10-14-2022

Assembly of Invaded Plant-pollinator Communities in a Fire-adapted Pine Rockland in the Lower Florida Keys

Brittany M. Harris
Florida International University, bharr063@fiu.edu

Recommended Citation

Harris, Brittany M., "Assembly of Invaded Plant-pollinator Communities in a Fire-adapted Pine Rockland in the Lower Florida Keys" (2022). *FIU Electronic Theses and Dissertations*. 5168.
https://digitalcommons.fiu.edu/etd/5168

FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

ASSEMBLY OF INVADED PLANT-POLLINATOR COMMUNITIES IN A FIRE-ADAPTED PINE ROCKLAND IN THE FLORIDA KEYS

A dissertation submitted in partial fulfillment of

the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

BIOLOGY

by

Brittany Harris

2022

To: Dean Michael R. Heithaus
College of Arts, Sciences and Education

This dissertation, written by Brittany Harris, and entitled Assembly of Invaded Plant-pollinator Communities in a Fire-adapted Pine Rockland in the Florida Keys, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

Hong Liu

Sparkle Malone

Mike Ross

Diego Salazar

Suzanne Koptur, Major Professor

Date of Defense: October 14, 2022

The dissertation of Brittany Harris is approved.

Dean Michael R. Heithaus
College of Arts, Sciences and Education

Andrés G. Gil
Vice President for Research and Economic Development
and Dean of the University Graduate School

Florida International University, 2022

DEDICATION

This dissertation is dedicated to my grandparents. Maw-maw and Paw-paw showed me through their love for each other, for others, and for the open road, that kindness, simplicity, and adventure is key to a happy life. From humble beginnings and endings, they taught me to be happy with whatever life brings, remembering that life does not bring what is not achieved through perseverance, and above all, the will to make a move.

ACKNOWLEDGMENTS

A dissertation is a work of the author, but it is never done in isolation. This work was supported by Kelly Foundation Tropical Botany, International Center for Tropical Botany and Institute of Environment, and the University Graduate School for two semesters of fellowship support to collect data (DEA), and two semesters of support to write the dissertation (DYF). I also want to thank TROPICs, The Tropical Fern & Exotic Plant Society, Kelly Foundation, the Judith Parker Travel grant, and FIU GPSC for support to present at two international conferences, to participate in the Bee Course, and to participate in the Organization for Tropical Studies ecology field course. These courses and conferences were instrumental in advancing my research and communication skills necessary to complete this dissertation.

I am grateful to the staff at the US Fish and Wildlife Service for providing housing and technical support on Big Pine Key during field work years. For this too, I thank Tie-Dye Micky for offering a room in his house on Big Pine Key after Hurricane Irma destroyed the shared USFWS housing. I am forever grateful for Micky's kindness and for sunset conversations while I pinned my insects after long hot days in the field.

Suzanne Koptur, my advisor, offered intellectual and emotional support throughout all aspects of this dissertation process. Her role has been that of teacher, cheerleader, and family. To my committee members, Diego, Hong, Sparkle, and Mike, thank you for your intellectual feedback and encouragement. I thank Diego most for his encouragement and for providing thorough feedback in every chapter of this dissertation. He is an incredible mentor and inspiration as a community ecologist. Hong was instrumental in motivating long-term monitoring and providing insight on bee invasions

and pollination. Sparkle offered feedback on disturbance and recovery; she was most speedy, thoughtful, and thorough in providing feedback. Mike inspired the idea to study fire history and provided many insightful discussions about Florida Keys pine rockland.

My lab mates in the Koptur Plant Ecology Lab and the GIS Remote Sensing Lab (including Daniel Gann and Jenny Richards) offered a welcome learning environment, as well as feedback, support, and friendship. I am grateful for the unconditional love of my siblings Jenn, Derrick, and Guy Rich. They believed in me and encouraged me when I needed it most (like every day of the dissertation).

ABSTRACT OF THE DISSERTATION

ASSEMBLY OF INVADED PLANT-POLLINATOR COMMUNITIES IN A FIRE-ADAPTED PINE ROCKLAND IN THE FLORIDA KEYS

by

Brittany Harris

Florida International University, 2022

Miami, Florida

Professor Suzanne Koptur, Major Professor

Most flowering plants rely on pollinators for their long-term survival. Increasing anthropogenic change has caused concern for declining pollinator populations and plant reproduction, yet we lack an understanding of the connection between pair-wise responses and those effects on the broader community. Here, I use a network approach and species-pair responses to understand how biological introductions and altered fire regimes influence plant-pollinator network dynamics, community stability, and plant reproduction in the globally imperiled pine rockland of the Florida Keys.

I analyzed shifts in the pollinator assemblage and reproductive output of an endangered buzz-pollinated plant before and after two tropical buzz-bees invaded the Florida Keys. Permutational multivariate analyses indicated high and sustained community turnover. Exotic orchid bees dominated the post-invasion assemblage, displacing the formerly dominant native buzz-bee, but providing similar pollination services.

Network analysis of the whole plant-pollinator community suggests that the displacement extended beyond the single plant assemblage; however, other buzz-bees were unaffected. To understand drivers of coexistence or competitive exclusion, I analyzed network subsets consisting of the whole plant-pollinator community and a buzz-bee subnetwork. The invaded networks were highly modular and specialized, with pollinators strongly partitioning resources compared to null models of abundances. Plant-pollinator co-occurrence and seasonal onset of flowering explained modularity and niche partitioning in the buzz-bee subnetwork but not the overall plant-pollinator network.

Lastly, I analyzed the effects of altered fire regimes on network dynamics and species diversity using a time-since-fire chronosequence in the fire-adapted pine rockland. Both flowering plant and interaction richness decreased with time-since-fire. Networks of recently burned areas were more specialized and modular than expected from null models, and deviation from random decreased with increasing fire return, suggesting that prolonged fire exclusion unravels complex plant-pollinator communities.

Introduced bees can disrupt pollinator communities, but partitioning niches across seasons can promote coexistence. Although invaded networks were modular and specialized, networks became less modular with prolonged fire suppression. Modularity and niche partitioning are thought to increase community resilience by confining disturbances rather than destabilizing whole networks. Therefore, understanding how abiotic and biotic change affects community dynamics and function is essential for reducing negative impacts of anthropogenic change.

TABLE OF CONTENTS

CHAPTER PAGE

LIST OF TABLES

LIST OF FIGURES

FIGURE PAGE

I. INTRODUCTION

Pollination by animals is a critical ecosystem service that enhances crop production and facilitates reproduction in over 90% of flowering plants (Ollerton et al., 2011). As a mutualistic service, pollinators depend on floral rewards that provide food or materials to provision their nests. Unlike antagonistic interactions, pollination involves competition and cooperation between two guilds of organisms with different life histories. Interactions between plants and pollinators are shaped by competition for resources, in which pollinators compete for flower resources and flowering plants compete for efficient pollinators.

The strength of interactions between plants and pollinators, when linked together, form complex networks with non-random structure (Barrat et al., 2004). Network dynamics can be analyzed to better understand drivers of community assembly. For example, species partition resources by differing from each other in their phenology, morphology, or spatial distribution. Resource partitioning produces a modular structure common in networks, in which groups of species are more likely to interact with each other than with other members of the community (Olesen et al., 2007; Vázquez et al., 2009). Furthermore, adaptive foraging and resource partitioning within guilds stabilize network structure by reducing competition (Valdovinos et al., 2016).

Anthropogenic driven changes in habitat quality or species invasions can potentially alter network structure and destabilize communities. The pine rockland of the Florida Keys was once considered the most endangered ecosystem in the United States (Noss & Peters, 1995) due to rapid coastal development, fire suppression, and salt-inundation from storm surge events (Ross et al., 2009). Pine rockland in the Florida Keys supports a high diversity of herbaceous flowering plants and is critical habitat for many rare and endemic species. Periodic fire and hurricanes are natural components of this ecosystem; however, disturbance regimes have been severely altered over the last century (Jones & Koptur, 2017). Invasive species further fuel changes with unknown outcomes for biodiversity or community persistence.

Pollination systems are thought to be resilient to change. Studies suggest that functional redundancy and some degree of asymmetry in the network stabilize pollination systems from disturbance (Bascompte et al., 2006). However, plant-pollinator communities have mostly been studied at the level of either individual species-pair responses, individual guilds, or of the structure of networks independent of species responses. Linking species and species-pair responses to the broader network better informs changes in community dynamics and ecosystem functioning in response to altered disturbance regimes and invasive species (Parra-Tabla & Arceo-Gómez, 2021).

In this dissertation, I aim to understand how plant-pollinator communities assemble in the face of biotic and abiotic anthropogenic change. In Chapter 1 (see pg.), I assess the effects of introduced solitary bees on community structure and composition, including the impacts of naturalization on specialized pollination services. We then zoom out to the broader plant-pollinator community in Chapter 2 (see pg.) and assess potential mechanisms structuring the invaded plant-pollinator community, particularly of native species with shared functional attributes as the introduced bees. Lastly, in Chapter 3 (see pg.), we analyze the effects of altered fire regimes on plant and pollinator diversity and of community network dynamics.

Specifically, I measure long-term impacts of two naturalized tropical solitary bees in the pine rockland plant-pollinator community on Big Pine Key, FL. *Euglossa dilemma* (Apidae) and *Centris nitida* (Apidae) are medium-large tropical bees with specialized floral diets. They can both can access pollen concealed in flowers with poricidal anthers, known as buzz-pollination. In 2015, they were observed visiting the flowers of the endangered buzz-pollinated legume, *Chamaecrista lineata* var. *keyensis*, which is endemic to the island. Using preliminary data (Liu & Koptur, 2003) before these bees naturalized on the island, we compared turnover in the pollinator community and changes in plant reproductive output of *C. keyensis*. I analyze the assemblage of the single plant to inform the impacts of the introduced bees on a specialized pollination system.

In Chapter 2, I analyze components of the plant-pollinator network to understand mechanisms driving network structure of the invaded community. I measure properties of the whole pine rockland plant-pollinator community on Big Pine Key and a subnetwork of the whole community composed of medium to large sonicating bees and the flowering plants they visit. By restricting the subnetwork to a specialized group of bees, pollinator morphology is controlled, and potential drivers of resource partitioning and coexistence amongst the native and introduced buzz-bees can be explored. I measure pollinator visits at flowers from March to November and calculate indices of modularity and pollinator niche partitioning for the whole network and the subnetwork. Network indices were compared to neutral and phenological null models to assess if network partitioning results from species abundances or from differences in phenological (i.e., seasonal) overlap in plants and pollinators. I was also interested if community modules are formed based on phenology of plants and pollinators in the whole network and subnetwork. In other words, do species in either network interact more closely with each other because they occur at the same time of the year compared to other potential partners in the network.

Finally, in Chapter 3, I analyze changes in network dynamics of the whole plant-pollinator community in response to altered fire regimes on the island. Pine rockland in the Lower Florida Keys historically ignited by lighting every 4-10 years (Bergh & Wisby, 1996). Controlled prescribed fires have replaced natural fires, but decades of fire suppression and infrequent prescribed burns have altered the landscape from open pine savannah to more densely vegetated forests. I construct 21 plant-pollinator networks from interaction frequency across a time-since-fire chronosequence in pine rockland on Big Pine Key to understand if network structure is resilient to altered fire returns. I measure plant and pollinator richness and the richness of their interactions across the chronosequence as well as network modularity and specialization and plant and pollinator niche overlap and partner diversity.

LITERATURE CITED

Barrat, A., Barthélemy, M., Pastor-Satorras, R., & Vespignani, A. (2004). The architecture of complex weighted networks. *PNAS*, *101*(11), 3747–3752. https://doi.org/10.1073/pnas.0400087101

Bascompte, J., Jordano, P., & Olesen, J. M. (2006). Asymmetric Coevolutionary Networks Facilitate Biodiversity Maintenance. *Science*, *312*(5772), 431–433.

Bergh, C., & Wisby, J. (1996). *Fire History of Lower Keys Pine Rocklands*. *305*, 296–3880.

Jones, I. M., & Koptur, S. (2017). Dead land walking: the value of continued conservation efforts in South Florida's imperiled pine rocklands. *Biodiversity and Conservation*, *26*(14), 3241–3253. https://doi.org/10.1007/s10531-017-1433-6

Liu, H., & Koptur, S. (2003). Breeding system and pollination of a narrowly endemic herb of the Lower Florida Keys: Impacts of the urban-wildland interface. *American Journal of Botany*, *90*(8), 1180–1187. https://doi.org/10.3732/ajb.90.8.1180

Noss, B. R. F., & Peters, R. L. (1995). *Endangered Ecosystems: A Status Report on America's Vanishing Habitat and Wildlife*.

Olesen, J. M., Bascompte, J., Dupont, Y. L., & Jordano, P. (2007). The modularity of pollination networks. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(50), 19891–19896. https://doi.org/10.1073/pnas.0706375104

Olesen, J. M., Eskildsen, L. I., & Venkatasamy, S. (2002). Invasion of pollination networks on oceanic islands: Importance of invader complexes and endemic super generalists. *Diversity and Distributions*, *8*(3), 181–192. https://doi.org/10.1046/j.1472-4642.2002.00148.x

Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, *120*(3), 321–326. https://doi.org/10.1111/j.1600-0706.2010.18644.x

Parra-Tabla, V., & Arceo-Gómez, G. (2021). Impacts of plant invasions in native plant–pollinator networks. In *New Phytologist* (Vol. 230, Issue 6, pp. 2117–2128). Blackwell Publishing Ltd. https://doi.org/10.1111/nph.17339

Ross, M. S., O'Brien, J. J., Ford, R. G., Zhang, K., & Morkill, A. (2009). Disturbance and the rising tide: The challenge of biodiversity management on low-island ecosystems. *Frontiers in Ecology and the Environment*, *7*(9), 471–478. https://doi.org/10.1890/070221

Valdovinos, F. S., Brosi, B. J., Briggs, H. M., Moisset de Espanés, P., Ramos-Jiliberto, R., & Martinez, N. D. (2016). Niche partitioning due to adaptive foraging reverses effects of nestedness and connectance on pollination network stability. *Ecology Letters*, *19*, 1277–1286. https://doi.org/10.1111/ele.12664

Vázquez, D. P., Chacoff, N. P., & Cagnolo, L. (2009). Evaluating multiple determinants of the structure of plant-animal mutualistic networks. *Ecology*. https://doi.org/10.1890/08-1837

II. DISPLACEMENT AND REPLACEMENT OF BUZZ-POLLINATION BY A NATURALIZED TROPICAL SOLITARY BEE

INTRODUCTION

Biological invasions threaten biodiversity by altering community structure and function and upending species interactions established over long evolutionary periods (Hui and Richardson 2017; Elton 1958). Invasion dynamics may offer key insights into our understanding of prominent theories in community ecology, such as species saturation (Sax and Gaines 2008) and competitive displacement (Reitz and Trumble 2002), and bridging these fields is vital (Latombe et al. 2021). Consequently, understanding the impacts of exotic species on the communities they invade is essential to conservation and a key challenge in ecology. Invasions in mutualisms, like plant-pollinator relationships, are particularly intriguing because outcomes are multifaceted. An exotic pollinator may share or compete with native pollinators for floral resources (Herbertsson et al. 2016; Garibaldi et al. 2013; Morales et al. 2013; Dohzono et al. 2008), and the effect on the flowering plants they visit could be positive, negative, or neutral (Brittain et al. 2013; Dohzono et al. 2008; Pemberton and Liu 2008). Further, the direction of these outcomes could change over time as species assimilate (Strayer et al. 2017).

