The Effects of Fire Season, Frequency, and Forest Structure on the Flowering Abundance of *Macbridea alba*

Chad T. Anderson[1,2], Samantha Dietz[1], Amy Jenkins[1], and Jason Drake[2]
[1]Florida Natural Areas Inventory, 1018 Thomasville Rd., Suite 200C, Tallahassee, FL 32303
[2]325 U.S. Forest Service, National Forests of Florida, John Knox Rd., Ste. F-100, Tallahassee, FL 32303

Abstract
White birds-in-a-nest (*Macbridea alba*) is a federally listed species endemic to the state of Florida and found in a relatively small range. Despite this, no quantitative studies have examined the habitat characteristics that best suit this species. We used data from forest monitoring plots to elucidate the relationships between *M. alba*, vegetation structure, and fire history. Overall, the number of *M. alba* flowering stems has likely increased since 2012 in the Apalachicola National Forest (ANF). Considering structural attributes of the five sites in our study, *M. alba* was more numerous at sites with a low to moderate amount of shrub cover and moderate herbaceous cover than at sites that were dominated by herbaceous cover. Plots with the greatest number of flowering stems had shrub cover between 15% and 45% and litter cover between 20% and 45%. Correspondingly, herb cover exceeding 80% seemed to negatively impact flowering stem count. Shrub richness was found to have a strong linear and positive effect on the flowering stem count. Across all sites, a fire return interval of 3.5-4.7 years with a balanced proportion of growing season to dormant season burning seemed to be beneficial to *M. alba*. Taken together, these results indicate that *M. alba*, unlike many other herbs, prefers moderate shrub cover, litter cover, and general conditions benefiting shrub diversity as opposed to frequently burned, highly herbaceous sites dominated by wiregrass (*Aristida stricta*). We recommend further investigations into the habitat dynamics of other rare species to better inform their conservation and management.

Background
White birds-in-a-nest (*Macbridea alba*), is a federally listed species endemic to Florida with a very narrow range. *M. alba* is found in the ecotone between wet prairie and flatwoods communities. Multiple known populations of *M. alba* occur (14 element occurrences in the BIOTICS database) in the Apalachicola National Forest (ANF). *M. alba* occurs in habitats historically maintained by frequent fires (Godfrey and Wooten 1981). In cooperation with the U.S. Forest Service, the Florida Natural Areas Inventory (FNAI) monitors *M. alba* through both opportunistic observations, project-based surveys, and permanent monitoring plots. For instance, prior to any timber harvests, searches are conducted to count the number of rare plants in the potentially affected areas. FNAI maintains a database of opportunistic counts and long-term monitoring plots which include known *M. alba* populations in the ANF (Figure 1). These permanent monitoring sites allow *M. alba* trends to be tracked over time. In addition to flowering stem counts, FNAI collected data on structure and species richness of these monitoring plots in 2020. This information can be used to assess how plant composition, structure, and management history can affect *M. alba* flowering stem counts.

