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Evaluating pathways by which fuels and fires influence vegetation response in a high-diversity plant community using structural equation models

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Running Headline: Above- and belowground fire effects on vegetation

Summary:

1. Fire strongly influences plant populations and communities around the world, making it an important agent of plant evolution. Fire influences vegetation through multiple pathways, both above- and belowground. Few studies have yet attempted to tie these pathways together in a mechanistic way through soil heating even though the importance of soil heating for plants in fire-prone ecosystems is increasingly recognized.

2. Here we combine an experimental approach with structural equation modeling (SEM) to simultaneously examine multiple pathways through which fire might influence herbaceous vegetation. In a high-diversity longleaf pine groundcover community in Louisiana, USA, we manipulated fine-fuel biomass and monitored the resulting fires with high-resolution thermocouples placed in vertical profile above- and belowground.

3. We predicted that vegetation response to burning would be inversely related to fuel load owing to relationships among fuels, fire temperature, duration, and soil heating.

4. We found that fuel manipulations altered fire properties and vegetation responses, of which soil heating proved to be a highly accurate predictor. Fire duration acting through soil heating was important for vegetation response in our SEMs, whereas fire temperature was not.

5. Our results indicate that in this herbaceous plant community, fire duration is a good predictor of soil heating, and therefore, of vegetation response to fire. Soil heating may be the key determinant of vegetation response to fire in ecosystems wherein plants persist by resprouting or reseeding from soil-stored propagules.

6. *Synthesis*. Our SEMs demonstrate how the complex pathways through which fires influence plant community structure and dynamics can be examined simultaneously. Comparative studies

of these pathways across different communities will provide important insights into the ecology, evolution, and conservation of fire-prone ecosystems.

Key-words: disturbance, fire duration, fire temperature, first- and second-order fire effects, longleaf pine savanna, residence time, resprouting, soil heating, structural equation modelling, vegetation dynamics.

Introduction

Fire is an important evolutionary and ecological force that influences plant life in most terrestrial ecosystems. As a potent agent of natural selection, fire shapes traits of plant species and has likely done so since plants first colonized land (Bond & Keeley, 2005; Keeley & Rundel, 2005; Scott & Glasspool, 2006). As an environmental filter, fire often determines which plant species occur within and dominate ecological communities (D'Antonio & Vitousek, 1992; Bond & Keeley, 2005; Keeley & Rundel, 2005; Pausas & Verdú, 2008). Because fire is pervasive in shaping vegetation structure and composition, and given the expectation that fire regimes will be altered under global change (IPCC, 2007; Bowman *et al.*, 2009), we should strive to understand the mechanisms by which fires influence plant populations and communities.

Fire influences vegetation through multiple, potentially interacting pathways that operate both above- and belowground. Aboveground heat can kill plant tissue and sometimes individuals outright. Although some trees can endure heat from fires, many fire-adapted plants persist by resprouting from belowground organs or from seeds stored in the soil (e.g., Whelan, 1995; Higgins, Bond & Trollope, 2000; Vesk & Westoby, 2004; Vesk, 2006). These organs and seeds are susceptible to damage when fires on the surface heat the soil beyond some lethal time-temperature threshold (e.g., temperatures above 60°C; e.g., Bradstock & Auld, 1995; Choczynska & Johnson, 2009). Elevated soil temperatures are presumed to be a function of aboveground fire temperature and duration (Steward, Peter & Richon, 1990; Bradstock & Auld, 1995). Because commonly used fire metrics are at best imperfect predictors of vegetation responses (Keeley, 2009 and references therein), there is much we do not know about how fire operates from a "plant's eye view" (*sensu* Harper, 1977).

Despite widespread interest in the role of above- and belowground effects of fire on plants (e.g., Keeley, 2009; Gagnon *et al.*, 2010 and references therein), empirical studies commonly rely on snapshot-like aboveground fire metrics that can be poor predictors of vegetation response. Such metrics include fire-line intensity, maximum fire temperature, and fire severity (Johnson, 1992; Whelan, 1995; Bond & van Wilgen, 1996; Bond & Keeley, 2005). Fire intensity refers to energy output during fire, whereas severity describes the amount of fuels consumed (Keeley, 2009). These metrics are valuable for modeling fuels and behavior of fires, but they can be poor indicators of damage to seed-banks and belowground plant organs, and therefore, of longer-term population and community dynamics (Hodgkinson & Oxley, 1990; Keeley, Brennan & Pfaff, 2008; Keeley, 2009). Such poor predictive power may be the result of failure by these metrics to incorporate elements of soil heating and potential interactions of above- and belowground processes on vegetation (Gagnon *et al.*, 2010). Given that many plant species survive fires belowground (Vesk & Westoby, 2004; Vesk, 2006), fire metrics that include some aspect of soil heating might better predict how fires affect plant populations and communities.

Here we combine an experimental approach with structural equation modeling (SEM) to examine above- and belowground pathways through which fires might influence vegetation. We manipulated fine-fuel biomass to produce variation in fire properties, then measured fire duration on the soil surface and temperatures in vertical profile. We developed hypotheses to explain how above- and belowground fire properties might influence vegetation response, then used SEMs to test the relative importance of multiple hypothesized pathways (Fig. 1) in a high-diversity longleaf pine groundcover community in Louisiana, USA. Prior to prescribed fires, we manipulated fuels and placed thermocouples at five different vertical positions. We predicted that vegetation response would be inversely related to fuel load owing to complex relationships among fuel load and fire properties above- and belowground. This prediction was validated, and we found soil heating to be a highly accurate predictor of vegetation response. Our results highlight the utility of SEMs for understanding complex, interrelated mechanisms through which fires may influence the structure and dynamics of plant populations and communities.

Methods

Study Site and Experiment

We studied prescribed fires and their effects at Camp Whispering Pines (30º 41' N, 90º 29' W; 25-50 m.a.s.l.), a species-rich longleaf pine (*Pinus palustris* Mill.) savanna in southeastern Louisiana, USA. Soils are Pleistocene-aged fine sands mixed with and capped by loess, and are among the most fertile pine-savanna soils (McDaniel, 1990). When we began the study, the site had been burned biennially during the early growing season (April-May) for the previous 15 years (Noel, Platt & Moser, 1998). Additional site information is available in Platt *et al*. (2006).

We manipulated fine fuels in our sample plots so that experimental fires would vary substantially in temperature and duration. The first experimental treatment was increased-fuels, in which we added 8 kg of dry, uncompacted longleaf pine needles, a highly flammable source of fuel in this ecosystem (Fonda, 2001). All pine needles were dried and stored outdoors in plastic bags under a rain shelter at the study site. We spread fuels evenly over the plots (each 2 x 2 m = 4-m^2) on the same mornings as the two fires. This quantity of fine fuel (2 kg · m^{-2}) mimicked the upper range of observed fuel loads at this productive site (Thaxton & Platt, 2006). The second treatment was reduced-fuels, in which we clipped and removed all biomass above 5 cm in height. The third set of plots comprised unmanipulated control-fuels. We assigned these treatments equally and randomly to 48 plots divided equally between two burn units (random blocks), which we burned under prescription near mid-day on two different days. To reduce variability of fuels among and within plots, we removed coarse woody fuels such as pinecones and downed branches. We manipulated fuels immediately prior to lighting the fires. Following fuel manipulations but before burning, we estimated total aboveground biomass by collecting all biomass from a series of nearby plots to which the same three treatments were applied, and then weighed the samples after drying for 48 hours at 100°C. Total aboveground biomass averaged 3076 g • m^{-2} (± 57 g • m^{-2} [1 SE]) in the increased-fuels treatment, 1076 g • m^{-2} (± 57 g • m^{-2}) in the control, and 444 g • m^{-2} (± 23 g • m^{-2}) in the reduced-fuels treatment. These quantities included natural herbaceous litter and any natural or added pine straw, plus naturally occurring fine fuels like small pine twigs. Additional details of the experiment and a description of bunchgrass responses to the fuel manipulations are in Gagnon *et al.* (2012).