Studies of invasions in plant-pollinator mutualisms have largely focused on invasive plants (Knight et al. 2018; Kaiser-Bunbury et al. 2011) or commercially managed social bees (Vanbergen et al. 2018; Dohzono and Yokoyama 2010). Further, these studies are mostly at the scale of species pair-wise effects (Liu and Pemberton

2009;) with little consideration for the broader community. For example, commercially managed bees (e.g., *Bombus* spp. and *Apis melifera*) can impact foraging behavior and abundances of native bees by exploiting floral resources (Vanbergen et al. 2018). Furthermore, their presence at flowers can impact reproductive success of native plants by resource robbing (Dohzono et al. 2008) and depositing interspecific pollen (Aizen et al. 2014). However, it is unclear if solitary naturalized bees exhibit similar competitive advantages to social bees (i.e., honeybees) in recipient communities. Such studies are currently limited (Graham et al. 2019; Pemberton and Liu 2008; Downing and Liu 2012). Further, natural disturbances, like hurricanes, can cause population and interaction shifts among plant-pollinator communities (Roubik and Villanueva-Gutiérrez 2009). Long-term studies permit investigation into disturbance recovery and potential *boom-bust* cycles of the invaded community (Strayer et al. 2017).

Here we present a multi-year study of the invasion dynamics of a solitary long-tongued orchid bee species, *Euglossa dilemma* (Bembé and Eltz), and its ecological impacts on the sub-tropical island community it invaded. This specialist tropical bee, native to Central America (Eltz et al. 2011), recently established itself across south Florida (Pascarella 2017) and Hispaniola (Genaro et al. 2020). This study is the first account of orchid bees in the Florida Keys. On Big Pine Key in 2015, we first observed these bees frequently visiting and sonicating anthers of *Chamaecrista keyensis*, a buzz-pollinated (Liu and Koptur 2003) and federally endangered herb, endemic to the island. We used a pre-invasion 2001 reference dataset of flower visitations and reproductive output of *C. keyensis* on the same island (Liu and Koptur 2003) before orchid bees naturalized to investigate:

1) Composition and structure of the flower visitor assemblage changed after orchid bees arrived

2) If and in which direction subsequent plant reproductive success changed

3) What role did urbanization have in structuring plant-pollinator interactions

4) If changes in community dynamics and plant reproductive success were sustained long-term over multiple flowering seasons, including following disturbance by a category-4 hurricane.

METHODS

2.1.1 Site Description

Our study occurred across the range extent of Big Pine partridge pea, *Chamaecrista lineata* var. *keyensis* (Pennell) H.S. Irwin and Barneby (Family: Fabaceae; henceforth referred to as *C. keyensis* or partridge pea). This federally endangered perennial herb (USFWS 2016) is endemic to the lower Florida Keys pine rockland, a globally endangered fire-dependent ecosystem. Populations are extant only on Big Pine Key (Fig. II.1; USFWS 2016). Fire history varies across pine rockland on Big Pine Key, and plants are most abundant where fire is frequent (Liu et al. 2005). Estimated fire return intervals for this ecosystem are 3-7 years; however, fragmentation by residential housing has resulted in fire suppression and delayed prescribed burns throughout (Bergh and Wisby 1996). Hurricanes occur every 10-20 years and the resulting saltwater intrusion can have lasting negative effects on pine rockland plant communities (Saha et al. 2011).

2.1.2 Species biology

Partridge pea is reproductively self-compatible, but its poricidal anthers must be sonicated for pollen to be released (Liu and Koptur 2003). Many groups of bees can sonicate (Cardinal et al. 2018), but only large sonicating bees can both initiate pollen removal and deposit it on the spatially separated stigma. Large *E. dilemma* bees, readily buzz pollen from partridge pea flowers. Flowering occurs during the rainy season from May through August. Flowers only offer pollen and are open for one day. Before *E.dilemma* arrived in the Florida Keys, *Xylocopa micans* Lepeletier (carpenter bees) and *Mellisodes communis* Cresson (long-horned bees) were the dominant buzz-pollinators (Liu and Koptur 2003).

2.1.3 Study Design

We sampled overlapping site locations from 2015-2019 where plants were surveyed in 2001 by Liu and Koptur (2003), before *E. dilemma* naturalized on the island. Three sites abutted residential areas (urban) and three were in forested tracts (forest). Comparable sites were substituted in some years depending on site accessibility and flowering abundances. Sites were approximately 250 m x 250 m, separated by a minimum of 400 m, and included north-south coverage of the 5.36 km^2 existing pine rockland on the 24.66 km^2 island. We surveyed sites at least three times per year during the entire flowering season from 2015 through 2019 (the earlier work surveyed only June and July). Comparable sites were substituted when fewer than 5 flowering plants were observed. Plots to examine pollinator interactions and plant reproduction were distributed haphazardly within sites where plants were flowering on survey days. On September 10, 2017, the center of a category 4 hurricane named Irma crossed the island. At that time, flowering had nearly concluded for the season, and we did not sample further in that year.

2.1.4 Pollinator Interactions

When open flowers were encountered within sites, we established 2 m diameter plots (Fig. II.1) and conducted single 10 min watches to observe pollinator interactions. Within plots, we measured the number of flowers (flower counts), the number of pollinators that visited at least one flower (abundances), and the number of flowers visited by each individual pollinator (flower visits). Pollinator interaction plots were separated by 25 m to reduce correlations between observations. We surveyed for pollinators on sunny days between 7:00 and 15:00, after which time flower visitors were scarce. Greater than 120 mins of watches occurred within forested and within urban sites each year, 2015 through 2019. We observed a total of 1,360 flowers, over 3,130 minutes, and across 288,475 m^2 throughout the five-year study.

In the pre-invasion study, Liu and Koptur (2003) measured flower visitation rates of species (Table II.1) as abundances at flowers per timed watch (A_p):

$$A_p = P \times F^{-1} \times t^{-1} \quad \text{Eq. 1}$$

P is the number of individuals that visited flowers in a plot (pollinator abundance), F is the number of flowers in a plot, and t is the observation time. The A_p is reported as species abundances visiting partridge pea flowers per hour, standardized by the number of open flowers in the observation plot. Yearly means for each site were used to compare pre-invasion A_p (2001) to the post-invasion A_p (2015-2019).

In the current study, we measured A_p, and we measured total flowers visited by pollinator species per timed watch (V_p):

$$V_p = V \times F^{-1} \times t^{-1} \quad \text{Eq. 2}$$

V is the number of flowers visited, F is the number of flowers and t is the observation time. V_p is visits per flower per hour. Yearly means for each site were used to compare V_p among post invasion years (2015-2019). Because each sonicating visit removes pollen and increases the probability of pollen deposition and reproduction in the self-compatible plant, then individual visits per flower (V_p) should be more relevant to resource competition and pollination.

All flower visitors were identified to species or genera, and a sample of all visitors were collected and preserved. The original dataset by Liu and Koptur (2003) identified legitimate “pollinators” to species, non-sonicating leafcutter bees (*Megachile* spp.) to genus, and all other species were lumped together as “others” (Table II.1). For the current work, we maintained this classification. In addition, we also analyzed differences in V_p of functional groups of pollinators in the post invasion assemblage (2015 – 2019) based on native or introduced status and attributes related to their ability to sonicate and pollinate flowers (Table II.1).

2.1.5 Plant reproductive success

We measured fruit and seed set in partridge pea plants to assess changes in reproductive success after *E. dilemma* bees naturalized. Reproduction plots were measured at all sites during the flowering season. Plots were circular with a 5m radius and haphazardly located throughout the sites (Fig. II.1) based on partridge pea flowering; they often overlapped with flower visitor observation plots. Within each plant-reproduction plot, we tagged up to three open flowers per each plant flowering in the plot. Labelled paper tags were attached directly below the flower petiole of open flowers. We did not observe differences in pollinator visitation between tagged and untagged flowers. Plots were revisited to record fruit set, which was visible within two weeks. Aborted fruits sometimes persisted, so fruit set was considered successful when pods were greater than 2 mm diameter and 10 mm length. We counted flowers that produced fruit containing at least one seed. If fruits were fully mature, we also counted seeds not damaged by herbivores. The pre-invasion data similarly comprised fruit and seed set from an open-pollination flowers at a forest and an urban site.

2.1.6 Statistical Analysis

Compositional changes in abundances (A_p) and visitation frequencies (V_p) to partridge pea's pollinator assemblage were assessed in two ways: first, to measure compositional turnover after *E. dilemma* bees naturalized (2001 and 2015), and second, to assess if compositional changes in the pollinator community were sustained after naturalization (2015-2019). These analyses were carried out in R ver. 4.1.0 (R Core Team 2020). To compare pollinator assemblages before and after invasion by *E. dilemma* (2001 and 2015), we computed Bray-Curtis distances on site-level mean A_p and tested the significance of compositional change in the community between the two time periods and across site urbanization types (urban and forest) with permutational Multivariate Analysis of Variance tests (9,999 random permutations; MANOVA) using the Adonis function in the Vegan package (Oksanen et al. 2020). Similarly, we compared pollinator assemblages among post-invasion years (2015-2019) by computing Bray-Curtis distances on site-level mean V_p and tested the significance of change in the community among the five time periods and across site urbanization factors with permutation MANOVA (9,999 random permutations). Significance tests for both analyses were done using *F*-tests based on sequential sums of squares from permutations of the site data for each sample year. We visualized temporal turnover across all years (2001 and 2015-19) using Non-metric Multidimensional Scaling (NMDS) based on the distance matrices of A_p. Dispersion ellipses for visualizing overlap between years were drawn using the veganCovEllipse function.

We assessed differences in V_p of functional groups of pollinators (Table II.1) across post-invasion years using Poisson regressions with site type (forest or urban) as a covariate. We were interested if V_p of large native buzz bees were collectively different from exotic buzz-bees, non-sonicating bees, or small buzz-bee visitors. We were also interested in how V_p of bee groups varied between habitats and across years, particularly after Hurricane Irma in 2017. Counts of visits were offset by the log of open flowers and watch times (log[flowers/min*60]) to standardize for observation length and flower patch sizes. The site urbanization variable (urban or forested) was also included in the models.

We used logistic regressions to assess if fruit set after (2001 and 2015) and across (2015 – 2019) post-invasion flowering seasons changed and Poisson regressions to assess differences in seed counts of fruits produced. For all Generalized linear models, we assessed model fit and assumptions using likelihood ratio tests and goodness-of-fit X^2 tests of residual deviances and degrees of freedom. We used negative binomial regressions for over-dispersed count data. Estimates and 95% confidence intervals (CI) reported were back-transformed (i.e., exponentiated). Means and standard errors are reported for V_p and A_p among pollinator species and groups. Data reported in this study can be accessed in the Knowledge Network for Biocomplexity data repository (Harris, et al. 2022).

RESULTS

1.2.1 Flower Visitor Assemblage

We observed 115 native bees (6 genera) to visit 222 flowers and 128 exotic *Euglossa dilemma* (orchid bees; Fig. II.2f) to visit 286 flowers of the 1,360 flowers observed, during the 2015 through 2019 flowering seasons. Among the native bees, five species (120 flower visits) sonicated and frequently touched stigmas while collecting pollen. Only three *Xylocopa micans* (carpenter bees), were observed at four flowers in total during these five years after orchid bees arrived at the island, despite 52 carpenter bee visitors recorded during watches in the single pre-invasion year, 2001 (Fig. II.2e). Most native buzz-bee visits were by *Melissodes communis* (Fig. II.2b; 25 visitors to 70 flowers), although visitors were variable across years (Fig. II.2g). *Megachile* spp. bees were not observed to sonicate flowers but were the second most frequent flower visitors in all years (Fig. II.2a). Exotic orchid bees buzzed flowers during all observations and were usually observed to brush against the stigma during visits.

The composition of the community of visitors to *Chamaecrista keyensis* (partridge pea) flowers changed significantly after orchid bees naturalized. There was a higher dissimilarity between pre-and post- invasion years than within them ($R^2 = 0.36$, $F_{(1)} = 4.55$ $P < 0.01$; Table II.2). Notably, orchid bees entered the assemblage and carpenter bees receded (Fig. II.2g). In 2001, 40% of all flower visitors were carpenter bees ($A_{p =}$ 0.48 ±0.08), but in the first year of our study, carpenter bees comprised only 3.3% of visitors in the assemblage (A_p = 0.08 ±0.08). Conversely, orchid bees (absent in 2001) contributed to 53.3% of all visitors at flowers in 2015 (A_p = 1.19 ±0.24).

Urbanization had little effect on community turnover (Table II.2), and flowers near forest or urban areas were equally as likely to be visited ($z_{(213)} = 0.64$, $P > 0.5$).

After the initial pollinator turnover, community composition remained consistent ($R_2 = 0.12$, $F_{(4)} = 0.85$, $P > 0.1$; Table II.2) across the next four flowering seasons. NMDS centroids exhibited separation of the pre-invasion pollinator assemblage from the overlapping post-invasion years (Fig. II.3). Once established, exotic orchid bees persisted as the primary visitors to *C. keyensis* flowers. They visited flowers at 5.73 (CI [3.44, 9.80]) times the rate of all large native buzz bees combined ($z_{(1187)} = 6.88$, $P < 0.001$; Fig. II.4b). Non-buzz-bees (*Megachile* spp.) were also significant flower visitors in the post-invasion assemblages ($z_{(1187)} = 2.70$, $P < 0.01$); these bees visited at twice the rate (CI [1.20, 3.67]) of native buzz-bees among seasons. Holding visitor species and habitat type steady, visitation frequency decreased slightly in consecutive years. However, departures from 2015 were only significant in the 2018 flowering season following Hurricane Irma, in which visitation rates were 64% lower ($z_{(1187)} = -2.53$, $P < 0.05$; Fig. II.4a).

1.2.2 Plant Reproduction

Reproductive output in partridge pea plants appeared unaffected by changes in the pollinator assemblage. After pooling sites for 2015, 42% (±0.02, N = 427) of all open flowers produced fruit containing an average of 8 seeds (7.7 ±0.47, N =23). Fruit set ($z_{(560)} = 0.874$ $P > 0.1$) and seeds per fruit ($z_{(110)} = 0.30$, $P > 0.5$) were approximately the same between pre- and post- invasion years (2001 and 2015); Fig. II.5a and II.5c). These averages were maintained for the five years post-invasion (2015-2019), except in 2018, after Hurricane Irma, when fruit set was 37% lower than in 2015 (CI [0.47, 0.94], $z_{(1292)} =$

-2.3, $P < 0.05$; Fig. II.5b). Seeds per fruit for all post-invasion years were not significantly different in any year (Fig. II.5d).

DISCUSSION

This study documents the rapid invasion of *Euglossa dilemma* (orchid bees), on an island in the lower Florida Keys and the subsequent disappearance of the largest native bee pollinator in the region. Our study establishes that orchid bees replaced the formerly dominant *Xylocopa micans* (carpenter bees) as buzz-pollinators of the federally endangered, island-endemic *Chameacrista keyensis* (Big Pine partridge pea). These compositional changes to the pollinator assemblage were sustained throughout our five-year study, including after the island was hit by a category-4 hurricane in late 2017.

Indeed, compositional changes in the pollinator assemblage were consistent over time and across space after invasion. We expected urban sites to harbor some native carpenter bees, as they were historically more associated with urbanization on the island (Liu and Koptur 2003), and *Euglossa* spp. bees are generally associated with forest cover in their native range (Roubik 1993). However, carpenter bees were essentially absent from all sites and orchid bees did not show preference for site conditions. We also expected that Hurricane Irma in late 2017 would have altered the composition of the pollinator assemblage in the following 2018 and 2019 flowering seasons. Visitation rates by orchid bees decreased in 2018, but compositional changes were not apparent, and rates recovered in 2019 to the 2015 levels. Fruit set also diminished slightly in 2018, but this too returned to 2015 levels in the following season. Hurricane disturbance can suppress native and non-native bee populations alike (Pascarella and Horvitz 1998). However, native and exotic bees seem to be resilient to recurrent disasters like hurricanes (Roubik and Villanueva-Gutiérrez 2009), and our study further supports such resiliency.

Replacement in buzz-pollinators did not translate to functional loss of pollination. Just as carpenter bees had done previously, the large orchid bees frequently visited and sonicated the poricidal anthers of partridge pea flowers and brushed against the stigma while manipulating flowers. Legitimate pollination resulted in fruit and seed set levels comparable to before orchid bees naturalized, when carpenter bees were the most abundant pollinators. These results differ from other noted pollinator invasions in specialized pollination systems of native plants (Hanna et al. 2014; Dohzono et al. 2008). In those studies, complex floral morphology limited the pool of pollinators capable of accessing flower rewards and facilitating plant reproduction, but invasive nectar robbers outcompeted legitimate pollinators, resulting in reduced fruit set. In another case, exotic *Euglossa dilemma* bees were successful buzz-pollinators of the invasive plant *Solanum torvum* in south Florida (Liu and Pemberton 2009). However, the current study is the first to reveal positive pollination services by a solitary bee to a specialized native plant but adverse effects to the resident pollinator community, including a potential local extinction.

