**Title**: Fire, flowers, and phenology: how fire changes floral resources in an old growth pine savanna

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**Introduction**

Many ecosystems fundamentally depend on the presence of fire. Fires are often patchy, and lightly burned and unburned areas, or refugia, are common within their perimeter (Kolden et al. 2012, Springer et al. 2018). Refugia can be permanent areas caused by differences in topography, vegetation, or soil moisture, or they can be ephemeral, caused by random chance during a particular fire event. Fire refugia, and areas adjacent to fire that are unburned, are important for sheltering fire sensitive organisms and repopulating burned areas (Robinson et al. 2016, Swan et al. 2016, Mutz et al. 2017). Prescribed fire is often used to reduce fire risk and increase habitat quality. However, management constraints often result in prescribed fires having a more homogeneous burn pattern than a natural fire would (Kolden et al. 2012, Blomdahl et al. 2019).

Heterogeneity within fires could be important for explaining the ecology of organisms that persist in frequent-fire ecosystems (Blomdahl et al. 2019) and for predicting the speed and likelihood of ecosystem recovery after fire (Mutz et al. 2017, Blomdahl et al. 2019). Several studies have addressed the ecological importance of large, permanent refugia for plants and animals (e.g. Robinson et al. 2016, Swan et al. 2016). However, relatively little is known about the potential roles of small-scale ephemeral refugia for enhancing habitat quality, and thus about the potential costs of eliminating refugia in managed burns.

Floral resources for pollinators are one example of an aspect of habitat quality that might be influenced by fire refugia. Pollinator declines are a matter of great concern, and fire is known to influence pollinator success. Several studies of the direct effects of fire on butterflies in prairie and savanna habitats have concluded that even taking into account immediate mortality from fire, the improvement in habitat quality from prescribed fires provides a net benefit for fire-adapted butterfly populations (e.g. Schultz and Crone 1998, Warchola et al. 2015, Henderson et al. 2018). These studies often find that the open habitat created by fires initially increase pollinator abundance. However, if these habitat conditions are not maintained, pollinator abundance decreases.

Fire timing and frequency are also known to influence the plants that provide floral resources required by pollinators. Fire affects the presence; abundance; and phenology, or the timing of life history events such as flowering, of many flowering plant species (e.g. Platt et al. 1988). If refugia flower at different times than burned areas this could extend the flowering season in the habitat as a whole, which could be good for pollinators. Fire is known to affect the timing and synchrony of flowering (Platt et al. 1988, Wagenius et al. 2020), so the presence of refugia could change the overall resource availability across a season for pollinators by creating more heterogeneity within a habitat. Flowering plants might exhibit different phenology in unburned areas by blooming earlier, or blooming with less synchrony or different abundance than their conspecifics in burned areas (Platt et al. 1988). A flowering season extended by landscape heterogeneity in burning could improve survival and reproduction of pollinator species by providing a longer window of resource availability. Studies have looked at the effects of fire on plant-pollinator relationships at the scale of an entire burn management unit (e.g. Welti and Joern 2018) or of a wildfire (e.g. Mola and Williams 2018). Some authors have suggested that some patches of habitat should remain unburned to insure that vulnerable life stages of a species are not lost from a community (e.g. Warchola et al. 2018). However none have yet examined how these small scale refugia as compared to burned areas might influence the phenology and abundance of floral resources.

Longleaf pine savanna is an ecosystem that is completely dependent on frequent fire and of conservation concern because less than X amount of the original extent of the habitat is left. This habitat is also managed with frequent prescribed burns, so understanding how best to burn to promote resources for pollinators is important for long-leaf pine management. Large scale burns are thought to maintain high plant diversity in long-leaf forests (Glitzenstein et al. 2012). These burns also recover from fire very quickly, with most plants resprouting within a week of burning, and several plants flowering within a week to a month of burning (MSW, KMR pers. obs.). Old growth longleaf pine savannas have distinctive canopy gaps that influence the pattern and intensity of fires. These small scale gaps are created by tree deaths have been shown to contribute to overall plant diversity in longleaf pine savannas (McGuire et al. 2001). These gaps are less likely to carry fire than the vegetation under the tree canopy, and this patchiness in fire has been demonstrated to be important for longleaf pine regeneration (Robertson et al. 2019). Fire patchiness could likewise influence resources for pollinators. Prescribed fire managers generally know under what conditions prescribed burns result in patchy versus continuously burned areas, such that improved understanding of effects of patchy burning on plants and pollinators could provide important guidance for conservation management. If small-scale fire refugia are important to the persistence of pollinators such as butterflies, land managers could use heterogeneous burns as part of their effort to achieve conservation goals.