To measure fire properties, we deployed high-resolution fire loggers at five positions in a vertical profile (Grace, Owens & Allain, 2005; Ellair & Platt, 2013). We built the fire loggers using HOBO® U12-014 J,K,S,T Thermocouple Data Loggers and Type K subminiature connectors (Onset Computer Corporation USA), and Inconel 600-insulated (10') Type K thermocouple wires (Omega Engineering, Inc. USA). We assembled the loggers and packaged them in waterproof plastic containers, which we buried 10 cm below the soil surface outside the sample plots on the morning of the fires (Grace, Owens & Allain, 2005). Although the data-loggers were capable of recording temperatures from 0 to 1250°C with an accuracy of ± 4 °C every second for 12 hours, the thermocouples to which they were attached were ultimately what determined data-logger accuracy. Rather than measuring true flame temperatures, thermocouples measure their own temperatures, which are subject to lags as a function of thermocouple thickness (i.e., mass); accordingly, they systematically underrepresent true temperatures (Kennard *et al.*, 2005, Wally, Menges & Weekley, 2006). Even so, their measurements are comparatively accurate, albeit systematically biased, and are useful for regression analyses (Kennard *et al.*, 2005) like those underpinning our SEMs. We located thermocouples at the soil surface in all 48 plots, and in four other positions (1 cm above the soil surface and 1, 2, and 4-cm below the soil surface) in 18 randomly selected plots (N = 6 plots/treatment; N = 3 plots/treatment/burn unit). We did so in a 1-m^2 sample quadrat in the center of each 4-m^2 plot on the morning of the fires. For belowground measurements, we used a marked wooden dowel to poke holes of appropriate diameter and depths, then inserted each thermocouple tip to the base of the appropriate hole; we then sealed the soil around each protruding thermocouple cable by lightly pressing the soil around it. In this way, we ensured that each thermocouple was buried to appropriate depth with minimal soil disturbance. We secured thermocouples at the surface using galvanized wire U-stakes ~3-cm from their tips. We additionally bent U-stakes into loops that held thermocouple cables at 1-cm height.

We ignited prescribed fires during late morning on two dry days with light breezes in late May 2007. We first set fires along the downwind perimeter of each of the two burn units; these backing fires traveled into the wind. We then set head-fires along the upwind perimeter of each burn unit; these burned through the plots in the direction of the wind. Reduced-fuel plots burned with fine-scale patchiness, whereas control- and increased-fuel plots all burned thoroughly. Fuels in all increased-fuel plots burned almost completely to ash. As fires in pine savannas burn quickly (fires at the surface in our control plots averaged 10 sec. residence times), we were able to remove even the belowground thermocouples from plots beginning 105 minutes after the fires. Following the fires that afternoon, we used a leaf-blower and blew residual ash from all burned plots. We collected and then replaced 0.5 kg of the ash on a random subset of plots; we found no measurable effect of ash on vegetation response, so we do not consider ash further.

Data Collection

We calculated two fire metrics for the soil surface in each plot. Maximum temperature increase was the difference between the hottest temperature during the fire and the ambient temperature prior to the arrival of the flame front (Box 1). The second was fire duration, defined as the time between when temperatures increased more than 0.3°C per second and the time they fell below 50°C. In those few plots in which temperatures never exceeded 50°C, we instead used the time following hottest temperature at which temperatures returned to within 5°C of pre-fire ambient temperature. We calculated maximum temperature increase from every logger and fire duration (i.e., residence time) from surface loggers only, using a custom R script.

We measured effects of fuel manipulations on vegetative cover in the 1-m^2 sample quadrats within the center of the 4-m^2 fuel-treatment plots. We took photos 2 m above every plot from a stepladder 3 weeks after the fires. By this time, *in situ* resprouting and some germination was already occurring across the burned area, while post-fire germination of seeds arriving from outside the plots was yet unlikely (Myers & Harms, 2011). Prior to fires, we inserted nails in each 1-m^2 sample quadrat at 10-cm intervals, creating a grid of 100, 10x10-cm “cells” visible in the photos. We counted the number of cells out of the 100 in each quadrat that contained any green vegetation. This yielded a proportion of cells containing green vegetation as a measure of short-term vegetation response. Prior to burning, this metric was 100% in all plots.

We examined effects of increased-fuels on post-fire germination from the soil seed-bank in a concurrent experiment at the same study site (Table S1 in Supporting Information). We applied two of the same fuel manipulations (control- and increased-fuels) to a separate set of plots located in the same two burn units (see Myers & Harms, 2011 for details). In each of 60, 2 × 3 m plots (N = 30 increased-fuels, N = 30 controls), we collected a 20 × 20 × 1 cm (length × width × depth) soil sample (excluding litter) within one week after prescribed fires, which was before most individuals began to germinate or resprout in the field. We sieved each soil sample as described by Ter Heerdt *et al.* (1996), spread each sieved sample thinly on top of sterilized soil in individual trays, and monitored seedling emergence and species composition in a climate-controlled growth chamber. We set light (16-h day length), temperature (32°C day, 22°C night), and relative humidity (90% day, 50% night) to approximate growing-season conditions. We watered and rotated trays regularly, recording abundance and species identity of germinating plants for two months, by which time new seedling emergence had virtually ceased.

In both burn units we quantified effects of fuel manipulations on species presence in a random subset of half the plots that contained surface fire-loggers. We identified all species with aboveground living tissues (*e.g.*, stems, leaves) in the 24, 1-m^2 central quadrats during two pre-fire censuses (conducted in July and October 2006) and two post-fire censuses (July and October 2007). We combined the 2006 censuses and combined the 2007 censuses because species were often more readily identified during either summer or autumn. To compare and contrast both species presence before and after the fires and relative patterns among functional groups, we examined their frequencies of occurrence in quadrats among fuel treatments pre- and post-fire.

Statistical models and analyses

We used linear mixed-effect models to analyze fire temperatures, densities of plants germinating from seed-bank samples, and species richness of seed-bank species. First we tested for differences in hottest temperatures (b in Box 1) among the three fuel manipulations and five vertical positions (Fig. 2, Table S2). For this analysis we used all 48 plots and fire loggers in all five vertical positions in an unbalanced design. Based on quantile-quantile plots, box-plots and a Shapiro-Wilk test, we log-transformed the response variable (hottest temperatures) to improve normality and homoscedasticity and to eliminate overdispersion. A box-plot of the transformed data and a Breusch-Pagan test both indicated heterogeneous variances, so we explored several variance structures before grouping by fire logger position (Zuur *et al.*, 2009). After determining the best-fit model using Akaike Information Criterion (AIC), we used post-hoc Tukey tests to determine significance among treatment groups and their interactions. We tested for differences in total species richness and in mean density of forbs and graminoids germinating from the seed-bank using fuel treatments (control- and increased-fuels; N = 30 per treatment) as fixed effects and blocks (burn units) as random effects (Myers and Harms, 2011). We performed all mixed modeling in R (v.3.0.2) using the nlme package and the Tukey post-hoc comparisons using lsmeans package (R Core Team, 2014).