Exploitative competition for pollen resources on the island may have caused displacement of carpenter bees from the pollinator assemblage. Buzz-pollinated flowers generally only offer pollen to flower visitors and only sonicating bees can access this non-replenishable and nutrient rich reward (De Luca and Vallejo-Marín 2013). Further, available floral resources and orchid bee foraging preference largely overlap in their native and introduced range, including many buzz-pollinated flowers (Pemberton and

Wheeler 2006; Villanueva-Gutiérrez et al. 2009). Species saturation (Sax and Gaines 2008) and limiting similarity in the island buzz-pollinator community could be acting in carpenter bee displacement. In other words, when resources are limited, and species exhibit similar functional traits and resource use, competition exceeds facilitation and coexistence is unlikely (Koffel et al. 2018). On the contrary, coexistence is apparent in nearly all documented pollinator invasions (Vanbergen et al. 2013; Downing and Liu 2012), apart from managed *Bombus* bees (Morales et al. 2013), even if native populations are slightly reduced (Taggar et al. 2021; Graham et al. 2019; Hanna et al. 2014). However, species saturation and limiting similarity may be more apparent on islands where resources are limited (Elton 1958), refuge habitat is sparse, and functional redundancy is generally low (Denslow 2003). Indeed, invasions are frequent on islands (Moser et al. 2018). Although extinctions of some vertebrates from islands is common, extinctions of insects are rarely documented (Sax and Gaines 2008).

Limiting similarity of shared functional traits may be more relevant in competitive exclusion of pollinators than phylogenetic relatedness (Junker et al. 2013); though previous studies of bee displacements among congeners would suggest otherwise (Dohzono and Yokoyama, 2010; Morales et al., 2013). Unlike co-occurring *Bombus* spp., *E. dilemma* is the only species of its tribe (Euglossini) in south Florida. While *B. terrestris* has been documented to cause population declines of other *Bombus*, the local decline of *Xylocopa micans* coincides with arrival and resource sharing of *E. dilemma*, a distantly related species of the family Apidae. Overlap in shared functional traits between the bees is high, such as their robust size, ability to sonicate, and use of ground nesting resources. Interestingly, *E. dilemma* co-exists alongside *E. viridissima* in its native range;

indeed, niche overlap is so high that they were initially mistaken as a single species (Eltz et al. 2011).

Long-term studies of the early phases of invasion are not well documented. Timely investigations of adverse effects of invasions may be beneficial for managing invasive species. In our study, ecological replacement of buzz-pollination services was thorough and sustained. It is not clear exactly when orchid bees arrived in the lower Florida Keys, though there appears to be no evidence of colonization on the island before 2015. Although our study demonstrates replacement of pollination service to the endangered, island endemic partridge pea, near local extinction of native *Xylocopa* bees could have subsequent ecological effects outside the scope of this single-plant species-focused study. Therefore, management decisions to control invasive pollinators should consider long-term consequences for the entire pollinator guild and for the flowering plants they frequently visit.

LITERATURE CITED

Aizen, M.A., Morales, C.L., Vázquez, D.P. V, Garibaldi, L.A., Sáez, A. and Harder, L.D. (2014). When mutualism goes bad: density-dependent impacts of introduced bees on plant reproduction. *New Phytol.*1–7

Aslan, C.E. (2019). Non-native insects dominate daytime pollination in a elevation Hawaiian dryland ecosystem. *Am. J. Bot.*, 106, 313–324.

Bergh, C. and Wisby, J. (1996). Fire History of Lower Keys Pine Rocklands, 296–3880.

Brittain, C., Williams, N., Kremen, C. and Klein, A.M. (2013). Synergistic effects of non-Apis bees and honey bees for pollination services. *Proc. R. Soc. B Biol. Sci.*, 280.

Cardinal, S., Buchmann, S.L. and Russell, A.L. (2018). The evolution of floral sonication, a pollen foraging behavior used by bees (Anthophila). *Evolution (N. Y).*, 72, 590–600.

De Luca, P.A. and Vallejo-Marín, M. (2013). What's the "buzz" about? The ecology and evolutionary significance of buzz-pollination. *Curr. Opin. Plant Biol.*, 16, 429–435.

Denslow, J. (2003). Weeds in Paradise : Thoughts on the invasibility of tropical islands. *Ann. Missouri Bot. Gard.*, 90, 119–127.

Dohzono, I., Kunitake, Y.K., Yokoyama, J. and Goka, K. (2008). Alien bumble bee affects native plant reproduction through interactions with native bumble bees. *Ecology*, 89, 3082–3092.

Dohzono, I. and Yokoyama, J. (2010). Impacts of alien bees on native plant-pollinator relationships: A review with special emphasis on plant reproduction. *Appl. Entomol. Zool.*, 45, 37–47.

Downing, J.L. and Liu, H. (2012). Friend or foe? Impacts of the introduced tropical oil bee *Centris nitida* on a threatened and specialized native mutualism in Southern Florida. *Biol. Invasions*, 14, 2175–2185

Elton, C.S. (1958). *The ecology of invasions by animals and plants*. Methuen, London.

Eltz, T., Fritzsch, F., Pech, J.R., Zimmermann, Y., Ramírez, S.R., Quezada-Euan, J.J.G., et al. (2011). Characterization of the orchid bee *Euglossa viridissima* (Apidae: Euglossini) and a novel cryptic sibling species, by morphological, chemical, and genetic characters. *Zool. J. Linn. Soc.*, 163, 1064–1076.

Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., et al. (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, 339, 1608–1611.

Genaro, J.A., Hinojosa-Díaz, I.A., Mcdowell, L., Barco, J. El, Lomoto, L., Altamira, C., et al. (2020). First record of the orchid bee *Euglossa dilemma* (Hymenoptera: Apidae) in Hispaniola, the Antilles. *Insecta mundi*, 0779, 1–5.

Graham, K.K., Eaton, K., Obrien, I. and Starks, P.T. (2019). *Anthidium manicatum*, an invasive bee, excludes a native bumble bee, *Bombus impatiens*, from floral resources. *Biol. Invasions*, 21, 1089–1099.

Hanna, C., Foote, D. and Kremen, C. (2014). Competitive impacts of an invasive nectar thief on plant-pollinator mutualisms. *Ecology*, 95, 1622–1632.

Harris, B., Liu, H. and Koptur, S. (2022). Multi-year dataset of flower visitors and reproductive output of Big Pine partridge pea. https://doi.org/10.5063/F1JD4V63

Herbertsson, L., Lindström, S.A.M., Rundlöf, M., Bommarco, R. and Smith, H.G. (2016). Competition between managed honeybees and wild bumblebees depends on landscape context. *Basic Appl. Ecol.*, 17, 609–616.

Hui, C. and Richardson, D.M. (2017). *Invasion dynamics*. Oxford University Press, Oxford, United Kingdom.

Junker, R.R., Blüthgen, N., Brehm, T., Binkenstein, J., Paulus, J., Schaefer, H.M., et al. (2013). Specialization on traits as basis for the niche-breadth of flower visitors and as structuring mechanism of ecological networks. *Funct. Ecol.*, 27, 329–341.

Kaiser-Bunbury, C.N., Valentin, T., Mougal, J., Matatiken, D. and Ghazoul, J. (2011). The tolerance of island plant-pollinator networks to alien plants. *J. Ecol.*, 99, 202–213.

Knight, T.M., Ashman, T., Bennett, J.M., Burns, J.H., Passonneau, S. and Steets, J.A. (2018). Reflections on, and visions for, the changing field of pollination ecology. *Ecol. Lett.*, 21,1282-1295

Koffel, T., Boudsocq, S., Loeuille, N. and Daufresne, T. (2018). Facilitation- vs. competition-driven succession: the key role of resource-ratio. *Ecol. Lett.*, 21, 1010–1021.

Latombe, G., Richardson, D.M., McGeoch, M.A., Altwegg, R., Catford, J.A., Chase, J.M., et al. (2021). Mechanistic reconciliation of community and invasion ecology. *Ecosphere*, 12.

Liu, H. and Koptur, S. (2003). Breeding system and pollination of a narrowly endemic herb of the Lower Florida Keys: Impacts of the urban-wildland interface. *Am. J. Bot.*, 90, 1180–1187.

Liu, H., Menges, E.S. and Quintana-Ascencio, P.F. (2005). Population viability analysis of *Chamaecrista keyensis*: Effects of fires season and frequency. *Ecol. Appl.*, 15, 210–221.

Liu, H. and Pemberton, R.W. (2009). Solitary invasive orchid bee outperforms co-occurring native bees to promote fruit set of an invasive *Solanum*. *Oecologia*, 159, 515–525.

Morales, C., Arbetman, M., Cameron, S. and Aizen, M. (2013). Rapid ecological replacement of a native bumble bee by invasive species. *Front. Ecol. Environ.*, 11, 529–534.

Oksanen, A.J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., et al. (2020). Community ecology package "vegan."

Pascarella, J.B. (2017). Range Extension of the Introduced Bee Species *Euglossa dilemma* (Hymenoptera: Apidae) in Monroe County, Florida, with Notes of Additional Range Extensions in Southern Florida. *Florida Entomol.*, 100, 209–210.

Pascarella, J.B. and Horvitz, C.C. (1998). Hurricane disturbance and the population dynamics of a tropical understory shrub: Megamatrix elasticity analysis. *Ecology*, 79, 547–563.

Pemberton, R.W. and Liu, H. (2008). Potential of invasive and native solitary specialist bee pollinators to help restore the rare cowhorn orchid (*Cyrtopodium punctatum*) in Florida. *Biol. Conserv.*, 141, 1758–1764.

Pemberton, R.W., and Wheeler, G.S. 2006. “Orchid Bees Don’t Need Orchids: Evidence from the Naturalization of an Orchid Bee in Florida.” *Ecology* 87 (8): 1995–2001

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Reitz, S.R. and Trumble, J.T. (2002). Competitive displacement among insects and arachnids. *Annu. Rev. Entomol*, 47, 435–65.

Roubik, D.W. (1993). Tropical pollinators in the canopy and understory: Field data and theory for stratum “preferences.” *J. Insect Behav.*, 6, 659–673.

Roubik, D. and Villanueva-Gutiérrez, R.(2009). Invasive africanized honey bee impact on native solitary bees: a pollen resource and trap nest analysis. *Biol. J. Linn. Soc.*, 98, 152–160.

Saha, S., Bradley, K.A., Ross, M.S., Hughes, P., Wilmers, T., Ruiz, P.L., et al. (2011). Hurricane effects on subtropical pine rocklands of the Florida Keys. *Clim. Change*.

Sax, D.F. and Gaines, S.D. (2008). Species invasions and extinctions: The future of native biodiversity on islands. *Proc. Natl. Acad. Sci.*, 105, 11490–11497.

Stout, J.C. and Morales, C.L. (2009). Ecological impacts of invasive alien species on bees. *Apidologie*, 40, 388–409.

Strayer, D.L., D’Antonio, C.M., Essl, F., Fowler, M.S., Geist, J., Hilt, S., et al. (2017). Boom-bust dynamics in biological invasions: towards an improved application of the concept. *Ecol. Lett.*

Taggar, A.K., McGrath, E. and Despland, E. (2021). Competition between a native and introduced pollinator in unmanaged urban meadows. *Biol. Invasions*, 23, 1697–1705.

USFWS. (2016). 50 CFR Part 17; Final Rule; Endangered Species Status for *Chamaecrista lineata* var. *keyensis* (Big Pine Partridge Pea), *Chamaesyce deltoidea* ssp. *serpyllum* (Wedge Spurge), and *Linum arenicola* (Sand Flax), and Threatened Status for *Argythamnia blodgettii*. *Fed. Regist.*, 81, 66842–66865.

Vanbergen, A.J., Espíndola, A. and Aizen, M.A. (2018). Risks to pollinators and pollination from invasive alien species. *Nat. Ecol. Evol.*, 2, 16–25.

Villanueva-Gutiérrez, R., Quezada-Euan, J, and Eltz, T. 2013. “Pollen diets of two sibling orchid bee species, *Euglossa*, in Yucatan, southern Mexico.” *Apidologie* 44 (4): 440–46.

TABLES

Table II.1. Flower visitors to *Chamaecrista keyensis* on Big Pine Key, FL. Insect visitors were classified according to the 2001 study and reclassified for some post-invasion analyses (2015-2019; Fig. II.4) by their ability to sonicate and deposit pollen on stigmas of partridge pea flowers.

Family	Visitor species	Authority	Classify 2001	Classify post-invasion
Apidae	*Centris errans*	Fox, 1899	Others	Native buzz-bee
Apidae	*Centris nitida*	Smith, 1874	Others	Exotic buzz-bee
Apidae	*Euglossa dilemma*	Bembé & Eltz, 2011	*Euglossa*	Exotic buzz-bee
Apidae	*Melissodes communis*	Cresson, 1878	*Melissodes*	Native buzz-bee
Apidae	*Xylocopa micans*	Lepeletier, 1841	*Xylocopa*	Native buzz-bee
Halictidae	*Augochloropsis anonyma*	Cockerell, 1922	Others	Small buzz-bee
Halictidae	*Lasioglossum surianae*	Mitchell, 1960	Others	Small buzz-bee
Megachilidae	*Megachile georgica*	Cresson, 1878	*Megachile*	Non-buzz-bee
Megachilidae	*Megachile pseudobrevis*	Mitchell, 1936	*Megachile*	Non-buzz-bee
Syrphidae	*Allograpta exotica*	Wiedemann, 1830	Others	NA
Syrphidae	*Pseudodorus clavatus*	Fabricus 1794	Others	NA

Table II.2. Permutational MANOVA (9,999 permutations) results comparing compositions ($A_{p,\ abundances/flower/hour}$) of *Chamaecrista keyensis* flower visitors before and after (2001 & 2015) invasion by *Euglossa dilemma* bees and among post-invasion years (2015 – 2019) in forest and urban sites.

