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Comparison of short term low, moderate, and high severity fire impacts to aquatic and terrestrial ecosystem components of a southern USA mixed pine/hardwood forest

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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 sought to quantify the impacts of low, moderate, and high severity fires, and their interaction with prior forest management practices, to several aquatic and terrestrial ecosystem components of a southern U.S. mixed pine/hardwood forest using a before–after, control-impact (BACI) approach. The ecosystem components we assessed were water quality, community composition of aquatic arthropods (wildfire impacts only), forest structure characteristics, community composition of understory vegetation, and community composition of ground-dwelling arthropods. We found that increasing fire severity 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, community composition of understory vegetation, and community composition of ground-dwelling arthropods in the initial years following burns. In contrast, high severity fires dramatically reduced fine and large fuel loads, increased diversity of understory vegetation, and influenced community composition of ground-dwelling arthropods. Further, wildfire severity was reduced in areas with a prior moderate severity prescribed burn, but not in areas with a prior low severity prescribed burn. Our results provide quantitative evidence for the role of fire severity as a primary factor influencing responses of ecosystems to fire, and indicate that forest management practices influence the impact of high severity fires on ecosystems.

1. Introduction

Climatic trends towards warmer and drier conditions, coupled with longstanding broad-scale fire suppression, have resulted in an increase in frequency of 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). The increase in wildfires is 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-dominated 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

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knowledge of similarities and differences between prescribed fire and wildfire 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 timing and burn frequency, particularly on vegetation (e.g., Cain et al., 1998; Sparks et al., 1998; Taylor, 2000; Webster and Halpern, 2010). However, much less is known about effects of burn severity, given that prescribed burns are typically low or moderate severity fires (Knapp et al., 2009). In contrast, high severity wildfires are unplanned and opportunities for comparative research are more limited.

Fire impacts many terrestrial ecosystem components, ranging from soil properties (Certini, 2005), to habitat selection of large mammals (Long et al., 2009). Fire has also been found to impact aquatic ecosystems in pine-dominated forests (e.g., Spencer and Hauer, 1991; Battle and Golladay, 2003). These aquatic ecosystems provide habitat for a variety of vertebrates (e.g., amphibians and fish) and invertebrates, with many threatened and endangered species dependent upon the presence and quality of aquatic environments in forested landscapes, such as the endangered Houston toad (*Bufo* [*Anaxyrus*] *houstonensis*), and threatened gila trout (*Oncorhynchus gilae*). With the exception of direct effects through increased water temperatures (Hitt, 2003) and burning when aquatic areas are dry (Sacerdote and King, 2009), fire primarily impacts aquatic components indirectly through a variety of impacts to the surrounding and adjacent terrestrial environment (Spencer and Hauer, 1991; Gresswell, 1999). Due to the interconnected nature of aquatic and terrestrial systems, fire research that incorporates effects on both ecosystem types is needed to improve our understanding of fire impacts to ecosystems (Bisson et al., 2003; Rieman et al., 2003).

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 the magnitude of inorganic 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 terrestrial and aquatic 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 inter- and intra-specific interactions. Thus, fire effects on biotic ecosystem components are inherently complex and difficult to extrapolate from one ecosystem to another. Further, the impacts of high severity fires are typically not short-lived, but rather a given fire can influence an ecosystem from 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., soil organic matter), which influences spacing of individual plants 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 low 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 the density of 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 equivocal and unpredictable, likely due to more complex trophic interactions and the ability of some taxa 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 some bird species (i.e., hermit thrush [*Catharus guttatus*] and western tanager [*Piranga ludoviciana*]) responded positively to low severity fire and negatively to high severity fire in the same study area, and Roberts et al. (2008) found equivalent responses in small mammals. Alternatively, by meta-analysis on bird and small mammal responses to fire severity, Fontaine and Kennedy (2012) concluded that fire severity did not consistently impact species response direction (e.g., a negative or positive impact), but response magnitude of animals increased with fire severity.

The above 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). In this study we sought to quantitatively assess the impacts of fire severity and forest management practices (i.e., prescribed fire, historic fire suppression, and their combinations) on both terrestrial and aquatic ecosystem components of a mixed pine/hardwood forest in central Texas. Specifically, we assessed impacts of low severity winter prescribed burns, moderate severity summer prescribed burns, moderate severity summer wildfires, and high severity summer wildfires on water quality, aquatic arthropods (data for wildfire impacts only), vegetation (live and dead), and terrestrial ground-dwelling arthropods. Based on previous research, we hypothesized that impacts to terrestrial components would increase with increasing fire severity, and subsequent effects on aquatic components would also be more pronounced as fire severity increased, and that prior forest management practices would influence the impacts of subsequent wildfires.

In addition to our basic interest concerning fire severity effects, we also have an applied interest specific to the impacts of fire on our study area, the Lost Pines ecoregion of Texas. This ecoregion is the last remaining stronghold for the federally endangered Houston toad, 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., 2013a,b). 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, 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 1948-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, 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 10 or more 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; winter burn intensities were low (hereafter LOWRX) and the summer burn intensity was moderate (hereafter MODRX) 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 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. Because these wildfires occurred shortly after the MODRX prescribed burn (i.e., under similar moisture and temperature conditions), were not extensive, and did not affect most of our sampling units, we included these wildfires in the MODRX category for this study. On 4 September 2011 a high severity wildfire (hereafter HIGHWILD) 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 (Fig. 1).

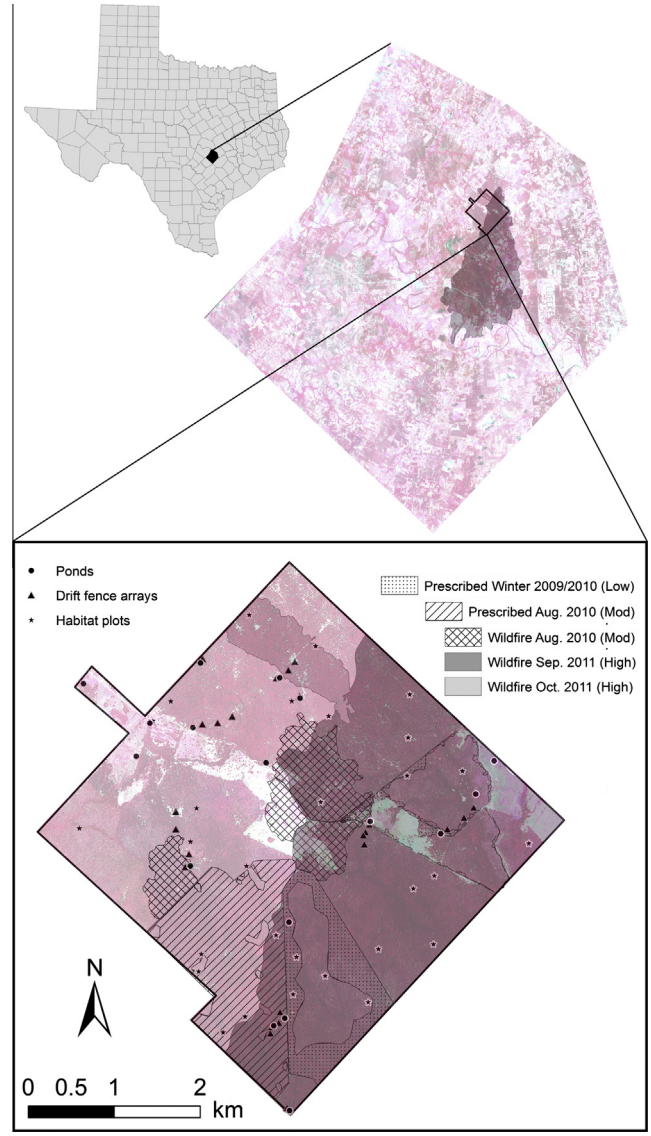

Fig. 1. Aerial image of the Griffith League Ranch (GLR), Bastrop County, Texas, USA, and its location with respect to a 13,406 ha high severity wildfire that occurred in the Lost Pines ecoregion in September 2011, with a breach of the fire break resulting in an additional 125 ha burned in October 2011. 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

The data sets described below differed in number of control and treatment sampling units and number of pre-fire and post-fire sampling events. To facilitate interpretation of our sampling effort and analyses, the number of sampling units and sampling events for each data set is provided in Table 1.

