that were part of the prior summer prescribed burn. Dashed lines represent treatment-burn status interactions and solid lines represent arthropod group associations with those interactions. Of the 49 arthropod groups included in the analyses, only the 9 to 15 showing the greatest interaction response were included for ease of interpretation. The analyses indicated low and moderate severity fires had no detectable effects on species composition of ground-dwelling arthropods, whereas several arthropod groups responded to the high severity fires.

4. Discussion

The results of our study indicated fire severity was an important factor influencing responses of the ecosystem components we assessed, and adds to the growing literature supporting severity as a critical determinant of fire effects on ecosystems (Schwilk *et al.*, 2006; Wayman and North, 2007; Knapp *et al.*, 2009). Further, based on the data used in this study and our qualitative observations in the study area, moderate severity prescribed burning was effective for reducing wildfire severity, and consequently tree mortality was much lower, litter and duff was reduced but not eliminated, and understory species diversity increased slightly. In contrast, the low severity fires did little to mitigate tree mortality or substrate burn severity. Overall, our study supports conclusions of the majority of studies assessing the efficacy of fuel reduction for reducing fire severity in pine-dominated forests; it is effective (Schoennagel *et al.*, 2004; Mitchell *et al.*, 2009; Safford *et al.*, 2012).

Interestingly, we found pine mortality was greater than oak or cedar at all fire severities. This result would appear to contradict the general consensus that pines in the southern United States are not only fire-adapted (Oosting, 1944; Moore *et al.*, 1999; Stambaugh *et al.*, 2011), but fire is necessary for long-term persistence of pine forests (Hartnett and Krofta, 1989; Waldrop *et al.*, 1992; Schulte and Mladenoff, 2005). We believe there are likely several interacting factors in our study responsible for this finding. The first is geographical; the Lost Pines loblolly pine community represents the westernmost edge of the loblolly pine distribution in the U.S. (Al-Rabah'ah and Williams, 2004). The climate in this region is warmer and drier than in the expansive East Texas Pineywoods ecoregion, and this disjunct population has managed to persist under what are likely suboptimal environmental conditions. As a result, the Lost Pines population may be more vulnerable to any disturbance with the potential to negatively impact survivorship. Secondly, and related to this, was the timing of the fires. The 2009 and 2010 low and moderate severity fires occurred following exceptional drought conditions throughout most of 2009. This drought killed 5.7% of the overstory loblolly pine trees, and 12.0% of the post oak trees, in our vegetation plots. In contrast, eastern red cedar appeared to be very drought resistant, with 0% overstory tree mortality. Thus, the remaining loblolly pines were likely more stressed, and thus more vulnerable to fire mortality, than if the burns occurred following several wet years. Third, the Lost Pines loblolly pine population currently has a significant pine engraver beetle (*Ips* spp.) infestation (personal observation). Pine engraver and bark beetles are known to select drought-stressed trees, and further increase vulnerability to mortality (Grosman and Upton, 2006; Schwilk *et al.*, 2006). Finally, fire intensities were potentially higher at the base of loblolly pines compared to the hardwoods due to higher pine needle fuel load densities, which are typically more flammable than hardwood leaves due to lower moisture and higher resin content (Hély *et al.*, 2000; Nowacki and Abrams, 2008). Based on haphazard sampling (3 independent samples per species) conducted in December 2008 to gauge differences in litter moisture content, it appeared that loblolly pine had the lowest litter moisture content (mean = 8.7%, SD = 1.6%), followed by post oak (mean = 8.9%, SD = 0.6%) and eastern red cedar (mean = 14.2%, SD = 4.9%).

We found all fire severities resulted in increased nutrient levels in ponds, and the magnitude of those increases were greatest following high severity fire. However, for all the fire severity analyses, the magnitude of effects was not substantially greater than the highest natural variability observed prior to burning, and further our results indicated that nutrient levels began returning to baseline levels fairly quickly following the fires. The observed increases were clearly influenced by precipitation-induced runoff following the fires, which is both intuitive and congruent with other studies (Gresswell, 1999; Battle and Golladay, 2003). Thus, if fire were to be used as a tool to stimulate aquatic productivity in oligotrophic ponds in similar ecosystems, both fire severity and timing are important considerations.

Despite the impacts of high severity fire on water quality, our analysis indicated those effects did not translate to changes in total captures or species composition of aquatic arthropods. Potential direct mortality of aquatic arthropods would likely have been caused primarily by significant increases in water temperature, which has been documented during high severity fires (Gresswell, 1999; Hitt, 2003; Pilliod *et al*., 2003). Unfortunately those data were not collected for our study site, or as far as we are aware, any water bodies within the wildfire zone, and thus we do not know if the wildfires impacted water temperature. Malison and Baxter (2010) reported a fire severity effect for benthic stream insects 5 to 10 years post-burn, with greater captures of emergent insects and greater larval biomass in higher severity stream reaches, and several other studies have reported impacts years after fire events (reviewed in Gresswell, 1999). Thus, it is possible the wildfires may affect the aquatic arthropod communities in our study area at a longer time-scale. However, given that water quality appeared to be returning to background levels by the end of the study, and all but 3 ponds on our study area dry periodically, we believe long-term impacts are unlikely for aquatic arthropods.

We found that in contrast to high severity fire, low and moderate severity fire in this severely fire-suppressed ecosystem was largely ineffective for enhancing vegetation diversity. This is probably directly related to less fine fuel consumption, and thus less open ground following the fires, as well as higher percent canopy cover due to the majority of trees surviving the fires. We found that even low severity fire was sufficient to top-kill yaupon holly, the pre-burn dominant shrub in our study area. However, this was followed by significant basal sprouting after the low and moderate severity fires, which agrees with other findings in central Texas (Mitchell *et al.*, 2005). In contrast, the high severity fires not only top-killed, but consumed entirely the majority of yaupon holly individuals, and this species did not appear to be reestablishing within the hottest areas of the wildfire zones within the time-frame of our study. Rather, pokeweed, a species rarely observed on the property prior to the wildfires, replaced yaupon holly as the dominant shrub in the wildfire zones. This positive fire severity response for pokeweed has been noted elsewhere (Glasgow and Matlack, 2007), and this species has likely persisted in the seedbank for over half a century. In addition, the dominant herbaceous vegetation shifted from panic grasses (*Dicanthelium* spp.) and flowering spurge (*Euphorbia corollata*), to panic grasses, sedges (*Cyperus* spp.), and horseweed (*Conyza canadensis*), another species rarely observed prior to the wildfires, but is known to respond positively to high severity fire (Barclay *et al.*, 2004).

Given the moderate severity fires affected subsequent fire severity, whereas the low severity fires did not, we expected that impacts to forest structure characteristics and understory vegetation composition would be different in the moderate severity plots re-burned during the high severity wildfires versus the prior control plots that burned during the high severity wildfires, and our analyses indicated that this was the case. However, we expected the opposite result for low severity plots, and our analyses indicated the low severity burn plots also differed from the prior control plots. The reasons for this are unclear, but may be a result of the low sample size (n = 2) for twice-burned low severity plots.

As with the vegetation results, we found that in contrast to high severity fire, low and moderate severity fire had no detectable effect on species composition of ground-dwelling arthropods. Further, the arthropod wildfire analysis did agree with our expectation for re-burned areas, traps in moderate fire severity zones would differ from those in high severity zones that were controls prior to the high severity wildfires; whereas, traps in low fire severity zones would be similar. However, there were few arthropod groups that seemed to have a strong response to fire within the time-frame of our study, and there was no clear correlations related to feeding guilds. Qualitatively, it appeared that the predator groups Scorpiones (scorpions [*Centruroides vittatus*]; Taber *et al.*, 2003), Opiliones (harvestmen) and Araneae (spiders) were negatively impacted, whereas the predatory beetle family Carabidae showed a positive response. Similarly, it appeared the herbivorous Gryllidae (crickets) showed a negative response, whereas the herbivorous Gryllacrididae (camel crickets) and Curculionidae (snout beetles) showed a positive response. However, our univariate analyses indicated most of these responses were not strong.

