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ABSTRACT

Fire frequency and severity have increased dramatically due to anthropogenic activity including historic fire suppression leading to fuel build-up. Investigating the influence of fire and fire-related characteristics (frequency, severity, spread, etc.) on organisms and their ecosystem services is therefore of high importance. This work is especially pertinent for arthropods, which constitute a large portion of global diversity and offer important ecosystem services, including pollination. Existing literature has demonstrated the susceptibility of many Lepidoptera to fire, but this has been variable across studies, underscoring the need to consider how fire-related variables impact survival. In addition, there continues to be a global decline of nocturnal moths, which are important but understudied floral visitors. I investigated the community structure and pollen transport networks of nocturnal moths along a time-since-fire gradient within the endangered rosemary balds of central Florida. I observed a decrease in moth abundance at sites burned one year ago, which contributed to communities being distinct from those from sites burned two years ago or left unburned. Declines in abundance had cascading effects on moth pollen transport networks as the number of pollen-transporting moths was smaller at sites burned one year ago. Yet, networks from burned sites were more complex and the proportion of moths transporting pollen remained constant across the gradient of time-since-fire. Overall, moth communities had extremely quick recovery times with all calculated diversity indices returning to pre-fire conditions after just two years. This relatively quick rebound in community structure might provide these fire-vulnerable organisms the chance to re-establish in between ever-increasing fire events.

**Cascading effect of recent fires on moth abundance alters pollen transport networks in
rosemary bald habitats**

by

Karma Kashmir
B.S., Weber State University, 2019

Thesis

Submitted in partial fulfillment of the requirements for the degree of
Master of Science in Biology.

Syracuse University

June 2023

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ACKNOWLEDGEMENTS

I want to take the time to thank numerous parties and people that my functioning and success has been dependent on throughout my time in graduate school. First, I need to thank all members of my committee who have helped me develop my research goals and this project. Namely, my advisor Dr. David Althoff, who has been patient and accommodating to my evolving beliefs, interests, and goals. I consider myself extremely lucky to have ended up with an advisor that has been so supportive in ways I would not have known would matter at the beginning of my graduate career. I would also like to thank Dr. Kari Segraves, who has been an epitome of excellence in academia. You have been instrumental to my understanding of what it takes to be a successful and respected scientist, and I have valued observing the hard work and dedication you apply to your own research as well as the research of your graduate students and collaborators. To Dr. Estelí Jiménez-Soto, I want to thank you for all the time you have given me, as I know this resource is especially limited for you. Developing our workshop proposal and receiving your advice and guidance was such a positive experience for me. Understanding your perspective on agroecology and the integration of socio-economic issues into traditional ecological research has provided clarity for so many of my own interests. Lastly to my newest committee member, Dr. Christopher Fernandez, thank you for your newfound support and your willingness to come on board and provide your perspective on my research. I'm excited to have you here, and I look forward to learning from your illustrious experience with ecological networks and interactions.

I would also like to thank many of my undergraduate professors at Weber State University. As a first-generation college student, I owe so much of my success to my undergraduate institution, which serves its community by providing accessible and hands-on education to non-traditional students. So many people have worked in collaboration with WSU to get me to where

I am today. First, I must thank my friend, Anja Wutz, who enrolled me in my first semester of classes. I also need to thank all the professors that I had, who have each left lasting impressions on me. In particular, thanks to Dr. Jonathan Marshall, who encouraged my involvement with academic outreach through the organization MAS (Multicultural Advancement in STEM) and helped me pursue numerous academic scholarships which *truly* got me through my education. To Dr. Ronald Meyers, who provided my foundation in undergraduate research—my time with you was invaluable to my transition into graduate school, thank you for opportunities. Lastly, to Dr. John Mull. The continued support and resources that you have given to me and so many WSU Zoology alumni is simply unsurpassable. Thank you so much for bringing me into the world of plant-insect interactions, I can't imagine where I would be without joining in your research. I have so appreciated having you in my corner.

For my friends and family, I will keep things short in hopes that you already know how much I appreciate you all for sticking by me throughout this chapter of my life. To my lab mates Thomas and Gwen—thank you for everything. Thank you, Anne, I don't know where I would be without your vast knowledge, experience, and willingness to help. Thanks to Anna and Haven, who have remained solid and dear friendships from afar. Thank you, Skylar, my partner in crime and life. While I probably could have done this without you, it would have been immeasurably more difficult and a whole lot less fun. You have been there to support me in every way I could have needed you, and our relationship has been my favorite mutualism. To my mom, my Aunt Rose, and Shoko, thank you for being my tiny family. A special thanks to my mom for the sacrifices you have made to support and enrich my life from the very beginning. To Rose, for consistently being family and friend throughout our lives. We started our journeys of advanced education so close to the same time, and we have finally reached the end.

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Cascading effect of recent fires on moth abundance alters pollen transport networks in rosemary bald habitats

(formatted for submission to *Ecological Entomology*)

Introduction

Anthropogenic activity and climate change have increased the frequency and severity of wildfires (Abatzoglou and Williams, 2016), resulting in major impacts on the environment, species diversity, and various ecosystem services, including pollination (Potts et al., 2003; Moretti et al., 2006). The positive feedback loop between increased CO₂, climate change, and fire frequency alters natural fire return intervals and intensities (Liu et al., 2019). These changes can have devastating effects on the abundance and species richness of pollinators, yet this response is taxon specific. For birds and beetles, the effect of fire on overall abundance can be neutral, or the effect can even be positive, as is true for some species of flies and bees (Carbone et al., 2019). Such positive effects support the “pyrodiversity begets biodiversity” hypothesis which predicts species diversity to increase after fire due to variation in fire regime (fire return interval, intensity, and other fire characteristics) that generates a mosaic of habitats and niches for diverse species to establish within (Martin and Sapsis, 1992; He et al., 2019). Support for this hypothesis, however, has not been observed in Lepidoptera. In response to wildfires, species richness of moths and butterflies may decline, and abundance is significantly reduced. These negative impacts are exacerbated as fire return intervals are shortened, and the ability for pollinator populations to recover is predicted to deteriorate (Carbone et al., 2019). This erodes population resilience and will likely have negative cascading effects on the pollination interactions of these floral visitors. This remains largely untested, however, particularly for nocturnal Lepidopteran pollinator species.

Lepidopterans, of which moths account for over 85% (Shields, 1989), are the most diverse pollinator group with more than 140,000 species of floral visitors that are eligible pollen transporters (Krenn, 2010; Wardhaugh, 2015; Walton, 2020). In addition to being speciose, moths can be highly abundant, which makes them potentially important pollinators due to their numbers. To date, very few studies have focused on examining the effect of nocturnal moths on plant reproduction and pollen flow in natural or agricultural systems (Atwater 2013; Macgregor et al., 2014; Hahn and Brühl, 2016; Banza et al., 2019; Walton, 2020). Recent work suggests that moths are important pollinators in many natural ecosystems, like Mediterranean meadows and Florida sandhills (Atwater 2013; Banza et al., 2015). They also benefit agro-ecosystems through direct pollination of economically important crops (Lu et al., 2021; Robertson et al., 2021) and “spill-over effect”, i.e., by helping to sustain neighboring wildflower populations, which in turn recruit other crop relevant pollinators (Hahn and Brühl, 2016; Walton, 2020). Additionally, moths are able to successfully pollinate flowers with diverse floral morphologies, and therefore are present in the majority of described pollination networks that include nocturnal visitors (Kashmir, unpublished data). In direct comparisons, nocturnal moth networks are at least as species rich and have similar or greater numbers of linkages as diurnal networks (Walton, 2020). Therefore, the ecological contribution of nocturnal moth pollinators towards overall pollination network stability is likely high.

We are only just beginning to understand the effects of fire on moth pollination networks and interactions. For example, Banza et al. (2019) demonstrated that fire in a montane shrubland ecosystem in Portugal impacts moths and their pollination interactions. Floral abundance increased post-burn, yet moth abundance was lower at burned areas, even though the fire event was eight months prior to sampling. The overall pollen transport by moths was significantly

higher in areas not impacted by fire where flowers were less abundant. Proxies for moth pollen-transport network tolerance to extinctions, linkage density and robustness, were reduced at burned sites. However, unique plant-moth interactions were detected at burned sites in comparison to unburned sites, suggesting that fire may drive context dependency of mutualistic interactions. Results from this study support the suggestion that the negative impacts of fire on moth communities will erode moth-plant pollination interactions, but there are relatively few studies, in general, from which to draw general patterns of the effect of fire on nocturnal moth communities and their interactions with plants.

