Insect Herbivory Following Fire on Lyonia fruticosa, an Ericaceous Shrub of Florida Scrub

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Abstract

The influential role of fire in shaping Florida scrub vegetation is well documented; however, relatively less is known about the role of fire on trophic interactions such as those between plants and herbivores. Here we examined the response of insect herbivory to time-since-fire and succession on *Lyonia fruticosa* (Michx.) G.S. Torr. (Ericaceae), a shrub found in scrub of south-central Florida. We measured herbivory on > 200 plants across a time-since-fire gradient of 7 sites (ranging from 0.6–8.7 yr) by (1) surveying recently flushed leaves for 3 mo to control for leaf age, and (2) surveying herbivory across whole plants irrespective of leaf age. We also recorded damage types (chewing, scraping, and mining) to determine how herbivore guilds were affected by time-since-fire. Using generalized additive models, we found herbivory increased for 5 to 6 yr post-fire with 59.8% of the deviance explained by time-since-fire in flushed leaf surveys and 76.6% in whole plant surveys. Chewing was the dominant damage type and increased for 5 yr post-fire. Scraping and mining damage were less frequent and unaffected by time-since-fire within the range studied. Additionally, we modeled the post-fire responses of *L. fruticosa* traits (height, stems, flowering, and leaf area), and found that most changes in growth and reproduction occurred within the first 4 to 6 yr post-fire. Herbivory levels increased as plants recovered and peaked in yr 5 and 6 post-fire indicating insect herbivores, like the plants, are well adapted to the dynamic, pyrogenic landscape.

Key Words: arthropod; plant damage; recovery; disturbance; generalized additive models

Resumen

El efecto influyente del fuego sobre la formación de la vegetación de matorral de la Florida está bien documentado; sin embargo, se sabe relativamente poco sobre el papel del fuego en las interacciones tróficas, como las que se dan entre plantas y herbívoros. Aquí, examinamos la respuesta de herbivoría de los insectos al tiempo transcurrido desde el incendio y la sucesión en *Lyonia fruticosa* (Michx.) G.S. Torr. (Ericaceae), un arbusto ericáceo que se encuentra en los matorrales del centro-sur de la Florida. Medimos la herbivoría en > 200 plantas a lo largo de un gradiente de tiempo desde el incendio de 7 sitios (que van de 0,6 a 8,7 años) mediante (1) el estudio de las hojas recientemente enrojecidas durante 3 meses para controlar la edad de las hojas, y (2) el estudio de la herbivoría en todo el territorio. plantas enteras independientemente de la edad de la hoja. También registramos los tipos de daño (masticación, raspado y minería) para determinar si los grupos de herbívoros se vieron afectados por el tiempo transcurrido desde el incendio. Usando modelos aditivos generalizados, encontramos que la herbivoría aumentó durante 5 a 6 años después del incendio con un 59,8 % de la desviación explicada por el tiempo transcurrido desde el incendio en estudios de hojas enrojecidas y un 76,6 % en estudios de toda la planta. La masticación fue el tipo de daño dominante y aumentó durante 5 años después del incendio. Los daños por raspado y minería fueron menos frecuentes y no se vieron afectados por el tiempo transcurrido desde el incendio dentro del rango estudiado. Además, modelamos las respuestas posteriores al incendio de los rasgos de *L. fruticosa* (altura, tallos, floración y área foliar) y descubrimos que ocurrieron cambios en el crecimiento y la reproducción dentro de los primeros 4 a 6 años posteriores al incendio. Los niveles de herbivoría aumentaron a medida que las plantas se recuperaron y alcanzaron su punto máximo en los años 5 y 6 posteriores al incendio, lo que indica que los insectos herbívoros, como las plantas, están bien adaptados a la dinamica pirogénica del territorio.