We used linear regressions to explore relationships among fire temperatures, durations, soil temperatures and vegetation response. We first examined proportion of cells containing green vegetation as the response variable, which we logit-transformed using a 0.025 adjustment factor to avoid 0 or 1 responses. Fire temperature, fire duration and soil temperatures (all log-transformed) served as predictor variables (Fig. 3). We examined soil heating as the response to fire temperature and duration at the soil surface, all log-transformed (Fig. S1). We performed these regression analyses using the lm function in R (v.3.0.2) base package.

We built structural equation models (SEMs) to examine hypothesized pathways and interactions through which fires on the surface might influence soil heating and vegetation response. Construction of SEMs is guided by theory and *a priori* knowledge of the relevant multivariate processes (including cause and effect) and is based on a series of bivariate relationships among the various factors (Figs. 3 and S1). By evaluating such hypotheses using SEMs, one can determine whether they are consistent with underlying patterns in the data. As with any regression-based analysis, a concern with SEMs is an unfounded assumption of causality among the proposed relationships, particularly when the data are observational. In this study, relationships between fuel manipulations (our treatment) and temperature, duration, and vegetation responses are all part of a controlled experiment. On the other hand, relationships among surface and belowground fire properties and vegetation response are observational; these we necessarily inferred from theory. We hypothesized that higher measured fire temperatures and longer durations on the surface should increase belowground temperatures and reduce post-fire resprouting and germination. Additionally, we hypothesized that increased fuels should increase fire temperatures and durations.

Ideally we would have explored these hypotheses using a single SEM, but we were constrained to building two separate models because of the limited size of our dataset of belowground conditions. Our first model examined these relationships using our dataset of surface conditions in all 48 plots (Fig. 1A). The diagram outlines our multivariate hypothesis describing the effects of fuel manipulations on temperature and duration at the soil surface during fire, and the combined effects of fuels, temperature and duration on vegetation response. In the second model, we examined the role of belowground soil temperatures from the 18 plots with fire loggers in vertical profile (Fig. 1B). We were unable to include fuel treatment in this model because of our small sample size. Instead, we infer the effects of fuel treatment on belowground temperatures from our mixed-model analysis (Fig. 2) and the results of the aboveground SEM (Fig. 4A and B).

All data were not normal, so we applied transformations before conducting SEMs. To correct for positive skew, we applied a natural log +1 transformation to above- and belowground temperature-increase and fire duration. We applied a logit transformation to correct for strong negative skew in vegetation response. All proposed relationships were linear following transformations based on box-whisker plots and Shapiro-Wilk tests (from the UNIVARIATE procedure in SAS release 9.3, SAS Institute Inc., Cary, North Carolina).

We included fuel treatments in the surface SEM as dummy-coded exogenous variables (Fig. 1A). Control-fuel treatment does not appear in the diagrams because it serves as baseline. The effects of increased- and reduced-fuel manipulations shown are in reference to this baseline.

To simplify the belowground model, we condensed the three measures of belowground temperature-increase (i.e., at -1, -2 and -4 cm depths) into one composite variable. For this, we used the first factor of a principal components analysis. This factor explained 95% of the variation among the three variables; all three had a factor score > 0.97.

We performed model estimation using maximum likelihood. We based model fit on chi-square values and their associated *P*-values and judged a model as not fitting the underlying structure in the data when it had a *P*-value < 0.05 based on a chi-square test. In the case of poor model fit, we examined residual covariances, located the largest residuals, and added a model pathway indicated by that residual. We did this only if the suggested pathway agreed with theory and our understanding of the system. We deemed a model with a new pathway to be of value if it satisfied a single degree of freedom chi-square test.

Path coefficients in our SEM figures indicate the strength of the various proposed effects (arrows). These partial regression coefficients represent the change expected in an endogenous variable if an exogenous variable is varied while the remaining exogenous variables remain constant. We report both standardized coefficients (in standard deviation units) and unstandardized coefficients. R^2 scores indicate the collective ability of the coefficients to explain variation in the endogenous variables. Multiplying the relevant standardized path coefficients indicates the strength of indirect effects.

To increase our confidence in the maximum-likelihood path coefficients, we conducted two additional analyses. First, we addressed a concern that our dataset had low sample sizes relative to the complexity of the models tested: for each model, the ratio (d) of sample size (n) to the number of unknown parameters being tested (a) was < 7. We therefore followed the recommendation of Lee & Song (2004) for Bayesian estimation. This produced results virtually identical to those of maximum likelihood estimation (for both models, path coefficients from Bayesian estimation differed with those from maximum likelihood estimation by < 1%). In our second analysis, we accounted for a potential block (burn-unit) effect by including block in the model as a dummy variable. We compared this model to one not including blocks and found no significant effect of block (e.g., block added just 0.01 to the R^2 score of vegetation response). Based on this result, we do not report results of models that included block. For all SEM analyses based on maximum likelihood estimation, we used the lavaan package in R v.3.0.2 (Rosseel, 2012; Beaujean, 2014; R Core Team, 2014); for the Bayesian estimation, we used IBM SPSS Amos version 20 as lavaan in R currently lacks this capacity (Arbuckle, 2011).

Results

Mixed modeling of fuel treatment effects on above- and belowground temperatures

Both fuel treatment and the position in vertical profile of thermocouples significantly affected the hottest temperatures loggers recorded during fires. Of the five vertical positions we examined, temperatures during fires were hotter by far at 1 cm aboveground and on the surface than belowground (Fig. 2). On the soil surface, reduced-fuels produced the lowest measured temperatures ($P < 0.001$ for reduced- vs. control-fuels at 0 cm; Tukey post-hoc tests), whereas temperatures from control- and increased-fuels did not differ ($P = 0.141$). At 1 cm belowground, mean hottest temperatures were only marginally hotter in increased-fuels relative to reduced-fuels ($P = 0.059$). At both 2 and 4 cm belowground, the hottest temperatures were under increased-fuels, whereas temperatures in control- and reduced-fuels were similar ($P < 0.001$ comparing increased- vs. control-fuels at both -2 and -4 cm; $P = 0.823$ and 0.801 comparing control- vs. reduced-fuels, respectively). Only the increased-fuels treatment raised belowground temperatures above 60°C – sometimes considered a lethal threshold – and not deeper than -2 cm.

Effects of fuel treatments on species composition

Increasing fuels reduced densities and species richness of seeds germinating from the soil seed-bank after fires (Fig. 5). We identified 11 species in seed-bank samples, including 5 of forbs (3 in the genus *Eupatorium*), 4 of C_3 grasses (all in the genus *Dichanthelium*), and 1 legume

(Table S1). Mean total densities of both forbs and graminoids were lower in increased-fuels plots relative to control-fuels, and species richness was significantly reduced (Fig. 5).

Fires in increased-fuels also reduced occurrence of most species compared to control plots based on plant censuses during the years before and after the fires (Table S3). With the exception of some C_3 grasses, during the year after the fires, most species occurred less frequently in increased-fuels plots than in control plots (Fig. S2). Several of the C_4 grasses occurred less frequently in the increased-fuels plots. Strikingly, increasing fuel loads eliminated over half of the forb species in the seed bank.

SEM of aboveground influences of fire on vegetation response

Our first SEM examined hypothesized relationships among fuel manipulations, fire temperatures (i.e., maximum temperature increase at the surface), duration, and vegetation response (see Figs. 3 and S1 for the bivariate relationships underlying this SEM and the next). Maximum likelihood estimation of this model produced a chi-square of 47.56 with 2 df ($P <$ 0.001), indicating that one or more important relationships in the data remained poorly described (Fig. 4A). An examination of residual covariances revealed a strong unspecified relationship between the increased-fuel treatment and vegetation response. A SEM that included this relationship (Fig. 4B) had a chi-square value of 1.10, which was substantially lower than the previous model, and easily passed the single degree of freedom chi-square test ($\Delta\chi^2 = 46.46 >> 3.841$). Also, this model had a *P*-value of 0.295 (df =1), indicating that it described the data adequately to merit interpretation here.