Taber *et al*. (2008) found that prescribed burning at another site in the Lost Pines positively impacted Diplopoda (millipedes), whereas we did not detect a strong response for diplopods, and the response direction was negative. Thus, as is typical with studies assessing fire impacts to terrestrial arthropods, our results were ambivalent and patterns were unclear.

This study has several implications with respect to management of the Houston toad using prescribed fire and in the Lost Pines post-wildfire landscape. First, one of the questions in relation to prescribed burning is whether winter or summer burns should be conducted. We believe there are benefits to both seasons. Summer burns were more effective for reducing fuel loads, and appeared to negatively impact some of the arthropod groups that are known predators of juvenile amphibians (Toledo, 2005), which are active during the summer in our study area (Brown *et al.*, 2011). In contrast, winter burns could positively impact tadpole growth and survivorship through increased aquatic productivity during the spring when the Houston toad breeds (Hillis *et al.*, 1984; Brown *et al*., 2013).

The wildfire dramatically impacted the terrestrial landscape. In our opinion, the most concerning of the impacts was complete overstory tree loss and elimination of fine fuel throughout much of the high severity wildfire zone. The Houston toad appears to show strong preference for heavily canopied environments (U.S. Fish and Wildlife Service, 1984), and the suitability of the post-wildfire landscape for this species is currently unclear. However, we note that although overstory canopy cover has been dramatically reduced, understory cover has dramatically increased. Further, although the majority of large fuel was consumed, which is the preferred refugia for adult Houston toads (Swannack, 2007), it is currently being rapidly replaced by fallen trees. Thus, although in general the soil is likely warmer and drier within the wildfire zone (i.e., increased probability of desiccation), Houston toads may be able to mitigate this problem in the short-term by seeking out suitable refugia. However, we note that natural pine regeneration following the 2011 wildfire is minimal across the burn zone and extremely patchy. Thus, assisted pine restoration through seedling tree planting is currently a major recovery initiative in the ecoregion.

With the increase in understory vegetation abundance and diversity an increase in overall arthropod abundance and diversity could occur in the coming years, which would be a positive impact on terrestrial food resources for the Houston toad (Neumann, 1991; Swengel, 2001; Moretti *et al.*, 2004; Buddle *et al.*, 2006). However, a concern with respect to arthropod responses is a potential increase in distribution and density of the invasive red imported fire ant (*Solenopsis invicta*), a known predator of juvenile Houston toads (Freed and Neitman, 1988), and possible predator of adult Houston toads (personal observation), given that abundance of this species appears to be inversely correlated with overstory canopy cover in our study area (Brown *et al.*, 2012). Thus, although the high severity wildfire could certainly have both short-term and long-term negative impacts on the Houston toad, it could also have positive impacts, and we believe it is inappropriate for managers to consider the burn zone as unsuitable habitat without the population trend data to support that assumption.

In conclusion, this study represented a unique opportunity to compare the influence of fire severity on several ecosystem components within a BACI framework, and our results indicated this factor affected all of the ecosystem components we assessed. Given our results, future work should seek to address if multiple low to moderate severity fires produce the desirable outcomes of high severity fires (e.g., increased diversity of understory vegetation), while minimizing the unwanted outcomes (e.g., significant loblolly pine mortality). We intend to continue monitoring the response of this ecoregion to the high severity wildfires to assess the longer-term impacts to biotic and abiotic ecosystem components, and to assist with recovery and management initiatives.

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V. FIRE ANTS IN HOUSTON TOAD HABITAT: ANNUAL ACTIVITY AND RESPONSES TO CANOPY COVER AND FIRE

Abstract

The red imported fire ant (RIFA; *Solenopsis invicta*) is an invasive species found throughout the south and southeastern U.S. Since its introduction, RIFA has been shown to negatively impact a wide range of native vertebrate and invertebrate species. The purposes of this study were to delineate the annual RIFA activity pattern, investigate the association between overstory canopy cover and RIFA captures, and evaluate the effects of low and moderate severity prescribed fire around pond edges on RIFA in the Lost Pines ecoregion of Texas, which provides habitat for most of the remaining endangered Houston toads (*Bufo* [*Anaxyrus*] *houstonensis*). We found that annual RIFA activity followed a quadratic curve, with above average activity between May and October. We found an inverse relationship between mean percent canopy cover near pond edges and mean number of RIFA captured. We found low and moderate severity prescribed burning had no significant influence on RIFA captures during our study period. However, strong spatial and temporal capture variability was apparent, and thus a strong impact would have been necessary to detect an effect. While this study provides evidence that should decrease concerns that wildlife managers, conservation biologists, and landowners in the Lost Pines ecoregion may have about exacerbating RIFA abundance when utilizing fire as an ecosystem management tool, we recommend additional work be conducted using a greater sample size, greater sampling effort, and longer study duration. We found that RIFA activity was highest during the time frame in which juvenile Houston toads emerge from ponds. Thus, RIFA control may be a useful Houston toad recovery tool where breeding ponds are not within dense canopy habitats.

Keywords: Houston toad; Lost Pines; prescribed fire; red imported fire ant; Texas.

Introduction

The red imported fire ant (RIFA; *Solenopsis invicta*) is an invasive species in the U.S., predominantly in the south and southeast. Since its introduction to Alabama in the 1930s, the distribution of RIFA has expanded east to North Carolina and west to central Texas (Callcott and Collins 1996), and the species has been introduced to California (Ward 2005). When introduced, RIFA has been shown to negatively impact a wide range of native vertebrate and invertebrate species (Porter and Savignano 1990; Allen et al. 1994; Allen et al. 2004; Stuble et al. 2009; Diffie et al. 2010; Epperson and Allen 2010). Vertebrates are particularly vulnerable to RIFA predation during early life-stages (Landers et al. 1980; Freed and Neitman 1988; Pedersen et al. 1996). Abundance and diversity of native arthropods can also be negatively affected by RIFA competition and predation (Morrison 2002; Plowes et al. 2007; Epperson and Allen 2010).

In the U.S. the RIFA prefers environments characterized by disturbance, and can use roads and powerline cuts as expansion corridors (Tschinkel 1988; Stiles and Jones 1998; Todd et al. 2008). In primarily forested habitats, RIFA tend to be more abundant in forest gaps (Colby and Prowell 2006). The RIFA is adapted to periodically flooded habitats (Allen et al. 1974), and has been found to prefer edges of ponds and other water bodies (Lyle and Fortune 1948; Tschinkel 1988; Stuble et al. 2009; Vogt et al. 2009). Because RIFA can be more flood tolerant than some native ant species, it may have a competitive advantage over these taxa in flood-prone environments (Vogt et al. 2009). The potential for high RIFA density around ponds is of concern in amphibian management, given the potential vulnerability of juvenile amphibians to RIFA predation when they enter the terrestrial landscape (Freed and Neitman 1988). Red imported fire ants prefer canopy gaps, thus ponds with less canopy cover or near the edges of forested fragments may have higher RIFA abundances and may subsequently have higher RIFA predation pressure on juvenile amphibians.

The RIFA arrived in Bastrop County, central Texas between 1973 and 1977, and are now well-established in the Lost Pines ecoregion (Cokendolpher and Phillips 1989; Taber and Fleenor 2003). This ecoregion is a 34,400 ha remnant of a pine-dominated forest that occurred in east and east-central Texas approximately 14,000 to 10,000 years ago (Bryant 1977). The Lost Pines houses the majority of the remaining breeding aggregations of the endangered Houston toad (*Bufo* [*Anaxyrus*] *houstonensis*; Gottschalk 1970), a species that has declined rapidly in the last half century due primarily to habitat loss and degradation (U.S. Fish and Wildlife Service 1984; Brown and Mesrobian 2005). The RIFA is known to prey upon Houston toads after their emergence from ponds as terrestrial juveniles (Freed and Neitman 1988).