Variable	Df	Sum of squares	R^2	F	Pr (> F)
Pre- & Post-invasion (2001 & 2015)	1	0.876	0.363	4.187	0.005
Urbanization class	1	0.076	0.031	0.364	0.841
Residual	7	1.465	0.606		
Post-invasion years (2015 – 2019)	4	0.854	0.119	0.854	0.656
Urbanization class	1	0.072	0.010	0.288	0.942
Residual	25	6.250	0.871		

FIGURES

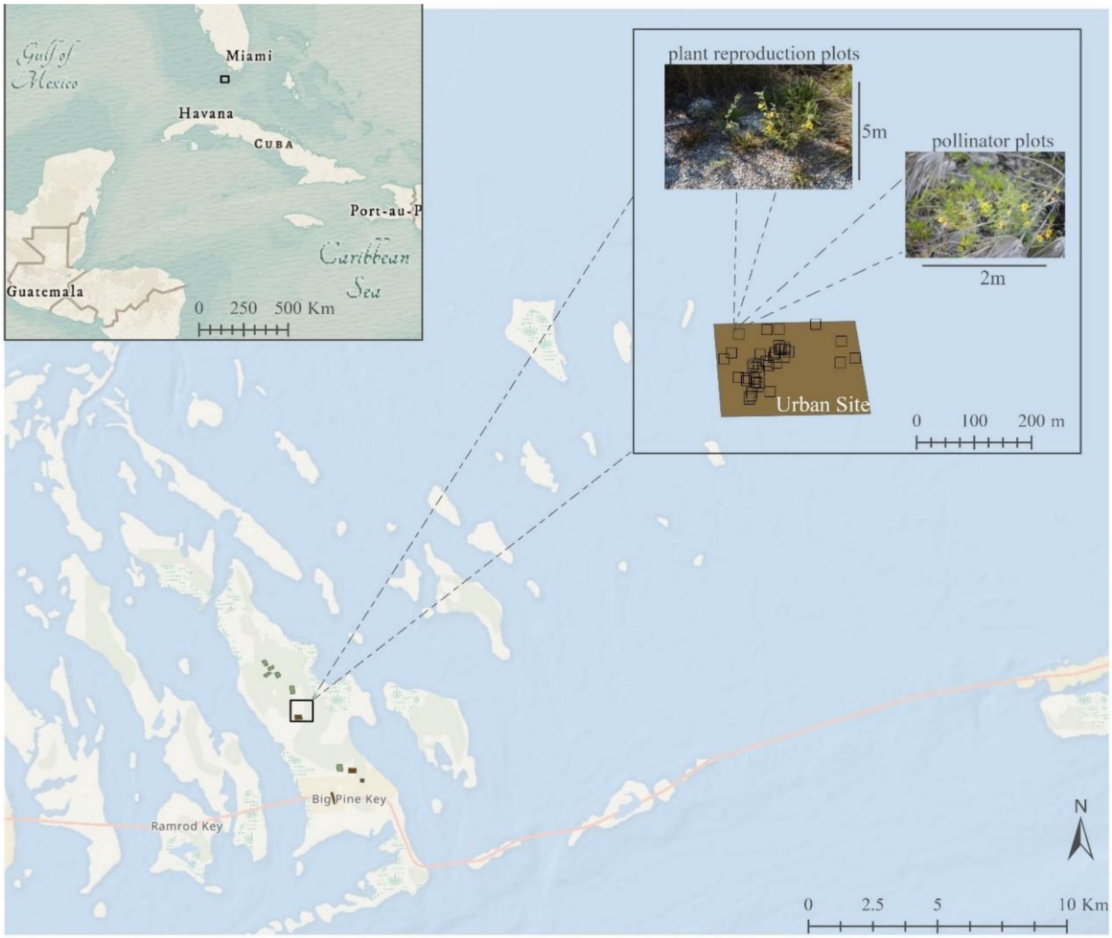

Figure III.1. Map of the study extent of *Chamaecrista keyensis* on Big Pine Key, FL USA in the lower Florida Keys. Plant reproduction and pollinator watch plots within urban and forest sites.

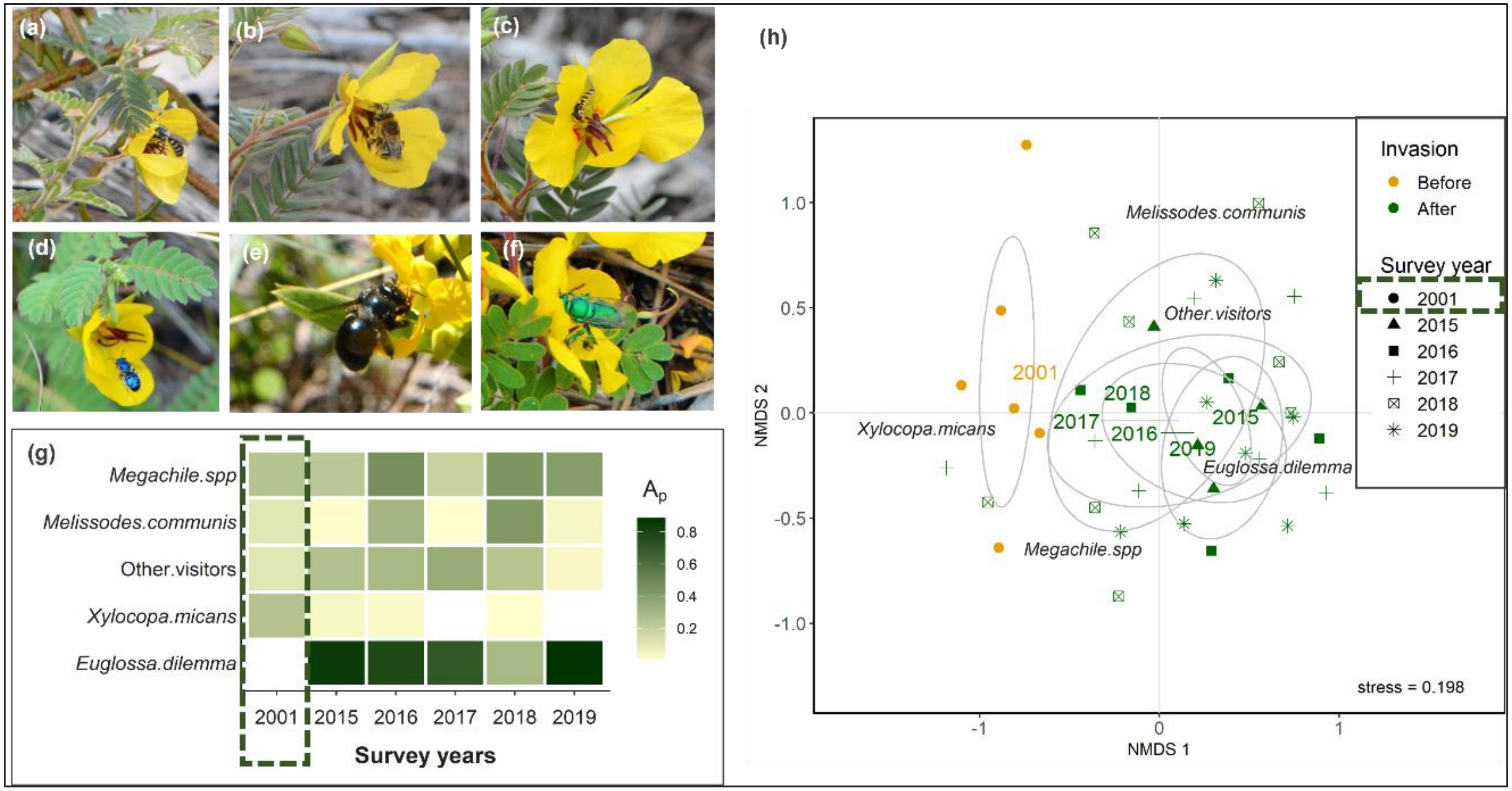

Figure III.2 Compositional differences in *Chamaecrista keyensis* flower visitors before (2001) and after (2015-2019) *Euglossa* bees naturalization. a) *Megachile georgica*. b) *Melissodes communis*. c) *Allograpta exotica*. d) *Augochloropsis anonyma*. e) *Xylocopa micans* f) *Euglossa dilemma*. g) Frequency matrix of mean visitor abundances (Ap; Eq.1) within sites and by years h) NMDS plot of visitation rates (Ap) across before and after invasion

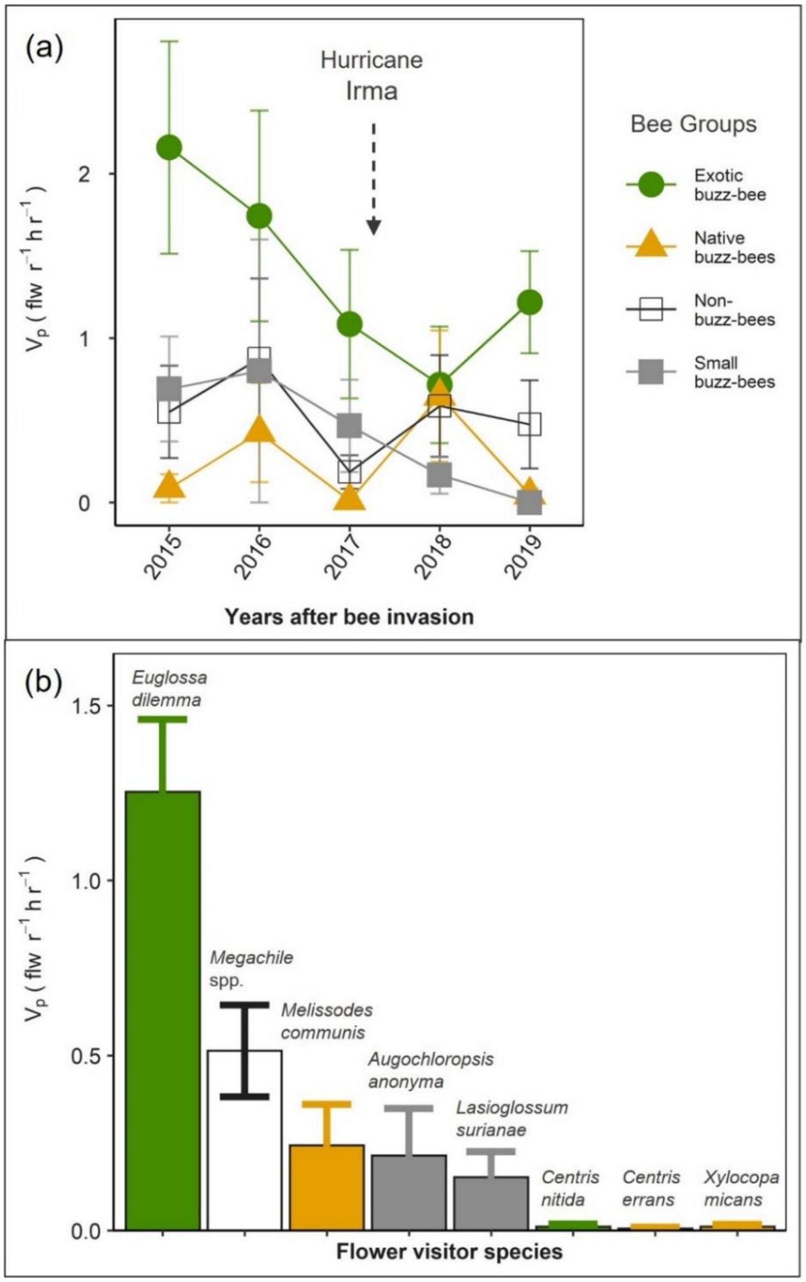

Figure III.3 Visitation frequencies (Vp = visits/flower/hour); Mean and SE) by pollinator functional groups to *Chamaecrista keyensis* after orchid bees naturalized in the Florida Keys. Only large sonicating bees, including exotic buzz-bees (*Euglossa dilemma*) and native bees, extract and transfer pollen. a) Vp of pollinator groups across years b) Vp of species within groups.

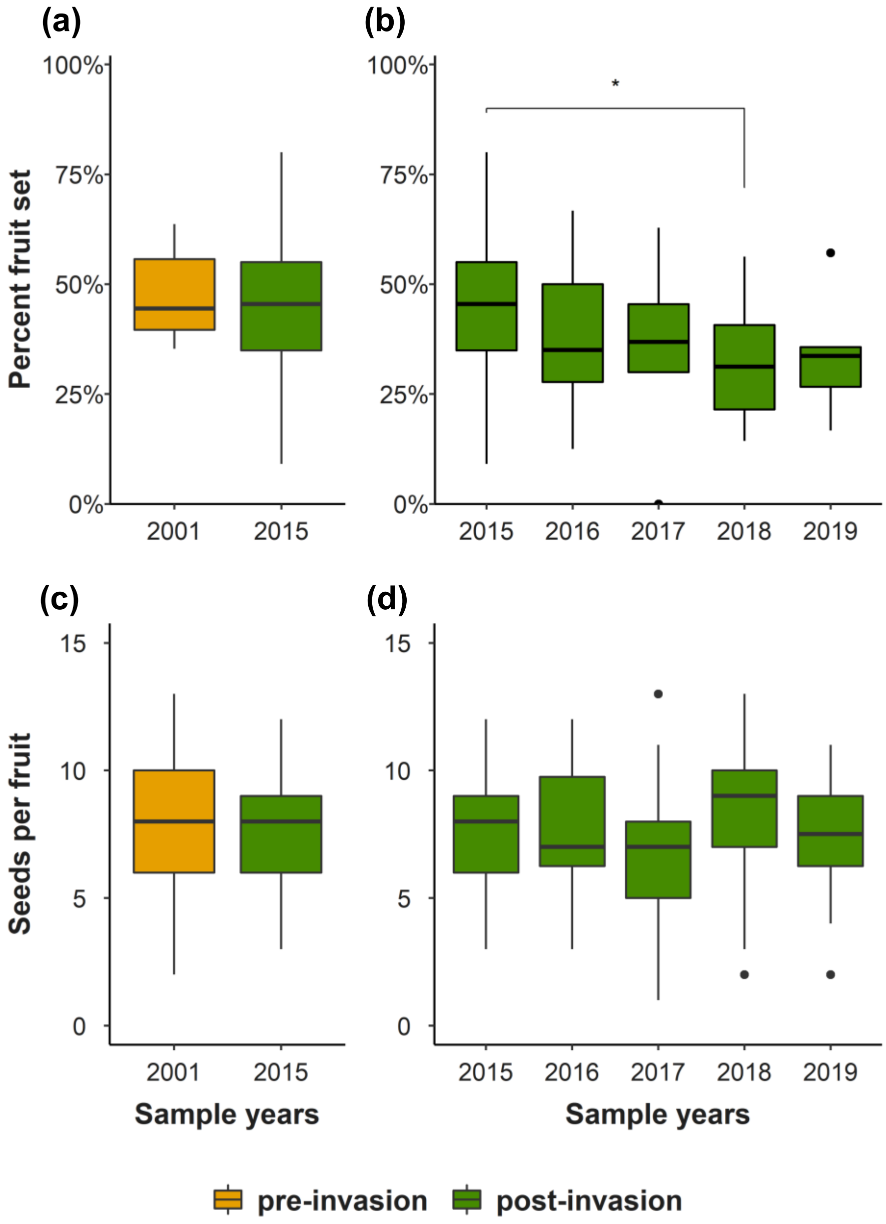

Figure III.4. Reproductive output of *Chamaecrista keyensis* before and after *Euglossa dilemma* invasion a) Percent of flowers producing fruit and b) seeds per fruit compared between the pre-invasion assemblage (2001) and the first year after (2015) orchid bees invaded. c) Fruit set and d) seeds per fruit between years (2015-2019) after E. dilemma bees invaded *Chamaecrista keyensis*'s flower visiting assemblage.

III. PLANT-POLLINATOR NETWORK SIZE AFFECTS SPECIES COEXISTENCE VIA PHENOLOGICAL DIFFERENCES

INTRODUCTION

Species invasions can alter community structure and function. Evaluating their impacts on recipient communities is therefore critical for biodiversity maintenance in a changing world (Pascal et al. 2010; Traveset and Richardson 2014). Despite advances in our capacity to predict invasions and sometimes manage them (Hui et al. 2016; Novoa et al. 2020), our understanding of community-wide impacts beyond single species interactions is limited (Sanders et al. 2003; Hui and Richardson 2017). Particularly, the role novel that interactions have in shaping recipient communities is not well established for mutualisms. In pollination, for example, species interact in non-random linkages, such that networks of interacting plants and pollinators are often modular (Olesen et al. 2007), connected (Thébault and Fontaine 2010), and nested (Krishna et al. 2008). Understanding the biological mechanisms that influence community structure is essential to assess potential impacts of invasions on recipient plant-pollinator communities.

Competition for shared resources is thought to be a strong force in assembling communities. Network architecture can explain how species partition resources to reduce competition and permit co-existence (Bastolla et al. 2009). The architecture of mutualistic networks has been well established (Bascompte and Jordano 2007, 2014; Olesen et al. 2011; Traveset et al. 2016); however, the relative importance of biological drivers to network dynamics is not well established (Vázquez et al. 2009b, a; Sonne et al. 2020). Morphology (Vizentin-Bugoni et al. 2014) and phenology (Encinas-Viso et al. 2012; Gonzalez and Loiselle 2016; Ramos–Jiliberto et al. 2018) are well-accepted drivers of specialization and niche partitioning in the community (Vázquez et al. 2009b) since they can allow or inhibit potential partner interactions. Morphologically similar pollinators and corresponding plant pollination syndromes (Armbruster et al. 2000) often form modules in community networks (Carstensen et al. 2016). For example, tubular fragrant white flowers provide sensory cues and restrict nectar access to long-tongued hawkmoths (Sazatornil et al. 2016). Similarly, rewards from flowers with poricidal anthers are restricted to sonicating bees, known as buzz-pollinators (Buchmann 1983).