Fuel manipulations had clear and strong relationships with both maximum temperature increase and fire duration at the soil surface (R^2 = 0.51 and 0.62 respectively; Fig. 4B). Plots with increased-fuels had hotter fires of longer duration than controls, whereas plots with reduced-fuels had cooler fires with similar durations compared to controls. According to our thermocouples, fire raised temperatures on the soil surface by an average of 361°, 216°, and 58°C and lasted an average of 35, 10 and 8 seconds respectively in increased-, control- and reduced-fuels.

The proposed model indicated that vegetation cover was strongly reduced following fires where we increased fuels and when fires at any given point lasted longer than 35 seconds (Fig. 3, Fig. 4B). Our increased-fuel treatment had a large direct effect on vegetation response, reducing it substantially (standardized path coefficient = -0.71). The second most important pathway was that of increased fire duration (-0.25), which also suppressed vegetation response. The pathway from temperature increase to vegetation response (-0.04) was not significant. For plots with increased-fuels but low fire durations, some contained new green vegetation in fewer than half of sampling cells, whereas others were revegetating more completely (Fig. 3). All control- and reduced-fuels plots contained green vegetation in more than 90% of sampling cells, but increased fire duration still caused a slight negative effect (Fig. 3 and Fig. 4B). In contrast to some direct pathways, indirect pathways from fuel manipulations to vegetation response were all relatively weak (e.g., the strongest was from increased-fuel treatment via duration at 0.71 × -0.25 = -0.18).

SEM connecting fire aboveground to soil heating and vegetation response

Our second SEM examined hypothesized relationships among fire temperature, duration, belowground soil temperature, and vegetation response. Maximum likelihood estimation of this model produced a chi-square of 2.75 with 2 df (P = 0.25), indicating that it described the data adequately. The proposed model indicated that fire duration was strongly associated with soil heating, whereas fire temperature at the surface was not (Fig. S1 and Fig. 4C). In turn, the model indicated that soil heating was strongly and negatively associated with vegetation response. Fire duration on the surface had a substantial indirect, negative association with vegetation response (0.63 × -0.92 = -0.58), whereas the indirect association between temperature increase at the surface and vegetation response was weak (0.14 × -0.92 = -0.13).

Discussion

Our structural equation models underscore the importance of fire duration operating through soil heating as a determinant of herbaceous vegetation response to burning. Post-fire resprouting and reseeding of herbs was strongly and negatively associated with shallow soil heating, which was in turn strongly associated with fire duration (Fig 4C). By contrast, aboveground maximum temperatures measured by thermocouples during fires were unimportant. These observations are consistent with the hypothesis by Gagnon *et al.* (2010) that fires with long residence times should send more heat into the ground and less upward into the air compared with intense, fast-burning fires. But we caution that this study was not designed as a test of that prediction and should not be interpreted as one; components of the study were necessarily correlative, including relationships among fire properties and vegetation response. Even so, the controlled experiment at the core of our study permits causal inferences about how fuels influence both fire properties and vegetation response.

This study addresses the paucity of research linking herbaceous vegetation response to fire, fuels and soil heating (as noted by Dickinson & Ryan, 2010; Stephan, Millar & Dickinson, 2010). In predicting vegetation response to fire, most previous studies have relied exclusively on aboveground metrics (e.g., Johnson, 1992; Whelan, 1995; Bond & van Wilgen, 1996; Odion & Davis, 2000; Bond & Keeley, 2005). Only a few studies have systematically examined the effects of soil heating on herbaceous vegetation, and fewer still have attempted to mechanistically link the effects of fire to response of herbaceous vegetation through soil heating (e.g., Bradstock & Auld, 1995; Santana, Baeza & Blanes, 2013). Our findings are consistent with the few other studies to have examined related questions. For example, Bova & Dickinson (2005) found that fire residence time was a much better predictor than fire intensity of both heat flux and depth of heating in tree trunks. Others have similarly concluded that fire temperatures are not particularly useful for predicting effects of surface fires on soils (e.g., Van Wagner & Methven, 1978, Bova & Dickinson, 2008).

Our short-term metric of herbaceous vegetation response is an accurate proxy for longer-term effects on vegetation. In a related study from the same plots and fires, Gagnon *et al.,* (2012) concluded that the increased-fuel treatment altered and suppressed the resprouting of individual bunchgrass tussocks for the duration of the growing season. Similarly, Myers & Harms (2011) monitored living, rooted plants in nearby plots at this same site after similar fuel manipulations and found community-wide effects that persisted for at least two growing season. Given the persistent effects we have documented elsewhere, it is likely that the reduced vegetative response we detected three weeks after fires reflected substantial damage and mortality to plants in our increased-fuel plots.

Surface fires typify our study ecosystem; fires that cause substantial soil heating reduce the likelihood that individuals will survive to contribute to post-fire vegetation. This is generally true regardless of a plants' species designation or functional group. Most plants we censused (> 90% of species) were herbaceous perennials that resprout to some degree; the large majority persisted through surface fires in control plots. Since soil heating beneath increased-fuels reduced overall vegetation cover, it is not surprising that frequency of occupancy generally decreased as well. Although in some cases elevated soil temperatures can increase recruitment from the soil seed-bank by triggering germination of fire-adapted seeds (e.g., Hodgkinson & Oxley, 1990; Michaletz & Johnson, 2007), we found little evidence of that here. Instead, seed-banking species produced a pattern similar to that of resprouting species, in that *per capita* mortality increased under heavier fuel loads, with few obvious differences among species or functional groups (Fig. 5, Fig S2). Given that many seedlings in our seed-bank study died before growing large enough to identify, and because our seed-bank samples each came from a single location in every sample plot, more extensive sampling of the seed-bank is needed to confirm this result. A possible exception was a handful of C_3 grasses with higher frequencies after fires in increased-fuels plots – one of these was *Panicum verrucosum*, a disturbance-tolerant annual. Several C_4 grasses declined or were extirpated following fires in increased-fuels, a pattern consistent with that reported by Gagnon *et al*. (2012) that bunchgrasses suffer under heavier fuel loads. In this way, locally severe fires in heavy fuels may increase the availability of microsites for colonization, a process that can influence spatial patterns of species diversity and community composition in post-fire landscapes (Myers & Harms, 2011). These same conditions may also increase abundances of disturbance-tolerant species (e.g., annual grasses), presumably owing to a combination of heat-induced germination and higher plant performance in more open microsites.

Soil temperature of 60°C is sometimes considered the lethal threshold for plant tissues (e.g., Bradstock & Auld, 1995; Choczynska & Johnson, 2009; but see Stephan, Miller & Dickinson, 2010). In this study, only under increased-fuels did measured soil temperatures exceed 60°C, and then not deeper than 2 cm belowground (Fig 2). Regardless, the reduced resprouting and germination in these plots indicate that this admittedly simplistic threshold based on thermocouple-measured temperature had merit for this system. Although various studies have found dehydrated seeds surviving substantially hotter temperatures (e.g., Stephan, Miller & Dickinson, 2010 and references therein), seeds in the soil of our study plots were killed by temperatures measured around 60°C; that and the observation that our soils were moist suggest that these seeds were hydrated and thus susceptible to the heat. Fire's influence on temperatures declined quickly with soil depth, supporting the observation that soil is an excellent insulator (Heyward, 1938; Beadle, 1940; Bradstock & Auld, 1995). That temperatures never approached the lethal threshold in unmanipulated fuel-controls underscores the importance of heavy fuels (e.g., downed branches, tree trunks and stumps) that burn for prolonged periods as gap-producing hotspots in the groundcover that might serve as sites for post-fire colonization (Thaxton & Platt, 2006; Myers & Harms, 2011; Wiggers *et al.,* 2013).