To determine how small-scale refugia in long-leaf pine savannah influenced floral resources for pollinators, we conducted an experiment that created protected plots (fire refugia) within a long-leaf pine ecosystem that has never had fire removed. For this experiment, we asked: 1.) Is floral abundance different between burned and protected plots? 2.) Are floral resource communities different between burned and protected plots? and 3.) Is flowering phenology different in burned and protected plots? To test these questions, we created small protected plots within prescribed fires in an old growth longleaf pine savanna. We predicted that flower abundance would be greater in burned plots than in protected plots, and that floral resource communities would be different in burned and protected plots. We also expected that plants would flower later and with greater synchrony (i.e. a shorter duration) in burned plots than in protected plots.

**Methods**

*Study system*

Our research was conducted at the Wade Tract, an 83 hectare tract of old growth longleaf pine savanna in southern Georgia, managed by Tall Timbers Research Station. The Wade Tract is divided into two burn units (east and west), both of which have been burned annually for most years in the past decade. The beginning of this timespan corresponds with the transition from dormant to growing season in southern Georgia. Prescribed fires at the Wade Tract are generally allowed to be patchy, depending on weather conditions conducive to burning, and are managed to minimize crown scorch and ignition of scars of mature trees on the property. Tall Timbers Research Station has kept detailed records of which areas have burned at the Wade Tract over the last 30 years. More than 500 species of flowering plants have been recorded at the Wade Tract (W.J. Platt and colleagues, unpublished data).

*Experimental methods*

To test the effect of fires in the current burn season on the floral resource community we established pairs of plots in which one was burned earlier in the same calendar year (as well as previous years) and one was burned in previous years and protected from fire in 2018. Plots were roughly circular with a diameter of 10 m. All plots were established in canopy gaps to simulate naturally occurring unburned patches, as gaps are where such patches are most likely to occur because of low pine needle litter fuel loads (Robertson et al. 2019). All plots were established prior to prescribed fires, in canopy gaps that had burned during every prescribed fire over the last 15 years, arranged so that plots were at least 50 m apart from each other and in separate gaps. Plots within each pair were randomly assigned the treatment of protected from fire (hereafter “protected” or allowed to burn (hereafter “burned”). We raked a fire break of ~0.5m around all protected plots to exclude fire before prescribed fires were ignited.

The Wade Tract consists of two burn units, east and west. The prescribed fire for the west burn unit was conducted in March 2018. This burn spread mostly during the early evening under mild fire conditions, and the resulting fire left many unburned patches behind. Three of the plots intended to burn were moved to the burned area nearest their original site. This maintained 7 pairs of burned and unburned plots in the west burn unit. In contrast, when the east burn unit was burned in May 2018, relative humidity was very low (only 19%), resulting in three protected plots burning during the initial fire. Protected plots that were lost during the prescribed burn could not be shifted to another unburned area. Areas that were naturally skipped by the fire might have remained unburned because of differences in hydrology, vegetation or other confounding factors. Since the purpose of our experiment was to compare burned and protected plots, all burned plots pairs without surviving protected plots were dropped from the study. Thus, on the east side, we only used four pairs of plots after our initial treatment.

We visited plots to survey flowers from mid-April through November 2018, and from March to mid-April 2019. From May through August 2018 floral surveys were done twice a week, and from September 2018 through April 2019 floral surveys were done weekly. Surveys in 2019 began on March 7, 2019 and continued until annual prescribed burns were applied, on March 27, 2019 for the east burn unit and on April 23, 2019 for the west burn unit. Within each plot we identified all plant species with open flowers and then counted the number of flowers present per species. When possible, we counted individual flowers in order to capture the best measure of reproductive effort and available floral resources for pollinators. For Asteraceae, in most cases we counted capitula (individual inflorescences of ray and/or disc flowers). For species in the genera *Eupatorium* and *Solidago*, counting capitula was impractical, so we counted flowering individuals instead. For other species with large inflorescences (e.g. in genera *Asclepias*, *Angelica*, *Rhus*, and *Callicarpa*), we counted umbels or individual inflorescences instead of individual flowers. Voucher specimens of most species identified were collected and placed in the FSU Godfrey herbarium. Wunderlin and Hansen (2011) was used to identify all plants.