We conducted this investigation as part of a larger study on the use of prescribed fire for Houston toad habitat recovery and conservation initiatives. The majority of the Lost Pines has been fire suppressed for the past century, resulting in heavy fuel loads and dense thickets of fire-intolerant shrubs, primarily yaupon holly (*Ilex vomitoria*). Currently there is limited published information on RIFA response to prescribed burning, and RIFA population responses to fire are unclear. Forbes (1999) documented short-term (i.e., five months post-burn) negative effects on RIFA due to prescribed burning in a Texas coastal prairie, presumably due to reduced soil moisture and food availability. Conversely, Norton (2003) found no effect of burning on RIFA abundance in habitats similar to those of Forbes (1999). In contrast, Hanula and Wade (2003) found that RIFA abundances increased with burn frequency in a Florida longleaf pine (*Pinus* *palustris*) forest. Thus, the results of the aforementioned studies present an unclear picture of whether the use of prescribed fire as a recovery tool in pine-dominated ecosystems may increase invasive potential for RIFA or whether fire may be an effective method to reduce RIFA in invaded pine forests.

The purposes of this study were to delineate the annual RIFA activity pattern in the Lost Pines ecoregion of Texas, and to investigate RIFA responses to overstory canopy cover and low and moderate severity prescribed fire. We were interested in temporal activity in order to better understand RIFA activity patterns in relation to Houston toad activity patterns, and to delineate optimum time intervals for RIFA control measures. Percent canopy cover is an easily quantifiable variable that could be used to determine which Houston toad ponds likely contain large RIFA populations, and thus where emergent Houston toads are most vulnerable to RIFA predation. Prescribed fire is a common habitat management tool used across the south and southeastern U.S., and thus it is important to know the impacts of fire on this invasive species.

Study Site

We conducted this study on the 1,900 ha Griffith League Ranch (GLR) in Bastrop County, Texas. The GLR is primarily forested, with vegetation typical of the Lost Pines ecoregion. The overstory is dominated by loblolly pine (*Pinus taeda*), post oak (*Quercus stellata*), blackjack oak (*Quercus marilandica*), and eastern red cedar (*Juniperus virginiana*), and the understory is dominated by yaupon holly (*Ilex vomitoria*), American beautyberry (*Callicarpa americana*), and farkleberry (*Vaccinium arboreum*).

The GLR contains three permanent ponds (i.e., ponds have not dried in at least 12 years), 10 semi-permanent ponds (i.e., ponds typically dry several times per decade), and dozens of ephemeral pools that hold water for days to months annually depending on rainfall. Ten of these ponds were used for this study. Three of the ponds were ephemeral (i.e. typically dry several times per year), six were semi-permanent (i.e., typically dry several times per decade), and one was permanent (i.e., has not dried in at least 11 years). Four of the pond edges were primarily covered by pine and oak leaf litter (>80% ground cover), with the remaining ponds having edges dominated by grasses and forbs (>80% ground cover). We chose these ponds because they spanned the distribution of size, hydroperiod, and canopy cover variability on the GLR, they were known Houston toad breeding ponds, and, when applicable, they were located in units projected to be burned. Houston toad calling activity occurred at all ponds used in this study within the previous two years (Duarte et al. 2011).

Methods

We conducted this study over a one-year period between 26 September 2009 and 10 October 2010, sampling the area around each of the 10 ponds a total of 27 times. Days between sampling ranged from 0 (i.e., consecutive sampling days) to 73, with a mean of 15 days between samples. We used a standard bait cup method for sampling ants (Porter and Tschinkel 1987; Mueller et al. 1999), which consisted of half a Vienna sausage placed in a 9-cm diameter round plastic dish. We placed between 3 and 15 dishes around the perimeter of each pond, depending on pond size (i.e., perimeter length). During each sampling event, we placed dishes 1-2 m from the pond edge at 3-4 m intervals, and allowed them to attract ants for 30 minutes. After 30 minutes we collected ants from each dish and euthanized them by freezing. We removed native ants from samples and RIFA were dried at ~50 °C for at least 48 hours. We then counted RIFA collected in each bait cup at each pond on each sampling date. Alternately, we weighed the cumulative number of ants in each bait cup at each pond on each sampling date, and sample weight was estimated to the nearest 1×10^{-4} g. We estimated RIFA abundances in these samples using an empirically-derived relationship between a known number of RIFA and the weight of the sample. This relationship was derived from samples collected from around study ponds on three randomly selected sampling dates ($n = 109$ samples, $y = 2140.8 \times \text{weight (g)}$, $r^2 = 0.92$). We used the estimated RIFA abundances as count data in statistical analyses.

Four of the ponds were subjected to prescribed burning, with all ponds sampled before and after burning. However, because ponds were spread over multiple burn units, areas around individual ponds were burned at different times of the year. The area around one pond was burned on 13 November 2009 (Pond 10), one pond on 10 January 2010 (Pond 13), and the remaining two ponds were burned on 21 August 2010 (ponds 14 and 15). This burn scenario created the ability to examine the effect of low severity winter fires (November and January) versus moderate severity summer fires (August). The goal for all fires was fuel reduction; burns removed the upper portion (i.e., 1 to 2 cm) of the leaf litter layer and charred but typically did not consume live woody vegetation.

In order to assess if RIFA counts were higher in open canopy areas, between 20 July 2008 and 16 April 2010, we estimated percent canopy cover around each pond between 4 and 24 times, depending on hydroperiod status at the time of sampling (i.e., estimates were not taken when ponds did not contain water). For each sample, we estimated percent canopy cover using a spherical densiometer (Forestry Suppliers Inc., Jackson, MS) at two to six randomly selected points at the pond edge, with higher numbers of estimation points corresponding to larger ponds. We then averaged the estimates at each pond per sampling date. For this study, we included measurements taken during the leaf-off period (December to March) because ponds with consistently high canopy cover at our study site were dominated by loblolly pine, which retains needles throughout the year.

Statistical analyses

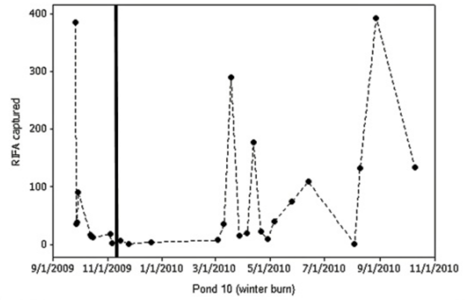
We used a Generalized Additive Model (GAM; Hastie and Tibshirani 1990) to summarize the annual activity pattern based on our sampling results. We used the CPUE at each pond on each day sampled (i.e., 27 samples with 10 observations per sample), included Day of Year (DOY) as a predictor, and fit a smoothing curve to the data (cubic regression spline), with the optimal amount of smoothing determined using a cross-validation algorithm (Zuur et al. 2009). Thus, the smoothing curve represented the model-fitted relationship between RIFA CPUE and DOY. Generalized Additive Models assume normality and homoscedasticity, and we investigated these assumptions using graphical diagnostics plots (Zuur et al. 2009). Because data appeared to violate the assumption of homoscedasticity, we transformed CPUE using the arcsinh (i.e., inverse hyperbolic sine) transformation (Fowler et al. 1998), which was effective. We performed this analysis using the program R (R Version 2.10.1, www.r-project.org), with the mgcv package (Wood 2004).