Here, I test how fires in Florida rosemary bald habitats (henceforth rosemary balds) can influence nocturnal moth communities and pollen-transport networks. Rosemary balds are geographically restricted habitats and host to endangered, endemic plants that occur along the Lake Wales ridge which extends down the center of the Florida peninsula (Abrahamson et al., 1984; Christman and Judd, 1990). These plant communities are relatively numerous at the Archbold Biological Station (ABS), which maintains a well-documented, long-term history of prescribed burns and documentation of fire-related variables. The pollination biology of many of the plants that occur in rosemary balds has not been described and this study has the potential to reveal the role of moth pollination in general for this community. Previous work examining moth pollination in nearby sandhill habitats documented moths visiting and transporting the pollen of 14 species that are commonly found throughout ABS (Atwater, 2013). A separate study comparing the contributions of nocturnal and diurnal pollinators to fruit set of *Lyonia lucida* found that moths were the primary pollinators of this plant (Benning, 2015). Further, there are 1,040 moth species found at ABS, and a literature search for each moth genus demonstrated that 4-14% of these species have been reported to be pollinators (Kashmir, unpublished data). Thus,

moths have the potential to be important pollinators in rosemary bald communities. Yet, their role as pollinators is possibly influenced by the fire regime associated within this habitat.

The structure of rosemary balds are altered greatly by fire for two major reasons. First, rosemary balds are adapted to relatively long fire-return intervals, suggesting there is a long period of re-establishment required for the community to return to pre-fire structure. Second, the most abundant plant species, Florida rosemary (*Ceratiola ericoides*), is fire-intolerant and has been suggested to alter the presence and abundance of neighboring plants through allelopathy. Therefore, fire has a strong probability of altering pollination interactions in rosemary balds.

Here, I generate and compare pollen transport networks of nocturnal moths at sites across a time-since-fire gradient. There are many fire-related variables that help describe fires and their ecological impacts such as time-since-fire, fire return interval, fire intensity, and severity. These factors can help explain and predict the differential effects of fire across studies and habitats (Mason et al 2021). For this study, I focused on the time-since-fire to evaluate moth community and pollen transport recovery after disturbance. This is helpful for predicting the impact of shortened fire-return intervals and how quickly moth pollination networks might recover after fire. I addressed the following questions: 1) how does time-since-fire impact moth community structure and re-establishment, 2) how does time-since-fire impact the proportion of moths transporting pollen, and 3) how does time-since-fire alter moth pollen transport networks?

Methods

Study system

This study was conducted in rosemary bald habitats at Archbold Biological Station (ABS) in central Florida (Venus, FL, USA). This distinctive plant community hosts a large number of endemic and threatened plants, although it is dominated by Florida rosemary (*Ceratiola*

ericoides). In addition to the presence of *C. ericoides*, rosemary balds are characterized by open, white sand knolls that are continuous in large patches. Within the rosemary balds, I conducted fieldwork in June 2022 at 9 sites which were sampled for moths once weekly for four weeks. These sites were selected based on their fire regime history and geographic distribution. Specifically, I selected three sites for each time-since-fire (TSF) treatment level as far apart as possible (>0.18 km). These TSF levels were TSF 1 year, TSF 2 years, and TSF 21+ years, or “unburned”. The unburned sites had not experienced a fire event since 2001-1991. As *C. ericoides* are fire-intolerant and thus obligate post-fire seeders (Abrahamson, 1984), they are posited to favor a fire return interval of 40 years according to modeling studies conducted in California (Malanson, 1985). Therefore, the historical fire return interval for the maintenance of rosemary balds is 20-60 years (Menges et al., 1993; Richardson and Hall, 2013). This makes these unburned sites adequate controls representing preserved rosemary balds.

Moth community structure

To determine moth community structure, moths were collected using Heath-style light traps (Heath, 1965), which were placed at the center of each site. These traps were baited with 36 LED lightbulbs coiled around 6-in long PVC pipe cylinders and were powered by 12 V batteries. The wavelength of the bulbs was 420-430 nm which is optimal for the attraction of moth species capable of long-distance flight (Macgregor et al., 2018). The traps were lit from sunset to sunrise. After each sampling event, individual moths were retained in separate vials and stored in a freezer to prevent pollen contamination among individual moths and to allow for future pollen analysis. Using the insect collection at ABS and local field guides, I identified moths to the lowest possible taxonomic level.

Floral abundance

To determine floral abundance at each site, I established four 15-m transects running in each ordinal direction at the center of every site where the traps were placed. Within 0.5-m on either side of the transect, the number of flowers per plant species was recorded to yield flower density as the number of flowers/60-m² for each species. I then identified all currently flowering plant species using field guides and the herbaria specimens available at ABS. Pollen samples were taken non-invasively from these flowers using fuchsin jelly which was later fixed on microscope slides to add to the existing pollen reference library at ABS. Samples were collected opportunistically for flowers blooming in neighboring habitats outside of the rosemary balds to allow for identification of potentially long-distance floral interactions.

Identifying moth-plant interactions via pollen identification

To identify moth-plant interactions using the moths I collected, I took pollen samples of most moth specimen. This was done by swabbing the mouthparts and abdomen with an insect pin dipped in fuchsin jelly (Beattie, 1971) that was then spread and fixed on a microscope slide. When possible, the proboscis was uncoiled and swabbed thoroughly. Pollen samples were not taken when moths were missing many of their abdominal scales as it was unlikely that any pollen would remain attached. Additionally, due to the often-invasive process of pollen swabbing, pollen samples were only taken from moths that were destined for specimen pinning and when they were large enough to remain intact after swabbing. Due to the high abundance of some species, pollen samples were only taken from 15 individuals per species, per site, per sampling event. I then quantified the number and identity of pollen grains per slide by examining them under a compound light microscope at 400x magnification. Pollen was identified using pollen characteristics such as shape, apertures, number of furrows/spores, and other morphological

structures. These features were compared to the previously generated pollen reference library to identify the plant species that moths were visiting.

Pollen load and transport

To analyze the composition of moth pollen loads, I determined the average number of pollen grains that moths transported per plant species flowering in the rosemary bald sites. This was calculated by dividing the number of pollen grains of a given plant species by the number of moths that acted as pollen vectors for this plant. Average pollen loads were calculated for each plant species overall as well as at each TSF level to determine if time-since-fire alters the quality of floral visitation interactions.

Pollen transport networks

Using the moth-plant interactions identified from the collected moths and analyzed pollen grains, I generated pollen-transport networks for plant species flowering within rosemary balds at each TSF treatment level. Resulting networks were analyzed using network metrics to evaluate the influence of TSF on interactions. These include NODF nestedness, linkage density (which is network complexity; Montoya et al., 2006; Banza et al., 2019), Shannon's diversity (interaction diversity and richness; Walton, 2020), connectance (proportion of possible mutualistic interactions that are realized; Jordano et al., 2006), network level specialization (H2'), and links per species. NODF nestedness and connectance are positively associated with stability in mutualistic networks (Okuyama & Holland, 2008; Thebault & Fontaine, 2010), while linkage density is positively correlated to resilience to species loss (Dunne et al., 2002). Additionally, H2' evaluates how specialized/opportunistic species interactions are (Blüthgen et al., 2006).