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 all 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 all fire events (i.e., 1–3 times within the first 2 weeks). We sampled water within 1 m of pond edges using 1 L Nalgene® collection bottles. Within 24 h 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 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

Table 1
Number of sampling units (control/treatment [RX]) and sampling events (pre-fire/post-fire) for ecosystem components used in this study to quantify the impacts of low severity prescribed fire (LOWRX), moderate severity prescribed fire/wildfire (MODRX), high severity wildfire (HIGHWILD), and their interactions with prior forest management practices (LOWRX + HIGHWILD; MODRX + HIGHWILD) on the Griffith League Ranch (GLR), Bastrop County, Texas, USA. The LOWRX fires occurred on 13 November 2009 and 10 January 2010, MODRX fires occurred on 7 August 2010 (prescribed fire) and 21 August 2010 (wildfire), and the HIGHWILD fires occurred on 4 September 2011 and 4 October 2011. The temporal distribution of sampling effort for each ecosystem component is described in the methods.

CONTROL vs.	Ecosystem component	Sampling units		Sampling events	
		CONTROL	RX	Pre-fire	Post-fire
LOWRX	Water quality	12	4	10	11
	Terrestrial vegetation	26	2	2	1
	Ground-dwelling arthropods	17	4	3	16
	Fire severity	NA	3	NA	1
MODRX	Water quality	12	4	15	8
	Terrestrial vegetation	9	3	3	1
	Ground-dwelling arthropods	17	4	13	6
	Fire severity	NA	5	NA	1
HIGHWILD	Water quality	9	7	14	4
	Terrestrial vegetation	9	13	3	1
	Ground-dwelling arthropods	10	7	19	5
	Aquatic arthropods	4	4	3	4
	Fire severity	NA	13	NA	1
LOWRX + HIGHWILD	Terrestrial vegetation	9	2	3	1
	Ground-dwelling arthropods	10	4	19	5
	Fire severity	NA	2	NA	1
MODRX + HIGHWILD	Terrestrial vegetation	9	1	3	1
	Ground-dwelling arthropods	10	4	19	5
	Fire severity	NA	2	NA	1

water column by filtering water through pre-combusted and pre-weighed A/E filters and then drying filters at 60 °C for 48 to 72 h, and re-weighing the filters. Quantification of non-volatile suspended solids (NVSS) was determined by subsequently combusting filters at 550 °C for 4 h and then taking weights (Heiri et al., 2001). We obtained filter mass values using a Mettler Toledo 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 on each sampling date, and used the average of the replicates for this study.

In addition to measuring water quality variables, we also estimated pond depth and percent canopy cover around each pond for use as covariables in water quality analyses. We estimated pond depth using permanent staff gauges located at the deepest point of each pond. 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 ponds of larger size. We averaged the estimates at each pond per sampling date.

2.3.2. Aquatic arthropods

Unfortunately, sampling of aquatic arthropods in ponds was initiated after the LOWRX and MODRX fires and most of the sampled ponds were not part of those fire treatments. Thus, we were only able to assess impacts of the HIGHWILD fire on the composition of pond arthropods. We sampled aquatic arthropods seasonally, collecting 7 samples at 8 ponds between August 2010 and January 2013 using a dip net (900 μm aperture netting). For each sampling event at each pond we sampled 3 points ca. 1 m from the perimeter, maintaining approximately even spacing between points, and performed 3 successive dip net sweeps per point. We combined the samples obtained at each pond and stored them in 95% ethanol. We identified insects to family, with the exception of Ephemeroptera (mayflies) and Odonata (dragonflies and damselflies), which we 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. Terrestrial vegetation

We used National Park Service (2003) fire monitoring guidelines to assess fire severity and impacts of the fires on forest structure characteristics and community composition of understory vegetation. We randomly placed thirty-one 20 m × 50 m plots in forested habitat, 29 of which were used in this study (Fig. 1). The remaining 2 plots were abandoned after fire breaks were accidentally installed within them during wildfires. Only 1 plot was burned in the 2010 MODRX wildfires, and this plot was used only in fire severity analyses. In addition, because no plots were burned in the November 2009 LOWRX prescribed fire, we installed 1 temporary plot adjacent to a permanent plot to assess fire severity.

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 LOWRX and MODRX fires. 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 (i.e., number of transect points intersecting vegetation), shrub and herbaceous vegetation abundance (i.e., number of stems detected in plots), litter and duff depth (mm), and fuel abundance (1 h [0–0.62 cm diameter], 10 h [0.63–2.54 cm diameter], 100 h [2.55–7.62 cm diameter], and 1000 h [>7.62 cm diameter]). We

identified shrubs, vines, and forbs to genus or, typically, to species. 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 (i.e., litter and duff) 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), with the same researcher performing all assessments to ensure consistency in ranks. Overstory canopy cover is not included in the National Park Service (2003) fire monitoring guidelines, but 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 (Fig. 1). 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 fires. 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. 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]) because our sampling design was likely inadequate for estimating relative abundance differences for flying taxa. 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.

2.4. Data analyses

We conducted similar analyses for the aquatic arthropod, terrestrial vegetation, and ground-dwelling arthropod data sets. We describe those analyses here, with additional, data set-specific, information given below. To assess community-level impacts of the fires we used redundancy analysis (RDA), which is an extension of principal components analysis (PCA), but includes explanatory variables. We chose RDA over canonical correspondence analysis (CCA) because detrended correspondence analyses (DCA) indicated our gradient lengths were short (<4), and our predictors were categorical (Leps and Smilauer, 2003). We tested for treatment × burn status interactions using Monte Carlo permutation tests (p-value in the results represents a permutation test for the first canonical axis). We included sampling unit identities (i.e., pond, array, plot) as covariates in the analyses. By including this covariate we subtracted the average values and assessed only value changes within each sampling unit (Leps and Smilauer, 2003). We $\log_{10}$ transformed the response data so that percentage rather than absolute changes in values were analyzed. In addition, when data were measured on different scales (e.g., forest structure characteristics), we centered and standardized the response data.

We conducted community composition analyses separately for the LOWRX, MODRX, and HIGHWILD fire categories because sampling units were often a member of multiple fire severity categories (e.g., controls during LOWRX fires were later burned in HIGHWILD fires). This allowed us to manipulate the sampling units and sampling events in each comparison so that only true controls and true treatment units were included in each comparison (see Table 1). For the HIGHWILD fire comparisons we separated sampling units into 3 categories, those that were controls prior to burning, those that burned in prior LOWRX fire, and those that burned in prior MODRX fire. This allowed us to investigate the influence of forest management practices on HIGHWILD impacts. We performed these analyses using the program CANOCO (version 4.5).

We conducted additional univariate analyses on the data sets to investigate fire impacts on total captures of aquatic arthropods and ground-dwelling arthropods, and to investigate species/variable-specific responses when they appeared to display a strong response in the RDA analyses. For these analyses we used generalized least squares. When data did not satisfy assumptions of normality and homoscedasticity we transformed them using the arcsinh (i.e., inverse hyperbolic sine) transformation, which was effective (Fowler et al., 1998). We accounted for non-independence in our repeated measures data using a continuous autoregressive term (corCAR1) nested within each sampling unit (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). We performed these analyses using the program R (version 2.14).

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 (Leps and Smilauer, 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).

Because the fires occurred at different times over the study period, we conducted 3 separate analyses, assessing impacts of LOWRX, MODRX, and HIGHWILD fire. To minimize the influence of fires not included in a given analysis, we removed ponds from the data set (i.e., sampling events) 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 LOWRX and MODRX fire analyses, we did not include any sampling events after the HIGHWILD fires, given that all but 1 of the ponds re-burned in those fires.

For all 3 analyses we included sampling period, pond depth, and canopy cover at the pond edge as covariates. Including sampling event 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 in a pond across all sampling events. 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 $\log_{10}$ 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. Terrestrial 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. 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.

For the community-level analysis of forest structure characteristics, we included 12 response variables: 1 h fuel, 10 h fuel, 100 h fuel, 1000 h fuel, total above-ground litter depth, total above-ground duff depth, overstory canopy cover, understory species cover, vegetation species richness, cedar seedling abundance, oak seedling abundance, and pine seedling abundance. In addition, we included cumulative precipitation between January and May (i.e., prior to initiation of sampling) for each sample year as a covariate. 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. 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. Additional univariate analyses including fuel (all classes), litter depth, duff depth, overstory canopy cover, understory species cover, and vegetation species richness, and the species yaupon holly, flowering spurge (*Euphorbia corollata*), pokeweed (*Phytolacca americana*), horseweed (*Conyza canadensis*), sedges (*Cyperus* spp.), and panic grasses (*Dicanthelium* spp.).