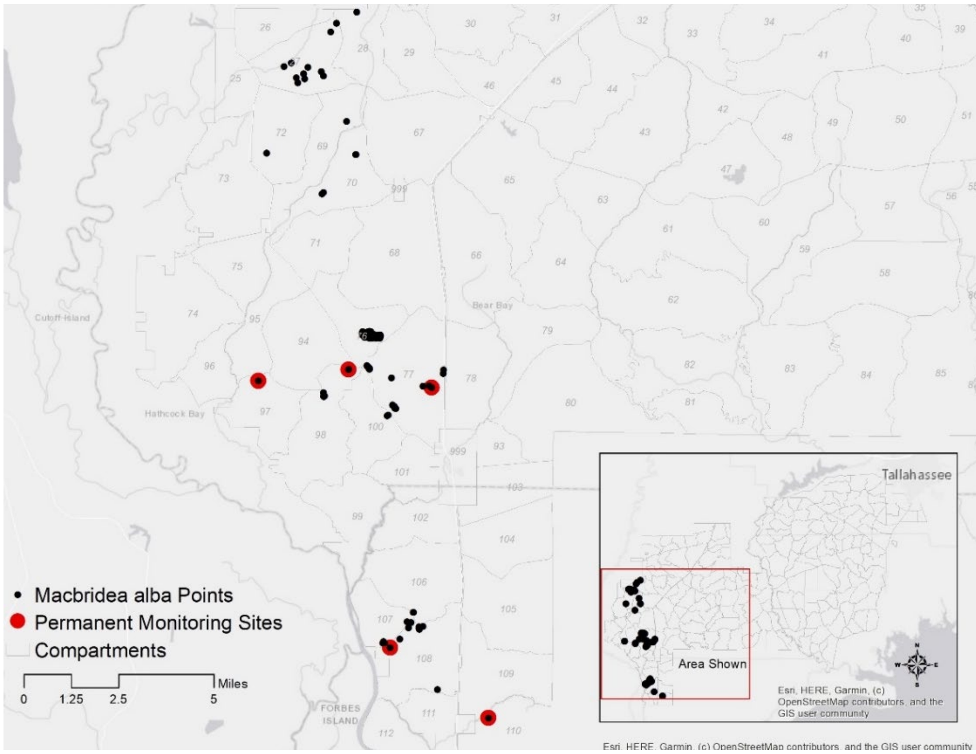

Figure 1. The locations of known Macbridea alba populations, permanent monitoring plots, and management compartments in Apalachicola National Forest

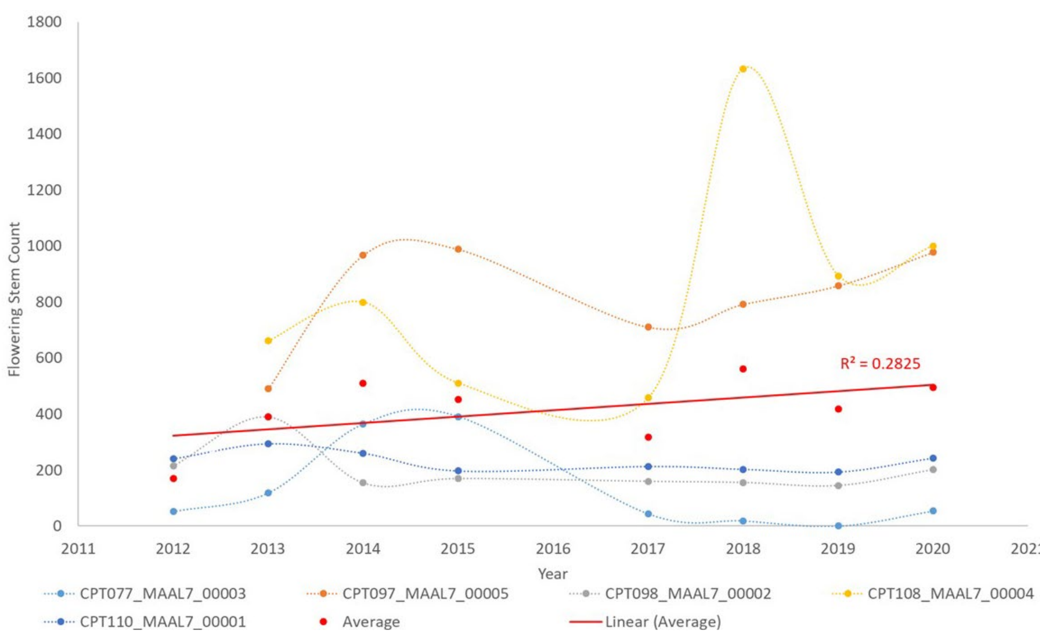

Figure 2. Counts of M. alba plants at each permanent monitoring plot since 2012. Compartment numbers correspond to the three numbers following "CPT" in each compartment code, and refer to the compartment where each monitoring plot is located.

The long-term monitoring plots in ANF are 20-m radius plots centered at five known populations of *M. alba*. These plots were established in 2012 to track counts of flowering stems and in 2020 a "crosshair" plot grid was added for additional sampling of the habitat structure (Figure 3). Each grid is comprised of 32 1-m x 1-m quadrats, with eight quadrats along each arm of the crosshair, resulting in 160 total quadrats. Arms of the crosshair extend in the each of the cardinal directions. Quadrats are offset at the center of the crosshair to prevent them from overlapping. In each quadrat, FNAI collected data on vegetation structure, species richness, and the number of *M. alba* stems present. Monitoring plots containing *M. alba* populations have been monitored since 2012 and occur in five compartments in ANF: 77, 97, 98, 108, and 110 (Figure 1). During 2020 surveys, FNAI counted the number of *M. alba* stems that occurred in each plot and quantified habitat structure (Figure 3).