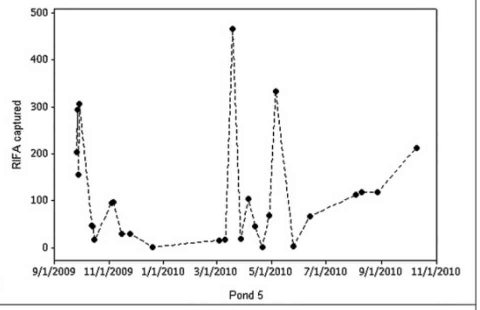
To examine the influence of canopy cover on RIFA CPUE, we utilized the RIFA capture and canopy cover data from all of the study ponds (*n* = 10), and calculated the mean percent canopy cover of each pond over the study period. We regressed mean RIFA CPUE on mean percent canopy cover for all ponds using ordinary least squares (OLS) linear regression, and gauged model fit using the coefficient of determination (r^2; Sokal and Rohlf 1995). We performed this analysis using program R (R Version 2.10.1, www.r-project.org).

To assess if prescribed fire influenced RIFA CPUE around ponds, we used the Before-After Control-Impact (BACI) approach described by Stewart-Oaten et al. (1986, 1992). One burn pond (Pond 13) was not included in the statistical analyses because we captured RIFA on very few sampling events, including none following the burn. We paired treatment (i.e., burned) ponds with control ponds that were similar in pre-burn temporal CPUE dynamics. For each pair, we computed the difference in CPUE between the control and treatment pond on each sampling occasion, and used a standard *t*-test to determine if the mean difference between the control and treatment ponds changed after the prescribed fire. An important assumption with this analysis is that effects are additive (Stewart-Oaten et al. 1986). We tested this assumption using Tukey's test of additivity (Tukey 1949), and two of the three pond pairs indicated non-additive effects ($P < 0.001$). We transformed CPUE for all ponds using the arcsinh transformation, which was effective for all pairs ($P = 0.904$ [ponds 5 and 10]; $P = 0.392$ [ponds 9 and 14]; $P = 0.407$ [ponds 16 and 15]), and used the transformed data for the *t*-tests. Levene's test for equality of variances indicated that variances were equal for all comparisons, and thus unequal variance *t*-tests were not used. However, results from unequal variance *t*-tests were equivalent. We performed this analysis using program SPSS (SPSS Statistics Version 20).

Results

We captured an estimated 18,050 RIFA during this study, with estimated number of captures among ponds ranging from 4 (Pond 13) to 3,642 (Pond 11; Fig. 1). The GAM model fit a quadratic curve to the CPUE-DOY relationship, with above average activity between May and October (Fig. 2). We found a strong negative relationship between percent canopy cover and mean RIFA CPUE (Fig. 3; $t_8 = 11.08$, $P < 0.0001$, $r^2 = 0.82$). We did not detect a prescribed fire effect on RIFA CPUE for ponds burned in the winter (Pond 10: $t_{25} = 1.338$, $P = 0.193$; Pond 13: number of pre-burn captures = 4, number of post-burn captures = 0). We also did not detect a prescribed fire effect on RIFA CPUE for ponds burned in the summer (Pond 14: $t_{25} = -0.316$, $P = 0.755$; Pond 15: $t_{25} = -0.630$, $P = 0.534$).


400
300
200
100
0
RIFA captured
9/1/2009
11/1/2009
1/1/2010
3/1/2010
5/1/2010
7/1/2010
9/1/2010
11/1/2010
Pond 10 (winter burn)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300
200
100
0
RIFA captured
9/1/2009
11/1/2009
1/1/2010
3/1/2010
5/1/2010
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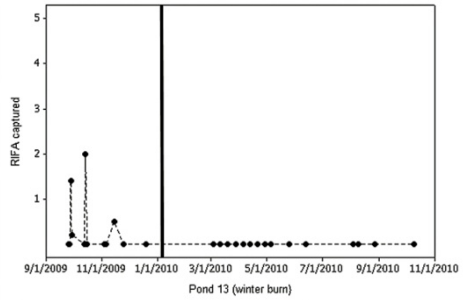
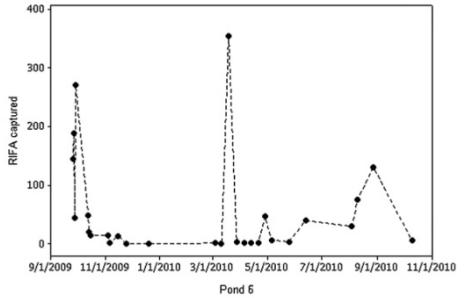
9/1/2010
11/1/2010
Pond 5


5
4
3
2
1
RIFA captured
9/1/2009
11/1/2009
1/1/2010
3/1/2010
5/1/2010
7/1/2010
9/1/2010
11/1/2010
Pond 13 (winter burn)


400
300
200
100
0
RIFA captured
9/1/2009
11/1/2009
1/1/2010
3/1/2010
5/1/2010
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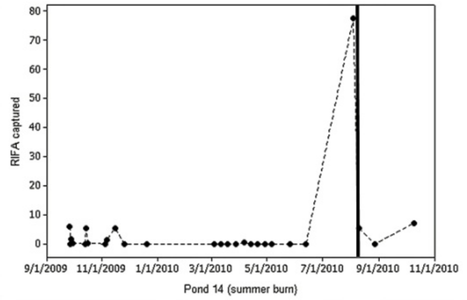
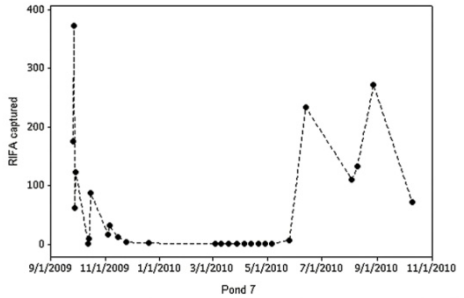
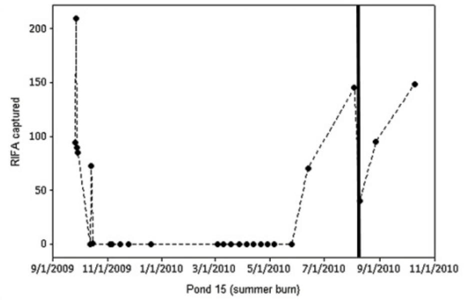
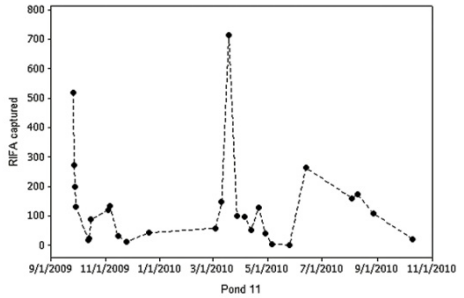
9/1/2010
11/1/2010
Pond 6


80
70
60
50
40
30
20
10
0
RIFA captured
9/1/2009
11/1/2009
1/1/2010
3/1/2010
5/1/2010
7/1/2010
9/1/2010
11/1/2010
Pond 14 (summer burn)


400
300
200
100
0
RIFA captured
9/1/2009
11/1/2009
1/1/2010
3/1/2010
5/1/2010
7/1/2010
9/1/2010
11/1/2010
Pond 7


200
150
100
50
0
RIFA captured
9/1/2009
11/1/2009
1/1/2010
3/1/2010
5/1/2010
7/1/2010
9/1/2010
11/1/2010
Pond 15 (summer burn)


800
700
600
500
400
300
200
100
0
RIFA captured
9/1/2009
11/1/2009
1/1/2010
3/1/2010
5/1/2010
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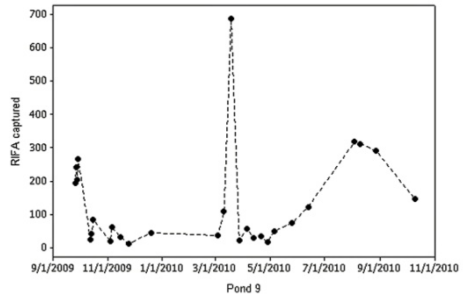
9/1/2010
11/1/2010
Pond 11


700
600
500
400
300
200
100
0
RIFA captured
9/1/2009
11/1/2009
1/1/2010
3/1/2010
5/1/2010
7/1/2010
9/1/2010
11/1/2010
Pond 9

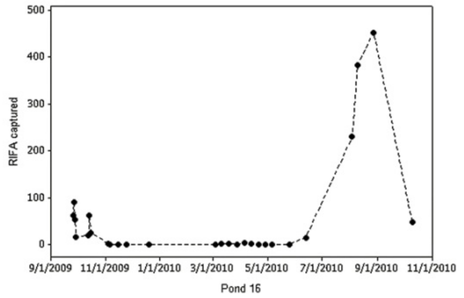

500
400
300
200
100
0
RIFA captured
9/1/2009
11/1/2009
1/1/2010
3/1/2010
5/1/2010
7/1/2010
9/1/2010
11/1/2010
Pond 16

Figure 1. Red imported fire ant (RIFA; *Solenopsis invicta*) captures at pond edges in the Lost Pines ecoregion of Texas. We sampled each pond 27 times between 26 September 2009 and 10 October 2010. The solid vertical bars delineate pre-burn and post-burn samples at burn ponds. Captures decreased immediately following a summer prescribed burn at ponds 14 and 15, but returned to background levels within weeks.