Phenological differences can further reduce niche overlap of groups with shared functional traits (Encinas-Viso et al. 2012; Morente-López et al. 2018; Souza et al. 2018). If species partition resources across seasons, for example, modules may emerge in which species co-occurring in time are more likely to interact with each other than with potential partners occurring at other times of the year (Morente-López et al. 2018). Interaction frequencies between potential partners can also change throughout seasons. A pollinator that interacts strongly with a plant in the beginning of a season may weakly interact with it later in the season, indicating either changes in resource availability/quality or changes in pollinator abundances (CaraDonna and Waser 2020).

On the other hand, network structure of plant-pollinator communities is sometimes attributable to neutral processes, like species abundances (Olesen et al. 2007; Vázquez et al. 2009b). It is unclear if network dynamics of invaded plant-pollinator communities are driven by biological or neutral processes. Invasive species can alter the structure of mutualistic networks in recipient communities (de M. Santos et al. 2012; Vizentin-Bugoni et al. 2019), but we are only beginning to investigate the biological processes that shape novel communities. Particularly, an understanding of how introduced specialists influence network dynamics is lacking (Olesen et al. 2002). If introduced species are resource specialists in a novel community, then modularity may persist and niche overlap of functionally or phenologically different species should remain low. However, if introduced species are generalists that link modules together, then niche overlap between species will increase and network specialization would be low.

I examined a plant-pollinator network on an island previously invaded by two non-native tropical specialist pollinators, *Euglossa dilemma* (orchid bee) and *Centris nitida* (oil-collecting bee), and one generalist cosmopolitan pollinator, *Apis mellifera* (honeybee) in the Lower Florida Keys, USA. Exotic *E. dilemma* is an effective pollinator of an endangered buzz-pollinated legume endemic to the island. However, since arrival on the island, it is thought to have displaced a large and previously common buzz-pollinator, *Xylocopa micans* (Chapter 1). Buzzing, or sonicating, at high frequencies allows bees to access pollen concealed in poricidal anthers. Buzz-bees represent an important group of pollinators for nearly 15,000 species of plants, including many economically valuable crops, such as blueberries and tomatoes (Buchmann 1983). Many phylogenetically unrelated groups of bees can buzz at high frequencies while foraging at flowers (Cardinal et al. 2018; Vallejo-mar 2019). Both *E. dilemma* and *C. nitida* can buzz-pollinate, but *A. mellifera* cannot sonicate at flowers. This specialized relationship can ensure a higher rate of pollen transfer for a plant species by permitting only a specialized subset of flower visitors to release pollen from its flowers.

In this study, I investigated network structure and potential drivers of modularity and niche partitioning at hierarchical scales in the invaded network: the whole plant-flower visitor network and the buzz-bee subnetwork (a hierarchical subset of the whole network). The pollinator-centered buzz-bee subnetwork includes all medium to large sonicating bees and the flowering plants they visit, regardless of whether the plants require buzz-pollination. By controlling for morphology in the network (Vizentin-Bugoni et al. 2014; Traveset et al. 2015; Sazatornil et al. 2016; Zapata-Mesa et al. 2017), then I can better determine the role of phenology or neutral processes in the network structure of the invaded community. I expected that the functionally similar buzz-bees (native and exotic) partitioned floral resources by seasons to reduce competition, but that phenology alone would not be important for the broader community. I aimed to address the following questions: 1) Are the determinants of network structure dependent on the scale of the community evaluated? 2) What role do phenological overlap and species abundances play in network modularity and resource partitioning among flower visitors in the hierarchical networks? and 3) How do the exotic bees integrate into the recipient network alongside native bees?

METHODS

3.1 Study site

I surveyed the pine rockland flowering plant and flower visitor community on Big Pine Key in the lower Florida Keys (24.699°N, 81.376°W) within the National Key Deer Refuge. Pine rocklands are fire dependent ecosystems with an average fire return of three to ten years (Bergh and Wisby 1996), and occur only on a few islands in the Florida Keys, separated from pine rockland on mainland peninsular Florida by over 100 km. Vegetation is characterized by a sparse canopy of slash pine (*Pinus elliottii* var. *densa* Engelm.), thatch palms, and a diverse understory of flowering herbs, vines, and shrubs including *Chamaecrista lineata* var. *keyensis* (Pennell) H.S.Irwin & Barneby (Big Pine partridge pea), *Pentalinon luteum* (L.) B.F. Hansen & Wunderlin (wild allamanda), and *Byrsonima lucida* (Mill.) DC (locust berry). Seasonality in the lower Florida Keys is marked by distinct wet and dry seasons with modest seasonal temperature differences (Fig. 1b). During the 2019 rainy season, (June to October) Big Pine Key received 5 to 6 in. of monthly accumulated rainfall and 1 to 2 in. monthly throughout the dry season (November to May). Accumulated monthly rainfall during our study year was consistent with 30-year averages on the island (Fig. 1b; NOAA 2022).

3.2 Flower-visitor interaction sampling

I established 24 semi-permanent 30m x 30m plots on Big Pine Key to sample plant-pollinator interactions. To achieve a representative sample, plots were randomly stratified within pine rockland burn units by time since last burned (Chapter 3) and each plot was separated by distances greater than 200 m from each other. I sampled plots every five weeks, from March to early November 2019; this included the late dry season, the complete wet season, and the early dry season. Daily sampling occurred between 07:00 and 17:00.

I conducted a series of timed observations of all entomophilous flowering plants in each site to quantify interactions between plants and flower visitors. Active time searching for open flowers between observations was 20 minutes (not including observation time) - the time needed to navigate once through each 900m^2 site. In this design, sampling effort is dependent on abundances of plants flowering at the time of the survey. When open flowers were encountered, I conducted 5-minute timed observations to all visible open flowers within 1m^2 of each other. I recorded flower abundances and abundances of flower visitors during observations. In this method, visits to multiple flowers on a single plant were counted once, but each new plant visited in the watch was counted as a recorded visit. Only visitors contacting reproductive parts of flowers were included as flower visitors, though there was no attempt to assess pollen deposited. As such, we do not refer to flower visitors as pollinators, although some degree of pollination is a likely outcome for visitors included. I identified visitors to species or genus when possible or collected and preserved them for later identification. Sonicating behavior in bees was also observed in the field to reference against published literature. Voucher specimens are in the possession of B. Harris, for eventual deposit in the Florida State Museum of Arthropods.

3.3 Network design

3.3.1 Plant-flower visitor network

To study network structure of the invaded plant and flower-visitor community, I built a cumulative quantitative plant-visitor network from timed watches (Vázquez et al., 2005). Counts of visits to each plant species were used as a proxy for interaction strength (Vázquez et al. 2015). I aggregated total visits of each insect species at flowering plants across sites and sample sessions. Species with few interactions (low species degree) are often depicted as specialists (Bascompte et al. 2003), but low species degree can be an indicator of species rarity or an artifact of sampling, as opposed to true specialization (Vázquez et al. 2009a). Therefore, I removed plants with fewer than three visits (n = 15) and pollinators that visited fewer than three flowers (n = 5) from community data before analyzing networks (Bluthgen et al. 2006). Network-level, guild-level, and species-level metrics were estimated for species of interest using the bipartite package (Dormann et al. 2008) in R version 4.1.0.

3.3.2 Buzz-bee subnetwork

I compared observed network dynamics of the whole plant-flower-visitor community to that of the plant-buzz-bee sub-community. For the buzz-bee subnetwork, I subdivided the community to include only medium-large sonicating bees and the flowering plants that they visited; therefore, the subnetwork is pollinator-centered. Sonication was based on observed behavior at flowers and supplemented by published literature (Cardinal et al. 2018). All other species and interactions were removed. The buzz-bee subnetwork included the two tropical exotic bees (*E. dilemma* and *C. nitida*) among other native buzz-bees. The same indices calculated for the whole network were also calculated for the buzz-bee subnetwork.

3.4 Network dynamics

3.4.1 Network indices

I calculated community modularity (Q_W), or network compartmentalization, using the DIRTLPAwb+ algorithm (Beckett 2016). This algorithm uses visitation frequency to detect and assign subsets (modules) of species that interact more frequently with each other than with other potential partners in the network. Additionally, I calculated network specialization (H_2'), weighted connectance, and weighted nestedness (wNODF). H_2' is a standardized version of the Shannon index (H_2) which measures interaction partitioning among all species (Bluthgen et al. 2006). It ranges from 0 to 1, where 0 indicates complete specialization in the network, and 1 indicates that all flower visitors interact with all plants. Nestedness indicates if specialists interact with a subset of the species with which generalists interact. I used the weighted index of nestedness (wNODF) which is nestedness standardized by the marginal sums of the interaction matrix.

3.4.2 Guild-level indices

I calculated plant and flower visitor niche overlap and weighted partner diversity. The pollinator niche overlap index measures mean similarity in flower visitor interactions and is calculated as Bray-Curtis similarity. Values near 0 indicate no common use of flowers, and values near 1 indicate complete overlap. Weighted partner diversity is the mean Shannon diversity of interactions for each guild. Higher values indicate higher interaction diversity for plants or flower visitors.

3.4.3 Species-level indices

I calculated species-level metrics to determine their roles in the network. I calculated the standardized specialization index (d') to measure insect visitor specialization on floral resources (Bluthgen et al. 2006). Like the H_2' index that measures network specialization, d' values are also derived from the Shannon diversity index and estimate how likely a potential pollinator is to visit a plant considering the abundance of flower resources available in the community sampled (Bersier et al. 2002; Bluthgen et al. 2006). I provided independent estimates of flower abundances within plots. Values closer to 0 indicate generalization and those closer to 1 specialization on a single plant. I also determined if interactions between plants and flower visitors were stronger or weaker than expected by species abundances, using observed flower visits and an independent measure of flower abundances (Vaughan et al. 2017).

3.5 Null models

3.5.1 Species abundance null model

To assess the relevance of network indices, observed values should be evaluated against null models (Dormann et al. 2009). Specifically, null models should incorporate independent measures of species abundances that account for resources available and not just resources used (Vázquez et al. 2009b; Vaughan et al. 2017). I evaluated the significance of network, guild, and species-level indices using null models based on species abundances. Flower abundances were calculated independently from plant-pollinator surveys and were included as available resources regardless of whether flowers were visited. Flower visitor abundances were estimated from sums of visits (column sums). We generated an ensemble of 1000 null networks based on the independent measures of flowering plant abundances and flower visitor abundances using an algorithm developed in the package econullnetr (Vaughan et al. 2017) in R ver 4.1.0. Species degree was allowed to vary for species in the null model simulations.

Network and guild-level indices were evaluated for significance by comparing the observed value to the distribution of generated null model values. I report mean predicted values of null models, the upper and lower confidence levels (CL), and standardized effect sizes (SES). Effect sizes were calculated for all significance tests as follows (Gotelli and McCabe 2002):

$$\text{SES} = \frac{(\text{observed value} - \text{mean predicted value})}{\text{standard deviation of null model simulations}} \qquad \text{Eq. 1}$$

3.5.2 Phenology null model

I calculated a probability matrix of plants and flower visitors co-occurring in time. I first constructed a matrix of plant abundances per month and of visitor abundances per month and then multiplied the matrices together. Temporally non-overlapping plants and flower visitors in the resulting matrix contained zeros, while those co-occurring contained the product of their abundances (Vázquez et al. 2009b). The resulting phenology matrix was normalized so that the sum of all cells in the matrix equaled one, creating a probability matrix of monthly co-occurrence. I simulated 1,000 binary networks from the probability matrix as a null model of phenological overlap (Vázquez et al. 2009b). The phenology null model was used to test the significance of network modularity (Q_W) and niche overlap in flower visitors.

3.6 Phenology and module formation

We further tested the probability that species were assigned to their respective network modules based on their phenology using multinomial logistic regressions (Morente-López et al. 2018). Assigned module number was the response variable and the week of the first flower visits recorded for each plant species was the predictor variable. I used the R package *nnet* to fit the multinomial model (Venables and Ripley 2002). In this analysis, phenology start week depended on the first week I observed flower visits, not flowering initiation. I used likelihood ratio χ^2 tests to evaluate model fit. To visualize frequencies of flower activity for each module across the weeks of our study, we used spindle diagrams (Valverde et al. 2016; Morente-López et al. 2018). Weeks ranged from the 10th to the 42nd, encompassing the late dry season through the wet season to the beginning of the following dry season in early November.

RESULTS

We surveyed 73 plant species for 8,675 minutes (144.5 hours). After removing plants and flower visitors with fewer than three observed interactions, our resulting network consisted of 42 plants visited by 47 pollinator species in a combination of 269 unique links. We observed 2,187 individual insects (abundances) visiting 12,775 flowers. All flowering plants in the resulting plant-pollinator network were native to the Florida Keys. *Alysicarpus vaginalis* (Fabaceae) was the only exotic flowering plant in our plots but was removed because our threshold of more than two visits was not met. The three exotic pollinators were all medium to large bees in the family Apidae, including *Apis mellifera* (European honeybee), *Centris nitida* (shining oil-collecting bee), and *Euglossa dilemma* (orchid bee).

The buzz-bee subnetwork consisted of six medium to large bees that visited 21 flowering plant species in a combination of 42 unique links. I observed 683 buzz-bees visit 3,092 flowers. Abundances were not evenly distributed among bee species. The most abundant buzz-bees were the exotic *Euglossa dilemma* (orchid bees) and the native *Centris errans* (oil-collecting bee), of which 272 and 271 individuals, respectively, were observed at flowers. The least abundant bees were the native *Xylocopa micans* (large carpenter bee) and the exotic *Centris nitida* (exotic oil-collecting bee), which were represented by only nine and seven individuals, respectively.

3.7 Network structure and Neutral processes

3.7.1 Whole plant-pollinator community

The indices used to quantify topology of the whole plant-pollinator community were all significantly different between our observed network and that predicted by the null model of species abundances. The observed network was much more specialized, less connected, less nested, and consisted of fewer interaction links than predicted (Table III.1; Figure IIII.2). Network specialization (*H_2’*) had the largest divergence from the null model. The observed H_2’ score was 0.466, which was significantly more specialized than predicted (Table III.1; *SES* = 67.9, *p* < 0.0001). Specialization was likely driven by low pollinator niche overlap. Resource sharing among flower visitors was significantly lower than predicted by species abundances (Table III.2; *niche overlap* = 0.069, *SES* = 15, *p* <0.0001). On the other hand, observed niche overlap in plants was 0.104 and was only 1 standard deviation (or 84%) lower than predicted.

The three exotic bees (*Apis mellifera, Centris nitida,* and *Euglossa dilemma*) varied in their flower resource use. *Apis mellifera* was the most generalized species with the widest niche breadth (*d’* = 0.1) and the highest partner diversity (*partner diversity* = 2.60, *SES* = 5.4, *p* < 0.0001) of all pollinators except a native leafcutter bee*, Megachile brevis* (Table III.5). In contrast, *Euglossa dilemma* was the most specialized bee (*d’* = 0.40), followed by the large native carpenter bee *Xylocopa micans* (d’ = 0.39). Partner diversity was significantly lower for *E. dilemma* than predicted (*partner diversity* = 1.05; *SES* = -9.2, *p* < 0.0001; Table III.5). Lastly, specialization (d’ = 0.27) and partner diversity (Table II.5) was intermediate for the exotic *Centris nitida* bee and for *C. errans* (d’ = 0.26), a native congener of the exotic bee.

3.7.2 Buzz-bee subnetwork

The buzz-bee subnetwork shared similar network-level attributes to the whole plant-pollinator network from which it was produced (Table III.3; Figure IIII.3). The subnetwork was more specialized and modular and less connected and nested than expected. Pollinator niche overlap was also lower than predicted by the null model of plant abundances (*niche overlap* = 0.09, *SES* = -8.9, $p < 0.0001$). Conversely, partner diversity differed in strength and direction between the hierarchical networks. While observed values were higher than predicted for the whole network, partner diversity was lower in the subnetwork (*partner diversity* = 1.62, *SES* = -19.3, $p < 0.0001$) than predicted (Table III.4).