Palabras Clave: artrópodo; daños a las plantas; recuperación; disturbio; modelos aditivos generalizados

Florida scrub is a pyrogenic ecosystem that relies on fire to periodically reshape and maintain the ecological communities (Menges 2007). Fire restructures vegetation by burning and top-killing dominant aboveground vegetation, initiating resprouting of dominant shrubs, stimulating the seed bank, altering resource availability, and changing the belowground microbial community (Menges 2007; Revillini et al. 2022). Although the influential role of fire in shaping Florida scrub vegetation is well documented (Menges & Kohfeldt 1995; Maguire & Menges 2011), relatively less is known about the role of fire on trophic interactions such as those between plants and herbivores. In Florida scrub, few studies have investigated herbivore establishment, community assembly, and herbivory with succession and time-since-fire, and such research is critical towards understanding how fire mediates trophic interactions for habitat management. Insect recovery time and the effects of time-since-fire on insect populations and their feeding damage are important considerations for habitat management through prescribed burns.

Fire has both direct and indirect effects on herbivore species. Fire can directly kill herbivores and surviving individuals can die off immediately after fire from changes in exposure and starvation due to lack of plant host tissue (Swengel 2001). Additionally, fires burn insect habitat, altering refuges and resource availability (Swengel 2001); yet,

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the indirect effects of fire on herbivore species populations and their feeding behavior may be just as numerous, but more subtle and potentially long-lasting. For example, fire alters habitat and vegetation structure changing acoustics benefiting some species (e.g., ease of locating mates for prairie mole crickets, Howard & Hill 2007). In Florida scrub, fire can indirectly affect herbivore communities through changes to habitat structure (Kim & Holt 2012) and host plant architecture or available material (Cronin et al. 2020). Additionally, fire indirectly affects resource availability and plant growth, which can affect host plant quality. For example, in Florida scrub, fire temporarily decreases foliar nitrogen and phosphorus, while temporarily increasing the foliar nitrogen to phosphorus ratio (Schafer & Mack 2014) and increasing soil moisture (Weekley et al. 2007). Furthermore, post-fire leaf production can increase, and leaves can be produced for a longer season (Lopes & Vasconcelos 2011), but the quality of new tissues can be affected by post-fire stress (Alves-Silva & Del-Claro 2013). Finally, fire indirectly can affect mechanical and chemical defenses of plants such as by temporarily decreasing leaf toughness (Kim & Holt 2012) and by increasing tannin (Wan et al. 2014) and resin defenses (Hood et al. 2015).

The pace of post-fire recolonization by herbivores will depend in part on the traits and life-history strategies of the individual herbivore species. Flighted, mobile species are likely to disperse more rapidly post-fire (Knight & Holt 2005; David et al. 2020), though some flighted species still may take years to recolonize (e.g., some cynipid gall-wasps in Florida scrub, Cronin et al. 2020). Additionally, dietary specialists recover slower than dietary generalists (García et al. 2016; Koltz et al. 2018; Bosc & Pauw 2020).

Here we investigated post-fire insect herbivory in Florida scrub using habitats that varied in their burn history. Using a time-since-fire gradient ranging from 0.6–8.7 yr, we quantified the herbivory of *Lyonia fruticosa* (Michx.) G.S. Torr. (Ericaceae) to address the following questions: (1) how does insect herbivory change with time-since-fire, and (2) do herbivore damage types (i.e., leaf chewing, scraping, and mining) vary with time-since-fire? These questions were asked to address the gap in our understanding of plant-herbivore interaction recovery after disturbance and to provide insight into how to manage Florida scrub for plants and insects with prescribed fires.

Materials and Methods

STUDY SITE

We conducted this study at Archbold Biological Station, located at the southern end of the Lake Wales Ridge in Venus, Highlands County, Florida. Archbold Biological Station encompasses 2,102 hectares of preserved Florida scrub that have been managed with prescribed burns since 1977 (Menges et al. 2017). The fire management plan at Archbold Biological Station results in a mosaic of prescribed burn size, fire return intervals, and patchiness to mimic that of the natural wildfire regime (Menges et al. 2017). The fire history variation across management units and fire history records allow for space-for-time studies of herbivory post-fire.