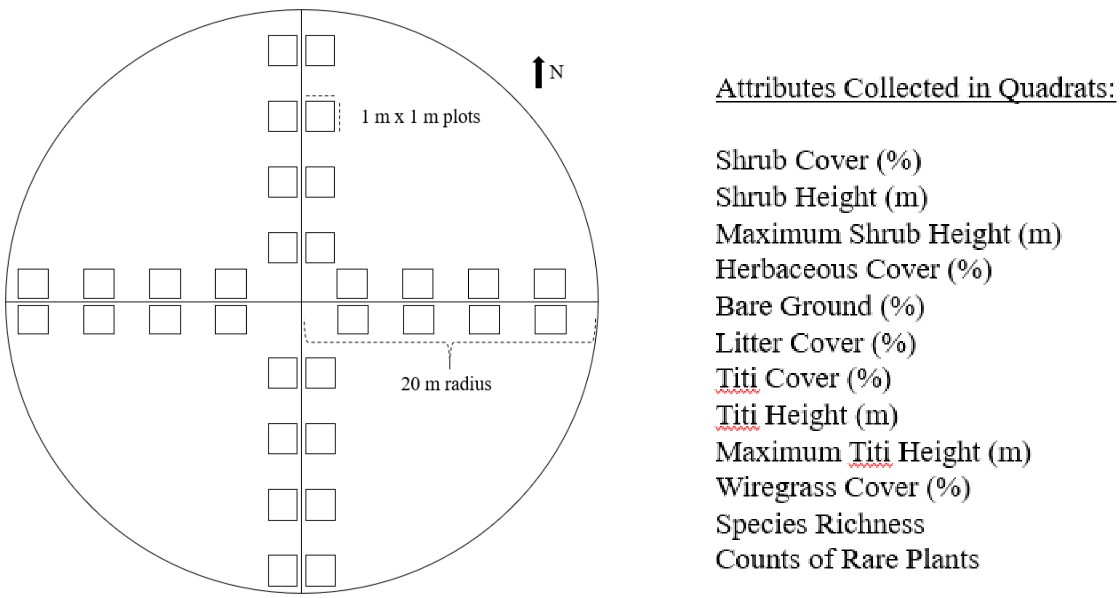

Figure 3. Plot layout and attributes collected in each quadrat.

To understand how fire history has affected these populations, we used fire data since 2006 to calculate the fire return interval (FRI) and the proportion of burns that occurred during the growing season for each plot. We normalized the count data by ranking each compartment by the total number of stems that were observed in quadrats during 2020 surveys. Rank "5" was assigned to the compartment containing the greatest number of total plants, and Rank "1" was given to the compartment with the fewest number of plants (Table 1).

Table 1. The number of M. alba stems at plots, the fire return interval, and the proportion of burns conducted in the growing season within each compartment surveyed.

Compartment	Total Stems in Plots	Rank	Fire Return Interval (years)	Time Since Fire (years)	Proportion of Growing Season Burns
77	54	1	2.8	1	0.6
97	978	4	3.5	1	0.5
98	202	2	4.7	0	0.3
108	1000	5	4.7	2	0.3
110	243	3	4.7	4	1

To better understand the habitat of *M. alba*, we first characterized the habitat across all five monitoring plots by determining the average vegetation structure within plots. We pooled and averaged each variable collected in the quadrats at each long-term monitoring site and then averaged the site values to calculate a mean and standard error for each variable to characterize the overall habitat preferences of *M. alba*. Further, to understand why some sites have more flowering stems than others, we compared the relationship between rank and vegetation structure using generalized additive models (GAM). By modeling these relationships using non-linear methods we were able to determine ideal thresholds and ranges for structural attributes, fire metrics, and species richness as they relate to *M. alba* counts. We conducted all analyses in R (R Core Team 2019) using the packages 'mgcv' (Wood 2011) and 'rcompanion' (Salvatore 2020).