2.4.3. Ground-dwelling arthropods

For both the community composition and univariate analyses, we included sampling season and cumulative precipitation during the 7-day sampling period as covariates. Univariate analyses for species groups included Araneae (spiders), Carabidae (ground beetles), Curculionidae (snout beetles), Diplopoda (millipedes), Gryllacrididae (raspy crickets), Scarabaeidae (scarab beetles), and Scorpiones (scorpions). 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., $\alpha = 0.017$).

3. Results

3.1. Water quality

The PRC analyses indicated a significant treatment × time interaction for the LOWRX ($P = 0.032$) and HIGHWILD ($P = 0.024$), categories, but not for the MODRX category ($P = 0.60$), with the first axis explaining 5%, 5%, and 4% of the variance, respectively. The PRC diagrams indicated increased pond nutrient levels following fire, with corresponding increases in chl-*a* concentrations (Fig. 2). Impacts on pH and DOC were equivocal, with pH decreasing following HIGHWILD fire, but increasing slightly after LOWRX fire, and DOC increasing following LOWRX fire, but decreasing after HIGHWILD fire.

3.2. Aquatic arthropods

We did not detect a HIGHWILD fire impact on total number of captured individuals of aquatic arthropods ($F_{1,52} = 0.71$, $P = 0.404$). Likewise, the RDA analysis indicated the HIGHWILD fire had no impact on community composition of aquatic arthropods ($P = 0.949$), with 3.2% of the variation explained by the model. In addition, the RDA biplot confirmed the statistical test, with all aquatic arthropod groups located either near the origin or nearly orthogonal to the treatment × burn status predictor.

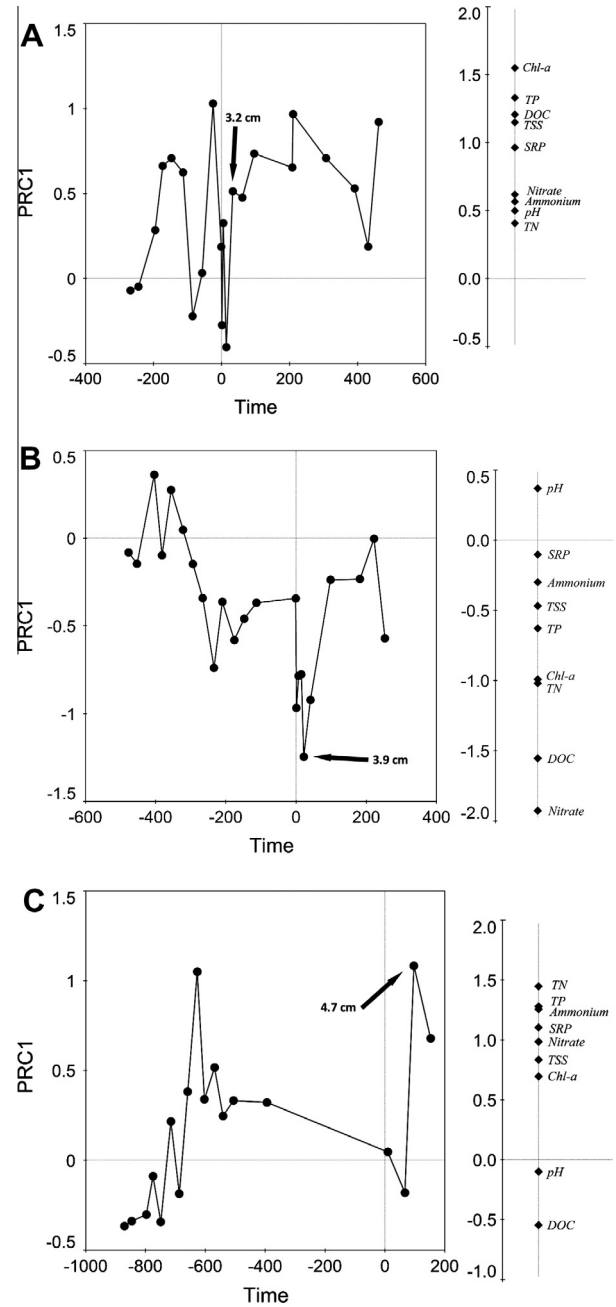

Fig. 2. Results from Principal Response Curve (PRC) analyses used to assess the impacts of low severity winter prescribed fires (A), moderate severity summer prescribed/wildfires (B), and high severity summer wildfires (C) on pond water quality on the Griffith League Ranch (GLR), Bastrop County, Texas, USA. Arrows indicate the first post-fire sampling event following significant precipitation (cm). Number of days before and after fires are shown on the *X*-axes, and PRC scores are 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: 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.

3.3. Terrestrial vegetation

3.3.1. Fire severity

The distribution of fire severity ranks to substrate ranged from 0.5 to 1.44 for the LOWRX fires, 0.5–2.5 for the MODRX fires, and 1.68–4 for the HIGHWILD fires when plots were controls prior to the fires (Fig. 3). Our plots indicated that burn severity for the

HIGHWILD fires was not affected by the prior LOWRX fires, but burn severity was dramatically reduced by the prior MODRX fires (Fig. 4).

Both overstory and pole-sized tree mortality was substantially greater in the HIGHWILD fire plots compared to the LOWRX and MODRX fire plots (Fig. 5). Similar to substrate impacts, our plots indicated that tree mortality following the HIGHWILD fires was not reduced in the LOWRX fire zones, but was dramatically reduced in the MODRX fire zones, with the exception of overstory cedar trees. For all of the fires, pine tree mortality was greater than either oak or cedar tree mortality.

3.3.2. Forest structure characteristics and understory community composition

The RDA analyses indicated the LOWRX fires had no significant impact on forest structure characteristics ($P = 0.133$) or understory community composition ($P = 0.145$), the MODRX fires had no significant impact on forest structure characteristics ($P = 0.102$) or understory community composition ($P = 0.082$), and the HIGHWILD fires did impact forest structure characteristics ($P = 0.002$) and understory community composition ($P = 0.002$). The amount of total variation explained by the HIGHWILD fire models was 18.1% and 9.6% for forest structure characteristics and community composition of understory vegetation, respectively.

The RDA biplot was congruent with significance tests (Fig. 6). No response variables were strongly associated with the LOWRX and MODRX fires, as indicated by the direction and length of response arrows. For plots that were controls prior to the HIGHWILD fires, overstory canopy cover ($F_{1,96} = 32.49$, $P < 0.001$), litter depth ($F_{1,96} = 66.63$, $P < 0.001$), duff depth ($F_{1,96} = 62.18$, $P < 0.001$), and amount of fuel in all fuel classes ($F_{1,96} = 24.55$, $P < 0.001$ [1 h fuel]; $F_{1,96} = 7.00$, $P = 0.010$ [10 h fuel]; $F_{1,96} = 11.49$, $P = 0.001$ [100 h fuel]; $F_{1,96} = 14.70$, $P < 0.001$ [1000 h fuel]) was reduced ca. 1 year after the fire, whereas species richness ($F_{1,96} = 4.08$, $P = 0.046$) was higher ca. 1 year after the fire. Understory vegetation cover was not significantly different ($F_{1,96} = 0.61$, $P = 0.44$).

For the vegetation taxa with a clear response to the wildfire, all responses were positive with the exception of yaupon holly. The univariate analyses supported the 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 negative response of yaupon holly ($F_{1,95} = 45.31$, $P < 0.001$), to HIGHWILD fire. The HIGHWILD analyses indicated that prior fires influenced the outcome for understory community composition. Abundance of flowering spurge ($F_{1,95} = 3.81$, $P = 0.054$) appeared to be positively associated with plots previously burned with LOWRX 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

Fig. 3. Examples of vegetation plots following low severity winter prescribed fires (A), moderate severity summer prescribed/wildfires (B), and high severity summer wildfires (C; 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 community 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 of understory vegetation.