Statistical testing

Moth community structure: To compare differences in moth communities across TSF levels, I calculated the following diversity metrics for all sites: species richness, abundance, Shannon diversity index, and Pielou's evenness. I calculated all metrics using base R "Bunny-Wunnies Freak Out" (Version 4.0.3). To evaluate the effect of TSF and sampling week on species richness and abundance, I used two separate generalized linear models (GLMs), both with poisson distributions and the log link function. Due to the established temporal variation associated with moth communities (Hahn and Brühl, 2016), time (week of moth sampling) was used as a fixed effect with TSF. Species richness and abundance were used as response variables. Differences in overall Shannon diversity index across TSF level were detected using paired t-tests while Pielou's evenness was evaluated simply by examining overlap in standard errors among TSF levels. Further community differences due to TSF were detected using Bray-Curtis dissimilarities in a nonmetric multidimensional scaling (NMDS) model with the R package vegan (Oksanen et al., 2020). To further evaluate the effect of TSF on species presence and to detect indicator species, I ran a point-biserial correlation coefficient analysis using the indicpecies package (De Caceres & Legendre, 2009) in R.

Pollen load and transport: To determine if TSF influenced the proportion of moths transporting pollen, I analyzed arcsine-transformed values using a two-way ANOVA with TSF and time (week of sampling) as fixed effects. I used two separate models, one using all collected pollen data, the other with just the pollen data from rosemary bald plants. These analyses were performed using the car package (Fox & Weisberg, 2019) in R.

Pollen transport networks: I constructed pollen transport networks using the bipartite package in R (Dormann et al., 2009). The effect of TSF on networks was determined by calculating the network-level metrics listed above (NODF, linkage density, Shannon's diversity, connectance,

H2', and links per species). Due to the impact that changes in network size have on network-level metrics, I calculated z-scores for each metric to allow for direct comparisons across TSF. This was done by first generating 500 null networks for each TSF network where the number of moth and plant species was conserved, but links (interactions) were randomized in each network. I then performed z-score calculations of each metric using the observed and respective null networks for each TSF level. To determine if observed network values were significantly different from their respective null values, z-scores were converted to p-values. These methods largely follow other work using null models to compare ecological networks (Dormann et. al, 2009; Dormann, 2022).

Results

Moth community structure

I collected a total of 1,530 moths across a minimum of 13 superfamilies, 28 families, 161 genera, and 292 species. Overall, superfamilies Pyraloidea and Tineoidea were dominant across TSF level and time, representing roughly 31-36% (Pyraloidea) and 21-25% (Tineoidea) of the total abundance (Figure 1). Only five species collected were previously identified as pollinators (*Samea multiplicalis*, *Spoladea recurvalis*, *Parachma ochracealis*, *Ufa rubedinella*, and *Idaea ostentaria*), and these species had a combined total of 32 individuals, which was 2.09% of the entire sampled community (Figure S1).

At the unburned (control) sites, species richness was 81.67 ± 4.81 (mean and SE) and abundance was 207 ± 44.54 (Table 1). One species, the geometer moth *Anavitrinella pampinaria*, occurred only at unburned sites and therefore had abundance values that varied significantly across TSF level according to the indicator species analysis ($P < 0.05$). This species has been found transporting pollen in the Ketona Dolomite Glades (LeCroy et al, 2013), but its

status as a reliable pollinator is not yet determined as most work focuses on their effect as agricultural pests of soy (Marston et al., 1983) and hops (Gargani et al., 2017). I detected additional differences in moth community structure when comparing the diversity values from unburned sites to those from the other two treatment levels.

I found significant differences in species richness across time ($F_{3,24} = 33.024$, $P < 0.05$), with richness generally increasing from week 1 to week 4 across all TSF levels. Time-since-fire, however, only had a marginal effect ($F_{2,24} = 18.190$, $P = 0.0735$) on species richness. When comparing across weeks, species richness varied in all contrasts ($P < 0.0004$ for 1-3 and 1-4; $P < 0.007$ for 2-3 and 2-4) except 1-2 and 3-4 ($P = 0.8230$ and 0.9999 respectively; Figure 2b). Similar patterns were detected for the effects of time and TSF on abundance, but both variables had a significant effect ($F_{3,24} = 152.989$, $P = 0.0037$; $F_{2,24} = 71.4$, $P < 0.05$, respectively). Abundance was significantly reduced at TSF-1 (recently burned) sites when compared to TSF-2 and unburned sites ($P < 0.0001$; Figure 3). Additionally, abundance varied among all weeks ($P < 0.0001$ for all contrasts but 2-4, where $P = 0.0017$) except when comparing weeks 1 and 2, where differences were marginal ($P = 0.0712$; Figure 3b).

Differences in abundance drove overall dissimilarity in moth community structure across TSF levels (NMDS model significance = 0.0432, ANOSIM statistic = 0.358). The NMDS detected grouping between moth communities at TSF-2 and unburned sites and a dissimilarity between these communities and those at TSF-1 sites (Figure 4).

Although there were significant differences in abundance, there were no differences in Shannon diversity index values across TSF levels. This was true when analyses were done using overall species counts across sites within each TSF level (unburned-TSF-1, $P = 0.1842$, $df = 873$; unburned-TSF-2, $P = 0.0971$, $df = 1157$; TSF-1-TSF-2, $P = 0.7826$, $df = 849$) and when I used

average species counts for each treatment (unburned-TSF-1, $P = 0.4774$, $df = 283$; unburned-TSF-2, $P = 0.3658$, $df = 385$; TSF-1-TSF-2, $P = 0.8831$, $df = 278$). There were, however, differences in evenness with moth communities at TSF-1 sites being more even than communities at the other TSF levels based on the non-overlapping SE of mean Pielou's evenness values (Table 1).

Floral abundance

Overall, the abundance of currently flowering plants was low both within the rosemary bald sites and in the broader landscape. The mean number of flowers/60m² (\pm SE) was 185 (\pm 96) at unburned sites, 61.33 (\pm 4.58) at TSF-2 sites, and 116 (\pm 115.5) at TSF-1 sites. Although the number of flowers/60m² was low, there was considerable range in sites within a TSF level, which resulted in overlap when comparing across TSF level (Table 2). Along the transects, only seven species of plants were in bloom. These species were Florida alicia (*Chapmannia floridana*), scrub palmetto (*Sabal etonia*), pineland scalypink (*Stipulicida setacea*), gopher apple (*Licania michauxii*), Atlantic St. John's wort (*Hypericum tenuifolium*), rusty lyonia (*Lyonia ferruginea*), and whitemouth dayflower (*Commelina erecta*). *C. floridana* and *S. etonia* are both Florida endemics, and *S. setacea* is endemic to the rosemary bald community (Abrahamson et al., 1984).

Pollen load and transport

I swabbed 1,143 moths, of which 363 (31.76%) were transporting pollen. This varied with time (week of sampling; $F_{3,24} = 21.11$, $P < 0.0001$; Figure 5b), but not across TSF level ($F_{2,24} = 2.21$, $P = 0.13$; Figure 5a). The proportion of moths with pollen was significantly higher the first week of sampling ($P < 0.0004$ when comparing weeks 1-2, 1-3, and 1-4). Proportions continued to

decline each progressive week, but differences were no longer significant when comparing weeks 2-3, 2-4, and 3-4 ($P = 0.20, 0.18, \text{ and } 0.99$ respectively). Weekly proportions ranged from 74-11% (unburned), 72-14% (TSF-2), and 85-28% (TSF-1). Across all weeks, however, moths were frequently transporting pollen of plants from outside the rosemary bald sites.

Once pollen transport data were isolated only to plant species found within rosemary bald sites, I found only 78 moths acted as pollen vectors across all TSF levels. This accounts for 21.49% of pollen bearing moths and just 6.79% of all moths that were swabbed for pollen. At unburned sites, there were 25 individuals, 15 individuals across TSF-1 sites, and 38 individuals across TSF-2 sites. Differences in the proportion of moths transporting pollen were significant across week (week of sampling; $F_{3,24} = 14.36, P < 0.0001$), but not TSF level ($F_{2,24} = 0.66, P = 0.53$). Weekly differences followed the same patterns of significance as seen above ($P < 0.0012$ when comparing weeks 1-2, 1-3, and 1-4; $P > 0.4$ when comparing weeks 2-3, 2-4, and 3-4). Despite the low number of individual moths acting as pollen vectors, 46 species of moths transported pollen grains of 6 out of 7 plant species that were blooming along the transects of rosemary bald sites.