SITE SELECTION

Seven management units were selected across Archbold Biological Station with varying time-since-fire: 0.6, 0.7, 2.7, 3.7, 4.7, 6.8, and 8.7 yr since fire (Table 1). The most recent fires in all 7 management units were prescribed burns occurring during the wet season between the end of May and mid-Aug. Using geographic information system vegetation and fire history maps (Menges et al. 2017) combined with initial field surveys, a population of *L. fruticosa* was identified in each unit in scrub habitat where the last burn was of highest intensity (vegetation and ground litter consumed by fire). The density of *L. fruticosa* was relatively even among our selected populations. In these *L. fruticosa* populations, 75 × 10 m belt transects were laid parallel to fire lanes bordering the management units 35 m into the scrub from the lane edges. Thirty plants then were selected randomly within each of the 7 belt transects.

STUDY SPECIES

Lyonia fruticosa is a shrub found in scrub and scrubby flatwoods habitats, and is a long-lived perennial that is a fire-adapted resprouter (Menges & Kohfeldt 1995; Maguire & Menges 2011). It resprouts rapidly after fire and persists in areas long unburned. From preliminary field surveys, we found that *L. fruticosa* is host to many insect herbivores, which feed throughout the wet and dry seasons, including Orthoptera, Coleoptera, Hymenoptera, Hemiptera, and Lepidoptera. These factors permit *L. fruticosa* to be used as a model for changes in insect herbivory with time-since-fire.

STUDY DESIGN

Herbivory was measured by (1) surveying recently flushed leaves over a 3 mo period to control for leaf age, and (2) surveying across whole plants irrespective of leaf age. In leaf surveys, 3 newly flushed leaves were tagged on 1 branch tip per plant during the first wk of Dec 2020 (first cohort). A second cohort of an additional 3 leaves was added to a second branch tip after approximately 3 wk. In cases where the only new growth was on the first tagged branch, the second cohort of leaves was added to the original branch tip. If new growth was not present on the plant, the leaves were added to the next closest plant

Table 1. Archbold Biological Station Management (mgmt) units' fire histories and sample sizes of flushed leaf surveys. Time-since-fire is from burn date to the last survey date of flushed leaf surveys (5 Mar 2021), 2 wk prior to leaf harvesting in whole plant surveys. Columns of total plants, total leaves, and total leaves in cohorts 1 and 2 are the sample sizes used in analyses of flushed leaf surveys.

Archbold Biological Station Management Units						
Mgmt unit	Date burned	Time-since-fire (yr)	Total plants	Total leaves	# of leaves (Cohort 1)	# of leaves (Cohort 2)
60C	13 Aug 2020	0.56	30	169	87	82
54B	23 Jun 2020	0.70	27	132	79	53
55	19 Jun 2018	2.71	30	163	86	77
43B	29 Jun 2017	3.68	31	153	83	70
41A	11 Jul 2016	4.65	33	140	81	59
46	28 May 2014	6.78	31	158	86	72
47A	10 Jul 2012	8.66	35	155	81	74

still within the bounds of the transect. In total 180 leaves on 30 to 38 plants were tagged in each of the 7 management units with varying time-since-fire (Table 1).

The tagged flushed leaves were surveyed weekly and percent herbivory was estimated visually for each leaf. Percent herbivory was scored 0 to 100% (0, 0.5, 1.0, 2.5, and continuing at increments of 2.5 to 100%). If herbivory was ≥ 90%, we stopped surveying the leaf in subsequent surveys because the remaining portion of the leaf usually dropped within 1 to 3 wk and additional herbivory was unlikely. Surveys were conducted for 85 d for the first cohort and 63 d for the second cohort, ending in the first wk of Mar 2021. Only the leaves surviving the entire survey period or leaves that had ≥ 90% herbivory were analyzed. While surveying for leaf damage, we observed herbivores feeding, which we identified to order in the field and, when possible, collected from neighboring *L. fruticosa* populations to rear to adulthood in the laboratory for identification to species or genus.

In whole plant surveys, samples of 60 leaves per tagged plant of the first cohort were harvested after the conclusion of the flushed leaf surveys in all 7 management units. A visual estimation of percent herbivory of each leaf was made using the same scoring as the flushed leaf surveys. We also recorded damage types (chewing, scraping, and mining). A mean of the sample of leaves was used to calculate an average percent herbivory of the whole plant.