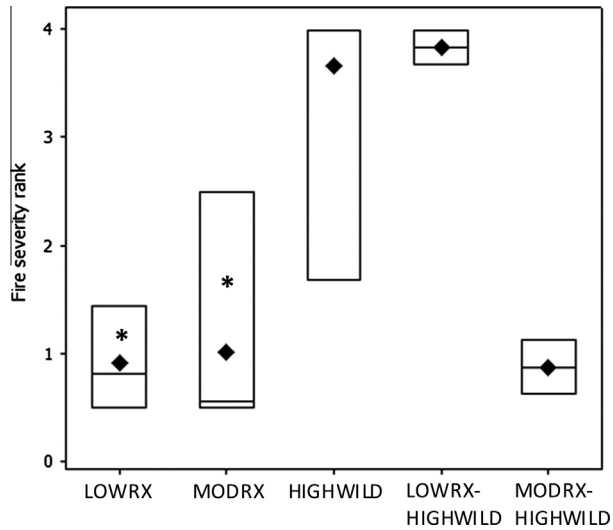

Fig. 4. Visual descriptive statistics displaying fire severity to substrate on the Griffith League Ranch (GLR), Bastrop County, Texas, USA for low severity winter prescribed fires (LOWRX), moderate severity summer prescribed/wildfires (MODRX), and high severity summer wildfires (HIGHWILD). We assessed 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 HIGHWILD fires included 3 categories: (1) plots that were controls prior to the fires [HIGHWILD (CONTROL)], (2) plots that were part of the prior LOWRX fires [LOWRX-HIGHWILD], and (3) plots that were part of the prior MODRX fires [MODRX-HIGHWILD]. Boxes enclose the range, diamonds show the mean, and horizontal bars delineate the median fire severity rank for each category. Stars in the LOWRX and MODRX severity categories denote the mean severity rank when unburned points were removed. Fire severity rank increased with fire severity, and prior MODRX fires reduced substrate burn severity from the HIGHWILD fires.

MODRX fires indicated the opposite associations ($F_{1,95} = 3.42$, $P = 0.068$ and $F_{1,95} = 27.97$, $P < 0.001$, respectively).

3.4. Ground-dwelling arthropods

We found no significant effect of fire on total captures of ground-dwelling arthropods in any of the fire severity analyses, as indicated by no significant treatment × burn status interaction effects (Table 2). The RDA analyses indicated LOWRX fire had no impact on community composition ($P = 0.110$); whereas, MODRX fire ($P = 0.024$) and HIGHWILD fire ($P = 0.002$) did affect community composition. However, the amount of total variation explained by the LOWRX, MODRX, and HIGHWILD models was low; 0.8%, 1.0%, and 2.9%, respectively. The RDA biplot indicated little or no response to fires for most arthropod groups (Fig. 7). However, the univariate analyses indicated several groups responded to fire. For areas that were controls prior to HIGHWILD fire, 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 positive response of Scarabaeidae to areas burned in both MODRX fire and HIGHWILD fire 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 HIGHWILD fire ($F_{1,594} = 0.54$, $P = 0.464$), or areas that were part of prior MODRX fire ($F_{1,594} = 1.32$, $P = 0.252$). Although Carabidae and Scorpiones appeared to show a moderate positive and negative response in areas that were controls prior to HIGHWILD fire, respectively, neither relationship was supported from univariate analyses ($F_{1,594} = 0.01$, $P = 0.943$ and $F_{1,594} = 1.42$, $P = 0.233$, respectively).

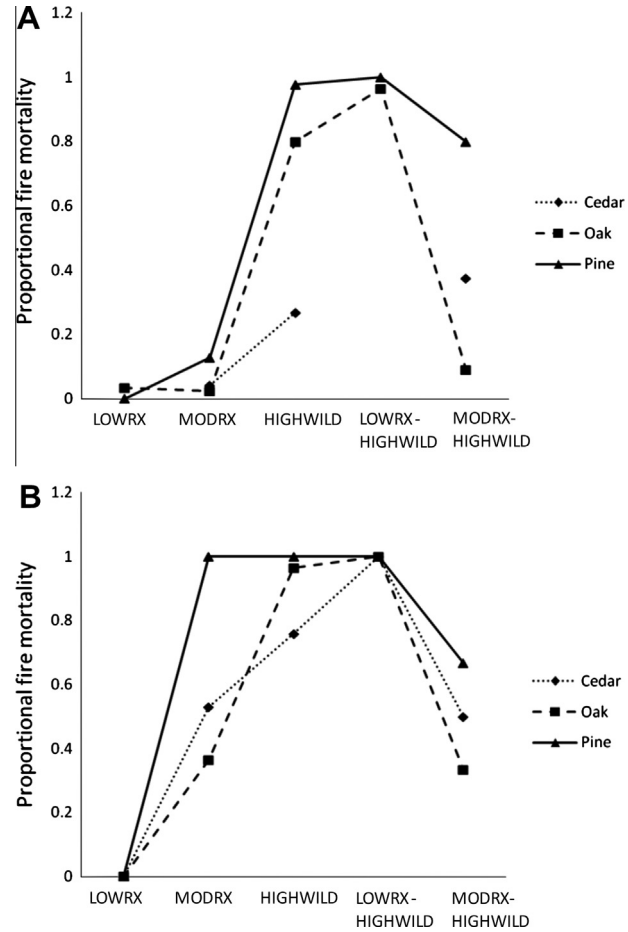

Fig. 5. Overstory (A) and pole-sized (B) tree mortality on the Griffith League Ranch (GLR), Bastrop County, Texas, USA following low severity winter prescribed fires (LOWRX), moderate severity summer prescribed/wildfires (MODRX), and high severity summer wildfires (HIGHWILD). The HIGHWILD fires included 3 categories: (1) plots that were controls prior to the fires [HIGHWILD (CONTROL)], (2) plots that were part of the prior LOWRX fires [LOWRX-HIGHWILD], and (3) plots that were part of the prior MODRX fires [MODRX-HIGHWILD]. 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 MODRX fires reduced tree mortality caused by the HIGHWILD fires. Note there were no overstory cedar trees in the LOWRX winter plots.

4. Discussion

The results of our study indicated fire severity influenced ecosystem response across scales and directly supports 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, MODRX fire was effective for reducing wildfire severity, and consequently tree mortality was much lower, litter and duff was reduced but not eliminated, and understory taxonomic diversity increased slightly. In contrast, LOWRX fire did little to mitigate tree mortality or substrate burn severity. Thus, managers seeking to use LOWRX fire for fuel reduction should expect that multiple burns will be necessary to achieve management goals. In contrast, higher severity fires are more effective for achieving immediate results, albeit with greater potential for unintended impacts. Overall, our study supports conclusions of the majority of studies, which concluded fuel reduction helps reduce fire severity in pine-dominated forests (Schoennagel et al., 2004; Mitchell et al., 2009; Safford et al., 2012).