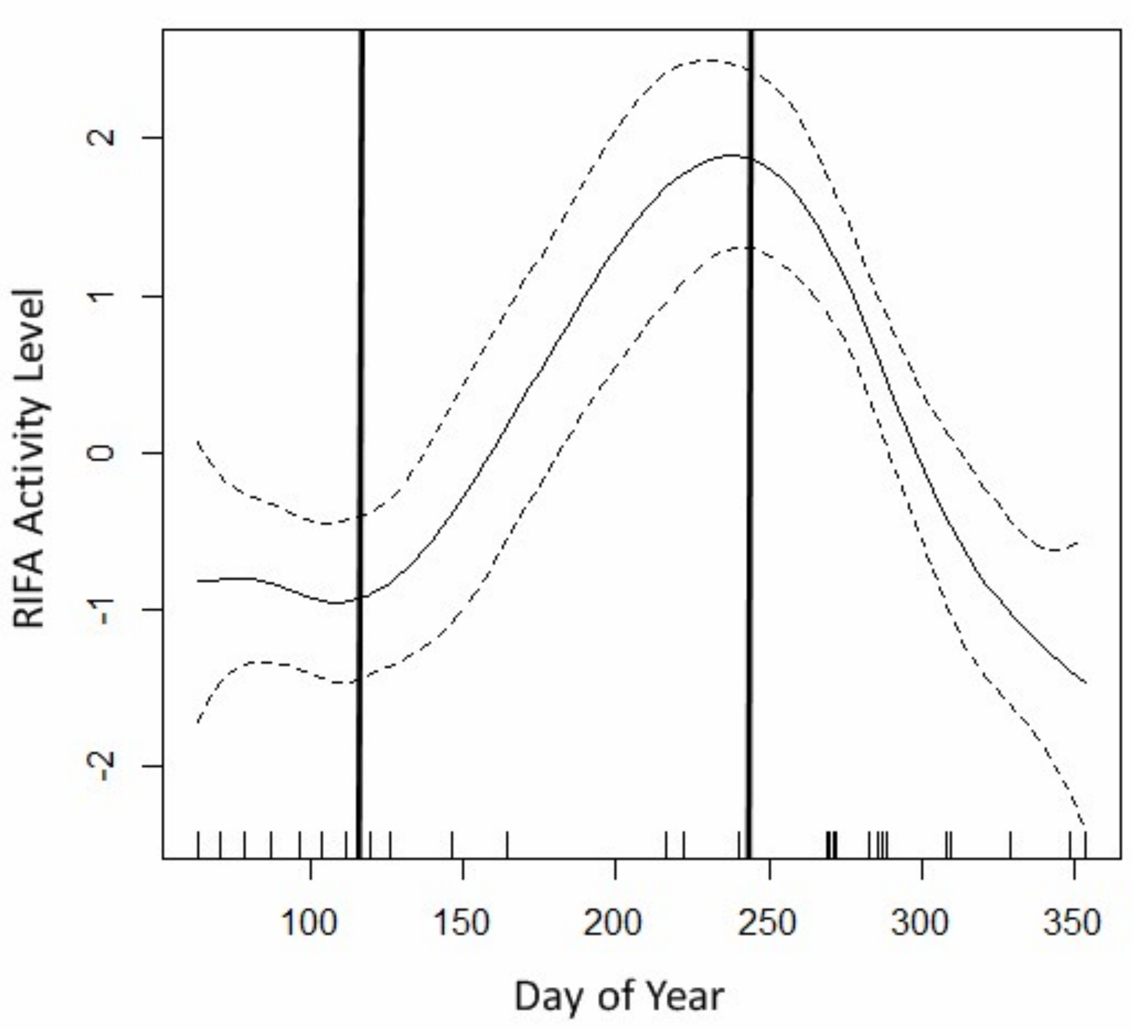


Figure 2. Annual activity pattern of red imported fire ants (RIFA) in the Lost Pines ecoregion of Texas based on captures-per-unit-effort (CPUE). We sampled RIFA 27 times at 10 ponds between 26 September 2009 and 10 October 2010. Sampling dates are shown with hash marks inside the x-axis. For this analysis we used CPUE at each pond on each day sampled (i.e., 27 samples with 10 observations per sample). We modeled CPUE as a function of Day of Year (DOY) using a Generalized Additive Model (GAM). The Y-axis shows the predicted activity level (with point-wise 95% confidence bands) based on results from days we sampled (inner tick marks) and relative to the observed mean CPUE for all observations (0). The vertical lines encase the time period in which terrestrial juvenile Houston toads (*Bufo houstonensis*) may be present near ponds.