Our study suggests that fire duration and soil heating will be most useful for predicting vegetation response in herbaceous, surface-fire systems like this longleaf pine savanna (Platt, 1999). Ecologists use many different measures of fire properties, and each is potentially useful depending on the context (Keeley, 2009). In many ecosystems, maximum temperatures are primarily a function of fine-fuel consumption (Beadle, 1940; Armour, Bunting & Neuenschwander, 1984; Keeley, Brennan & Pfaff, 2008; Keeley, 2009), whereas fire duration reflects the consumption of coarse or packed fuels (Hartford & Frandsen, 1992; Varner *et al.*, 2005; Michaletz & Johnson, 2007; Varner *et al.,* 2007, Varner *et al.,* 2009). The latter is more likely to heat the soil (Gagnon *et al.*, 2010 and references therein; Massman, Frank & Mooney, 2010). We expect the relative importance of fire duration to increase additionally in ecosystems where duff layers might alternately retain moisture and thus insulate the soil during relatively brief fires, or dry out and heat the soil intensely when it combusts and smolders for prolonged periods (Armour, Bunting & Neuenschwander, 1984; Hartford & Frandsen, 1992; Michaletz & Johnson 2007; Varner *et al.,* 2007; Varner *et al.,* 2009; Butler & Dickinson, 2010).

Increasing fuel load had a substantial direct effect on vegetation response beyond anything operating through fire temperature or duration (Fig. 4B). We view the most likely cause as the difference in spatial scales between how we measured fire properties versus how we measured vegetation response. Within our 1-m^2 sampling quadrats, we measured vegetation response within one hundred small cells, whereas we measured fire metrics on the soil surface at one single point per quadrat. Fire properties could vary greatly over very short distances because fuels, and therefore combustion, were intrinsically spatially heterogeneous despite that we specifically designed fuel manipulations to homogenize fire properties across the quadrat. Fuels and fire temperatures, and thus thermocouple point measurements, are all inherently noisy at fine spatial scales, and thermocouples are imperfect at best for measuring true flame temperatures (Kennard *et al.,* 2005; Wally, Menges & Weekley, 2006). For similar studies in the future, we recommend that researchers design tighter coupling of fire and vegetation metrics both in scale and in space, for example by measuring fire metrics at multiple points within each sample plot and then measuring vegetation response at those same points. We postulate that doing so here would have produced a stronger effect of fuel treatment on vegetation via fire temperature and/or duration, and a weaker direct effect of fuel manipulations (Fig. 4B). Alternatively, the direct effect of increased-fuels on vegetation response may have been caused by an increase in ash and accompanying soil nutrients on post-fire environmental conditions, residual aboveground biomass, or biotic interactions (e.g., soil microbes, seed predators, plant competitors; Myers & Harms, 2011; Gagnon *et al.,* 2012; Brown *et al.,* 2013). We view these as unlikely possibilities because we applied fuel manipulations on the same days as burning and blew away ash immediately afterwards, and subsequent ash manipulations had no effect on vegetation response.

An improvement to our method would be to use multiple, replicated plots across a broad area, with each containing replicated thermocouple probes. Such a setup would enable data capture during prescribed fires at broad scales but with high resolution both at the soil surface and belowground; data could then be analyzed as we have done using SEM. By coupling this setup with thermal imaging (e.g., Hiers *et al.*, 2009; Kremens, Dickinson & Bova, 2012), scientists might partition fires into various constituent components (e.g., conductive, radiative, and convective heat) to simultaneously compare the role of each on soil heating and subsequent vegetation response. Data from such studies could inform predictive models of first- and second-order fire effects (as per Dickinson & Ryan, 2010; Massman, Frank & Mooney, 2010; Stephan, Millar & Dickinson, 2010) for the benefit of fire managers.

Our findings about the importance of fire duration relative to fire temperatures have implications for conservation and management of both forests and herbaceous-dominated systems. Soil heating is the key determinant of herbaceous vegetation response to fire in surface-fire systems because those plants that persist through fires do so by resprouting from belowground organs or by germinating from soil-stored seeds (Whelan, 1995; Higgins, Bond & Trollope, 2000; Vesk & Westoby, 2004; Vesk, 2006). Thus, only by cooking their belowground regenerative tissues are fires likely to kill plants outright (Flinn & Wein, 1977; Hodgkinson & Oxley, 1990; Bradstock & Auld, 1995; Schimmel & Granstrom, 1996; Odion & Davis, 2000; Brooks, 2002; Choczynska & Johnson, 2009; Gagnon *et al.*, 2010). Our results underscore the need for extreme caution with dry, packed fuels that can smolder for prolonged periods at the soil surface and thus heat the soil substantially (as per Varner *et al.*, 2009; Butler & Dickinson, 2010 and references therein). In addition, our results suggest that fire managers should consider the advantages of fast-moving head fires that might cause less soil heating than creeping backfires with longer residence times.

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Data Accessibility

- The complete dataset used for both ANOVA and SEM analyses: DRYAD entry doi: xx.xxxx/dryad.xxxx.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Table S1 Abundance and frequency of species emerging from soil seed-bank samples.

Table S2 Results of mixed effects model of soil heating.

Table S3 Species list, functional group classifications, and numbers of quadrats in which each species was found, relative to prescribed fires and by fuel treatments.

Figure S1 Bivariate regressions of the relationships between soil heating at 3 different depths and fire temperature or duration at the soil surface on log-log scales.

Figure S2 Comparison of frequency across quadrats of species found in increased-fuels compared to control-fuels during the growing season after burning.

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Figure Legends

BOX 1. Diagram of a typical time-temperature series from a fire-logger located on the soil surface including: (a) pre-fire ambient temperature, (b) hottest temperature, (c) maximum temperature increase, (d) fire residence time, and total heat (shaded area).

FIG. 1. Hypothesized structural equation models of direct and indirect pathways: (A) from fuel manipulations to surface fire temperature and duration to vegetation response, and (B) from surface fire temperature and duration to soil heating to vegetation response. Circles (e1-e3) signify error terms; double-headed arrows indicate significant correlations.

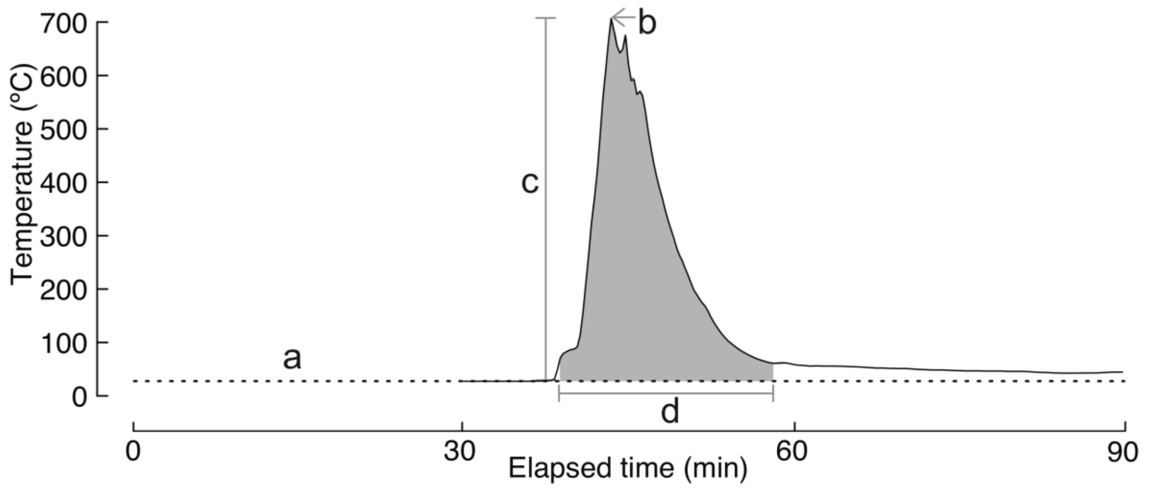
FIG. 2. Aboveground and belowground temperatures in the three fuel treatments. Boxes represent the median and 25th/75th percentile. Whiskers extend to 1.5 times the interquartile range. Letters above boxplots indicate statistical difference. Temperatures on the Y-axis are log scale. Horizontal dotted line demarcates soil temperature of 60°C. Vertical lines differentiate different depths; black line represents the soil surface.