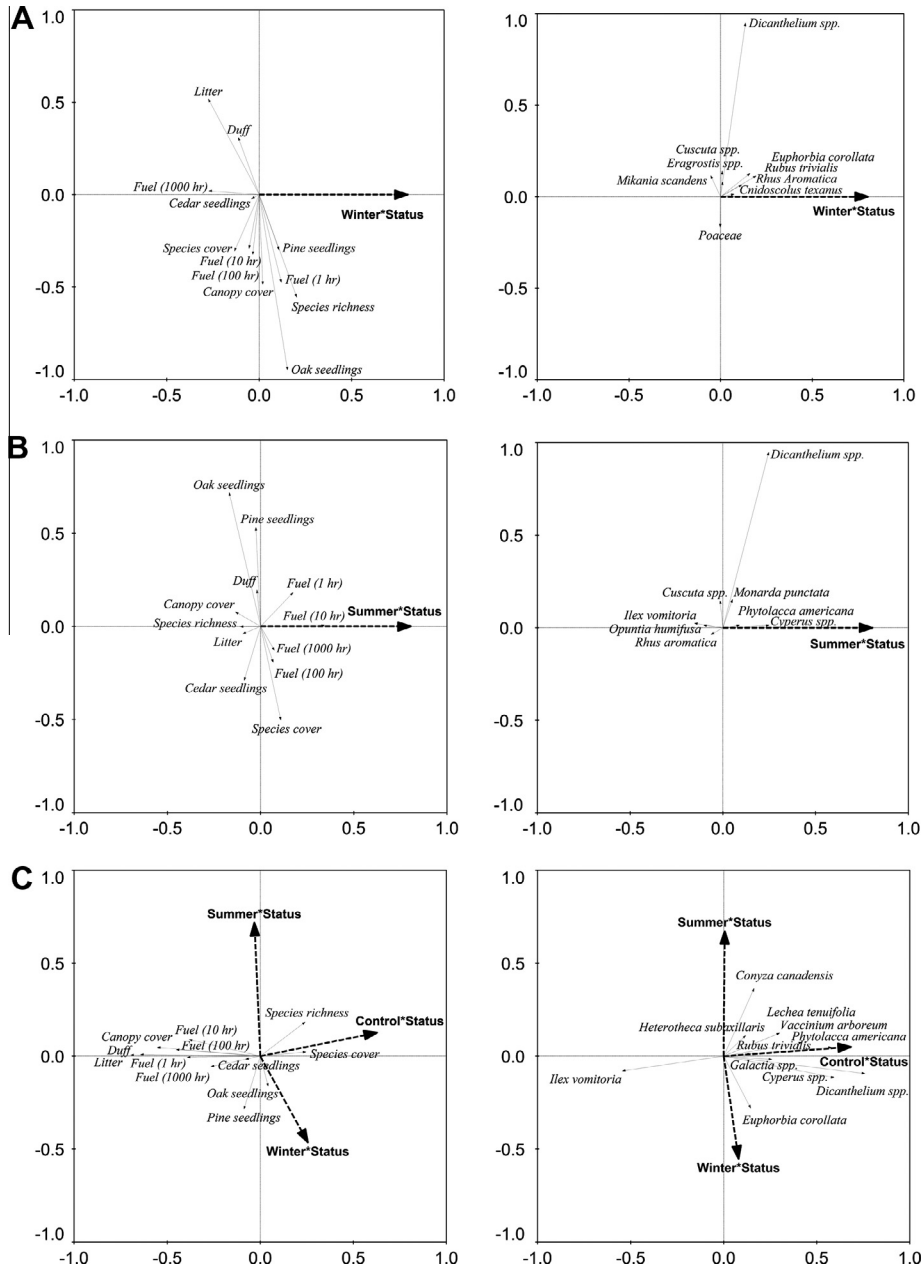

Fig. 6. Results from Redundancy Analyses (RDA) used to assess the impacts of low severity winter prescribed fires (A), moderate severity summer prescribed/wildfires (B), and high severity summer wildfires (C) on forest structure characteristics (left biplot) and community composition of understory vegetation (right biplot) on the Griffith League Ranch (GLR), Bastrop County, Texas, USA. The high severity summer wildfires included 3 categories: (1) plots that were controls prior to the wildfire, (2) plots that were part of the prior low severity fires, and (3) plots that were part of the prior moderate severity 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 8–11 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 community composition of understory vegetation. In contrast, high severity fires dramatically reduced fine and large fuel loads, and increased diversity of understory vegetation.

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 across scales responsible for this finding, the first factor being the timing of the fires. The 2009 and 2010 LOWRX and MODRX fires occurred following exceptional drought conditions (based on the Palmer Drought Severity Index) 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 drought resistant, with 0% overstory tree mortality. Thus, the remaining loblolly pines were likely stressed, and thus more vulnerable to fire mortality, than if the burns occurred following several average rainfall or wetter than average years. Secondly, the Lost Pines loblolly pine population currently has a pine engraver beetle (*Ips* spp.) infestation (KES Consulting and Forstner, 2007). Pine engraver and bark beetles are known to select drought-stressed trees, and further increase vulnerability to mortality (Grosman and Upton,

Table 2
Results of generalized least squares analyses used to assess if a low severity winter prescribed burn (LOWRX), a moderate severity summer prescribed burn (MODRX), and high severity summer wildfires (HIGHWILD) 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 LOWRX fire, MODRX fire, and HIGHWILD fires occurred on 13 November 2009, 7 August 2010, and 4 September 2011 and 4 October 2011, respectively. The HIGHWILD fires included 3 categories: (1) plots that were controls prior to the wildfire (CONTROL), (2) plots that were part of the prior LOWRX fire (LOWRX-HIGHWILD), and (3) plots that were part of the prior MODRX fire (MODRX-HIGHWILD). The lack of significant treatment × burn status interaction effects indicated the fires did not significantly impact total abundance of ground-dwelling arthropods.

Fire	Coefficient (±SE)	*F*-value	df	*P*
LOWRX				
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
MODRX				
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
HIGHWILD				
Season	0.101 (0.05)	2.87	1,590	0.091
Precipitation	0.007 (0.00)	16.15	1,590	<0.001
Treatment (LOWRX-HIGHWILD)	−0.154 (0.23)	2.45	1,590	0.118
Treatment (MODRX-HIGHWILD)	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 (LOWRX-HIGHWILD)	−0.148 (0.42)	0.00	1,590	0.944
Treatment × status (MODRX-HIGHWILD)	−0.914 (0.42)	3.66	1,590	0.056
Treatment × status (CONTROL)	−0.427 (0.35)	1.48	1,590	0.224

2006; Schwilk et al., 2006). Third, 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 opportunistic sampling (3 independent samples per tree 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%). The final possible explanation 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 drier than in the expansive East Texas Pineywoods ecoregion (Owen, 1989), 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 climate change and related disturbance (e.g., increased prevalence of wildfires) impacts. Higher vulnerability to climate change and related disturbance impacts at distribution edges, particularly dry edges, appears to be common for conifers (Galiano et al., 2010; Littell et al., 2010; Coops and Waring, 2011; Benavides et al., 2013).

We found that fire severity impacted pond nutrient level increases, with the magnitude of those increases greatest following HIGHWILD fire, which agreed with our hypothesis that aquatic impacts would increase as terrestrial impacts increased. 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 within 200 days 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. Conversely, ponds and associated drainage zones should be excluded from prescribed burns when temporary nutrient increases are viewed as harmful to aquatic ecosystem integrity.

Despite the impacts of HIGHWILD fire on water quality, our analyses indicated those effects did not translate to changes in total captures or community 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, or as far as we are aware, any water bodies within the HIGHWILD fire 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 5–10 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 (i.e., lagged responses in population growth rates). 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 HIGHWILD fire, LOWRX and MODRX fire in this severely fire-suppressed ecosystem were largely ineffective for enhancing vegetation diversity in the initial years following burns. 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 LOWRX 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

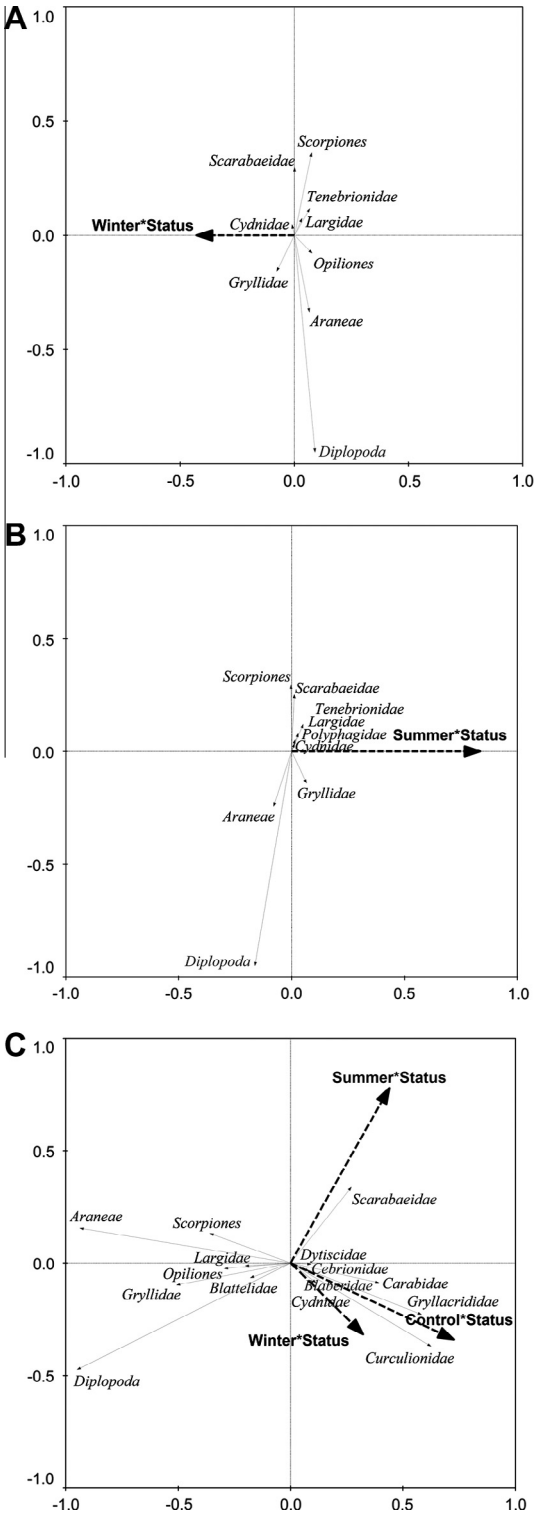

Fig. 7. Results from Redundancy Analyses (RDA) used to assess the impacts of a low severity winter prescribed fire (A), moderate severity summer prescribed/wildfires (B), and high severity summer wildfires (C) on ground-dwelling arthropods in the Lost Pines ecoregion of Texas, USA. We sampled arthropods using drift fence arrays with pitfall traps. The high severity wildfires included 3 categories: (1) traps that were controls prior to the wildfire, (2) traps that were part of the prior low severity fire, and (3) traps that were part of the prior moderate severity fires. 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 9–15 showing the greatest interaction response were included for ease of interpretation. The analyses indicated low and moderate severity fires had no detectable effects on community composition of ground-dwelling arthropods, whereas several arthropod groups responded to the high severity fires.