Results

General Characterization of Habitat Structure

We generalized values across all five sites to characterize the typical characteristics of *M. alba* habitat. Overall in ANF, the number of *M. alba* flowering stems has likely been stable or increasing since 2012 (r^2=0.28, Figure 2). Across all permanent monitoring sites in 2020, there was a 21.2% (SE: ± 0.05) probability of *M. alba* occurring in a given square meter quadrat. Average shrub cover in *M. alba* habitat is 18.2% (SE: ± 3.8). Shrub height was relatively low, with an average shrub height of 0.5 m (SE: ± 0.1) and the average maximum shrub height was similar at 0.6 m (SE: ± 0.1). Average herb cover at these sites was relatively high at 63.5% (SE: ± 13.1) across all sites. Similarly, average wiregrass (*Aristida stricta*) cover was 52.3% (± 15.3). Average bare soil was low, at only 0.41% (SE: ± 0.4). Average litter cover was found to be 26.7% (SE: ± 6.8) in *M. alba* habitat. The average species richness, including both shrub and herb species, was 13.9 (SE: ± 1.0) species per plot. The average number of shrub species per plot was 3.4 (± 0.5) and the average number of herb species per plot was 10.4 (SE: ± 1.1). On average, all sites were generally found to be within the recommended range considering all metrics for high quality mesic flatwoods (FNAI 2009).

Drivers of Variation Between Sites

We found strong relationships between the number of flowering stems and the vegetation structure of the sites. Herbaceous cover had a negative effect on flowering stem count once it exceeded 80% cover (edf= 2.0, F= 145.3, $p < 0.001$, Figure 4). This occurred at plots 98 and 77, which had average herb covers of 92% and 93%, respectively. Similarly, wiregrass cover had a negative effect on count once it exceeded 70% cover (edf= 2.0, F= 67.6, $p < 0.001$). Similar to herbaceous cover, plots 98 and 77 had the highest wiregrass cover of all five plots (91% and 79%, respectively). In contrast, sites with greater numbers of flowering stems were characterized by higher levels of shrub cover and richness. There was a positive effect on the number of flowering stems when shrub cover was between 15% and 45%. However, when shrub cover was below 15% there was a negative effect on flowering stem counts (edf= 1.9, F= 16.7, $p < 0.001$, Figure 4). Average shrub height below 0.5 m had a negative effect on flowering stem count, but this relationship was not significant (esf= 1.3, F= 1.3, p= 0.2). However, maximum shrub heights less than 0.6 m had a marginally significant negative effect on flowering stem count (esf= 1.3, F= 4.7, p= 0.04). Shrub richness had a linear negative effect on the number of flowering stems when the number of species per site was lower than four (edf= 1, F= 78.4, $p < 0.001$). Litter cover between 20% and 45% had a positive effect on flowering stem count (esf= 2.0, F= 90.6, $p < 0.001$, Figure 4). In addition, litter cover below 20% had a negative effect on flowering stem count (Figure 4). The absence of bare ground was negatively correlated with of flowering stems at the site level, but this relationship was only marginally significant (edf= 1.6, F= 2.7, p= 0.05). We found no significant effect of titi cover (edf= 1, F= 2.2, p= 0.1), height (edf= 1.5, F= 3.1, p= 0.1), or maximum titi height (edf= 1.6, F= 1.7, p= 0.3) on flowering stem counts.

Fire history was an important predictor of *M. alba* flowering stem counts (Figure 5). The average fire return interval was less than five years across all sites, ranging from 2.8 to 4.7 years. A fire return interval less than 3.5 years had a negative effect on flowering stem counts (edf= 2.0, F= 2.9, $p < 0.001$). Sites that were burned greater than four times since 2006 had a negative effect of flowering stem count (edf= 2.0, F= 2.9, $p < 0.001$). Similarly, flowering stem count was negatively affected if the time since last burn was less than one year (edf= 2.0, F= 37.4, $p < 0.001$). The proportion of burns that occurred during the growing season had a positive effect on flowering stem counts when it was less than 50% (edf= 2.0, F= 16.8, $p < 0.001$). Sites that were burned more frequently had less shrub cover (edf= 1.4, F= 9.6, p= 0.003), lower average shrub heights (edf= 1, F= 11.7, p= 0.001), lower maximum shrub heights (edf= 1.8, F=23.0, $p < 0.001$), and lower litter cover (edf= 2.0, F= 2.0, $p < 0.001$).