Moth pollen loads across plant species were very low and did not change with TSF level for all but one plant species. *Lyonia ferruginea* pollen grains were not found on any moths transporting pollen within TSF-1 sites. However, *L. ferruginea* is also the species with the highest number of pollen grains, 22, found on one moth. This is also the species with the highest overall average pollen load of 3.59 grains per moth. When comparing average *L. ferruginea* pollen loads of moths from unburned and TSF-2 sites, however, values were very similar at 2.71 and 4 grains per moth respectively. All other plant species had overall average pollen loads of 1-1.28 grains per moth with little variation across TSF levels.

Moth-plant interactions based on pollen transport

I found 100 species of moths interacting with a minimum of 83 species of plants from within and beyond the rosemary bald sites. This seemed to vary across TSF levels, as there were 45 species of pollen vectors for 56 plant species at unburned sites, 64 species of pollen vectors for 45 plant species at TSF-2 sites, and 46 species of pollen vectors for 58 plant species at TSF-1 sites. Many of the plant species that moths were interacting with were not present within rosemary balds as they were not detected at any of the sites, along transects or otherwise. For the seven plant species flowering within the sites, there were 46 species of moths transporting pollen grains. One species, *Commelina erecta*, only had two flowers blooming at just one site and no moths were found transporting its pollen. At the TSF-2 and unburned sites, there were 27 and 21 species of moths engaged in pollen transportation for 6 plant species. At TSF-1 sites, however, there were just 13 moth species transporting the pollen of five plant species. The only plant species that did not have moth pollen vectors at TSF-1 sites (aside from *C. erecta*) was *Lyonia ferruginea*, which had the overall highest number of moth vectors and the strongest species-specific interactions out of all the plant species across sites.

Overall, there were 69 unique plant-moth species interactions, 23 at unburned sites, 37 at TSF-2 sites, and just 16 at TSF-1 sites. Out of the 363 moths with pollen on them, 85 were transporting grains that I was unable to identify. This is largely due to the pollen grains being damaged in some way or obscured, preventing me from confidently classifying them.

Pollen transport networks

Using observed moth-plant interactions, I generated interaction networks for each TSF level. Raw network metrics varied across TSF level (Table 3), largely due to changes in network size. The measure of nestedness, NODF, was much lower in the unburned network than either of the

burned ones (unburned: 4.3, TSF-2: 19.6, TSF-1: 17). Connectance was also lowest in the unburned network, however it was comparable to the burned networks (unburned: 0.18, TSF-2: 0.23, TSF-1: 0.25). Linkage density and links per species were highest in the TSF-2 network (linkage density—unburned: 2.7, TSF-2: 4.4, TSF-1: 2.8; links per species—unburned: 0.85, TSF-2: 1.12, TSF-1: 0.89). Interaction diversity and richness (network Shannon's diversity) was similar across TSF levels, although it was lowest in the TSF-1 network (unburned: 3.1, TSF-2: 3.5, TSF-1: 2.8). Network specialization ($H2'$) was extremely low in the TSF-1 network and highest in the unburned network (unburned: 0.59, TSF-2: 0.31, TSF-1: 0.0). To analyze the impact of differences in network size, I directly compare networks using z-scores derived from the raw metric values and the null networks.

When comparing network metrics using calculated z-scores, the TSF-1 network had higher values relative to the distribution of its null networks for all metrics except $H2'$, which remained highest in the unburned network (Table 3). Therefore, when adjusting for size, NODF, linkage density, Shannon's diversity, connectance, and links per species are all highest in the TSF-1 network and followed by the TSF-2 network. No observed network metrics were significantly different from the mean null models for the TSF-1 or TSF-2 networks. Contrarily, in the unburned network all observed network metrics were significantly lower than the mean nulls, except for $H2'$, which was significantly higher (Table 3).

Discussion

Lepidopterans, a key component of pollination networks in every terrestrial habitat, are experiencing a general decline in Europe and North America likely due to climate change and habitat degradation (Thomas et al., 2004; Fox, 2013; Ollerton, 2017). Part of this decline may be linked to increased fire events as lepidopteran abundance responds negatively to wildfire. Many

lepidopteran larvae are canopy feeders with only moderate mobility, making them susceptible to fire and its environmental impacts (Kral et al., 2017). Fire has the potential to change and reshape lepidopteran communities and thus influence pollination networks. One of the major gaps in our understanding of lepidopteran communities and pollination networks is how fire impacts nocturnal moths and their floral interactions.

Here I examined how time-since-fire may influence adult moth communities and their pollination networks in the endemic and endangered Florida rosemary bald habitat that occurs on the Lake Wales Ridge of central Florida. Fire events are a natural part of the rosemary bald habitat, and this community is maintained by long fire return intervals of approximately 20 years (Menges et al., 1993; Richardson and Hall, 2013). These habitats and other Lake Wales Ridge habitats are host to many endemic invertebrates (Deyrup, 1989; Deyrup, 1990), and the way these invertebrates respond to fire is less clear. The goal of this study was to understand how fire events change the community composition of moths, the proportion of moth species transporting pollen, and the moth-pollen transport network structure for plants within the rosemary balds.

Moth community structure

Overall, rosemary balds are visited by a diverse set of nocturnal moths, with species from at least 28 families and 161 genera. The results of the analyses of community structure highlight how very recent fires alter moth communities, making them structurally different from those found at sites that have not been burned for two or more years. These differences are driven by changes in moth abundance rather than species composition, as abundance was significantly decreased at sites that were burned one year ago whereas species richness remained consistent across TSF levels (Table 1; Figures 2b and 3b). The decrease in abundance at sites burned one year ago served to increase evenness at these burned sites. Increased evenness following recent fire events

is not surprising, as disturbances frequently act to “reset”, or equalize, species abundances and fire is also commonly used to help maintain diversity by promoting evenness of many taxa including arthropods, plants, and soil organisms (Crowder et al., 2012). Maintaining evenness may also serve to preserve overall interactions within a community and ultimately ecosystem function (Hillebrand et al., 2008).

Beyond abundance and evenness, other diversity metrics remained consistent across TSF levels. Shannon diversity indices and species richness were similar across TSF levels. This finding is consistent with previous work on lepidopteran responses to fire. Two studies based on meta-analyses, demonstrate that fire generally has no significant impact on species richness in lepidoptera. (Carbone et al., 2019; Mason et al., 2021). In rosemary balds, maintained species richness might indicate that most moth species that visited rosemary balds do not have a strong larval dependency or a dependence on nectar for the plant species present in this plant community. Additionally, the preservation of species richness could be due to the long flight distances that most moths are capable of traveling (Young, 2002; Barthelmess et al., 2005; Macgregor et al., 2018), which would allow them to move into and out of the burned areas. Moths collected from rosemary balds had pollen from plants that were not present in balds, suggesting that moths were indeed traveling beyond the rosemary bald sites.

In addition to time-since-fire, moth community structure changed over time (week of sampling event). Both species richness and abundance increased significantly throughout the sampling period (Figures 2c and 3c). Similar temporal variation has been shown in numerous studies examining moth communities, although it is typically observed over a greater period, whether that be monthly (Jonason et al., 2014), seasonally (Banza et al., 2019), or even annually (Alarcón et al. 2008a; Devato et al., 2011). The fact that moth communities exhibit temporal

changes underscores the importance of conducting more sampling events across longer timescales. Sampling should also include investigations of ecological interactions at each time point, as there is likely large seasonal, phenological variation in interactions.

Pollen load and transport

Out of the 292 captured moth species, over 100 species carried pollen and approximately 32% of all individuals were transporting pollen from over 80 plant species. The number of pollen grains on an individual moth ranged from 1-40, with an average of 1.5 grains (SE = 0.12). Moths were mostly visiting and transporting the pollen of plant species beyond the rosemary balds, as plant species identified within rosemary balds sites were only 7% (6/83) of the species visited by moths. For plant species in the rosemary bald sites, the number of pollen grains found on moths ranged from 1-22, with an average of 1.8 grains.