Additionally, we measured a number of plant traits to quantify the growth and reproduction of *L. fruticosa* across post-fire environments. These traits were measured on the initial 30 plants in each unit used in flushed leaf surveys. In Jan 2021, we measured plant height and the number of stems. In Mar 2021, we recorded flowering (presence or absence) and measured leaf length and width for 5 randomly selected leaves per plant. Leaf area was calculated as the area of an ellipse: π × (length / 2) × (width / 2).

STATISTICAL ANALYSIS

To allow for non-linear effects of time-since-fire on insect herbivory, we constructed generalized additive models using the mgcv package version 1.8-38 (Wood 2004) in R version 4.1.2 (R Core Team 2021). The response variables of percent herbivory, number of leaves damaged, and number of leaves damaged by type (chewing, scraping, mining) were first averaged across sampled leaves of a plant, then averaged across the management unit to avoid pseudoreplication within units. Following preliminary analyses, generalized additive models were fit using 3 knots. We also constructed similar 3-knot generalized additive models investigating the response of *L. fruticosa* to time-since-fire using the response variables height, number of stems, proportion of plants flowering, and leaf area. Height and number of stems were first averaged across the management unit, and leaf area was averaged by plant then by management unit. Generalized additive models were evaluated based on Akaike information criteria (an estimator of prediction error and thereby relative quality of statistical models for a given set of data). We report the generalized additive model percent deviance explained, which is the proportion of the null deviance explained by the model: $(1 - (\text{Dev}_{\text{Model}} / \text{Dev}_{\text{Null}})) \times 100$.

Results

We observed insects from the orders Orthoptera, Coleoptera, Hymenoptera, Hemiptera, and Lepidoptera feeding on *L. fruticosa* during our weekly surveys. The most abundant observed herbivores were *Floritettix nigropicta* (Hebard) (Orthoptera: Acrididae), a species of Pyralidae (Lepidoptera), *Nemoria catachloa* (Hulst) (Lepidoptera: Geo-

metridae), Cryptocephalinae (Coleoptera: Chrysomelidae), and leaf miners (Lepidoptera). The Pyralid sp. was exclusively observed feeding on the youngest leaves at branch tips, and *N. catachloa* also was most frequently observed feeding on such leaves. All other taxa observed fed on both young and old tissue. Leaf chewing (41.9% leaves damaged) was the dominant damage type, followed by scraping (2.9%) and mining damage (0.5%). Chewing herbivores were primarily *N. catachloa* and Orthoptera including *F. nigropicta.* Pyralid larvae and Cryptocephalinae larvae scraped the leaves. Lastly, leaf mining was likely caused by at least 2 species of Lepidoptera as we observed both leaf miner tunneling and blotching.

Herbivory on our flushed leaves after 3 mo averaged 14.8% ± 1.0% with 34.6% of leaves exhibiting damage. Percent herbivory increased for 5 yr post-fire and peaked at about 23% (59.8% of deviance explained). After peaking, herbivory decreased by about 1.5% per yr post-fire. Time-since-fire did not affect the proportion of leaves damaged within the range of time-since-fire studied (0.6–8.7 yr). Across whole plants irrespective of leaf age, *L. fruticosa* leaves averaged 8.7% ± 0.16% herbivory, and 44.3% of leaves exhibited damage. On whole plants, we observed a strong effect of time-since-fire on herbivory with 76.6% of the deviance explained in our generalized additive model of percent herbivory with time-since-fire. Percent herbivory increased then peaked in the sixth yr post-fire (Fig. 1). Similarly, the proportion of leaves damaged increased for 5 yr post-fire and then decreased (78.2% deviance explained; Fig. 1). These results were primarily driven by chewing damage, which increased for 5 yr post-fire before declining (84.9% deviance explained). Scraping and mining damage were less frequent and were not explained by the range of time-since-fire (Fig. 2).