FIG. 3. Bivariate relationships between vegetation response and fire properties. The proportion of cells containing green plants 3-weeks after burning represents vegetation response (Y axes, on logit scale). Fire properties include temperature and duration on the surface and temperature at three soil depths (X axes, on log scale) during experimental prescribed fires. We incorporated these relationships into structural equation models. Black lines are best-fit lines; gray areas encasing lines are 1SE envelopes.

FIG. 4. Structural equation models describing proposed relationships among fuels, fires and vegetation. The models include: (A) our starting, theory-driven model describing relationships aboveground (χ^2 = 47.56, df = 2, P < 0.001); (B) the same model but with an additional pathway from increased-fuels to vegetation response (χ^2 = 1.10, df = 1, P =

0.295); and (C) our proposed model examining effects belowground (χ^2 = 2.75, df = 2, *P* = 0.25). Pathways are accompanied by standardized partial regression coefficients. The significance of the coefficients is shown with differently weighted/colored lines (thin gray = non-significant, medium black = $P \leq 0.01$, and thick black = $P \leq 0.001$). Models in panels A and B have 48 samples, while the model in panel C has 18 samples. Circles (e1-e3) signify error terms, double-headed arrows indicate significant correlations, and R^2 values indicate the total variation explained by a model up to those points in the diagram.

FIG. 5. Seed density and species richness from 20 × 20 × 1 cm soil samples collected 1 week after fires in control- and increased-fuels plots. Panels include: (A) density of forbs, (B) density of graminoids, and (C) total species richness. Bars = back-transformed (density only) least squares means ± 1 SE; N = 30. *P*-values from ANOVA are listed in panels.



TERM	**DEFINITION**	**UNITS**
Ambient temperature	Average temperature prior to fire onset; (a) above.	°C
Hottest temperature	Highest temperature measured by a firelogger at a given location; (b) above. Locations were in vertical profile at soil surface and buried 1, 2, and 4 cm in the soil.	°C
Temperature increase	Difference between hottest fire temperature and pre-fire ambient temperature; (c) above.	°C
Fire duration	Time between fire onset and fire end as recorded by surface firelogger at given location; (d) above.	minutes:sec
Fire onset	First time temperature increased more than 0.3°C per second at given location	time of day
Fire end	Time at which temperature fell below 50°C at surface following fire at a given location	time of day
Fuel load	Quantity of combustible fuels at a given location comprising mostly grasses, herbs, pine needles and cones. Includes both fuels *in situ* and pine needles added experimentally in our fuel addition plots.	kg/m^2

Box 1.

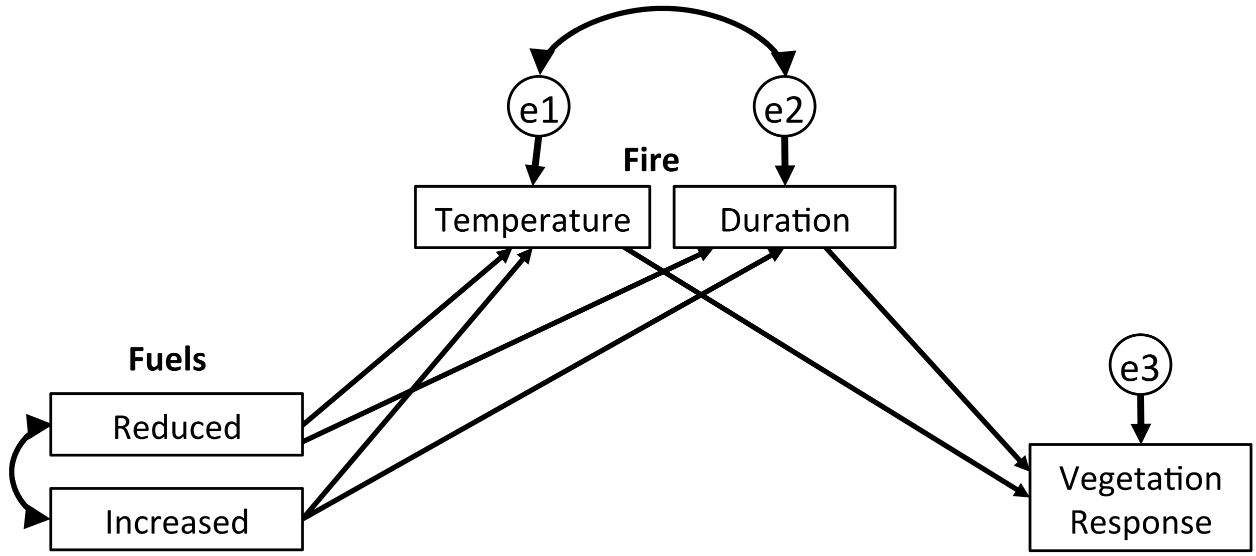


Figure 1A.