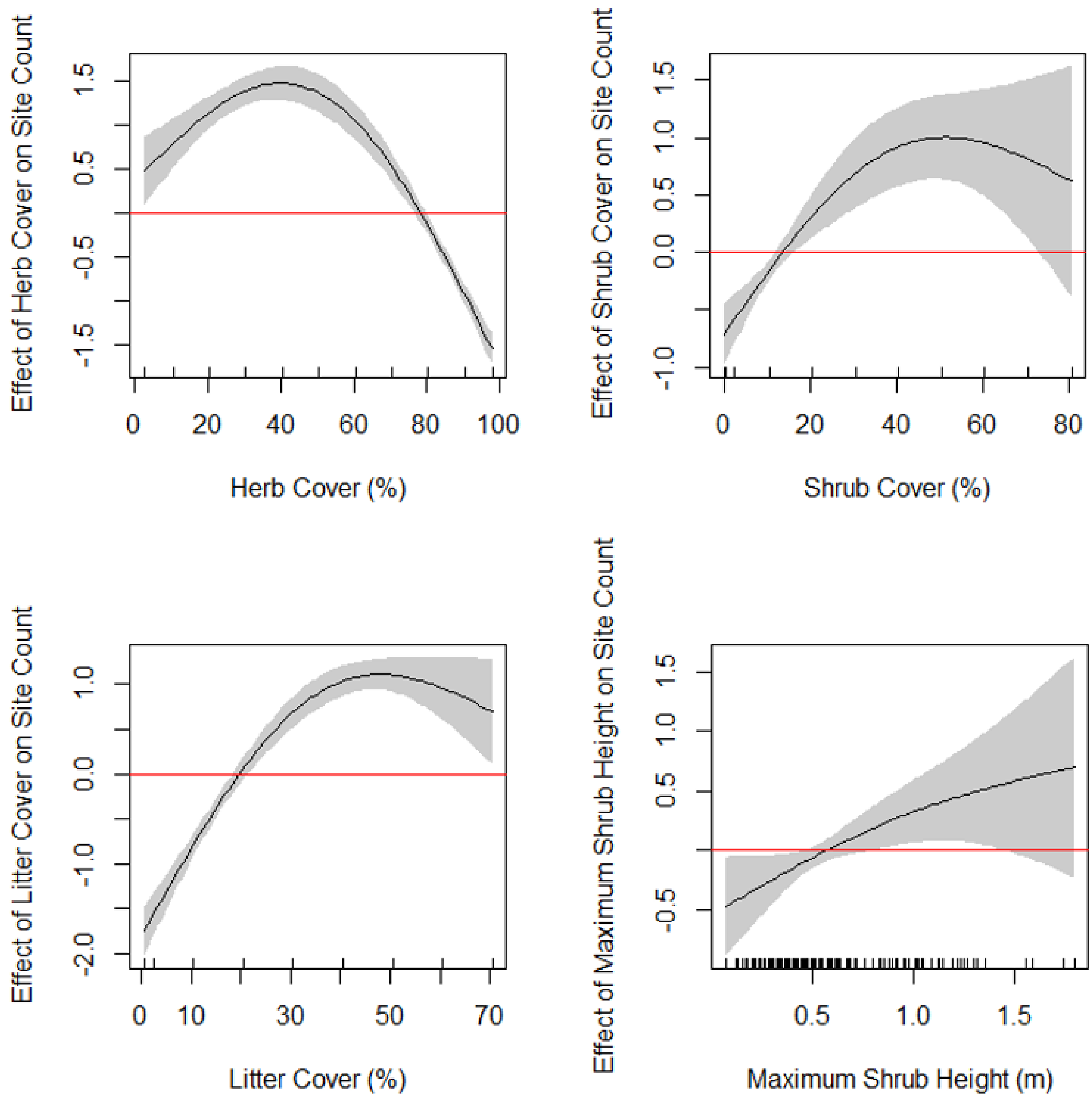

Figure 4. The effect of structure on the number of flowering Macbridea alba stems at each site. The curve above the red line represents the values of the parameter that have a positive effect on flowering stem count, and the curve below the line represents the values of the parameter that have a negative effect on flowering stem count.