*Statistical methods*

*Floral abundance and community*

To compare total floral abundance for the suite of flowering species between burned and protected plots, we used a repeated measures analysis in which number of flowers in each week was the response variable and burn status and week as factors, plot pair as a blocking variable, and burn unit as a categorical covariable. We used our complete dataset to test for patterns in floral abundance. Plot pairs were included as a random effect in the model to account for site heterogeneity and repeated measures at each plot. Main effects and interactions were tested, using the *lmer* and *car* packages in R v3.X.X. Plot pairs (i.e. spatial block) were included as a random effect in the model to account for repeated measures taken at each plot and the overall heterogeneity of the field site. We modeled the log total number of flowers found per visit by treatment and time of year, with burn unit as a fixed effect and plot pair as a random effect. We included a square term to allow the model to curve.

To test whether the suite of flowering species differed between burned and protected plots, we used NMDS to visualize differences in composition among plots and their changes over time, and then ran a PERMANOVA on a distance matrix using Bray-Curtis community dissimilarity scores (*vegan* package in R). Rare species can have an outsized effect on community analyses, so we used the inflection point of the species accumulation curve for our data to determine how many species to include in the NMDS plots and all further community analysis. We used a subset of the 55 most abundant species for the NMDS plots and the PERMANOVA analysis to compare community composition between burned and protected treatments. We first compared communities by treatment over the entire year of sampling. We also used PERMDISP to compare the homogeneity of flowering response within each treatment relative to among treatments. For both the PERMANOVA and PERMDISP analyses, we tested responses of the suite of flowering species to protected and burned treatments, week of year, and interactions between treatment and week of year. To separate effects of abundance from the effects of species identity, we also ran the PERMANOVA and PERMDISP analyses using species’ presence or absence.

Personal observation over the course of the experiment suggested that there were distinctive phenological flowering guilds, so in addition to analyses of the entire year we split our data into five phenological flowering guilds. This allowed us to ask whether differences in burned and protected treatments differed over the season; it is possible that effects of burning would only be apparent in spring and summer, and have faded by fall. The seasonal phenological guilds were determined based on field observations, and then checked by comparing boxplots of the flowering duration by week of year for dominant species (Fig 1). Based on our inspection of distributions of flowering times, we split the data into partitions for spring 2018 (weeks 14 to 28 early summer (weeks 29 to 35), late summer (weeks 36 to 42), fall (weeks 43 to 47), and spring 2019 (weeks 10 to 16).

*Flowering phenology*

To compare flowering phenology (the timing of flowering) between protected and burned plots we calculated first, last, and peak flowering dates and flowering durations for all species that were observed in both burned and protected treatments and that had been observed in at least five separate visits. Previous studies have shown that the timing of fire can affect whether plants show a flowering response or not (Platt et al. 1988), so we also looked at the timing of first, peak, and last flowering, and the duration of flowering separately for the two burn units. For most species we did not have sufficient replication to test formally for species-level differences in phenology between protected and burned treatments. Instead, we compared average differences in phenology for the entire suite of flowering species, using the phenology of each species as a data point. First (last) flowering date was calculated as the week of year of the first (last) observation of a species’ open flower, across all plots within a treatment and burn unit. Peak flowering was calculated as the week of year with the highest abundance of flowers for a species, across all plots within a treatment and burn unit. Duration of flowering was calculated as the number of weeks between the observation of the first and last open flower. We compared first, last, and peak flowering dates, and duration between treatments using a t-test, with degrees of freedom equal to the number of species for which we were able to estimate phenology data. We tested for effects on average phenology in each burn unit separately, because the timing and intensity of the fires was different between the two burn units. The west unit was burned at the end of the dormant season and the east unit was burned at the beginning of the fire season for southern Georgia. Previous research suggests that the season of burn also affects how plants respond to fire (Platt et al. 1988).

Since we hypothesized that refugia might increase the landscape-level duration of flowering, we also calculated species’ phenological scores using the first flowering date in any plot (protected or burned) and the last flowering date in any plot (protected or burned). The phenological scores from the combined plots, representing the hypothetical phenology for a landscape with spatial patchy burning, was compared to the phenological scores from only the burned plots, representing a more homogenous “clean” burn strategy. Again, we used a t-test to compare flowering duration in current season burn plots to the combined flowering duration of protected and current season burn plots, with degrees of freedom equal to the number of species observed flowering over at least five visits and in both plot types. We again tested for effects on average phenology in the burn units separately.

**Results**

*Floral abundance and community*

We collected data on 93 species or genera of flowering plants over the course of the experiment. While we preferred to identify plants to species, some sets of species were impractical to ID in the field (e.g. *Pityopsis,* some *Desmodium* species), so in some instances we binned plants of the same genus together for data analysis. *Desmodium* could be separated into smaller bins based on similar morphological characteristics (e.g. leaf shape or growth form) even when they could not be easily distinguished to an individual species, so this genus was divided into three separate groups to provide a better picture of *Desmodium* diversity. *Desmodium floridanum* was easily identified in the field and left as a separate species for all analyses.