Time-since-fire did not alter the proportion of moths transporting pollen of rosemary bald plants, or those in the broader landscape (Figure 5a). This suggests that moths may be a consistent source of pollen transportation within the rosemary balds, as their interactions are not directly altered after fire events. Additionally, the overall proportion of moths transporting pollen was significantly higher the first week of sampling which suggests a strong temporal component to moth-plant interactions. During the first week of sampling, 77% of moth individuals across all TSF treatments were transporting pollen, but this value declined each week (Figure 5b). This, in addition to the fact that moth pollination services do not seem to be perturbed by recent fires, suggests that moths might provide nocturnal pollination to plants in this habitat, especially earlier in the season when floral availability is higher. Furthermore, the abundance of previously identified pollinating moth species was consistent across TSF treatments (Figure S1), although I only collected 5/42 of these species. This incomplete collection of previously identified

pollinators suggests that continued work observing the pollination interactions of moths in the rosemary balds would be fruitful.

Pollen transport networks

Time-since-fire impacted pollen transport networks for plants that were flowering in rosemary balds during the sampling period. Across all treatment levels there were 69 unique plant-moth interactions between 46 species of moths and 6 species of plants. Recent fire reduced moth-plant interactions, as there were only 13 species of moth pollen vectors at TSF-1 sites while there were 21 and 27 at Unburned and TSF-2 sites. Although the mean number of flowers/60m² within the rosemary bald sites was low across TSF levels, 6 out of the 7 plant species blooming had pollen transported by moths. The low number of available flowers likely contributed to the small pollen loads carried by most moths. The only plant species that was not visited by moths at any TSF level was *Commelina erecta*, which had only two flowers blooming at just one site.

Examination of network structure at unburned sites revealed that most network metrics were significantly lower than the null network values (Table 3; Figure 6). Nestedness (NODF), linkage density and links per species, Shannon diversity, and connectance were significantly lower than expected in a network of its size (based on number of participating plant and moth species/individuals). Lower values of these metrics suggest that networks for unburned sites were less complex and had fewer interactions among moths and plants as would be predicted by a random network of a similar size. In contrast, H2' was incredibly high at 0.51, making this the network with the highest degree of specialization. Thus, unburned sites are characterized by fairly specialized interactions in which moths tend to visit the same plant species and are likely to transfer pollen among conspecific individuals.

In contrast to network metrics from unburned sites, metrics from sites that experienced fire

did not differ substantially from null networks based on their sizes (Table 3). These networks had larger values for Nestedness (NODF), linkage density and links per species, Shannon diversity, and connectance suggesting that fire increased the complexity of size corrected, nocturnal pollen transport networks. This result is interesting given that fire significantly reduced moth abundance at TSF-1 sites but not TSF-2 sites. Thus, fire served to restructure moth-pollen transport networks irrespective of changes in abundance. The other effect of fire was to reduce $H2'$ values, especially for the TSF-1 network where this value is 0. In the TSF-2 network, $H2'$ values begin to return to the unburned. These smaller values suggest that moth-plant interactions are less specialized with moth species carrying pollen from a wider range of flowering plant species. Taken together the results from the network analyses suggest that the rate and pollination quality in terms of moths visiting conspecific plant individuals is decreased within rosemary balds that have been recently burned (TSF-1 sites), as there are simply less moths, and moths that are present do not specialize on specific plant species.

Conclusion

Fire is a natural and integral part of the rosemary bald habitat ecology, but it also serves to reduce moth abundance in this habitat. Through this work I have ascertained that moth community structure is altered, largely due to reduced abundance, after recent fires. Despite these structural changes, species richness and overall diversity are conserved. These nocturnal communities have demonstrated quick recovery rates, as all diversity indices returned to pre-fire conditions after just two years post-fire. Further, the proportion of moths transporting pollen is similar across the gradient of time-since-fire. Even so, there are cascading effects on pollination networks during the recovery phase which could erode moth pollination services at recently burned sites. While the overall complexity of pollen transport networks is higher for TSF-1 and

TSF-2 networks, species-specific pollen transport and specialization is much higher at undisturbed rosemary bald sites and declined abundance at TSF-1 sites could have cascading effects on pollination. Although I did not test the strength of selection or the direct role that moths have in the sexual reproduction of plants, I believe that the evaluation of moth pollen transport networks in response to an ever-increasing cataclysm such as fire provides important data for moth and ecosystem conservation.

Table 1. Calculated diversity indices of nocturnal moth communities sampled at Archbold Biological Station reported as mean and SE for each time-since-fire treatment (TSF) level.

	Unburned	TSF-2	TSF-1
Species richness	81.67 ± 4.81	82 ± 4.51	61.33 ± 11.35
Abundance	207 ± 44.54	181.67 ± 5.55	121.33 ± 16.42
Shannon's diversity	3.78 ± 0.13	3.9 ± 0.08	3.73 ± 0.16
Pielou's evenness	0.86 ± 0.04	0.89 ± 0.01	0.91 ± 0.002

Table 2. Floral abundance of every plant species flowering at Archbold Biological Station during nocturnal moth sampling. Flowering individuals were recorded within 0.5-m of the two 15-m transects established at each rosemary bald site. Abundance is reported as flowers/60m² for each flowering species. TSF is time-since-fire in years.

TSF-Level	<i>Stipulicida setacea</i>	<i>Licania michauxii</i>	<i>Chapmannia floridana</i>	<i>Sabal etonia</i>	<i>Hypericum tenuifolium</i>	<i>Lyonia ferruginea</i>	<i>Commelina erecta</i>	Total
Unburned	0	0	1	0	0	0	2	3
Unburned	3	222	0	0	0	0	0	225
Unburned	0	0	0	239	61	29	0	329
TSF-2	0	10	0	0	0	0	0	10
TSF-2	18	2	2	0	0	0	0	22
TSF-2	0	0	0	148	0	0	0	148
TSF-1	0	0	0	0	0	0	0	0
TSF-1	0	0	1	0	0	0	0	1
TSF-1	139	0	0	208	0	0	0	347

Table 3. Calculated network metrics for nocturnal moth communities sampled at Archbold Biological Station for each time-since-fire treatment (TSF) level. The “value” column reports raw network metrics, and the “z-score” column reports z-scores of the observed metric value in relation to the mean metric values from the 500 null networks calculated for each TSF level. Significant differences between observed values and mean null values are indicated by an asterisk.

	Unburned		TSF-2		TSF-1	
Metric	value	z-score	value	z-score	value	z-score
NODF	4.3	-2.8*	19.6	-0.4	17.0	1.0
Linkage density	2.7	-2.7*	4.4	-1.0	2.8	0.9
Shannon’s diversity	3.1	-2.6*	3.5	-0.6	2.8	0.9
Connectance	0.18	-2.3*	0.23	-0.3	0.25	0.9
Network specialization ($H2'$)	0.59	2.6*	0.31	0.6	0.0	-0.9
Links per species	0.85	-2.3*	1.12	-0.3	0.89	0.9