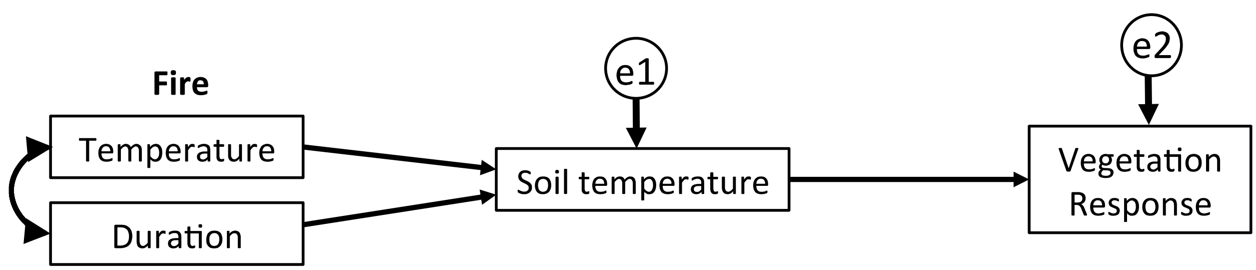
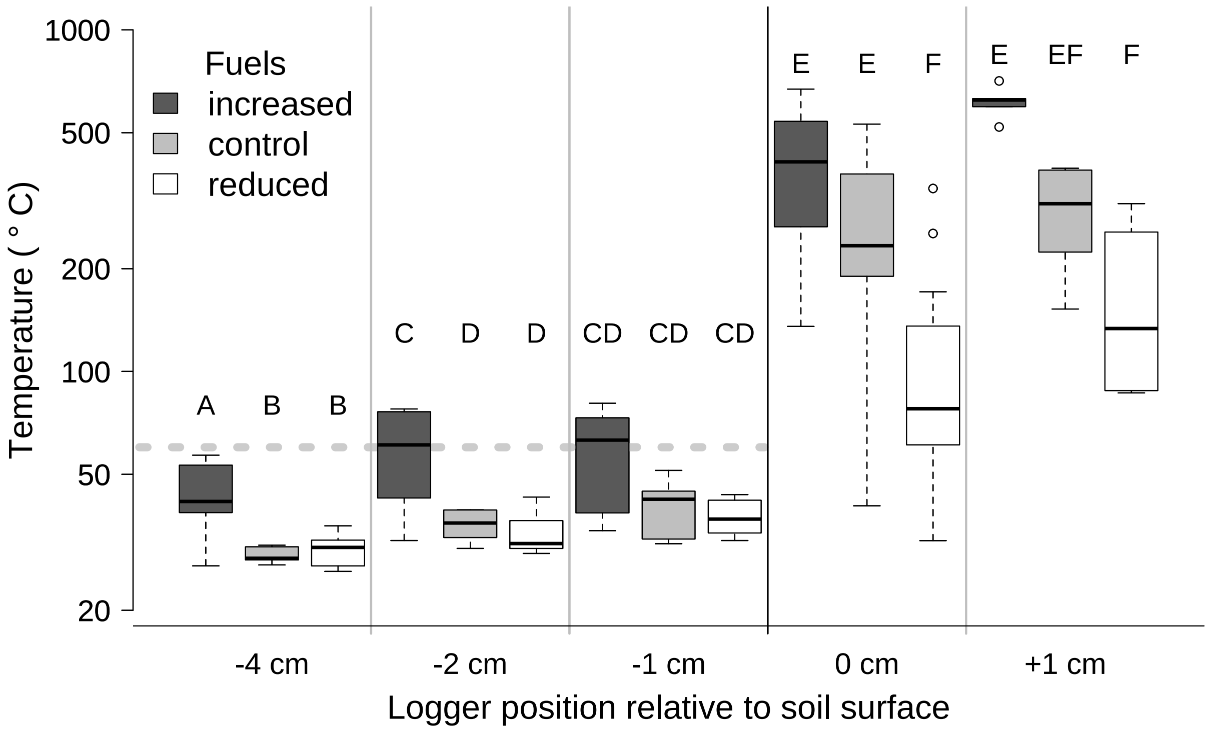


Figure 1B.



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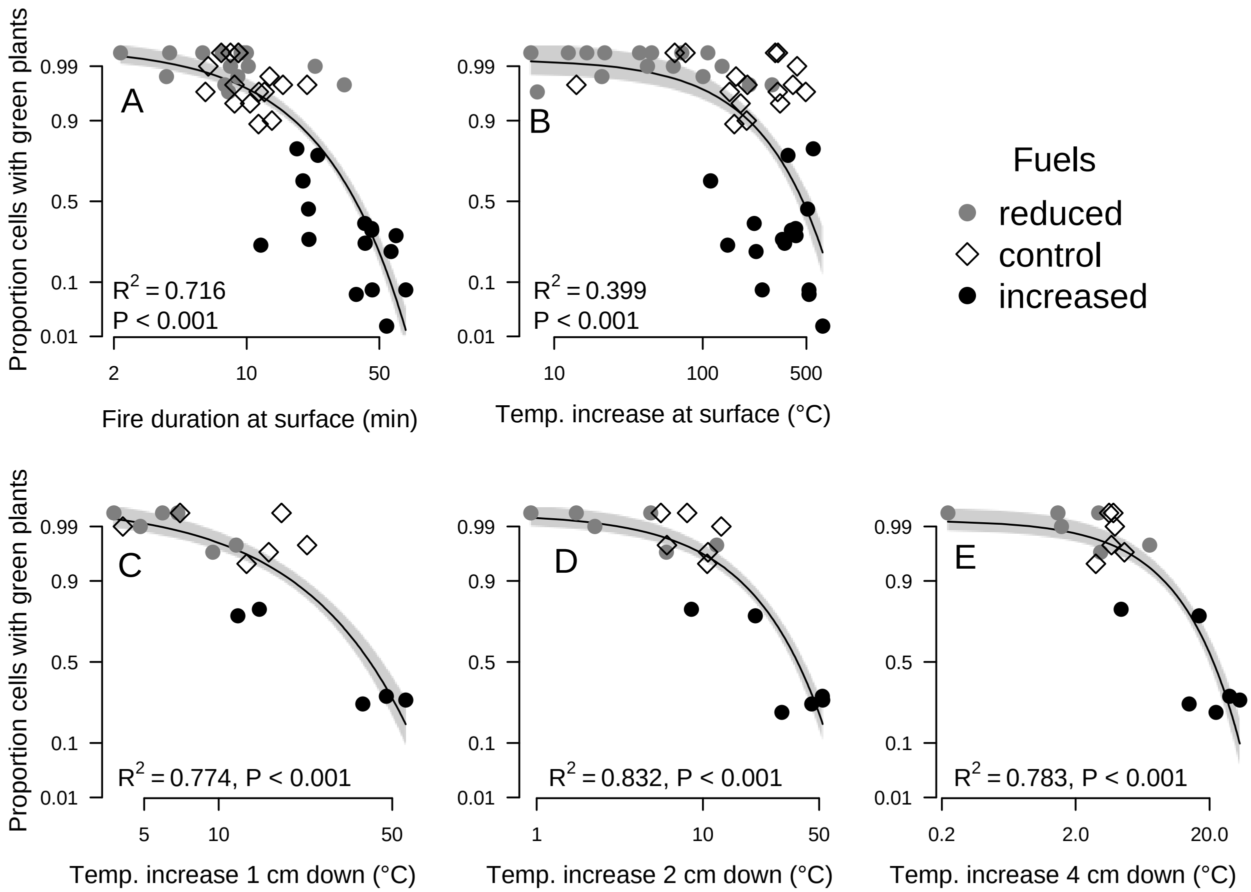
727 Figure 2.



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729 Figure 3.

730

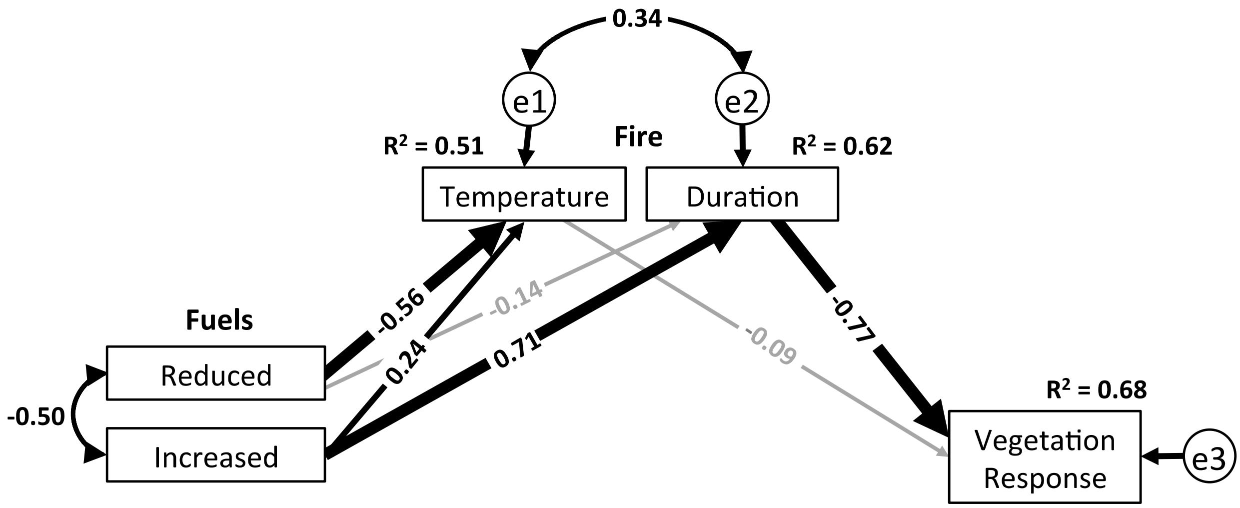

Figure 4A.