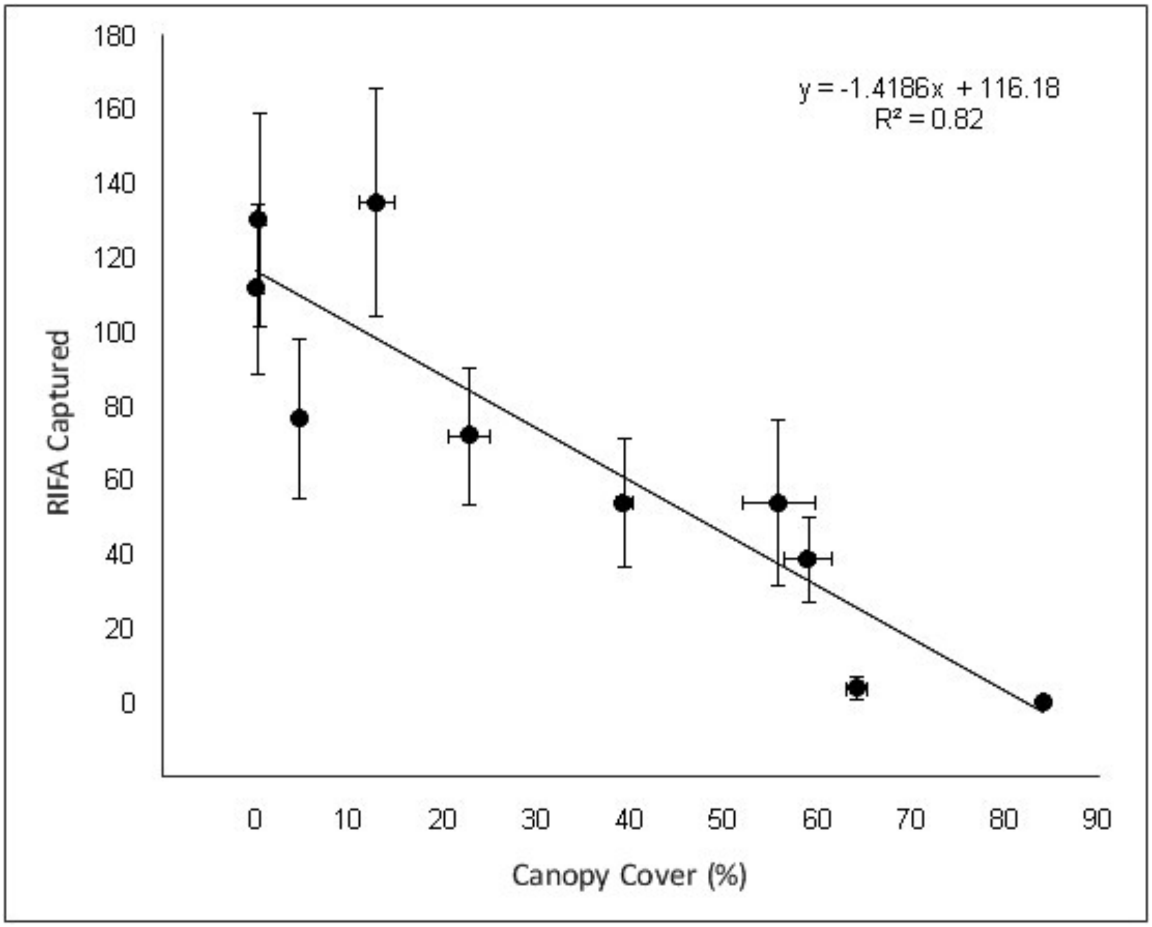


Figure 3. Relationship between mean percent canopy cover (± SE) and mean red imported fire ant (RIFA) captures (± SE) at 10 ponds in the Lost Pines ecoregion of Texas. We sampled RIFA at ponds 27 times between 26 September 2009 and 10 October 2010 and used the mean of the samples for this analysis. For percent canopy cover we used the mean of 4 to 24 samples taken between 20 July 2008 and 16 April 2010. We found a strong inverse relationship between mean RIFA captures and percent canopy cover.

Discussion

The results of this study indicate that disturbance from low and moderate severity prescribed burning did not affect RIFA abundance around ponds in our study area. This finding is in contrast to other studies reporting that disturbance from livestock use or vegetation-clearing can lead to increases in RIFA abundance (Lofgren et al. 1975; Stiles and Jones 1998; Todd et al. 2008; Vogt et al. 2009). In the present study, the number of RIFA captured at the two summer burn ponds decreased immediately after burning, but returned to background levels within weeks. The winter burns were conducted during a period of low RIFA activity at all ponds, and no short-term changes were apparent. These results indicate that, at least in the short-term, prescribed burning did not benefit RIFA. However, each experimental pond was burned only once, and burn frequency may increase RIFA abundance (Hanula and Wade 2003). Additional research is needed concerning effects of burn frequency and severity on RIFA in both forest and non-forest systems. Further, due to strong spatial and temporal capture variability a strong impact would have been necessary to detect an effect. Future work on this topic would benefit from greater sample sizes, greater sampling effort, and longer study durations. We also note that RIFA were present at our study ponds prior to burning, and thus we did not address the potential for habitat invasion following disturbance through fire.

Percent canopy cover was a viable predictor of RIFA CPUE in our study area. This result was not surprising, as this species is known to select for open and edge habitats (Stiles and Jones 1998; Colby and Prowell 2006). We recommend that future studies seek to determine whether substrate-type (i.e., litter-dominated or vegetation-dominated) is an important RIFA CPUE predictor in forested environments, as fire can increase understory herbaceous vegetation density by removing litter and sunlight-capturing woody vegetation (Hodgkins 1958; Sparks et al. 1998;

Donato et al. 2009). Because of constantly shifting pond borders due to deposition of precipitation and evapotranspiration, we were unable to test substrate-type in this study, as substrate-type shifted at several ponds. Quantifying substrate relationships would potentially increase predictive power for estimating RIFA densities around ponds, as well as increase our understanding of the causal mechanisms behind fire effects on RIFA.

Monitoring RIFA over the course of a year showed that activity varied seasonally, with highest activity between May and October. This includes the period where juvenile Houston toads are vulnerable to predation near ponds. Houston toad emergence from ponds in the Lost Pines typically occurs between March and June, and juveniles remain near the pond for the first one to two months after emergence (Greuter and Forstner 2003; Greuter 2004). Given that they are active, RIFA abundance differences could potentially significantly affect survivorship rates of terrestrial juvenile Houston toads. Thus, future research on juvenile Houston toad predation by the RIFA is warranted.

Based on the results of this study, low and moderate severity prescribed burning did not decrease RIFA CPUE around pond margins, suggesting that this kind of fire does not appear to be a useful management tool for eliminating RIFA. Chemical control has been shown to be locally effective, but insecticides can have severe impacts non-target wildlife, particularly amphibians (Lofgren et al. 1975; Boone and James 2003; Relyea 2003). If chemical control is necessary for managing RIFA in the Lost Pines ecoregion, we hypothesize that fall or winter application may have the lowest amphibian impact because amphibian activity is low relative to spring and summer (Brown et al. in press). Further, although broadcast application is the most effective way to control RIFA, strategic bait placement (e.g., on mounds) can also be effective (Williams et al. 2001; Allen et al. 2004). Because amphibians do not appear to actively avoid soils contaminated with harmful chemicals (Hatch et al. 2001; Storrs Méndez et al. 2009), and these chemicals can be readily absorbed through the skin, strategic bait placement is a more attractive management option. Biological controls, such as the fire ant decapitating fly (*Pseudacteon curvatus*) and the disease-causing protozoan *Thelohania solenopsae*, may eventually prove to be effective broad-scale control agents (Brinkman and Gardner 2001; Porter 2010).

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VI. WILDFIRE IMPACTS ON RED IMPORTED FIRE ANT CAPTURES IN THE LOST PINES ECOREGION OF TEXAS

Abstract

The impacts of high intensity wildfires on red imported fire ant (*Solenopsis invicta*) abundances in forest systems are currently unknown. The purpose of this study was to evaluate the effects of a high intensity wildfire around pond edges on red imported fire ant captures in the Lost Pines ecoregion of Texas, which provides habitat for most of the remaining endangered Houston toads (*Bufo houstonensis*). The red imported fire ant is a known predator of Houston toads, and thus there is interest in understanding the potential and realized impacts of this species on Houston toad survivorship. Our results suggested the wildfire did not directly impact captures-per-unit-effort, but it had indirect positive impacts through reductions in canopy cover due to overstory tree mortality. The results of this study indicate that both area occupied by red imported fire ants and site-specific red imported fire ant densities could increase dramatically in the Lost Pines as a result of the wildfire and subsequent human-based recovery efforts.

Keywords: Canopy cover; Houston toad; Lost Pines; red imported fire ant; Texas; wildfire.

Introduction

The red imported fire ant (RIFA; *Solenopsis invicta*) is an invasive species in the southern and southeastern U.S. It was introduced to Alabama in the 1930s, and has since expanded east to North Carolina and west to central Texas (Callcott and Collins 1996), and has been documented in California (Ward 2005). Negative ecological impacts of RIFA invasion have been demonstrated for a wide range of vertebrates and invertebrates (Porter and Savignano 1990; Allen et al. 1994; Allen et al. 2004; Stuble et al. 2009; Diffie et al. 2010; Epperson and Allen 2010). Among vertebrates, juveniles tend to be particularly vulnerable to RIFA predation (Landers et al. 1980; Freed and Neitman 1988; Pedersen et al. 1996).

The red imported fire ant appeared in Bastrop County, central Texas between 1973 and 1977, and has since become well established throughout the Lost Pines ecoregion (Cokendolpher and Phillips 1989; Taber and Fleenor 2003), which has historically been the last remaining stronghold for the federally endangered Houston toad (*Bufo* [*Anaxyrus*] *houstonensis*; U.S. Endangered Species Act [ESA] 1973, as amended). This species is a known predator of juvenile Houston toads (Freed and Neitman 1988), and thus there is interest in understanding the potential and realized impacts of RIFA on Houston toad survivorship.