the LOWRX and MODRX fires (D.J. Brown, personal observation), which agrees with other findings in central Texas (Mitchell et al., 2005). In contrast, the HIGHWILD fires not only top-killed, but consumed entirely the majority of yaupon holly individuals, and this species did not reestablish 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 HIGHWILD fires, replaced yaupon holly as the dominant shrub in the HIGHWILD fire zones. This positive fire severity response for pokeweed has been noted elsewhere (Glasgow and Matlack, 2007). 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 HIGHWILD fires, but one that is known to respond positively to high severity fire (Barclay et al., 2004).

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

As with the vegetation results, we found that in contrast to HIGHWILD fire, LOWRX and MODRX fire had no detectable effect on community composition of ground-dwelling arthropods. Further, the arthropod HIGHWILD analysis agreed with our expectation for re-burned areas, traps in MODRX zones would differ from those in HIGHWILD zones that were controls prior to the HIGHWILD fires; whereas, traps in LOWRX 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 were no clear correlations related to feeding guilds. Qualitatively, the predators Scorpiones (scorpions [*Centruroides vittatus*]; Taber and Fleenor, 2003), Opiliones (harvestmen) and Araneae (spiders) were negatively impacted, whereas the predatory beetle family Carabidae showed a positive response. Similarly, 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 LOWRX fire 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 (KES Consulting and Forstner, 2007). We believe there are benefits to conducting burns in 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 may 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., 2013a,b). However, we note the relationships between pond productivity and tadpole growth and time-to-metamorphosis have not been examined for the Houston toad, and we recommend future research on this topic.

The HIGHWILD fire 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 HIGHWILD zone. The Houston toad exhibits strong preference for heavily canopied environments (U.S. Fish and Wildlife Service, 1984), and the suitability of the post-2011 HIGHWILD landscape for this species is currently unclear. However, we note that although overstory canopy cover has been dramatically reduced, understory cover has increased since the completion of this study (D.J. Brown, personal observation). 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 and large limbs. Thus, although in general the soil is likely warmer and drier within the wildfire zone (i.e., increased probability of desiccation), Houston toads could potentially mitigate this problem in the short-term by seeking out suitable refugia. However, we note that natural pine regeneration following the 2011 HIGHWILD fire was low and patchy across most of the burn zone. Thus, assisted pine restoration through seedling tree planting is currently a major recovery initiative in the ecoregion (Lost Pines Recovery Team, 2012).

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 (M.C. Jones, personal observation), given that abundance of this species appears to be strongly inversely correlated with overstory canopy cover in our study area (Brown et al., 2012, 2013a). However, with the increase in understory vegetation 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). Thus, although the HIGHWILD fire 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 HIGHWILD fire 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. Our results indicated this factor affected the ecosystem components we assessed, and prior forest management practices influenced the response of several ecosystem components to HIGHWILD fire. Given our results, future work should seek to address if multiple LOWRX to MODRX fires produce the desirable outcomes of HIGHWILD 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 HIGHWILD fires to assess the longer-term impacts to biotic and abiotic ecosystem components, and to provide data that can assist with recovery and management initiatives.

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References

Agee, J.K., 1996. Achieving conservation biology objectives with fire in the Pacific Northwest. Weed Technol. 10, 417–421.
Al-Rabah'ah, M.A., Williams, C.G., 2004. An ancient bottleneck in the Lost Pines of central Texas. Mol. Ecol. 13, 1075–1084.
Allen, C.D., Savage, M., Falk, D.A., Suckling, K.F., Swetnam, T.W., Schulke, T., Stacey, P.B., Morgan, P., Hoffman, M., Klingel, J.T., 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. Ecol. Appl. 12, 1418–1433.
Arkle, R.S., Pilliod, D.S., 2010. Prescribed fires as ecological surrogates for wildfires: a stream and riparian perspective. For. Ecol. Manag. 259, 893–903.
Baker, F.E., 1979. Soil Survey of Bastrop County. Texas. U.S, Department of Agriculture, Soil Conservation Service, Washington, D.C..
Barclay, A.D., Betancourt, J.L., Allen, C.D., 2004. Effects of seeding ryegrass (*Lolium multiflorum*) on vegetation recovery following fire in a ponderosa pine (*Pinus ponderosa*) forest. Int. J. Wildland Fire 13, 183–194.
Battle, J., Golladay, S.W., 2003. Prescribed fire's impact on water quality of depressional wetlands in southwestern Georgia. Am. Midl. Nat. 150, 15–25.
Benavides, R., Rabasa, S.G., Granda, E., Escudero, A., Hodar, J.A., Martinez-Vilalta, J., Rincon, A.M., Zamora, R., Valladares, F., 2013. Direct and indirect effects of climate on demography and early growth of *Pinus sylvestris* at the rear edge: changing roles of biotic and abiotic factors. Plos One 8, e59824.
Bisson, P.A., Rieman, B.E., Luce, C., Hessburg, P.F., Lee, D.C., Kershner, J.L., Reeves, G.H., Gresswell, R.E., 2003. Fire and aquatic ecosystems of the western USA: current knowledge and key questions. Forest Ecol. Manag. 178, 213–229.
Brown, D.J., Baccus, J.T., Means, D.B., Forstner, M.R.J., 2011. Potential positive effects of fire on juvenile amphibians in a southern USA pine forest. J. Fish Wildlife Manage. 2, 135–145.
Brown, D.J., DeVolld, B., Nowlin, W.H., Forstner, M.R.J., 2012. Fire ants in Houston toad habitat: annual activity and responses to canopy cover and fire. J. Fish Wildlife Manage. 3, 142–149.
Brown, D.J., Preston, D.B., Ozel, E., Forstner, M.R.J., 2013a. Wildfire impacts on red imported fire ant captures in the Lost Pines ecoregion of Texas. J. Fish Wildlife Manage. 4, 129–133.
Brown, D.J., Swannack, T.M., Forstner, M.R.J., 2013b. Predictive models for calling and movement activity of the endangered Houston toad (*Bufo houstonensis*). Am. Midl. Nat. 169, 303–321.
Bryant Jr., V.M., 1977. A 16,000 year pollen record of vegetational change in central Texas. Palynology 1, 143–156.
Buddle, C.M., Langor, D.W., Pohl, G.R., Spence, J.R., 2006. Arthropod responses to harvesting and wildfire: implications for emulation of natural disturbance in forest management. Biol. Conserv. 128, 346–357.
Cain, M.D., Wigley, T.B., Reed, D.J., 1998. Prescribed fire effects on structure in uneven-aged stands of loblolly and shortleaf pines. Wildl. Soc. Bull. 26, 209–218.
Certini, G., 2005. Effects of fire on properties of forest soils: a review. Oecologia 143, 1–10.
Collins, B.M., Stephens, S.L., Moghaddas, J.J., Battles, J., 2010. Challenges and approaches in planning fuel treatments across fire-excluded forested landscapes. J. Forest. 108, 24–31.
Coops, N.C., Waring, R.H., 2011. Estimating the vulnerability of fifteen tree species under changing climate in Northwest North America. Ecol. Model. 222, 2119–2129.
Crumpton, W.G., Isenhart, T.M., Mitchell, P.D., 1992. Nitrate and organic N analyses with second-derivative spectroscopy. Limnol. Oceanogr. 37, 907–913.
Davis, C., 2001. The west in flames: the intergovernmental politics of wildfire suppression and prevention. Publius 31, 97–110.
Dickson, B.G., Noon, B.R., Flather, C.H., Jentsch, S., Block, W.M., 2009. Quantifying the multi-scale response of avifauna to prescribed fire experiments in the southwest United States. Ecol. Appl. 19, 608–621.
Duarte, A., Brown, D.J., Forstner, M.R.J., 2011. Estimating abundance of the endangered Houston toad on a primary recovery site. J. Fish Wildlife Manage. 2, 207–215.
Duran, J., Rodriguez, A., Fernandez-Palacios, J.M., Gallardo, A., 2010. Long-term decrease of organic and inorganic nitrogen concentrations due to pine forest wildfire. Ann. For. Sci. 67, 207.
Earl, S.R., Blinn, D.W., 2003. Effects of wildfire ash on water chemistry and biota in south-western USA streams. Freshw. Biol. 48, 1015–1030.
Engstrom, R.T., 2010. First-order fire effects on animals: review and recommendations. Fire Ecol. 6, 115–130.
Fontaine, J.B., Kennedy, P.L., 2012. Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in U.S. fire-prone forests. Ecol. Appl. 22, 1547–1561.