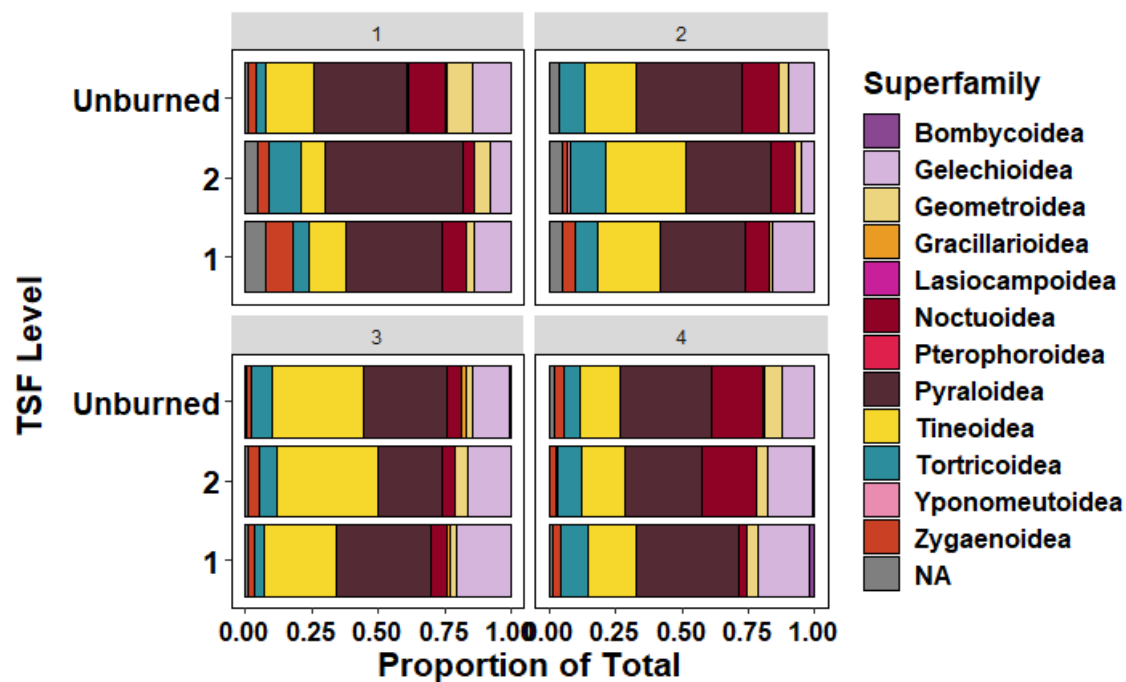


Figure 1. Frequency of all moth superfamilies trapped at Archbold Biological Station for each time-since-fire treatment (TSF) level for each week. The number of each panel corresponds to the week of sampling. The proportion each superfamily contributes to the total collection is reported along the x-axis.

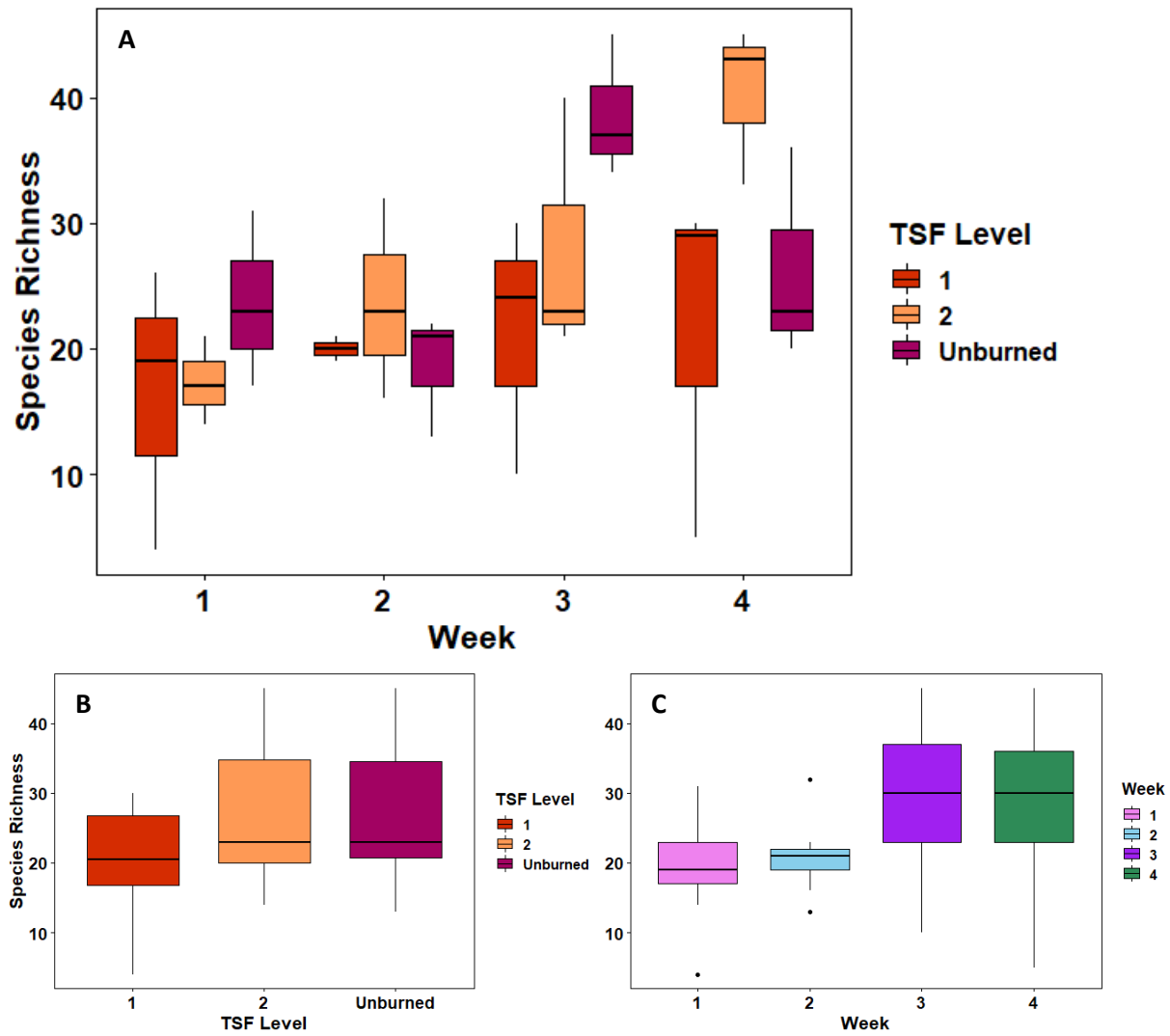


Figure 2. Species richness of moths trapped at Archbold Biological Station with regards to time-since-fire (TSF) and sampling week **a)** mean richness at each TSF level for every week, **b)** mean weekly richness at each TSF level, and **c)** richness averaged across TSF level each week. Significant differences are seen in **b)** when comparing weeks 1 and 2 to weeks 3 and 4. There are no differences in **a).**