Brown et al. (2012) recently conducted a study in the Lost Pines aimed at delineating annual RIFA activity patterns, elucidating the relationship between overstory canopy cover and RIFA captures, and evaluating the effects of low intensity prescribed fire around pond edges (where juvenile Houston toads are vulnerable to predation after emergence) on RIFA captures. Brown et al. (2012) found that annual RIFA activity was highest between May and October, which includes the period in which juvenile Houston toads disperse from ponds. They also found a strong inverse relationship between RIFA captures and canopy cover near pond edges. It is possible that greater sunlight exposure, and thus greater heat, in open-canopied environments results in more suitable habitat for RIFA (Vogt et al. 2003). Lastly, Brown et al. (2012) detected no effects of low intensity prescribed fire on RIFA captures, indicating no sustained direct impact of fire on the species. However, the authors noted that research on high intensity fire impacts was warranted, given the greater potential for habitat alteration consequent of hotter fires.

On 4 September 2011 a high intensity wildfire began in the Lost Pines. The fire was unstoppable due to wind gusts in excess of 58 kph caused by tropical storm Lee, coupled with extreme drought conditions in central Texas. After 18 days the fire was 95% contained, with the total burn area encompassing 13,406 ha (ca. 39% of the Lost Pines ecoregion). Seven of the 10 ponds used in the Brown et al. (2012) study burned in the wildfire, allowing us the opportunity to assess the impacts of a high intensity wildfire on RIFA in the Lost Pines ecoregion using 7 burned and 3 unburned ponds. Given the inverse relationship between canopy cover and RIFA captures found in the previous study, we hypothesized that RIFA captures would increase at ponds with substantial tree mortality caused by the wildfire.

Study Site

We conducted this study on the 1,948 ha Griffith League Ranch (GLR). Vegetation on the GLR is typical of the Lost Pines ecoregion, with an overstory dominated by loblolly pine (*Pinus taeda*), post oak (*Quercus stellata*), blackjack oak (*Quercus marilandica*), and eastern red cedar (*Juniperus virginiana*), and an understory dominated by yaupon holly (*Ilex vomitoria*), American beautyberry (*Callicarpa americana*), and farkleberry (*Vaccinium arboreum*). The GLR contains three permanent ponds (i.e., ponds have not dried in at least 12 years), 10 semi-permanent ponds (i.e., ponds typically dry several times per decade), and dozens of ephemeral ponds that hold water for days to months annually depending on rainfall. For this study we used the 7 burned and 3 unburned ponds with RIFA sampling data prior to the wildfire, all of which are known Houston toad breeding ponds. Three of the ponds were ephemeral, six were semi-permanent, and one was permanent.

Methods

The pre-wildfire RIFA capture data used in this study was collected between 26 September 2009 and 10 October 2010, with the area around each of the 10 ponds sampled a total of 27 times (Brown et al. 2012). We collected post-wildfire RIFA capture data for this study between 25 September 2011 and 4 August 2012, sampling the area around each of the 10 ponds a total of 11 times. To maximize comparability we used an identical sampling design to that of Brown et al. (2012). Days between sampling ranged from 15 to 78, with a mean of 31 days between samples. We used a standard bait cup method for sampling ants (Porter and Tschinkel 1987; Mueller et al. 1999), which consisted of half a Vienna sausage placed in a 9-cm-diameter round plastic dish. We placed between 4 and 14 dishes around the perimeter of each pond, depending on pond size (i.e., perimeter length). During each sampling event, we placed dishes 1−2 m from the pond edge at 3−4 m intervals, and allowed them to attract ants for 30 minutes. After 30 minutes we collected ants from each dish and euthanized them by freezing. We removed native ants from samples and counted the number of RIFA individuals collected in each bait cup at each pond on each sampling date. Because the number of bait cups varied by pond and sampling date, we calculated captures-per-unit-effort (CPUE; defined as the number of captures / number of bait cups), and used CPUE as our response variable.

The pre-wildfire canopy cover data used in this study was collected between 20 July 2008 and 16 April 2010, with percent canopy cover around each pond estimated between 4 and 24 times, depending on hydroperiod status at the time of sampling (i.e., estimates were not taken when ponds did not contain water; Brown et al. 2012). We estimated percent canopy cover around each pond four times between 18 April 2012 and 27 June 2012. For both studies, we estimated percent canopy cover using a spherical densiometer (Forestry Suppliers Inc., Jackson, MS) at two to six randomly selected points at the pond edge, with higher numbers of estimation points corresponding to larger ponds. We then averaged the estimates at each pond per sampling date. For this study we used the difference between the mean pre-wildfire and post-wildfire canopy cover estimates as a predictor of post-wildfire RIFA CPUE.

Statistical analyses

Our data included both spatial (multiple samples were taken from around the same pond) and temporal (the same ponds were sampled repeatedly) non-independence. To account for this we used a mixed effects modeling approach for our analyses, treating within-day sample nested within pond as a random effect. Preliminary analyses indicated a strong positive relationship between air temperature and RIFA captures, and thus we included mean daily temperature as a covariate in our final analyses. We obtained temperature data from the Austin-Bergstrom International Airport weather station, located approximately 36 km from the GLR (station number: 410429).

We initially tested interactions among and between treatment (control/wildfire), time (pre-burn/post-burn), and canopy cover change (change in mean % canopy cover between the pre-wildfire and post-wildfire sampling periods). This analysis indicated an interaction between canopy cover change and time, and changes in canopy cover were not consistent among ponds due to variability in tree mortality caused by the wildfire, as well as pond size (canopy cover at the edge of ponds typically increases as pond size increases). Thus, we analyzed each pond individually using mixed effects models to determine if RIFA CPUE differed by burn status. We investigated assumptions of normality and homoscedasticity using graphical diagnostics plots (Zuur et al. 2009). Because the data appeared to violate the assumption of normality, we transformed RIFA CPUE using the arcsinh (i.e., inverse hyperbolic sine) transformation (Fowler et al. 1998). We performed these analyses with the program R (R Version 2.10.1, www.r-project.org) using the nlme (Pinheiro et al. 2009) package. We considered effects to be significant at $\alpha = 0.05$. Finally, we tested the relationship between changes in RIFA CPUE between sampling periods and changes in mean % canopy cover between sampling periods using ordinary least squares (OLS) regression (Sokal and Rohlf 1995). For this analysis we used RIFA captures between May and early August (i.e., the peak RIFA activity months common to both the pre-wildfire and post-wildfire sampling periods). We considered effects to be significant at $\alpha = 0.05$.

Results

The initial analysis testing interactions among and between treatment, time, and canopy cover change indicated no treatment x time x canopy cover change interaction effect ($F_{1,365} = 0.03$, $P = 0.853$), no treatment x canopy cover change interaction effect ($F_{1,6} = 1.72$, $P = 0.237$), and no treatment x time interaction effect ($F_{1,365} = 0.02$, $P = 0.902$). However, we detected a time x canopy cover change interaction effect ($F_{1,365} = 27.52$; $P < 0.001$). These results indicate changes in CPUE between sampling periods (i.e., time) were not directly associated with the wildfire. Rather, CPUE differed between sampling periods, and the effect was influenced by changes in % canopy cover. The pond-specific tests indicated a time effect on RIFA CPUE at 5 of the 10 ponds, including 1 of 3 control ponds, and 4 of 7 wildfire ponds (Table 6.1). The time coefficients indicated that post-burn CPUE decreased at the control pond (Pond 6), decreased at two of the wildfire ponds (ponds 10 and 11), and increased at two of the wildfire ponds (ponds 13 and 14). The directional change in RIFA captures for all of these ponds was inversely related to canopy cover change (Pond 7 [+5.14%]; Pond 10 [+5.01%]; Pond 11 [+17.52%]; Pond 13 [-11.30%]; Pond 14 [-41.86%]). The OLS regression indicated that RIFA CPUE decreased with increased mean % canopy cover ($F_{1,7} = 13.17$; $P = 0.008$; $r^2 = 0.65$; Figure 6.1).