Ford, W.M., Menzel, M.A., McGill, D.W., Laerm, J., McCay, T.S., 1999. Effects of a community restoration fire on small mammals and herpetofauna in the southern Appalachians. For. Ecol. Manag. 114, 233–243.

Fowler, J., Cohen, L., Jarvis, P., 1998. Practical Statistics for Field Biology, second ed. Wiley, New York.

Freed, P.S., Neitman, K., 1988. Notes on predation of the endangered Houston toad, *Bufo houstonensis*. Tex. J. Sci. 40, 454–456.

Gaertner, J.P., Brown, D.J., Mendoza, J.A., Forstner, M.R.J., Bonner, T., Hahn, D., 2012. Geographic variation in *Batrachochytrium dendrobatidis* occurrence among populations of *Acris crepitans blanchardi* in Texas. USA Herpetol. Rev. 43, 274–278.

Galiano, L., Martinez-Vilalta, J., Lloret, F., 2010. Drought-induced multifactor decline of scots pine in the Pyrenees and potential vegetation change by the expansion of co-occurring oak species. Ecosystems 13, 978–991.

Gaston, M.A., Fuji, A., Weckerly, F.W., Forstner, M.R.J., 2010. Potential component allee effects and their impact on wetland management in the conservation of endangered anurans. Plos One 5, e10102.

Gauthier, S., Bergeron, Y., Simon, J.-P., 1996. Effects of fire regime on the serotiny level of jack pine. J. Ecol. 84, 539–548.

Gebert, K.M., Black, A.E., 2012. Effect of suppression strategies on federal wildland fire expenditures. J. Forest. 110, 65–73.

Geluso, K.N., Bragg, T.B., 1986. Fire-avoidance behavior of meadow voles (*Microtus pennsylvanicus*). Am. Midl. Nat. 116, 202–205.

Gilliam, F.S., 1988. Interactions of fire with nutrients in the herbaceous layer of a nutrient- poor coastal plain forest. B. Torrey Bot. Club 115, 265–271.

Gilliam, F.S., Platt, W.J., 1999. Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (longleaf pine) forest. Plant Ecol. 140, 15–26.

Glasgow, L.S., Matlack, G.R., 2007. Prescribed burning and understory composition in a temperate deciduous forest, Ohio, USA. For. Ecol. Manag. 238, 54–64.

Greenberg, C.H., Forrest, T.G., Waldrop, T., 2010. Short-term response of ground-dwelling arthropods to prescribed fire and mechanical fuel reduction in a southern Appalachian upland hardwood forest. For. Sci. 56, 112–121.

Greenberg, C.H., Waldrop, T.A., 2008. Short-term response of reptiles and amphibians to prescribed fire and mechanical fuel reduction in a southern Appalachian upland hardwood forest. For. Ecol. Manag. 255, 2883–2893.

Gresswell, R.E., 1999. Fire and aquatic ecosystems in forested biomes of North America. Trans. Am. Fish. Soc. 128, 193–221.

Grosman, D.M., Upton, W.W., 2006. Efficacy of systemic insecticides for protection of loblolly pine against southern fine engraver beetles (Coleoptera: Curculionidae: Scolytinae) and wood borers (Coleoptera: Cerambycidae). J. Econ. Entomol. 99, 94–101.

Hall, S.A., Burke, I.C., Hobbs, N.T., 2006. Litter and dead wood dynamics in ponderosa pine forests along a 160-year chronosequence. Ecol. Appl. 16, 2344–2355.

Hanberry, B.B., Dey, D.C., He, H.S., 2012. Regime shifts and weakened environmental gradients in open oak and pine ecosystems. Plos One 7, e41337.

Hartnett, D.C., Krofta, D.M., 1989. Fifty-five years of post-fire succession in a southern mixed hardwood forest. B. Torrey Bot. Club 116, 107–113.

Heiri, O., Lotter, A.F., Lemcke, G., 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. J. Paleolimnol. 25, 101–110.

Hély, C., Bergeron, Y., Flannigan, M.D., 2000. Effects of stand composition on fire hazard in mixed-wood Canadian Boreal Forest. J. Veg. Sci. 11, 813–824.

Hillis, D.M., Hillis, A.M., Martin, R.F., 1984. Reproductive ecology and hybridization of the endangered Houston toad (*Bufo houstonensis*). J. Herpetol. 18, 56–72.

Hitt, N.P., 2003. Immediate effects of wildfire on stream temperature. J. Freshwater Ecol. 18, 171–173.

Hodgkins, E.J., 1958. Effects of fire on undergrowth vegetation in upland southern pine forests. Ecology 39, 36–46.

Houghton, R.A., Hackler, J.L., Lawrence, K.T., 2000. Changes in terrestrial carbon storage in the United States. 2: The role of fire and fire management. Glob. Ecol. Biogeogr. 9, 145–170.

Jones, D.D., Conner, L.M., Storey, T.H., Warren, R.J., 2004. Prescribed fire and raccoon use of longleaf pine forests: implications for managing nest predation? Wildl. Soc. Bull. 32, 1255–1259.

KES Consulting, Loomis Austin, Forstner, M.R.J., 2007. Lost Pines Habitat Conservation Plan for Bastrop County, Texas. <http://www.co.bastrop.tx.us/site/content/lostpineshabitat> (accessed 06.17.13).

Knapp, E.E., Estes, B.L., Skinner, C.N., 2009. Ecological Effects of Prescribed Fire Season: A Literature Review and Synthesis for Managers. U.S. Department of Agriculture, General Technical Report PSW-GTR-224, Redding, CA.

Knebel, L., Wentworth, T.R., 2007. Influence of fire and southern pine beetle on pine-dominated forests in the Linville Gorge Wilderness, North Carolina. Castanea 72, 214–225.

Lecomte, N., Simard, M., Fenton, N., Bergeron, Y., 2006. Fire severity and long-term ecosystem biomass dynamics in coniferous Boreal Forests of Eastern Canada. Ecosystems 9, 1215–1230.

Leps, J., Smilauer, P., 2003. Multivariate Analysis of Ecological Data Using CANOCO. Cambridge University Press, New York.

Lewis Jr., W.M., 1974. Effects of fire on nutrient movement in a South Carolina pine forest. Ecology 55, 1120–1127.

Littell, J.S., Oneil, E.E., McKenzie, D., Hicke, J.A., Lutz, J.A., Norheim, R.A., Elsner, M.M., 2010. Forest ecosystems, disturbance, and climatic change in Washington State. USA Clim. Change 102, 129–158.

Long, R.A., Rachlow, J.L., Kie, J.G., 2009. Sex-specific responses of North American elk to habitat manipulation. J. Mammal. 90, 423–432.

Lost Pines Recovery Team, 2011. Bastrop County complex fire Lost Pines Region: Resource Assessment & Response Report. Lost Pines Recovery Team, Bastrop County, Texas, USA. <http://bastroprecovery.org> (accessed 06.17.13).

Lost Pines Recovery Team, 2012. Bastrop Lost Pines habitat Recovery Project Master Plan. Lost Pines Recovery Team, Bastrop County, Texas, USA. <http://bastroprecovery.org> (accessed 06.17.13).

Malison, R.L., Baxter, C.V., 2010. Effects of wildfire of varying severity on benthic stream insect assemblages and emergence. J. N. Am. Benthol. Soc. 29, 1324–1338.