Burn treatment, week of year, and the interaction between treatment and time all significantly affected floral abundance (p<0.001 for all, Table 1). Burned plots had more flowers than protected plots, and this difference was greatest at peak flowering (Fig 2). Peak flowering for both burned plots and protected plots occurred in September.

We found that burn treatment, time of year, and the interaction between treatment and time all had significant effects on community composition (PERMANOVA: burn treatment: p<0.001, pseudo r2=0.01; week of year: p<0.001, pseudo r2=0.03; interaction: p<0.001, pseudo r2= 0.006; NMDS stress=0.075). The burned community was significantly more homogeneous than the burned community (PERMDISP: p<0.001).

The floral community still differed by burn treatment when we used presence-absence values instead of abundances (PERMANOVA: Burn treatment: p<0.001, pseudo r2=0.02; week of year: p<0.001, pseudo r2= 0.07; interaction: p<0.001, pseudo r2= 0.007; NMDS stress=0.71). Floral community showed a larger difference by week of year for presence-absence data than for abundance data.

When we ran the NMDS, PERMANOVA and PERMDISP analyses for each phenological flowering guild, we found that burn treatment and week of year had a significant effect in all seasonal communities, but that late summer and fall communities did not show a significant interaction between burn treatments and week of year, or a significant difference in dispersion in burned and protected treatments. In spring of 2019, floral communities were still different between burned and protected plots (PERMANOVA: burn, p=0.001; week of year, p=0.001; interaction, p=0.06), suggesting that the two communities had not yet converged by the time prescribed fires were carried out in 2019.

Spring 2018 and early summer floral communities were more homogeneous in the burned treatment than in the protected treatment (PERMDISP: spring 2018, p=0.003; early summer, p<0.001). By spring of 2019, the plots in the current year treatment became significantly less homogenous than their protected counterparts (PERMDISP, spring 2019 p<0.001).

*Floral phenology*

For the east burn unit, which was burned in a hot fire in May, both first and peak flowering dates were significantly later in the burned treatment than in the protected treatment (t-test: first flowering, p=0.001; peak flowering, p=0.01). The west burn unit, which was burned as a cooler fire in March, showed no significant difference in flowering phenology by treatment. Neither burn unit showed a significant difference in flowering duration by burn treatment. When data from both burn units was considered together, peak flowering was the only phenological event that showed any significant difference between burned and protected treatments, with peak flowering occurring slightly later for plots in the burned treatment (t-test, p=0.04).

Even though average flowering duration was not different in burned and protected treatments, the combination of burned and protected treatments did extend flowering duration for the whole community compared to the flowering duration of burned alone. For the west burn unit, the fire treatment combination extended flowering duration by 1.67 weeks, which is a marginally significant difference from the burned flowering duration alone (t-test: p=0.08). However, for the east unit, the fire treatment combination significantly extended flowering duration (3.25 weeks longer, t-test, p=0.01).

**Discussion**

Our results suggest that the heterogeneity created by fire refugia could provide greater floral resource diversity and extend the amount of time that floral resources are available. These are the first experimental results that we know of that show that small-scale fire refugia could have an important effect on the abundance, composition, and availability of floral resources for pollinators.

Burned treatments had a greater abundance of flowers than protected treatments (Fig. 2). Other studies in longleaf pine savannas have shown similar results with floral abundance increasing after fires (Platt et al. 1988). An increase in abundance of flowers certainly provides more potential resources for pollinators. Whether it is beneficial for plant reproduction even if it increases the amount of conspecific pollen a plant receives, might depend on how rates of outcrossing also change.

The suite of species that flowered in protected plots was significantly different from the suite that flowered in burned plots (Fig. 3x). Even though longleaf pine ecosystems recover from fire quickly, the effects of protecting plots were still apparent a year later (Fig 3y.) Some species had very strong responses to the burned and protected treatments. *Tephrosia virginiana* flowered a month after fire and only in areas that had been burned. *Penstemon australis* was already flowering before the May fire, but these same plants regrew and flowered again after the prescribed burn. *Penstemon australis* flowers were often visited by butterflies (MSW pers. obs.) and *Penstemon* is a bee pollinated genus. Flowering twice in a year could certainly provide more resources for pollinators, but using double the resources to be able to produce seeds might not be beneficial for the *Penstemon*.