Lyonia fruticosa height, number of stems, flowering, and leaf area changed the most within the first 4 to 6 yr post-fire. Height (95.6% deviance explained) and flowering probability (73.2%) increased with time-since-fire, while leaf area (50.9%) and stems (85.2%) decreased (Fig. 3). Height continued to increase through time, but the annual growth rate decreased with time since fire. Stems decreased following high production post-fire, then began to plateau after 5 yr post-fire. Flowering was less frequent or delayed for the first 5 yr following fire. Lastly, leaf area was highest within yr 1 following fire, then decreased and plateaued with time-since-fire.

Discussion

Insect recovery post-fire is an important, yet often overlooked consideration for management of Florida scrub. In this study, we found that insect herbivory increased for 5 to 6 yr post-fire, suggesting that herbivore populations are establishing and growing during this time. After peaking in yr 5 or 6 post-fire, we found herbivory leveled off or slightly declined. A longer range of time-since-fire is necessary to determine if, after peaking, herbivory plateaus or declines in long unburned scrub.

The effects of time-since-fire on herbivory differed between the damage types: leaf chewing, scraping, and mining. Leaf chewing was the dominant damage type and drove the trend of total herbivory. Chewing damage increased during the first 5 yr then peaked. An effect of time-since-fire was not found on scraping and mining damage types suggesting scraping and mining herbivores likely recovered before 0.6 yr since fire and were then unaffected by time-since-fire within the range studied (0.6–8.7 yr). However, scraping and mining herbivory were observed less often and low sample sizes could have affected the results. It appears that these results agree with similar studies performed by Kim and Holt (2012) and Lopes and Vasconcelos

(A) **Herbivory**
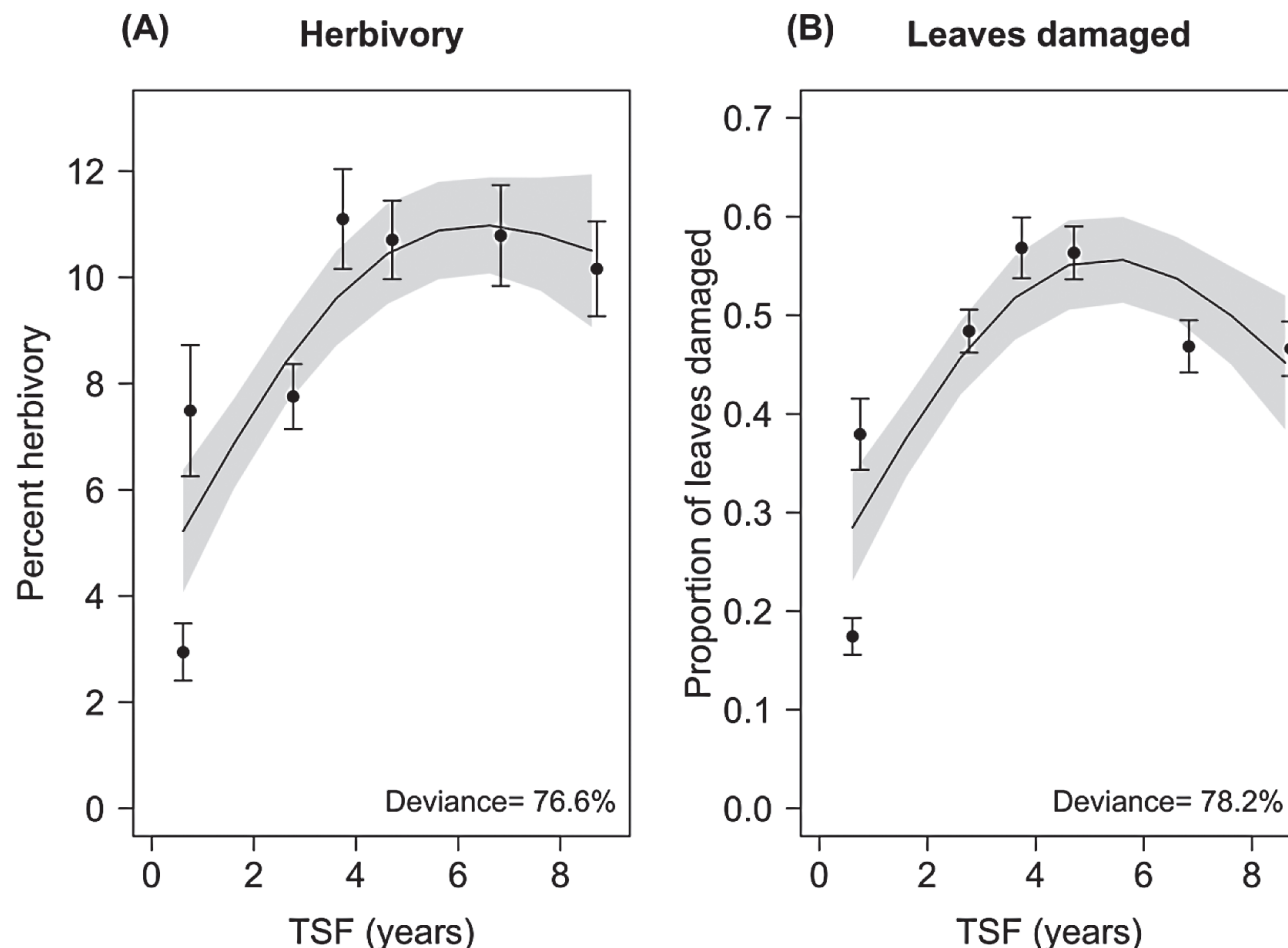
(B) **Leaves damaged**