McEachern, P., Prepas, E.E., Gibson, J.J., Dinsmore, W.P., 2000. Forest fire induced impacts on phosphorus, nitrogen, and chlorophyll a concentrations in Boreal subarctic lakes of northern Alberta. Can. J. Fish. Aquat. Sci. 57, 73–81.

Miller, J.D., Safford, H.D., Crimmins, M., Thode, A.E., 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, R., Cathey, J.C., Dabbert, B., Prochaska, D.F., DuPree, S., Ron, S., 2005. Managing yaupon with fire and herbicides in the Texas Post Oak Savannah. Rangelands 27, 17–19.

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

Moore, B., 1977. Bastrop County 1691–1900, revised ed. Nortex Press, Wichita Falls, TX.

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

Moretti, M., Obrist, M.K., Duelli, P., 2004. Arthropod biodiversity after forest fires: winners and losers in the winter fire regime of the Southern Alps. Ecography 27, 173–186.

Moritz, M.A., Parisien, M.-A., Batllori, E., Krawchuk, M.A., Van Dorn, J., Ganz, D.J., Hayhoe, K., 2012. Climate change and disruptions to global fire activity. Ecosphere 3, article 49.

National Park Service, 2003. Fire Monitoring Handbook. Fire Management Program Center, Boise, ID.

Neumann, F.G., 1991. Responses of litter arthropods to major natural or artificial ecological disturbances in mountain ash forest. Aust. J. Ecol. 16, 19–32.

Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and "mesophication" of forests in the eastern United States. Bioscience 58, 123–138.

Oosting, H.J., 1944. The comparative effect of surface and crown fire on the composition of a loblolly pine community. Ecology 25, 61–69.

Owen, J.G., 1989. Patterns of herpetofaunal species richness: relation to temperature, precipitation, and varience in elevation. J. Biogeogr. 16, 141–150.

Pilliod, D.S., Bury, R.B., Hyde, E.J., Pearl, C.A., Corn, P.S., 2003. Fire and amphibians in North America. Forest. Ecol. Manag. 178, 163–181.

Rieman, B., Lee, D., Burns, D., Gresswell, R., Young, M., Stowell, R., Rinne, J., Howell, P., 2003. Status of native fishes in the western United States and issues for fire and fuels management. Forest Ecol. Manag. 178, 197–211.

Roberts, S.L., van Wagtendonk, J.W., Miles, A.K., Kelt, D.A., Lutz, J.A., 2008. Modeling the effects of fire severity and spatial complexity on small mammals in Yosemite National Park, California. Fire Ecol. 4, 83–104.

Sacerdote, A.B., King, R.B., 2009. Dissolved oxygen requirements for hatching success of two ambystomatid salamanders in restored ephemeral ponds. Wetlands 29, 1202–1213.

Safford, H.D., Stevens, J.T., Merriam, K., Meyer, M.D., Latimer, A.M., 2012. Fuel treatment effectiveness in California yellow pine and mixed conifer forests. For. Ecol. Manag. 274, 17–28.

Schoennagel, T., Veblen, T.T., Romme, W.H., 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. Bioscience 54, 661–676.

Schulte, L.A., Mladenoff, D.J., 2005. Severe wind and fire regimes in northern forests: historical variability at the regional scale. Ecology 86, 431–445.

Schwilk, D.W., Knapp, E.E., Ferrenberg, S.M., Keeley, J.E., Caprio, A.C., 2006. Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. For. Ecol. Manag. 232, 36–45.

Shang, Z., He, H.S., Lytle, D.E., Shifley, S.R., Crow, T.R., 2007. Modeling the long-term effects of fire suppression on central hardwood forests in Missouri Ozarks, using LANDIS. For. Ecol. Manag. 242, 776–790.

Simmons, M.T., Windhager, S., Power, P., Lott, J., Lyons, R.K., Schwope, C., 2007. The response of old world bluestem to mid- and late-summer fire in two grassland ecoregions in central Texas. In: Masters, R.E., Galley, K.E.M. (Eds.), Proceedings, 23rd, Tall Timbers Fire Ecology Conference: Fire in Grassland and Shrubland Ecosystems. Tall Timbers Research Station, Tallahassee, FL, pp. 246–250.

Smucker, K.M., Hutto, R.L., Steele, B.M., 2005. Changes in bird abundance after wildfire: importance of fire severity and time since fire. Ecol. Appl. 15, 1535–1549.

Sparks, J.C., Masters, R.E., Engle, D.M., Palmer, M.W., Bukenhofer, G.A., 1998. Effects of late growing-season and late dormant-season prescribed fire on herbaceous vegetation in restored pine-grassland communities. J. Veg. Sci. 9, 133–142.

Spencer, C.N., Hauer, F.R., 1991. Phosphorus and nitrogen dynamics in streams during a wildfire. J. N. Am. Benthol. Soc. 10, 24–30.

Spencer, C.N., Gabel, K.O., Hauer, F.R., 2003. Wildfire effects on stream food webs and nutrient dynamics in Glacier National Park, USA. For. Ecol. Manag. 178, 141–153.

Stambaugh, M.C., Guyette, R.P., Marschall, J.M., 2011. Longleaf pine (*Pinus palustris* Mill.) fire scars reveal new details of a frequent fire regime. J. Veg. Sci. 22, 1094–1104.

Swannack, T.M., 2007. Modeling Aspects of The Ecological and Evolutionary Dynamics of The Endangered Houston Toad. PhD dissertation. Texas A&M University, College Station, Texas, pp. 155.
Sweeney, J.R., Biswell, H.H., 1961. Quantitative studies of the removal of litter and duff by fire under controlled conditions. Ecology 42, 572–575.
Swengel, A.B., 2001. A literature review of insect responses to fire, compared to other conservation managements of open habitat. Biodivers. Conserv. 10, 1141–1169.
Taber, S.W., Fleenor, S.B., 2003. Insects of the Texas Lost Pines. Texas A&M University Press, College Station.
Taber, S.W., Fleenor, S.B., Privette, J.L., 2008. Arthropod abundance following a prescribed burn in the Lost Pines forest of central Texas. Southwest. Entomol. 33, 65–77.
Taylor, A.H., 2000. Fire regimes and forest changes in mid and upper montane forests of the southern Cascades, Lassen Volcanic National Park, California, USA. J. Biogeogr. 27, 87–104.
Thies, W.G., Westlind, D.J., 2012. Validating the Malheur model for predicting ponderosa pine post-fire mortality using 24 fires in the Pacific Northwest, USA. Int. J. Wildland Fire 21, 572–582.
Tinker, D.B., Knight, D.H., 2000. Coarse woody debris following fire and logging in Wyoming lodgepole pine forests. Ecosystems 3, 472–483.
Toledo, L.F., 2005. Predation of juvenile and adult amphibians by invertebrates: current knowledge and perspectives. Herpetol. Rev. 36, 395–400.
U.S. Fish and Wildlife Service., 1984. Houston Toad Recovery Plan. U.S. Fish and Wildlife Service, Albuquerque, New Mexico, USA. <http://ecos.fws.gov/speciesProfile/profile/speciesProfile.action?spcode=D004>.
Van den Brink, P.J., Ter Braak, C.J.F., 1999. Principal response curves: analysis of time-dependent multivariate responses of biological community to stress. Environ. Toxicol. Chem. 18, 138–148.
Vose, J.M., 2000. Perspectives on using prescribed fire to achieve desired ecosystem conditions. In: Moser, W.K., Moser, C.E. (Eds.), Proceedings, 21st, Tall Timbers Fire Ecology Conference: Fire and Forest Ecology: Innovative Silviculture and Vegetation Management. Tall Timbers Research Station, Tallahassee, FL, pp. 12–17.
Waldrop, T.A., White, D.L., Jones, S.M., 1992. Fire regimes for pine-grassland communities in the southeastern United States. For. Ecol. Manag. 47, 195–210.
Wan, S., Hui, D., Luo, Y., 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. Ecol. Appl. 11, 1349–1365.
Wayman, R.B., North, M., 2007. Initial response of a mixed-conifer understory plant community to burning and thinning restoration treatments. For. Ecol. Manag. 239, 32–44.
Webster, K.M., Halpern, C.B., 2010. Long-term vegetation responses to reintroduction and repeated use of fire in mixed-conifer forests of the Sierra Nevada. Ecosphere 1, article 9.
Wetzel, R.G., Likens, G.E., 2000. Limnological Analyses, third ed. Springer, New York.
Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer Science + Business Media, New York.