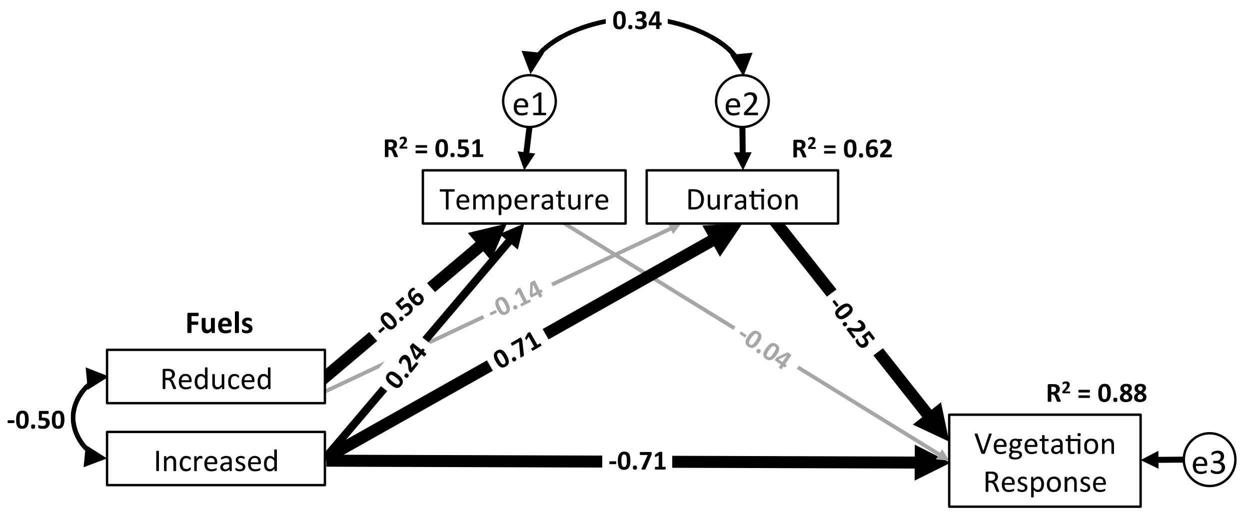

Figure 4B.

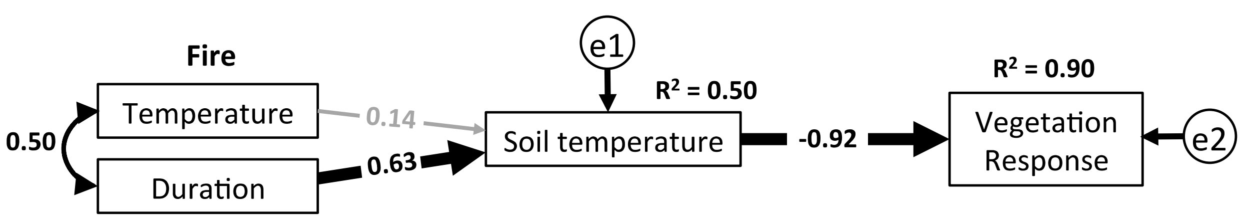

Figure 4C.

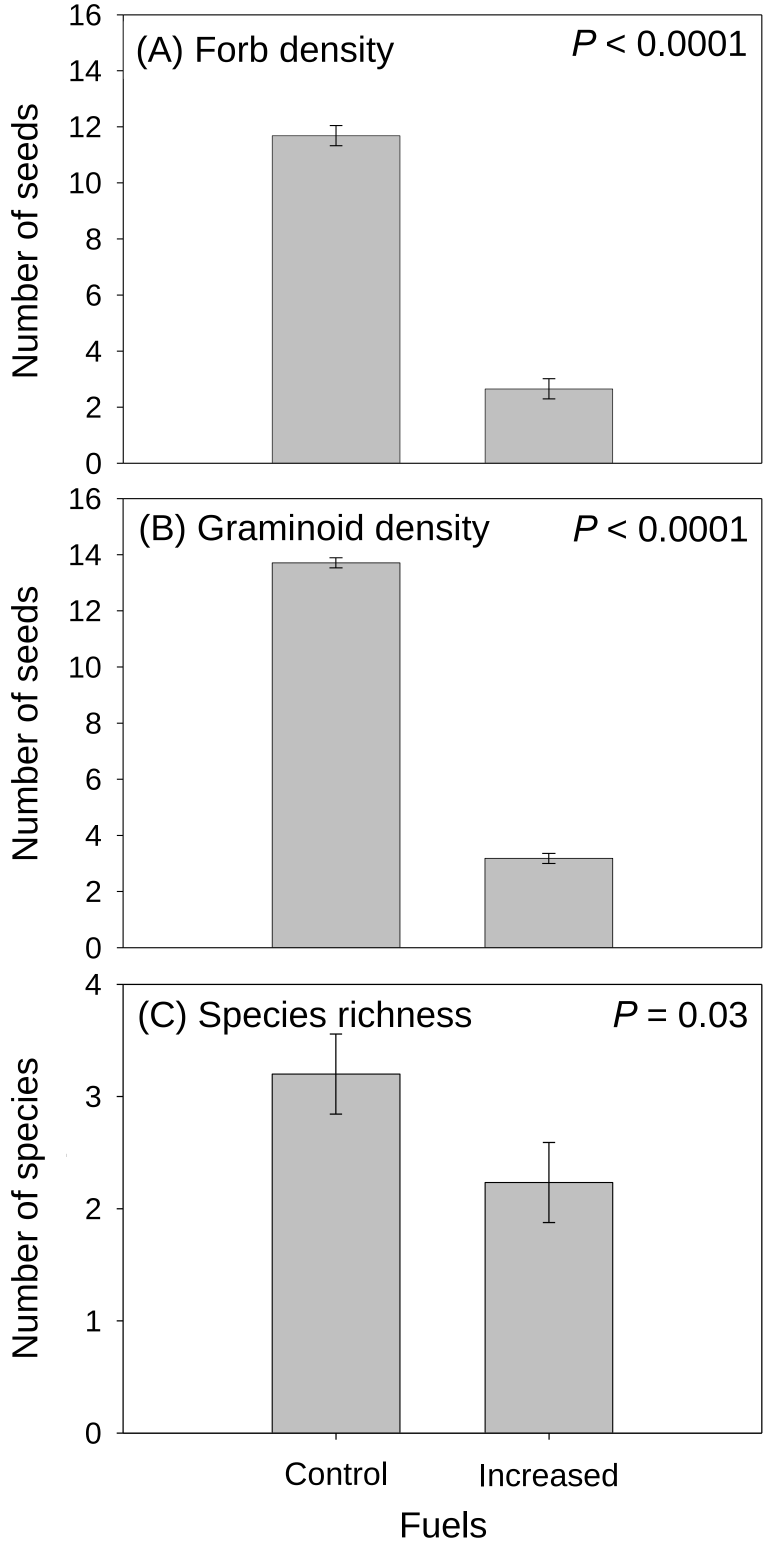
(A) Forb density
P < 0.0001
Number of seeds
0
2
4
6
8
10
12
14
16
(B) Graminoid density
P < 0.0001
Number of seeds
0
2
4
6
8
10
12
14
16
(C) Species richness
P = 0.03
Number of species
0
1
2
3
4
Control
Increased
Fuels

Figure 5.