Fig. 1. Time-since-fire and herbivory across whole plants. (A) Percent herbivory with time-since-fire; (B) proportion of leaves damaged with time-since-fire. For both panels, points show the mean ± 1 SE of plants within a management unit. Generalized additive models were fitted using the mean values (see text for details). Solid regression lines and the shaded areas show the predicted values with 1 SE.
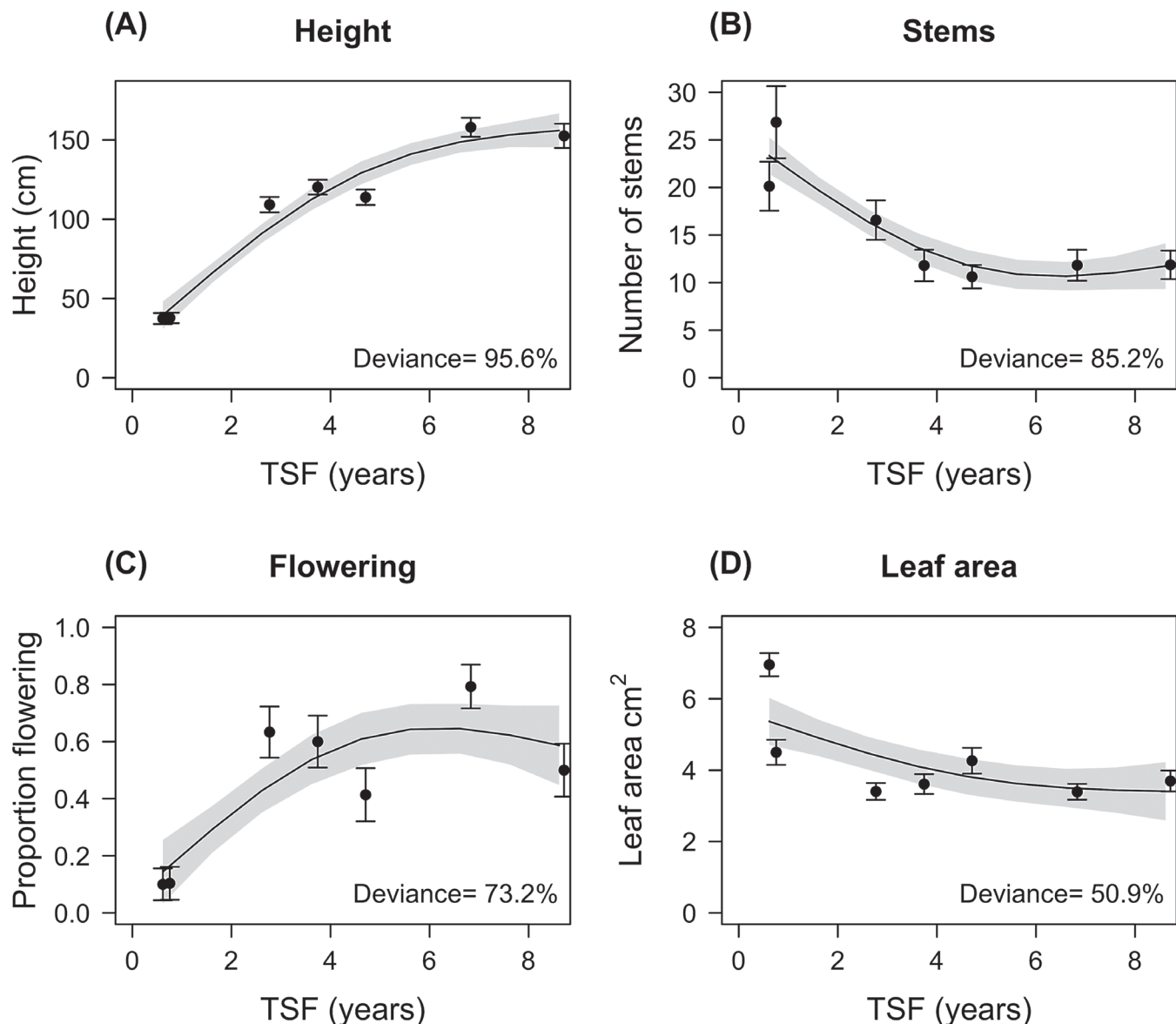