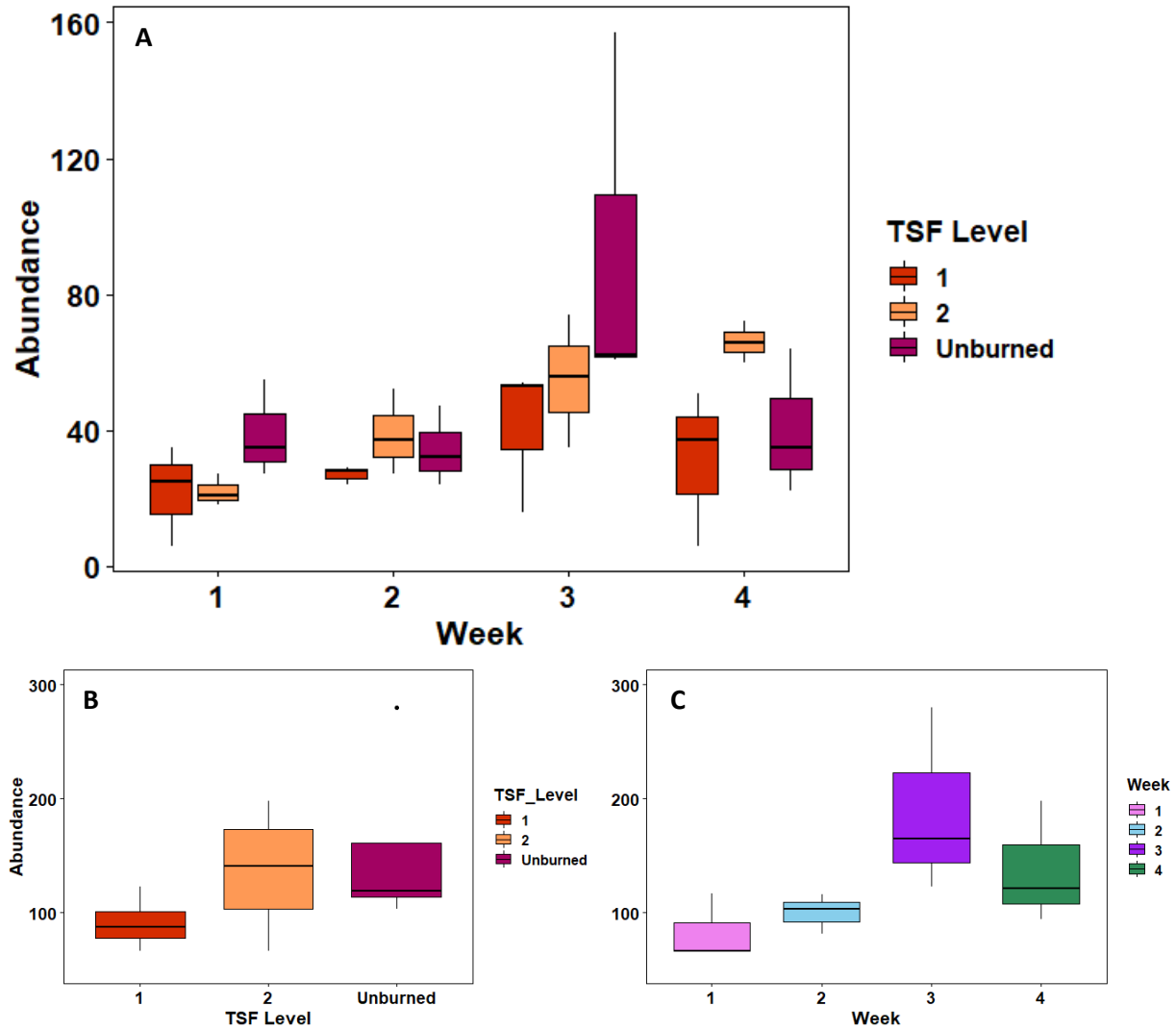


Figure 3. Abundances of moths trapped at Archbold Biological Station with regards to time-since-fire (TSF) and sampling week. **a)** mean moth abundance at each TSF level for every week, **b)** mean weekly moth abundance at each TSF level, and **c)** moth abundance averaged across TSF level each week. Significant differences are seen in **a)** when comparing TSF-1 to TSF-2 and unburned and in **b)** in all weekly comparisons except for week 1 vs. week 2.

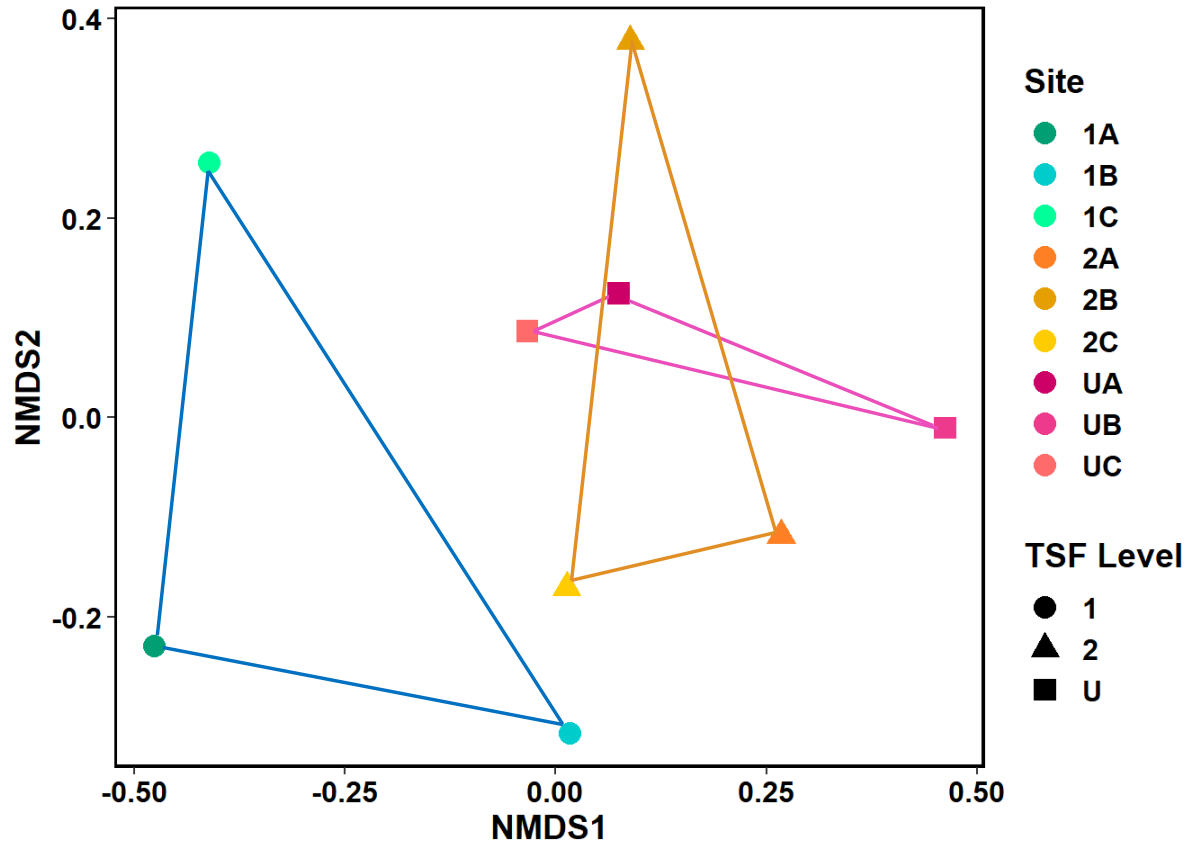


Figure 4. NMDS plot depicting moth community (site) dissimilarity at Archbold Biological Station across time-since-fire treatment (TSF) levels. TSF level is distinguished by shape (circle = TSF-1, triangle = TSF-2, and square = unburned) and the three sites within each treatment color coded (blues = TSF-1 sites, oranges = TSF-2 sites, and pinks = unburned sites). Lines highlight statistically significant clustering. NMDS model significance = 0.0432, ANOSIM statistic = 0.358.

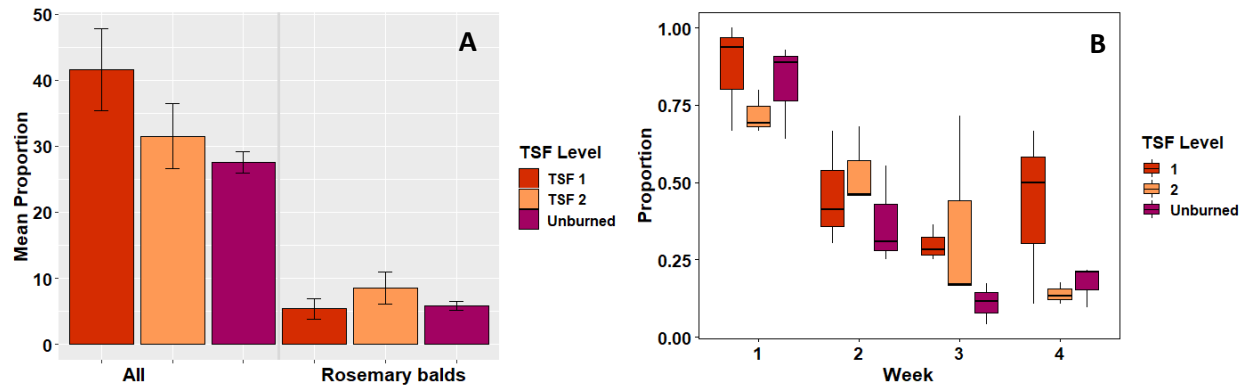


Figure 5. Proportion of moths transporting pollen at Archbold Biological Station for each time-since-fire treatment (TSF) level. **a)** mean proportion with error bars representing standard error. The left panel shows pollen from all plant species, the right panel shows pollen only from plants found along transects of rosemary bald sites. There are no significant differences across TSF level within either panel. **b)** mean proportion of moths transporting pollen from all plant species at each TSF level across time (week of sampling). Averaging across TSF levels, weekly proportion is significantly highest at week 1 and all other weekly comparisons are nonsignificant.