3.8 Modularity and Phenology

3.8.1 Whole plant-pollinator community

The whole plant-pollinator community was compartmentalized into six modules, and all three exotic bees, *Apis mellifera, Centris nitida*, and *Euglossa dilemma* belonged to modules separate from each other (Figure III.4a). The observed modularity (Q_W) for the weighted network was significantly higher ($Q_W = 0.52$; $z = 92.16$, $p < 0.0001$) than predicted from species abundances. Conversely, the phenology null model (the probability of plant and flower visitor activity overlapping each month) predicted a significantly more modular network than observed (Figure III.4b, $z = -19.0$, $p < 0.0001$). Weekly interaction frequency varied among modules, but most activity within the six modules spanned all seasons (Figure III.4c). Additionally, the multinomial logistic regression indicated that seasonal start of flower visitor activity for each plant species was not significant to module formation of the whole plant-pollinator network (Likelihood Ratio tests: $\chi^2 = 6.8$, $df = 5$, $p > 0.1$). Niche overlap in flower visitors was slightly lower than predicted by overlapping phenology (Table III.2; $z = -1.95$, $p < 0.05$).

3.8.2 Buzz-pollinator subnetwork

The buzz-bee subnetwork was compartmentalized into four modules. Three of the six buzz-bees, including *Euglossa dilemma*, formed their own respective modules (Fig. III.5a). A fourth module contained two native buzz-bees (*Xylocopa micans* and *Centris errans*) and the exotic congener *C. nitida* (Figure III.5a, Module 1). Modularity for the weighted subnetwork was slightly higher than the whole network and was significantly higher than predicted by species abundances ($Q_W = 0.55$; $z = 34.0$; $p < 0.0001$).

Phenology was essential to module assignment for the subnetwork. Observed modularity was predicted solely by the probability of monthly co-occurrence of plants and pollinators ($Q_W = 0.55$, $z = 0.196$, $p > 0.1$). Modules 1-3 contained mostly specialized bees with high specialization scores (d'). Module 4 included only *Melissodes communis* (native long-horned bees), which was more generalized ($d' = 0.18$) than the other buzz-bees. Weekly interactions appear to be partitioned across the four modules (Figure III.5c). Multinomial logistic regression indicated that onset of buzz-bee activity at flowers was a significant predictor of module formation ($\chi^2 = 19.3$, $df = 3$, $p < 0.0001$). Buzz-bee niche overlap was also predicted by phenology (*niche overlap* = 0.087, $Z = 0.064$, $p > 0.1$).

DISCUSSION

The structure of the plant-pollinator network in the pine rockland forest of the lower Florida Keys was not driven by neutral processes. The whole network was more specialized and modular than expected if interactions were determined only by species abundances. The network was also less connected and nested than predicted. In the tropics, where warm temperatures provide year-round productivity, mutualistic networks tend to be more modular, specialized, and nested than previously described in temperate regions (Sonne et al. 2020). Longer seasonal activity increases diversity and network resilience by increasing opportunities for niche partitioning (Encinas-Viso et al. 2012).

Although high modularity and specialization is a common feature of many large networks (Olesen et al. 2007), contributions of connectedness and nestedness to network structure are less straightforward. Connectedness (most species interact) and nestedness (specialists are thought to interact with a subset of generalists) were traditionally thought to increase species persistence and network stability (Bascompte et al. 2003; Bascompte and Jordano 2007). However, those early studies consisted of qualitative interactions instead of quantitative ones weighted by interaction frequency, and species can adapt their foraging behavior by shifting resource use based on resource availability (Chacoff et al., 2018). When adaptive foraging is considered, such as in weighted networks, niche partitioning of floral resources increases and connectedness and nestedness are less prevalent (Valdovinos et al. 2016). High niche partitioning was also suggested as a driver of specialization and low nestedness in antagonistic flower-florivore networks (Cordeiro et al. 2020).

The plant-buzz bee subnetwork shared similar attributes to the larger community, but drivers of network dynamics were different between the two. Indeed, high modularity, specialization, and niche partitioning within flower visitor species were observed in both the whole network and the buzz-bee sub-network. Neither were shaped by neutral processes, but phenology played different roles in explaining the dynamics of the hierarchical networks. Modularity in the buzz-bee subnetwork was predicted by phenological overlap in plants and bees and by the onset of interaction activity across the year. For the larger community, the phenology null model predicted higher modularity than was observed, and modules were not formed based on the onset of visitor activity at flowers. Buzz-bees strongly partitioned niches based on phenological overlap with the flowers available. Phenology appeared to also play a modest role in pollinator niche partitioning for the larger community. Few studies have compared drivers of network attributes between a whole community and a hierarchical subset. However, phenology seems to be a critical driver of modularity for small and specialized networks (Gonzalez and Loiselle 2016) in the Arctic where seasonal activity is limited, and seasonal changes are abrupt (Morente-López et al. 2018; Ramos–Jiliberto et al. 2018).

Functional morphology may be more important than phenology when phenological forbidden links are not considered and *vice versa* (Vázquez et al. 2009b). In the larger yearly network, three of six buzz-bees were contained in one module, while the exotic orchid bee, *Euglossa dilemma*, was assigned a module that mostly contained butterflies. Considering *E. dilemma'*s exceptionally long-tongue (Fig. 7d), overlap with butterflies for nectar plants is not surprising. However, in the buzz-bee subnetwork, where morphological differences in flower visitors are limited, modularity and niche partitioning is driven by phenology. In Brazilian forests, several species of oil-provisioning plants in the family Malphigiaceae exhibit sequential flowering over short phenophases, reducing temporal overlap and competition for oil-collecting pollinators (Barônio and Torezan-Silingardi 2017). Indeed, the oil-collecting bees in our buzz-bee network, *Centris errans* and the exotic *Centris nitida*, forage in the late dry season when the oil-provisioning *Byrsonima lucida* is at its flowering peak. *Centris* bees are also frequent visitors of the buzz-pollinated *Senna mexicana* var. *keyensis,* which coincides in flowering with *B. lucida*. Conversely, the exotic *Euglossa dilemma* interacts most frequently with the buzz-pollinated *Chamaecrista lineata* var. *keyensis*, which is most active in the peak rainy season.

The three exotic bees in the flower-visitor network did not exhibit similar foraging behavior. In fact, the exotic bees were positioned across both ends of the generalization-specialization spectrum. *Apis mellifera* was an extreme generalist, *Euglossa dilemma* was an extreme specialist, and *Centris nitida* was intermediate in specialization. All three exotic bees were in separate modules in the whole network, and *Centris* spp. and *E. dilemma* were in separate modules in the buzz-bee subnetwork, indicating differences in foraging. Additionally, the abundances of the three bees were different. *Euglossa dilemma* and *A. mellifera* were relatively frequent flower foragers, but *Centris nitida* was uncommon in the network. Interestingly, *Centris errans*, the native conger, was as abundant as *E. dilemma*. While the native *C. errans* and exotic *E. dilemma* largely partitioned floral resources, overlap between the two *Centris* bees was high. These combinations of trait differences among the three exotic bees suggest that generalist foraging is not universal among invasive species.

Modularity and pollinator niche partitioning was unexpected in the small sub-network with two exotic bees. Invaded flower-visitor networks previously described are often dominated by generalist exotic bees, like *Apis mellifera*, with high foraging overlap with other pollinators (de M. Santos et al. 2012; Aslan et al. 2019). In a study of Brazilian flower-visitor networks, *Apis mellifera* was abundant at flowers and held a central role in connecting modules (de M. Santos et al. 2012). *Apis mellifera* plays a similar generalist role in the Big Pine Key flower-visitor network. Conversely, the two exotic buzz-bees in our study were more specialized. A Hawaiian seed-dispersal network composed primarily of novel interactions by exotic birds also appeared to be highly modular and specialized (Vizentin-Bugoni et al. 2019). Those authors suggest that long evolutionary history may not be necessary for complexity in seed-dispersal networks, and our findings agree.

The results of this study suggest that network attributes may be dependent on the scale and extent of the community evaluated. The underlying mechanisms driving network structure may shift in strength or direction at different scales, such that relative contributions of different mechanisms to network complexity vary. However, the significance of network scale to differences in network structure is not novel. Network dynamics can vary depending on the temporal scale chosen, from hourly networks within a day to yearly networks within century (CaraDonna and Waser 2020; CaraDonna et al. 2020). In this study, phenology is a critical driver of network modularity in the buzz-bee network, because morphology was restricted, but not in the larger network that includes many morphologically different visitors.

Indeed, analyzing subsets of communities may be essential to determine drivers of community assembly among functional equivalents or those occurring in the same seasons. However, there are potential drawbacks to hierarchical subsets that influence interpretation of certain levels of the network. For example, plants in hummingbird-plant networks (Dalsgaard et al. 2009) and in our buzz-bee-plant network are visited by other pollinators that are excluded from analyses (Izquierdo-Palma et al. 2021). Excluding interactions is common in analysis of specialized networks, such as hummingbird (Dalsgaard et al. 2009), hawkmoth (Sazatornil et al. 2016), or bird pollination networks (Gonzalez and Loiselle 2016). In our pollinator-centered buzz-bee network, all interactions of buzz-bees were considered, including plants that do not require buzz-pollination. Only three plants from the buzz-bee network have poricidal anthers: *Senna mexicana* var. *chapmannii, Chamaecrista lineata* var. *keyensis,* and *Solanum erianthum*. Of these, *S. chapmannii* is state endangered and *C. keyensis* is federally endangered. However, if we restricted the subnetwork to only plants with poricidal anthers and the buzz-bees that pollinate them, then modularity would be completely driven by phenology, considering that flowering does not overlap among them.

Partitioning of resources can promote species co-existence by reducing competition for the same rewards. Invasions by specialist pollinators may have more rapid and intense effects on native species with shared attributes if those species are vying for the same flowers. In the case of our study, *Euglossa dilemma* shares few resources with other medium to large sonicating bees. *E. dilemma* has evidently displaced, *Xylocopa micans,* a bee of comparable morphology from certain shared flowering plants, but perhaps other bees utilizing the same resources would be less affected if those bees also forage from many other resources, such as the case in the generalist foraging behavior of *Melissodes communis*, long horned-bees. Modularity driven by phenology may be relevant for post-disturbance recovery and community resiliency. Because interacting partners in modules act nearly independently from those in other modules, each specialized subnetwork may profit from differences in phenology that would otherwise affect species with shared morphology. Disturbances like hurricanes and fires that are relatively common in pine rocklands of Big Pine Key (Saha et al. 2011) are often seasonal, and if subsets of the community specialize on season, then negative effects of disturbance may be isolated among modules (Olesen et al. 2007).

CONCLUSION

Phenology was the primary driver of network modularity and pollinator niche overlap in the buzz-bee subnetwork, in which pollinators shared similar functional attributes. For the whole community, phenology was only slightly important for pollinator niche overlap and largely underpredicted network modularity. The idea that network attributes are scale-dependent is not new; this trend has been detected in almost all mutualistic networks, including plant-pollinator (Chacoff et al. 2012), seed-dispersal (Costa et al. 2016), and ant-extrafloral nectary networks (Falcão et al. 2016). However, these studies investigated differences in sampling method (Gibson et al. 2011), sampling size, or type of network type (quantitative or qualitative). To our knowledge, this is the first study to evaluate differences in drivers of network dynamics in a hierarchical network consisting of a whole community and a specialized subset. The relatively simple community of flowering plants and flower visitors of pine rocklands invaded by several different bees provided an excellent opportunity to examine these differences.

LITERATURE CITED

Armbruster WS, Fenster C, Dudash M (2000) Pollination “principles” revisited: specialization, pollination syndromes, and the evolution of flowers. *The Scandanavian Association for Pollination Ecology* 39:179–200

Aslan CE, Shiels AB, Haines W, Liang CT (2019) Non-native insects dominate daytime pollination in an elevation Hawaiian dryland ecosystem. *Am J Bot* 106:313–324. https://doi.org/10.1002/ajb2.1233

Barônio GJ, Torezan-Silingardi HM (2017) Temporal niche overlap and distinct bee ability to collect floral resources on three species of Brazilian Malpighiaceae. *Apidologie* 48:168–180. https://doi.org/10.1007/s13592-016-0462-6

Bascompte J, Jordano P (2014) Mutualistic Networks. Monographs in Population Biology (53). Princeton University Press

Bascompte J, Jordano P (2007) Plant-Animal Mutualistic Networks: The Architecture of Biodiversity. *Annu Rev Ecol Evol Syst*. https://doi.org/10.1146/annurev.ecolsys.38.091206.095818

Bascompte J, Jordano P, Melian CJ, Olesen JM (2003) The nested assembly of plant-animal mutualistic networks. *Proc Natl Acad Sci* https://doi.org/10.1073/pnas.1633576100

Bastolla U, Fortuna MA, Pascual-García A, et al (2009) The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature.* https://doi.org/10.1038/nature07950

Beckett SJ (2016) Improved community detection in weighted bipartite networks. R Soc Open Sci. https://doi.org/10.1098/rsos.140536

Bergh C, Wisby J (1996) Fire History of Lower Keys Pine Rocklands. 296–3880

Bersier L-F, Banasek-Richter C, Cattin M-F (2002) Quantitative descriptors of food-web matrices. *Ecology* 23:2394–2407. https://doi.org/https://doi.org/10.1890/0012-9658(2002)083[2394:QDOFWM]2.0.CO;2

Bluthgen N, Menzel F, Blüthgen N (2006) Measuring specialization in species interaction networks. *BMC Evol Biol* 12:. https://doi.org/10.1186/1472-6785-6-9

Buchmann SL (1983) Buzz-pollination in angiosperms. In: CE J, RJ L (eds) Handbook of experimental pollination biology. Scientific and Academic Editions, New York, NY, US, pp 73–113

CaraDonna PJ, Burkle LA, Schwarz B, et al (2020) Seeing through the static: the temporal dimension of plant–animal mutualistic interactions. *Ecol Lett* 24:149–161. https://doi.org/10.1111/ele.13623

CaraDonna PJ, Waser NM (2020) Temporal flexibility in the structure of plant–pollinator interaction networks. *Oikos* 129:1369–1380. https://doi.org/10.1111/oik.07526

Cardinal S, Buchmann SL, Russell AL (2018) The evolution of floral sonication, a pollen foraging behavior used by bees (Anthophila). *Evolution* (N Y) 72:590–600. https://doi.org/10.1111/evo.13446

Carstensen DW, Sabatino M, Morellato LPC (2016) Modularity, pollination systems, and interaction turnover in plant-pollinator networks across space. *Ecology* 97:1298–1306. https://doi.org/10.1890/15-0830.1

Chacoff NP, Vázquez DP, Lomáscolo SB, et al (2012) Evaluating sampling completeness in a desert plant-pollinator network. *Journal of Animal Ecology* 81:190–200. https://doi.org/10.1111/j.1365-2656.2011.01883.x

Cordeiro J, de Oliveira JHF, Schmitz HJ, Vizentin-Bugoni J (2020) High niche partitioning promotes highly specialized, modular and non-nested florivore–plant networks across spatial scales and reveals drivers of specialization. *Oikos* 619–629. https://doi.org/10.1111/oik.06866

Costa JM, da Silva LP, Ramos JA, Heleno RH (2016) Sampling completeness in seed dispersal networks: When enough is enough. *Basic Appl Ecol* 17:155–164. https://doi.org/10.1016/j.baae.2015.09.008

Dalsgaard B, Martín González AM, Olesen JM, et al (2009) Plant-hummingbird interactions in the West Indies: Floral specialisation gradients associated with environment and hummingbird size. *Oecologia* 159:757–766. https://doi.org/10.1007/s00442-008-1255-z

de M. Santos G, Aguiar CML, Genini J, et al (2012) Invasive Africanized honeybees change the structure of native pollination networks in Brazil. *Biol Invasions* 14:2369–2378. https://doi.org/10.1007/s10530-012-0235-8

Dormann CF, Gruber B, Fründ J (2008) Introducing the bipartite package: analysing ecological networks. R News 8:8–11

Encinas-Viso F, Revilla TA, Etienne RS (2012) Phenology drives mutualistic network structure and diversity. *Ecol Lett* 15:198–208. https://doi.org/10.1111/j.1461-0248.2011.01726.x