Herbivory by damage type
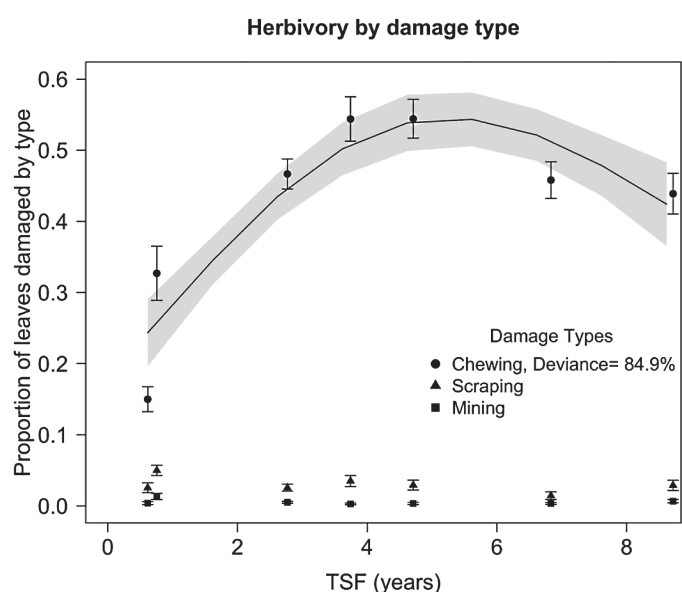
Fig. 2. Time-since-fire and herbivore damage by type across whole plants. Points show the mean ± 1 SE of plants within a management unit. Generalized additive models were fitted using the mean values for each management unit to avoid pseudoreplication. When significant, solid regression lines and the shaded areas show the predicted values with 1 SE.