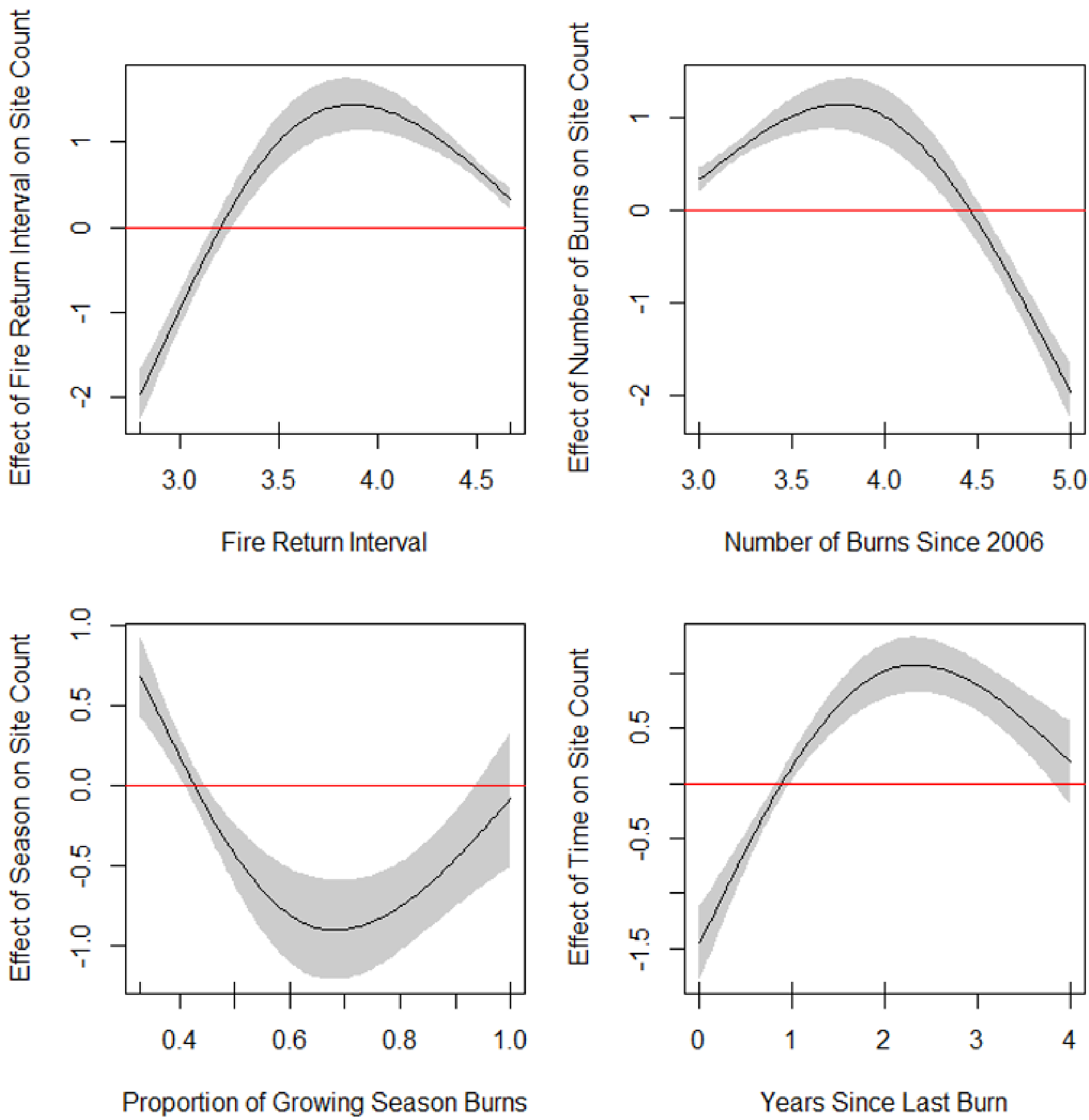

Figure 5. The effect of fire history on the number of flowering Macbridea alba stems at each site. The curve above the red line represents the values of the parameter that have a positive effect on flowering stem count, and the curve below the line represents the values of the parameter that have a negative effect on flowering stem count.

Discussion

Fire plays an important role in shaping pine ecosystems in the Southeastern United States. Historically, fire is believed to have occurred in these ecosystems with relatively high frequency and primarily during the growing season (Huffman et al. 2006). Today, fire prescription regimes generally adhere to these patterns (Keane et al. 2009). The accepted recommended fire return interval for pine flatwoods varies across sources, but is generally considered to be two to four years (Heyward 1939; Garren 1943; FNAI 2010). Though there is much debate, many believe frequent growing season burning is superior to dormant season burning for flowering plant species in the coastal plain (Glitzenstein et al. 2003; Lemon 1949; Meyers 1990; Platt et al. 1998). In fact, most of the available, but limited, research suggests that herbaceous species generally benefit from shorter fire return intervals. However, the exact needs of many species are unknown and it is likely that some species prefer the latter part of the typical return interval or longer.