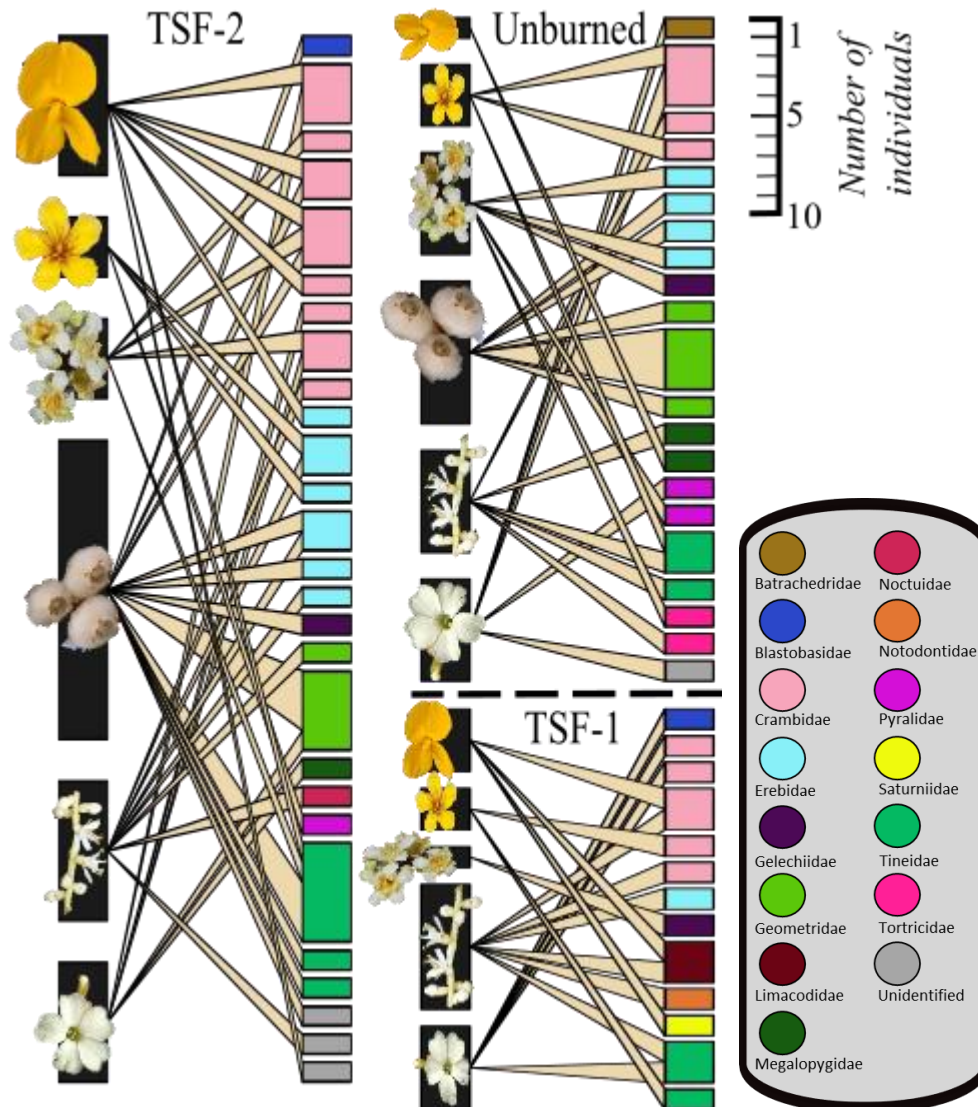


Figure 6. Pollen transport networks constructed for nocturnal moth communities sampled at Archbold Biological Station for each time-since-fire treatment (TSF) level within the rosemary balds. Each box represents a distinct species, and box width is proportional to the number of individuals. Link width represents the number of individuals participating in a given species specific, moth-plant interaction based off the presence of pollen on moth bodies. From top to bottom, flowering plant species are: *Chapmannia floridana*, *Hypericum*, *Licania michauxii*, *Lyonia ferruginea* (absent from TSF-1 network), *Sabal etonia*, and *Stipulicida setacea*.

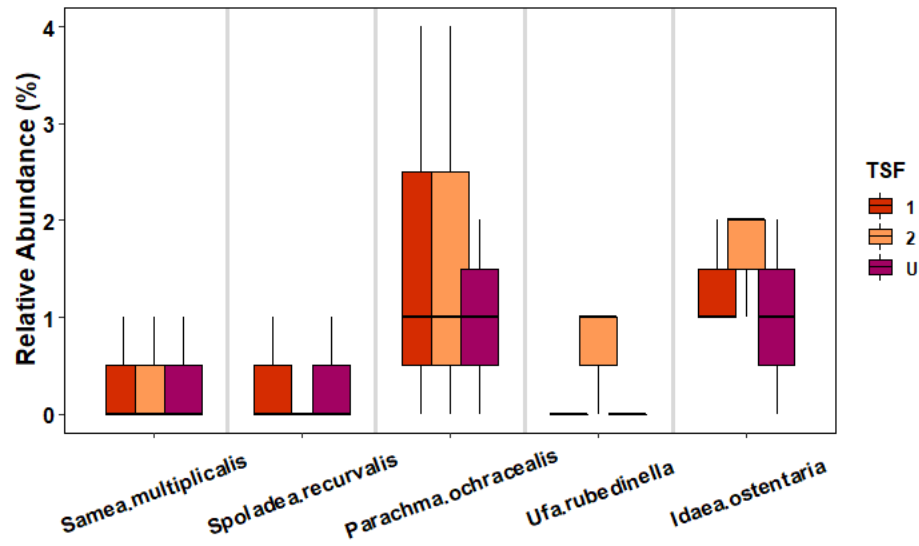


Figure S1. Relative abundance (percent of the total moth community) of five moth species previously identified as pollinators at Archbold Biological Station for each time-since-fire (TSF) level. Each species' abundance was similar across TSF levels.

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Dr. Dave Althoff, Syracuse University

Managed and analyzed multiple large datasets and interpreted/communicated the results in meetings. Developed research questions, conceptualized experimental design, managed budgets, conducted field work, and ran statistical analyses on ecological data.

Field work consisted of plant and insect collection and identification within various sites along a treatment variable. Sites were selected based on geospatial data (habitat distribution, disturbance type, and distance). I visualized these results into quality figures and tables.

Found and successfully secured multiple sources of funding by writing grant proposals.

- Presented at the **7th Annual Archbold Research Symposium**, January 2023

May 2019—December 2019

Dr. John Mull, Weber State University

Independent field work studying monarch butterflies and their oviposition host preference using two native milkweed species. Successfully secured funding, aided in the conceptualization of experimental design, reared greenhouse plants, conducted field work, analyzed data, and produced a thesis.

Field work consisted of surveying milkweed for monarch butterfly eggs and larvae, identifying milkweed species, counting monarch larvae, and recording monarch instar and plant condition, life stage, and approximate age. Took place in temperate forests, local parks, and wetlands.

Created and maintained garden plots and ran thin-layer chromatography experiments to compare chemical profile of milkweed leaves within and between species.

- Presented at the **Ecological Society of America** in August 2020
- Presented at the **Undergraduate Research Symposium** in March 2020
- Presented at the **National Conference on Undergraduate Research** in 2020

August 2019—October 2019

Dr. Jon Marshall, Weber State University

Field work in desert climates capturing and identifying Western fence lizards.

2016—2018

Dr. Ronald Meyers, Weber State University

Responsible for handling bird tissue samples which I processed into microscope slides using a cryostat-microtome. Followed lab protocols to stain samples using various chemicals so that I could determine the proportion of distribution of muscle fiber types in different muscles. Generated graphs and assembled high resolution microscope images using computer software. I successfully funded the research and laboratory through the acquisition of a grant.

- Presented at the **Undergraduate Research Symposium** in March 2018

Notable Accomplishments and Awards

- Honorable Mention of the Graduate Research Fellowship Program (GRFP) through the National Science Foundation (NSF)
- Recipient of the 2019-2020 Evolutionary Ecology Award through Weber State University
- Graduated cum laude and with departmental honors
- Completion of an undergraduate senior thesis

Volunteer Experience

- Bird Banding Station; Ogden, Utah
- Lantern House; homeless shelter; Ogden, Utah
- Ogden Wildlife Rehabilitation Center; Ogden, Utah
- Humane Society of Northern Utah; Ogden, Utah

Work Experience

- August 2021—Current
Biology Teaching Assistant, Syracuse University Instructing and guiding introductory biology laboratory and discussion sections for undergraduate students. Responsible for ensuring that students understand the material and maintain lab safety guidelines. Managed student communications and grades. Supervisors: Mary Graziano (teaching assistant coordinator), David Althoff (professor), Jason Wiles (professor)