Some plant species at the Wade Tract also appear to rely on unburned areas for sexual reproduction. Ericaceous species, particularly *Vaccinium* and *Gaylusacia*, and *Rubus* species flowered early in the year, and were already fruiting when prescribed fires were applied at the Wade Tract. Unlike the *Penstomon* and *Ceanothus*, they did not reflower after fire. While these species are all generally long-lived perennials, losing the opportunity for sexual reproduction could still potentially have important effects on genetic diversity. These species are all important early season pollinator resources. The fruits of these species are also potentially important food sources for birds, mammals, and insects, so it seems likely that the effects of fire refugia on flowering could benefit far more than just pollinators.

Canopy gaps in longleaf pine savannas have also been shown to have distinctly different plant communities than the areas under the tree canopy (McGuire et al. 2001), suggesting that areas where ephemeral refugia are more likely can have an impact on community composition. Canopy gaps have also been shown to be important for longleaf pine regeneration, in part because it is more likely for these gaps to be skipped during fires, which allows seedlings and saplings to survive during their brief fire-vulnerable lifestages (Robertson et al. 2019).

The presence of protected plots within the burned area also increased the total duration of time that floral resources were available (Fig 4). For example, *Ceanothus americanus*, an important pollinator resource as well as the host of a rare native skipper (Elfin Elders pers. comm.), flowered at different times in burned and protected plots. Flowering dates between treatments barely overlapped, with burned *Ceanothus* just beginning to flower as the unburned *Ceanothus* was finishing. *Ceanothus* had apparently not previously been shown to flower directly after fire at the Wade Tract (Elfin Elders, pers. comm.).

Timing and intensity of burn (the effects of which can’t be separated in this study) also appeared to affect flowering phenology, with plants that were burned in the hot May fire showing more synchrony in flowering than plants burned in the cool March fire (Fig 8). Other research also suggests that fire can increase synchrony of flowering in longleaf pine ecosystems, and that the timing of fires determines whether flowering is more synchronized after fire or not (Platt et al. 1988). While research suggests that decreasing synchrony of flowering reduces plant reproduction (Wagenius et al. 2020), the overall increased flowering duration could be beneficial for pollinators, particularly since it appears refugia can maintain an important pollinator resource in longleaf pine savannas while burned areas are recovering.

In general, our results suggest that small-scale fire refugia potentially increase resources for pollinators and other organisms in longleaf pine savannas. These results could be applicable outside of longleaf pine ecosystems as well. For example, different intensities of fire (which also result in heterogeneity and refugia within a burn) have been shown to affect community composition in lodgepole dominated forests in Yellowstone National Park (Turner et al. 1997). Application of prescribed has been shown to increase the reproduction of a rare *Echinacea* species in the Midwest (Wagenius et al. 2020). Several studies have also shown that fire affects the presence, abundance, and behavior of pollinators, often mediated through the effects fire has had on habitat (Mola and Williams 2018, Welti and Joern 2018).

The Wade Tract, and longleaf pine savannas in general, are extremely heterogeneous communities. While all our PERMANOVA analyses had low R2 values, that any signal at all was noticed suggests that heterogeneity in fire disturbance could be important for maintaining community diversity, even when fire is a frequent and strong filter for species present in that community. We also don’t know the relative value of every plant observed for pollinators, which limits our understanding for how increases in flowering duration might affect some pollinators, particularly specialist bees. However, for generalists like Lepidoptera, the demonstrated effect heterogeneity within a fire has on flowering duration seems useful.

There are several areas where future research is needed. While we have shown that abundance, community, and phenology of floral resources might be different between fire refugia and the surrounding burned matrix at our study site, these data don’t show us if the presence of refugia can change plant reproductive success. It would be useful to explore if fire refugia also have a significant effect on reproductive success in plant species. While we can speculate on how pollinators might respond to differences in floral resources between small scale fire refugia and the surrounding burned matrix, our current data also don’t show us any pollinator response. Testing if the presence of certain pollinators are different between refugia and the burned matrix is an important next step for understanding the larger tropic effects that small scale fire refugia might have. Previous studies also suggest that fire refugia could be directly important to pollinators, particularly for insuring that fire vulnerable life stages of otherwise fire-reliant species continue to survive in a habitat (Schultz and Crone 1998, Thom and Daniels 2017, Henderson et al. 2018). Other studies also suggest that insects and other invertebrates survive fires within refugia (citations needed).

**Conclusions**

Prescribed fire managers generally know under what conditions prescribed burns result in patchy versus continuously burned areas, such that improved understanding of effects of patchy burning on plants and pollinators could provide important guidance for conservation management. If small-scale fire refugia are important to the persistence of pollinators such as butterflies, land managers could use heterogeneous burns as part of their effort to achieve conservation goals.

**Acknowledgements**

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**Figures** (forthcoming in separate document)