Current research regarding *M. alba* management suggests that prescribed fire be applied at least every four years to maintain the preferred habitat, but provides no empirical evidence to support this claim (Schulze et al. 2002). Likewise, the 2009 U.S Fish and Wildlife 5-yr review suggests the ideal fire return interval be four to five years, but no citation supporting this claim is provided in the text. Here, we provide empirical support for these recommendations based on multiple structural and fire history metrics. *M. alba* may prefer fewer growing season burns than is typical of some graminoids in pine flatwoods, such as the well-studied wiregrass. A longer fire return interval was strongly associated with shrub cover, litter cover, and the number of flowering stems at a site. The data for these 5 sites suggest that a fire return interval of around 4 years is optimal and a fire return interval of less than 3.5 or greater than 4 years may be detrimental to *M. alba.* A number of plausible mechanisms exist which may explain this dynamic. Shrubs may provide refugia from fire or other environmental stressors (e.g. solar radiation) by creating an important microclimate for germination, water retention, or nutrient composition (Jankju 2013). Frequent fire may negatively affect recruitment success of *M. alba* or cause a net deficit in carbohydrate cycling. However, identifying the mechanism would require extensive additional research.

We also found that the proportion of burns applied during the growing season affected flowering stem counts. Increasing growing season burning is generally considered the ideal fire regime to benefit flowering herbs and limit shrub growth. We found that flowering stem count decreased when more than half of burns were applied during the growing season. The data suggest that a mix of growing and dormant season burns may be important for *M. alba*. The relationships between fire history and flowering plant counts warrant further investigation, but to our knowledge provide the best available information about *M. alba* habitat structure and the effects of fire history.

In our study, we represented the number of flowering stems in each plot using a rank. However, we also investigated the effect of structure on *M. alba* flowering stem counts and *M. alba* presence (frequency). We found similar patterns of vegetation structure driving count and presence, but rank had a stronger effect than either of the other flowering stem indices. These patterns indicate that the effect of structure greatest was at the site level, rather than the quadrat level. The long-term monitoring sites in this study are spread across most of the known populations of *M. alba* in ANF (Figure 1), and likely represent a comprehensive assessment of the known habitat. Even so, we recommend an additional site or sites be placed in the northern cluster of populations to sample the full extent of this species in ANF.

Compartment 77 is of particular interest in our study, as it has the fewest number of plants and plant counts have declined relatively drastically since 2015 (Figure 2). Compartment 77 had the shortest fire return interval relative to the other compartments and a high proportion of growing season burns. Long-term monitoring was performed in this site from 1996 to 2012 by the USFS (but in a smaller plot of 50 x 25 feet) and showed similarly low counts. In this plot, 47 plants were counted in 1996 but in 2000-2012 no count was recorded above 26 plants. As one might expect based on the fire frequency and season of burn, Compartment 77 has highest mean herb cover of 93.1% while the plot with the most plants has 50% herb cover. Compartment 77 also has the lowest shrub cover of all the compartments (7%) and while the site with the most plants had about four times as much shrub cover. Further, Compartment 77, along with compartments 98 and 110, are the wettest of the monitoring plots and the plots with the lowest flowering stem counts. Additional sites in these compartments that sit in the drier end of the habitat spectrum may help to answer questions about why these plots have lower *M. alba* counts. Compartment 77 is frequently burned, especially in recent years, due to the presence of frosted flatwoods salamander (*Ambystoma cingulatum*) ponds. It is possible that frequent burning in growing season conditions have expanded the wet prairie overtime and this long-term plot is no longer ideally situated in the ecotone, which may explain the reduction in count over time. Despite the potential impacts to *M. alba*, an aggressive burning regime to this area may still be warranted given their critically declining status. However, we encourage studies to assess the effectiveness of the current burning regime for *A. cingulatum*, as documentation of the effectiveness of managing their habitat through fire and its surrogates has been limited (Gorman et. al 2013).

This work to characterize *M. alba* habitat and understand the drivers of flowering stem count demonstrates the importance of studies investigating important habitat structure thresholds and determining the ideal conditions for rare and threatened species. The information gathered through these studies are designed to help shape management and create dynamic recommendations that can aid in the adaptive management cycle. We recommend further and extended monitoring of all federally listed plant species, including *M. alba*, using the methodology presented here. Data collected using this methodology, which is relatively inexpensive and efficient, can elucidate habitat requirements and inform management decisions of the rare plants in ANF.

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