Table 6.1. Results from pond-specific tests of a burn status (pre-wildfire/post-wildfire) effect on red imported fire ant (RIFA; *Solenopsis invicta*) captures-per-unit-effort (CPUE) around pond edges in the Lost Pines ecoregion, Bastrop County, Texas, USA. We used mixed effects models to test for burn status effects, treating within-day sample nested within pond as a random effect, and we included mean daily temperature as a covariate. Pre-burn status coefficients show the direction of change in RIFA captures between sampling periods (pre-wildfire sampling period: September 2009 to October 2010; post-wildfire sampling period: September 2011 to August 2012), with positive coefficients indicating higher pre-wildfire RIFA captures.

Pond	Treatment	Pre-burn status coefficient (± SE)	$F_{1,35}$	P
5	Control	0.53 (0.61)	0.76	0.388
6	Control	0.86 (0.34)	6.33	0.017
7	Control	0.81 (0.56)	2.07	0.159
9	Wildfire	0.85 (0.53)	2.57	0.118
10	Wildfire	1.14 (0.45)	6.55	0.015
11	Wildfire	1.27 (0.53)	5.79	0.022

13	Wildfire	-0.50 (0.17)	8.17	0.007
14	Wildfire	-1.46 (0.45)	10.68	0.002
15	Wildfire	-0.67 (0.50)	1.80	0.188
16	Wildfire	0.27 (0.41)	0.42	0.523

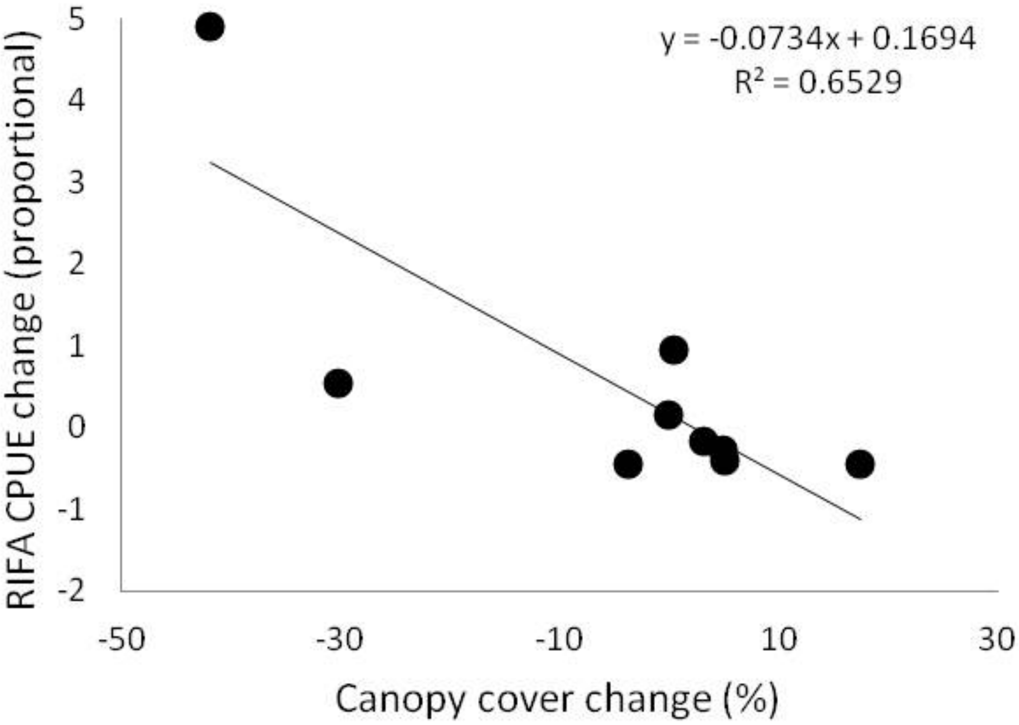

Figure 6.1. Ordinary least squares (OLS) regression assessing the relationship between differences in mean % canopy cover between the pre-wildfire (September 2009 to October 2010) and post-wildfire (September 2011 to August 2012) sampling periods, and red imported fire ant

(RIFA; *Solenopsis invicta*) captures-per-unit-effort (CPUE) between May and early August (i.e., the peak RIFA activity months common to both the pre-wildfire and post-wildfire sampling periods) around pond edges in the Lost Pines ecoregion, Bastrop County, Texas, USA. The analysis indicated post-wildfire RIFA CPUE was typically higher around ponds where % canopy cover was lower during the post-wildfire sampling period, and typically lower around ponds where % canopy cover was higher during the post-wildfire sampling period ($F_{1,7} = 13.17$; $P = 0.008$). One pond (Pond 13) was removed from this analysis because we obtained no captures during the pre-burn sampling period and thus could not calculate the proportional change in CPUE. For this pond the mean % canopy cover change was -11.3% and the mean post-wildfire CPUE during the peak RIFA activity period was 21.4.

Discussion

We found that a high intensity wildfire did not have a direct impact on RIFA CPUE, which was the same conclusion found for low intensity prescribed fires in this system (Brown et al. 2012). Rather, CPUE differences between the two sampling periods were driven by changes in canopy cover. Our results indicated the wildfire indirectly benefited RIFA through overstory tree mortality (and thus canopy cover reduction), supporting our hypothesis based on previous research (Brown et al. 2012). We speculate that the two wildfire ponds with significant post-wildfire decreases in RIFA CPUE actually positively impacted RIFA, but the effect was masked by an increase in canopy cover at these ponds due to heavy rainfall in fall 2011 that resulted in the pond edges reaching into the adjacent upland forest canopy.

Our primary motivation for conducting research on RIFA is to assist with management activities that benefit recovery of the Houston toad. The results of this study are cause for concern in that the wildfire burned a significant portion of the Lost Pines ecoregion (ca. 39%), with an estimated overstory tree loss of 78% across the burned area (Lost Pines Recovery Team 2011). Based on 13 randomly placed 20 m x 50 m vegetation plots on the GLR within the wildfire zone, the mean overstory tree loss was 81.9%, with a corresponding 30.2% decrease in canopy cover (D.J. Brown, unpublished data). Further, the Federal Emergency Management Agency (FEMA), Bastrop County, and local landowners are currently removing a substantial amount of dead trees due to conflicts with human-based recovery needs. Red imported fire ants are known to prefer forest gaps (Colby and Prowell 2006), and to use openings such as roads and powerline cuts as expansion corridors (Tschinkel 1988; Stiles and Jones 1998; Todd et al. 2008). Thus, the mortality and subsequent removal of trees in the Lost Pines has the potential to dramatically increase both area occupied by RIFA and site-specific RIFA densities in the Lost Pines.

The research conducted in this study and Brown et al. (2012) has increased our understanding of the spatial and temporal habitat use of RIFA in the Lost Pines ecoregion. It is clear that these patterns overlap with those of the Houston toad (Brown et al. 2012), and thus RIFA has the potential to be a serious threat to the persistence of the Houston toad. However, although we know that RIFA prey upon juvenile Houston toads (Freed and Neitman 1988), and we have evidence that they also prey upon adult Houston toads (M. C. Jones, Texas State University, personal communication), we do not have a good understanding of their impacts on Houston toad survivorship rates. Thus, it is possible that RIFA predation is partially or entirely compensatory (i.e., some or all of the mortality caused by RIFA could be substituting for mortality that would have occurred due to other factors). However, we believe the increased prevalance of RIFA in the Lost Pines as a result of post-wildfire canopy cover loss will likely add additional stress to Houston toad persistance in the ecoregion. Fortunately, RIFA control through insecticides, if warranted, is a viable option for Houston toad recovery efforts.

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