Falcão JCF, Dáttilo W, Rico-Gray V (2016) Sampling effort differences can lead to biased conclusions on the architecture of ant – plant interaction networks. *Ecological Complexity* 25:44–52. https://doi.org/10.1016/j.ecocom.2016.01.001

Gibson RH, Knott B, Eberlein T, Memmott J (2011) Sampling method influences the structure of plant-pollinator networks. *Oikos* 120:822–831. https://doi.org/10.1111/j.1600-0706.2010.18927.x

Gonzalez O, Loiselle BA (2016) Species interactions in an andean bird-flowering plant network: Phenology is more important than abundance or morphology. *PeerJ* 2016:1–22. https://doi.org/10.7717/peerj.2789

Gotelli NJ, McCabe DJ (2002) Species co-occurrence: A meta-analysis of J. M. Diamond’s assembly rules model. *Ecology* 83:2091–2096. https://doi.org/10.1890/0012-9658(2002)083[2091:SCOAMA]2.0.CO;2

Hui C, Richardson DM (2017) Invasion dynamics. Oxford University Press, Oxford, United Kingdom

Hui C, Richardson DM, Landi P, et al (2016) Defining invasiveness and invasibility in ecological networks. *Biol Invasions* 18:971–983. https://doi.org/10.1007/s10530-016-1076-7

Izquierdo-Palma J, del Coro Arizmendi M, Lara C, Ornelas JF (2021) Forbidden links, trait matching and modularity in plant-hummingbird networks: Are specialized modules characterized by higher phenotypic floral integration? *PeerJ* (9) https://doi.org/10.7717/peerj.10974

Krishna A, Guimaraes JPR, Jordano P, Bascompte J (2008) A neutral-niche theory of nestedness in mutualistic networks. *Oikos*. https://doi.org/10.1111/j.1600-0706.2008.16540.x

Morente-López J, Lara-Romero C, Ornosa C, Iriondo JM (2018) Phenology drives species interactions and modularity in a plant - Flower visitor network. *Sci Rep* 8:1–11. https://doi.org/10.1038/s41598-018-27725-2

Novoa A, Richardson DM, Pys P, et al (2020) Invasion syndromes : a systematic approach for predicting biological invasions and facilitating effective management. *Biol Invasions* 22:1801–1820. https://doi.org/10.1007/s10530-020-02220-w

Olesen JM, Bascompte J, Dupont YL, Jordano P (2007) The modularity of pollination networks. *Proc Natl Acad Sci* 104:19891–19896. https://doi.org/10.1073/pnas.0706375104

Olesen JM, Eskildsen LI, Venkatasamy S (2002) Invasion of pollination networks on oceanic islands: Importance of invader complexes and endemic super generalists. *Divers Distrib* 8:181–192. https://doi.org/10.1046/j.1472-4642.2002.00148.x

Olesen JM, Stefanescu C, Traveset A (2011) Strong, Long-Term Temporal Dynamics of an Ecological Network. *PLoS One* 6:2–6. https://doi.org/10.1371/journal.pone.0026455

Pascal M, le Guyader H, Simberloff DS (2010) Biological invasions and the conservation of biodiversity.

Ramos–Jiliberto R, Moisset de Espanés P, Franco–Cisterna M, et al (2018) Phenology determines the robustness of plant–pollinator networks. *Sci Rep* 8:1–10. https://doi.org/10.1038/s41598-018-33265-6

Saha S, Bradley KA, Ross MS, et al (2011) Hurricane effects on subtropical pine rocklands of the Florida Keys. *Clim Change*. https://doi.org/10.1007/s10584-011-0081-1

Sanders NJ, Gotelli NJ, Heller NE, Gordon DM (2003) Community disassembly by an invasive species. *Proc Natl Acad Sci* 100:2474–2477

Sazatornil FD, Moré M, Benitez-Vieyra S, et al (2016) Beyond neutral and forbidden links: morphological matches and the assembly of mutualistic hawkmoth–plant networks. *Journal of Animal Ecology* 85:1586–1594. https://doi.org/10.1111/1365-2656.12509

Sonne J, Vizentin-Bugoni J, Maruyama PK, et al (2020) Ecological mechanisms explaining interactions within plant-hummingbird networks: Morphological matching increases towards lower latitudes. *Proceedings of the Royal Society*: Biological Sciences 287:. https://doi.org/10.1098/rspb.2019.2873

Souza CS, Maruyama PK, Aoki C, et al (2018) Temporal variation in plant–pollinator networks from seasonal tropical environments: Higher specialization when resources are scarce. *Journal of Ecology* 106:2409–2420. https://doi.org/10.1111/1365-2745.12978

Thébault E, Fontaine C (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* (1979) 853–856. https://doi.org/10.1126/science.1188510

Traveset A, Olesen JM, Nogales M, et al (2015) Bird-flower visitation networks in the Galápagos unveil a widespread interaction release. *Nat Commun* 6:. https://doi.org/10.1038/ncomms7376

Traveset A, Richardson DM (2014) Mutualistic Interactions and Biological Invasions. *Annu Rev Ecol Evol Syst* 45:89–113. https://doi.org/10.1146/annurev-ecolsys-120213-091857

Traveset A, Tur C, Trøjelsgaard K, et al (2016) Global patterns of mainland and insular pollination networks. *Global Ecology and Biogeography* 25:880–890. https://doi.org/10.1111/geb.12362

Valdovinos FS, Brosi BJ, Briggs HM, et al (2016) Niche partitioning due to adaptive foraging reverses effects of nestedness and connectance on pollination network stability. *Ecol Lett* 19:1277–1286

Vallejo-mar M (2019) Buzz pollination: studying bee vibrations on flowers. *New Phytologist* 224:1068–1074. https://doi.org/10.1111/nph.15666

Valverde J, Gómez JM, Perfectti F (2016) The temporal dimension in individual-based plant pollination networks. *Oikos* 125:468–479. https://doi.org/10.1111/oik.02661

Vaughan IP, Gotelli NJ, Memmott J, et al (2017) econullnetr: An r package using null models to analyse the structure of ecological networks and identify resource selection. *Methods Ecol Evol* 1–6. https://doi.org/10.1111/2041-210X.12907

Vázquez DP, Bluthgen N, Cagnolo L, Chacoff NP (2009a) Uniting pattern and process in plant-animal mutualistic networks: A review. *Ann Bot* 103:1445–1457. https://doi.org/10.1093/aob/mcp057

Vázquez DP, Chacoff NP, Cagnolo L (2009b) Evaluating multiple determinants of the structure of plant-animal mutualistic networks. *Ecology*. https://doi.org/10.1890/08-1837.1

Vázquez DP, Ramos-Jiliberto R, Urbani P, Valdovinos FS (2015) A conceptual framework for studying the strength of plant-animal mutualistic interactions. *Ecol Lett* 18:385–400. https://doi.org/10.1111/ele.12411

Venables WN, Ripley BD (2002) Modern Applied Statistics with S, Fourth edi. Springer

Vizentin-Bugoni J, Maruyama PK, Sazima M (2014) Processes entangling interactions in communities: Forbidden links are more important than abundance in a hummingbird-plant network. *Proceedings of the Royal Society: Biological Sciences* 281:. https://doi.org/10.1098/rspb.2013.2397

Vizentin-Bugoni J, Tarwater CE, Foster JT, et al (2019) Structure, spatial dynamics, and stability of novel seed dispersal mutualistic networks in Hawai'i. *Science.* 364(6435): 78-82. https://doi.org/10.1126/science.aau8751

Zapata-Mesa N, Montoya-Bustamante S, Murillo-García OE (2017) Temporal variation in bat-fruit interactions: Foraging strategies influence network structure over time. *Acta Oecologica* 85:9–17. https://doi.org/10.1016/j.actao.2017.09.003

TABLES

Table III.1 Standard effect size (S.E.S) and confidence levels (C.L.) of the observed network-level indices for the weighted flower-visitor network compared to that predicted by the null model of flowering plant abundances in pine rockland of Big Pine Key, FL. (N.S. = not significant; * = < 0.05; ** = < 0.01; *** = < 0.001; **** = < 0.0001).

Network Index	Observed	Predicted	Lower.CL	Upper.CL	S.E.S.	
wNODF	22.73	46.73	42.46	51.03	-10.90	****
Linkage Density	6.31	8.70	8.52	8.87	-27.50	****
wConnectance	0.07	0.13	0.12	0.13	-16.40	****
Interaction Evenness	0.60	0.64	0.63	0.65	-5.20	****
H_2'	0.47	0.15	0.14	0.16	67.90	****

Table III.2. Standard effect size (SES) and confidence levels (CL) of the observed trophic-level indices for the weighted flower-visitor network compared to that predicted by the null model of flowering plant abundances in pine rockland of Big Pine Key, FL. Significance of P-value calculated from two-tailed Z-scores (N.S. = not significant; * = < 0.05; ** = < 0.01; *** = < 0.001; **** = < 0.0001).

Pollinators	Observed	Null	Lower CL	Upper CL	SES	
Niche Overlap	0.07	0.18	0.16	0.19	-14.93	****
Partner Diversity	2.59	2.41	2.36	2.47	6.43	****

Plants						
Niche Overlap	0.10	0.12	0.09	0.14	-1.00	N.S.
Partner Diversity	1.62	2.84	2.83	2.85	-230	****

Table III.3. Standard effect size (SES) and confidence levels (CL) of the observed network indices for the weighted buzz-pollinator subnetwork compared to that predicted by the null model of flowering plant abundances in pine rockland of Big Pine Key, FL. (N.S. = not significant; * = < 0.05; ** = < 0.01; *** = < 0.001; **** = < 0.0001).

Buzz-network Index	Observed	Null	Lower.CL	Upper.CL	SES	
wNODF	25.16	49.60	42.30	57.01	-6.20	****
Linkage Density	2.48	4.51	4.26	4.79	-15.20	****
wConnectance	0.08	0.17	0.15	0.18	-10.40	****
Interaction Evenness	0.47	0.64	0.62	0.66	-17.60	****
H_2'	0.72	0.28	0.25	0.31	29.30	****

Table III.4. Confidence levels (CL) and standard effect sizes (SES) of the observed buzz-pollinator indices for the weighted buzz-pollinator network compared to that predicted by the null model of flowering plant abundances in pine rockland of Big Pine Key, FL. (N.S. = not significant; * = < 0.05; ** = < 0.01; *** = < 0.001; **** = < 0.0001).

Buzz-Pollinators	Observed	Null	Lower.CL	Upper.CL	SES	
Niche Overlap	0.09	0.22	0.19	0.25	-8.95	****
Partner Diversity	1.62	2.67	2.88	3.09	-19.25	****

Table II.5. Confidence levels (CL) and Standard effect sizes (SES) of observed and predicted Partner Diversity Index of all flower visitors in the pine rockland plant and flower visitor network on Big Pine Key, Florida. Flower visitors are indicated by a combination of the first three letters of their generic epithet and the first three letters of their specific epithet. (N.S. = not significant; * = < 0.05; ** = < 0.01; *** = < 0.001; **** = < 0.0001).

Pollinator species	Observed	Null	Lower CL	Upper CL	SES	
APIMEL	2.600	1.894	1.789	1.995	13.484	****
MEGBRE	2.781	2.022	1.904	2.134	12.706	****
MELCOM	2.150	1.670	1.505	1.824	5.708	****
EPHBRU	1.440	1.088	0.932	1.242	4.476	****
MEGADD	1.236	0.631	0.206	0.973	3.423	***
MEGGEO	2.141	1.887	1.725	2.038	3.180	***
MEGMEN	1.366	0.846	0.536	1.199	3.070	**
PSECLA	1.930	1.480	1.124	1.776	2.660	**
ANTNOT	2.112	1.753	1.399	2.075	2.102	*
LASSUR	2.138	2.053	1.970	2.140	1.942	NS
AGRVAN	1.386	0.911	0.000	1.386	1.443	NS
OCYFUS	1.586	1.361	0.925	1.778	1.045	NS
CERDUP	1.772	1.602	1.240	1.970	0.899	NS
EURLIS	1.099	0.942	0.637	1.099	0.699	NS
COESOL	1.653	1.620	1.270	1.919	0.204	NS
Campsomeris sp2	0.637	0.589	0.000	1.099	0.190	NS
Trichopoda sp1	1.040	1.039	0.562	1.386	0.003	NS
CENNIT	1.255	1.350	0.900	1.733	-0.390	NS
TRIRUF	0.000	0.094	0.000	0.693	-0.395	NS
Campiglossa sp1	0.000	0.154	0.000	0.673	-0.604	NS
STRIST	0.637	0.857	0.000	1.099	-0.731	NS
Vespidae sp1	0.000	0.302	0.000	0.693	-0.877	NS
XYLMIC	0.736	1.085	0.377	1.733	-1.000	NS

PACNAS	0.000	0.420	0.000	0.693	-1.240	NS
HYLFOR	0.000	0.248	0.000	0.535	-1.661	NS
PHOAGA	0.500	1.013	0.500	1.609	-1.802	NS
Crabronidae sp1	0.000	0.554	0.000	0.693	-1.993	*
LEPCAS	0.000	0.563	0.000	0.693	-2.077	*
Polistes sp1	1.115	1.612	1.180	2.018	-2.268	*
MEGPRU	1.491	1.730	1.528	1.935	-2.385	*
ASBCAP	0.000	0.858	0.000	1.332	-2.582	**
HEMCER	0.796	1.476	0.796	1.946	-2.597	**
LARSUC	0.869	1.305	0.959	1.610	-2.621	**
PACERY	1.434	1.818	1.570	2.089	-2.846	**
WALOTH	1.128	1.693	1.272	2.069	-2.911	**
ZETSLO	1.351	1.856	1.531	2.137	-3.130	**
CENERR	0.884	1.048	0.955	1.143	-3.260	***
AUGANO	1.276	1.758	1.477	2.038	-3.303	***
MEGBAH	0.224	1.117	0.790	1.467	-5.089	****
EUGDIL	1.191	1.925	1.799	2.047	-11.366	****

FIGURES

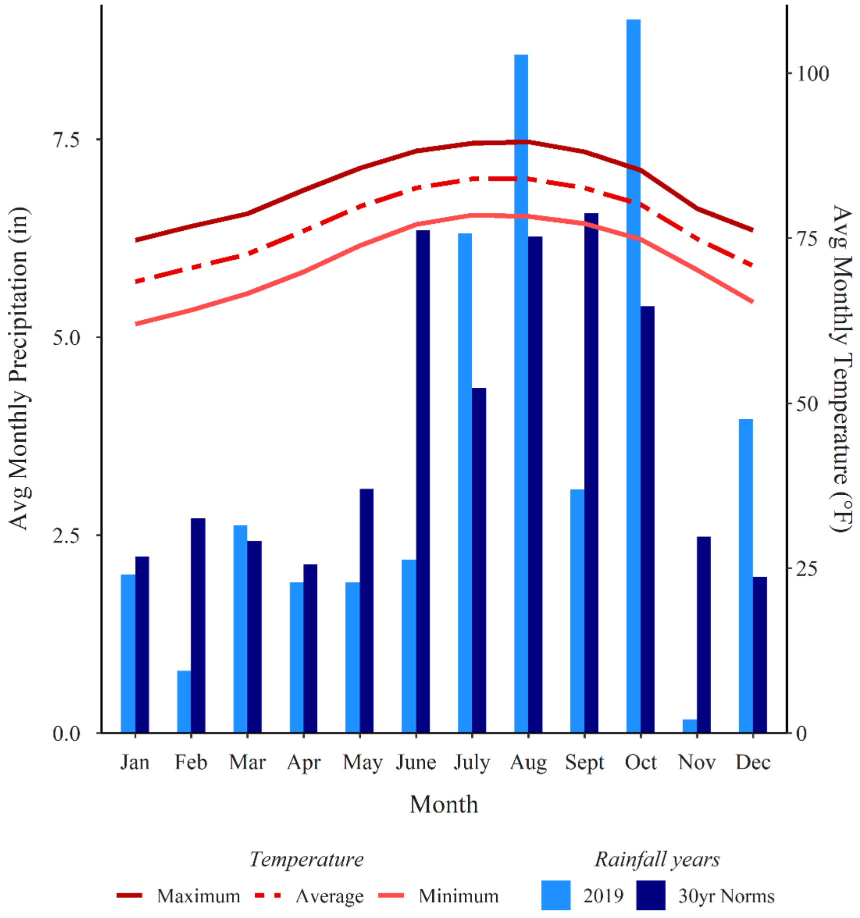

Figure IIII.1. Climatograph of 2019 average monthly temperatures (°F) and precipitation (in.) on Big Pine Key, FL and adjacent islands compared to 30-year averages (NOAA, 2021). Monthly averages calculated from daily averages.