(2011) that indicate herbivore communities and guilds can respond uniquely post-fire. Differences in dispersal ability, survival in post-fire habitat, and post-fire host plant quality may explain the variation in insect establishment after fire. For example, many species of Florida scrub leaf chewing grasshoppers are flightless (Deyrup 1989), which could delay their dispersal and colonization of post-fire habitat compared to flighted insects (Knight & Holt 2005). One such flightless species we often observed chewing leaves was *F. nigropicta*, which is likely slower to disperse than the Pyralid moth we observed. We found that the effects of time-since-fire varied across herbivore guilds, and future research on how and when insects establish post-fire is necessary for insect management in Florida scrub.

Our different sampling approaches yielded slightly different results. While we observed a clear increase in whole plant herbivory and proportion of damaged leaves with time-since-fire, on tagged flushed leaves we observed a moderate effect of time-since-fire on percent herbivory and no effect on the proportion of leaves damaged. The difference in the results and their strength between our survey methods could be a product of leaf age; however, we observed leaves senescing at the end of Mar and estimate that most *L. fruticosa* leaves are less than 1 yr old. Therefore, the strong effect of time-since-fire on herbivory across whole plants is more likely due to an increase in herbivore populations and feeding with time-since-fire than due to herbivore exposure time. The difference also could be explained by biasing

(A)
Height

(B)
Stems

(C)
Flowering

(D)
Leaf area

Fig. 3. *Lyonia fruticosa* traits with time-since-fire: (A) height, (B) number of stems, (C) proportion of plants flowering, and (D) leaf area. For all panels, points show the mean ± 1 SE of plants within a management unit. Generalized additive models were fitted using the mean values for each management unit to avoid pseudoreplication. Solid regression lines and the shaded areas show the predicted values with 1 SE.

herbivore damage in tagged flushed leaf surveys towards insects specializing on new tissue (e.g., Pyralid sp.) which may recover at different rates compared to herbivores feeding across entire plants including older tissues (e.g., *F. nigropicta*). Lastly, the smaller sample size of our tagged flushed leaf surveys also could be a contributing factor to the differences in the results.

The architecture and phenology of the recovering plants post-fire could play a role in shaping the resulting herbivory. Post-fire, *L. fruticosa* individuals were bushy, growing many short stems with large leaves with reduced or delayed flowering compared to individuals in long unburned habitat. As time-since-fire progressed, stems thinned, height growth continued, leaf area reduced, and the proportion of flowering plants increased. These changes in both architecture and reproductive stage or phenology of *L. fruticosa* may impact herbivore habitat and host plant quality potentially altering host plant selection and herbivore performance. Cronin et al. (2020) found time-since-fire

indirectly affects herbivores through changes to host plant architecture or available host plant material, and Kim and Holt (2012) found that time-since-fire indirectly influences herbivore communities through habitat structure. We found *L. fruticosa* traits (height, stems, flowering, and leaf area) changed the most within the first 4 to 6 yr post-fire, similar in timing to the response of herbivore damage. Thus, we find herbivore establishment takes place as *L. fruticosa* post-fire growth changes are still occurring. These findings indicate that herbivores may be well adapted to changes in habitat and host plants that occur with time-since-fire.

Reduced herbivory herbivory following fire after fire suggests fire provides temporary relief from herbivore pressure; however, it is possible that while herbivory is reduced, it could be more damaging on resprouting plants due to reduced aboveground biomass, fire damage, and stress from rapid regrowth. Further research should address the effects of herbivory on plant fitness post-fire for plant management.

It is vital that insects and other arthropods are considered in Florida scrub management. The preserved scrub at Archbold Biological Station alone is home to at least 1,112 species of Lepidoptera (Minno 1992), 102 ant species (Deyrup & Trager 1986), and 113 bee species (Deyrup et al. 2002). There are 46 arthropods known to be endemic to Florida scrub, and this number is expected to be only a fraction of the total endemics (Deyrup 1989). The post-fire establishment of insects is essential for ecosystem functioning as insects provide crucial services such as pollination and are a key component of trophic interactions. Post-fire, insects may be even more vital for trophic interactions as a source of food and nutrition for omnivores while vegetative sources are limited (e.g., reduced acorn production post-fire; Abrahamson & Layne 2002). We found herbivory increased relatively quickly after fire, revealing insect herbivores, like the plants, are well adapted to the dynamic, pyrogenic landscape. Herbivory increased through the first 5 to 6 yr post-fire indicating that herbivores still were establishing during this time, and prescribed fire return intervals should be at least 5 yr apart to allow for insect recovery. However, insect guilds can respond uniquely and fire's effects on individual herbivore taxa and specialist insects in Florida scrub should be considered in future studies. Finally, herbivory should be studied across a longer range of time-since-fire to determine how long unburned scrub affects insects and trophic interactions.

Acknowledgments

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