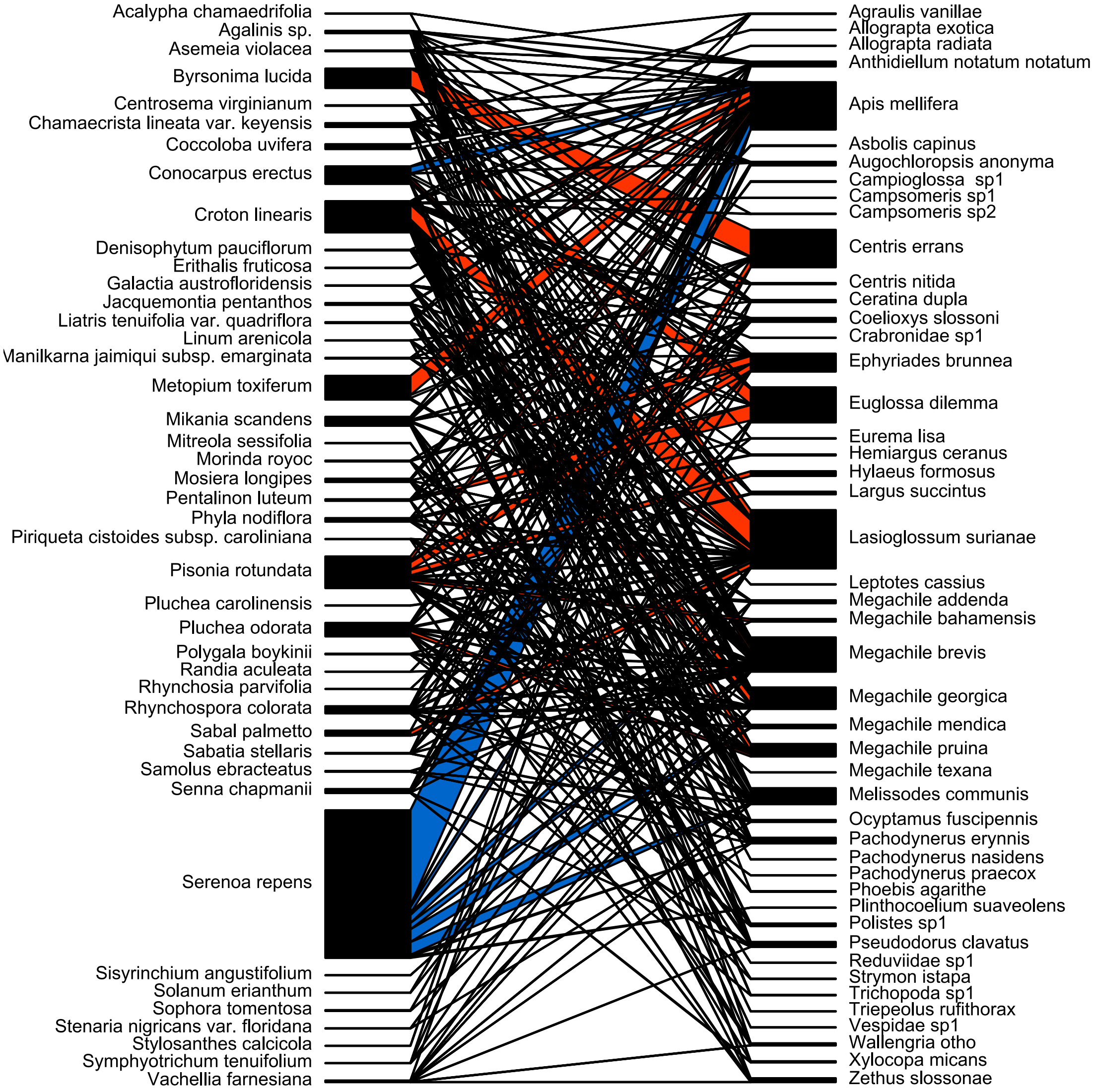

Figure IIII.2. Flower-visitor network on Big Pine Key, FL. Bar heights indicate abundance of flowers (left) and abundance of buzz-bees (right). Edge widths are equal to relative interaction frequency, with red links as statistically stronger, blue links as weaker, and grayish links as expected from a null model (100 simulations) of flower abundances.

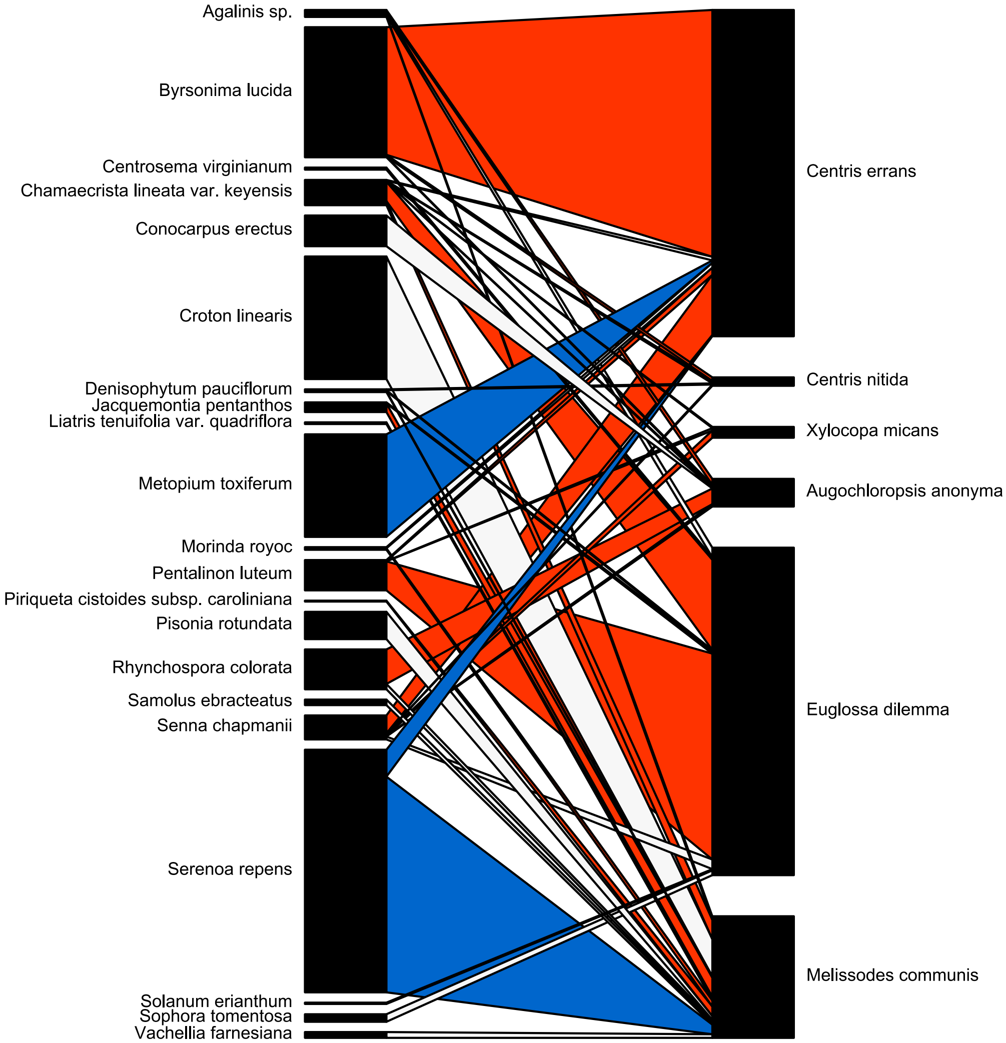

Figure IIII.3. Buzz-bee bipartite network on Big Pine Key, FL. Bar heights indicate abundance of flowers (left) and abundance of buzz-bees (right). Edge widths are equal to relative interaction frequency, with red links as statistically stronger, blue links as weaker, and grayish links as expected from a null model (100 simulations) of flower abundances.

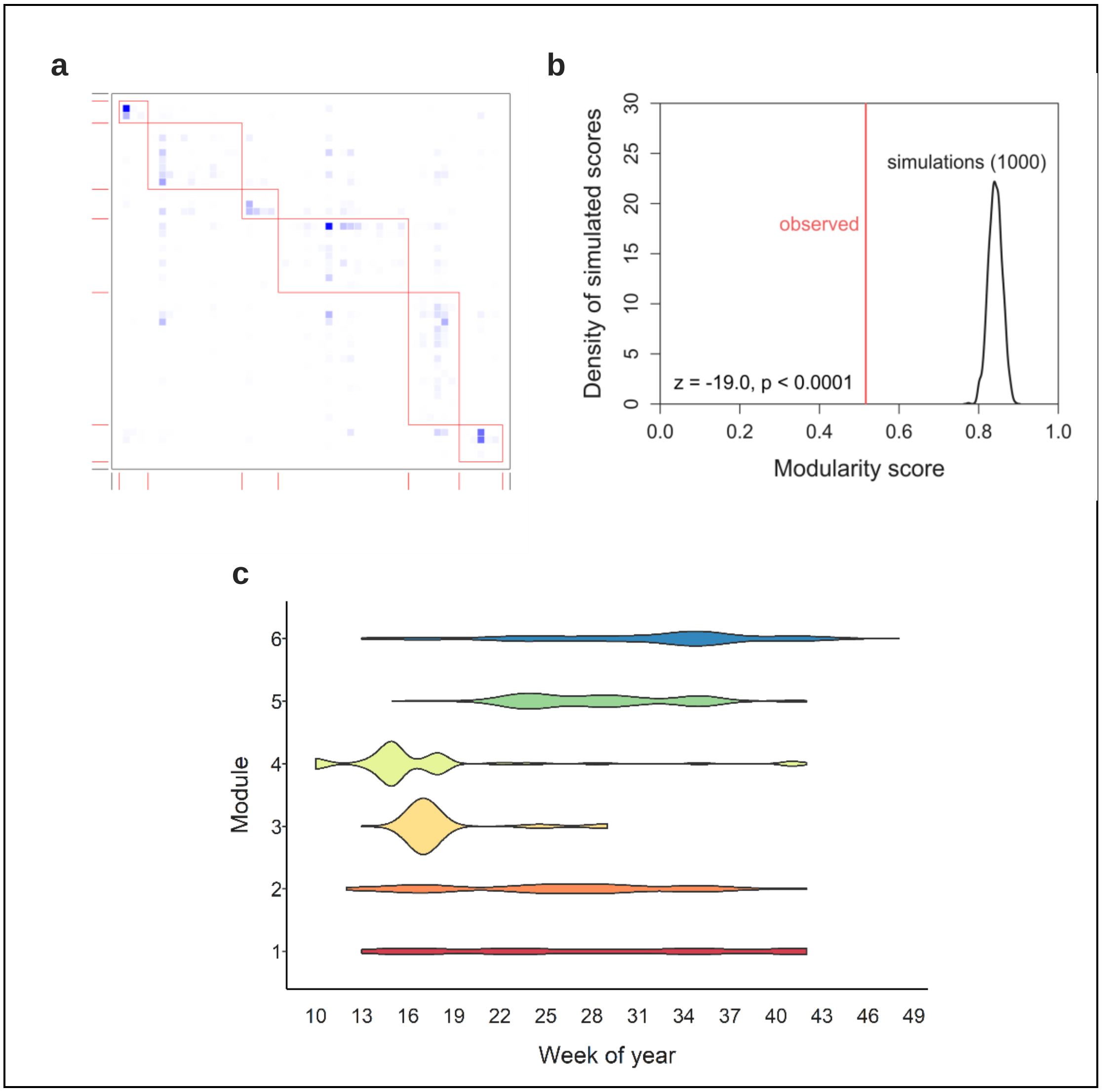

Figure III.4. Modularity and pollinator niche overlap of the whole flower-visitor network on Big Pine Key, FL. A) Observed network compartmentalization of plants and flower visitors that are more likely to interact among each other than with members of other modules B) Observed modularity index and C) pollinator niche-overlap compared to that predicted by the null model of phenological overlap (simulations = 100).

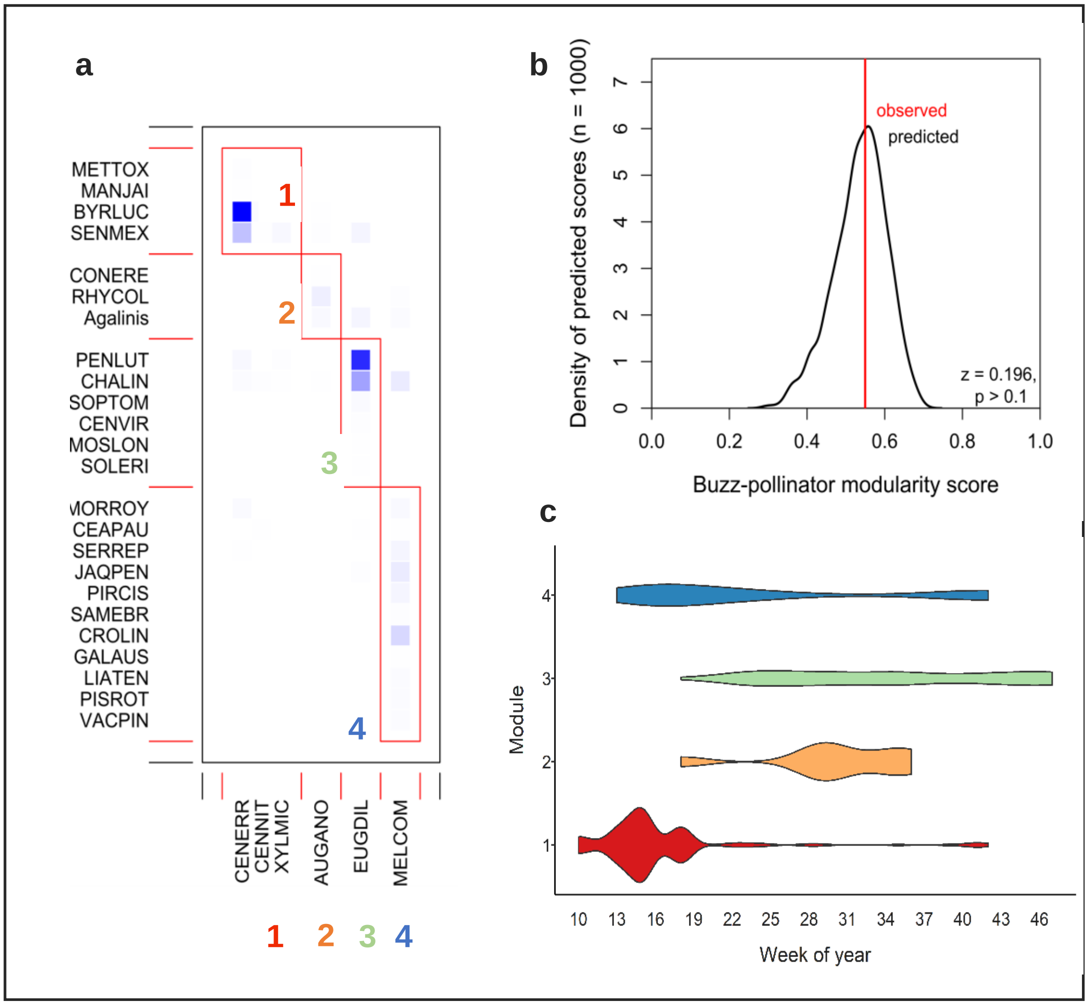

Figure III.5 Buzz-bee subnetwork modularity and pollinator niche overlap in pine rockland on Big Pine Key, FL. A) Observed network compartmentalization of plants and buzz-bees. B) Observed modularity index and C) buzz-bee niche-overlap compared to that predicted by the null model of phenological overlap (simulations = 1000).

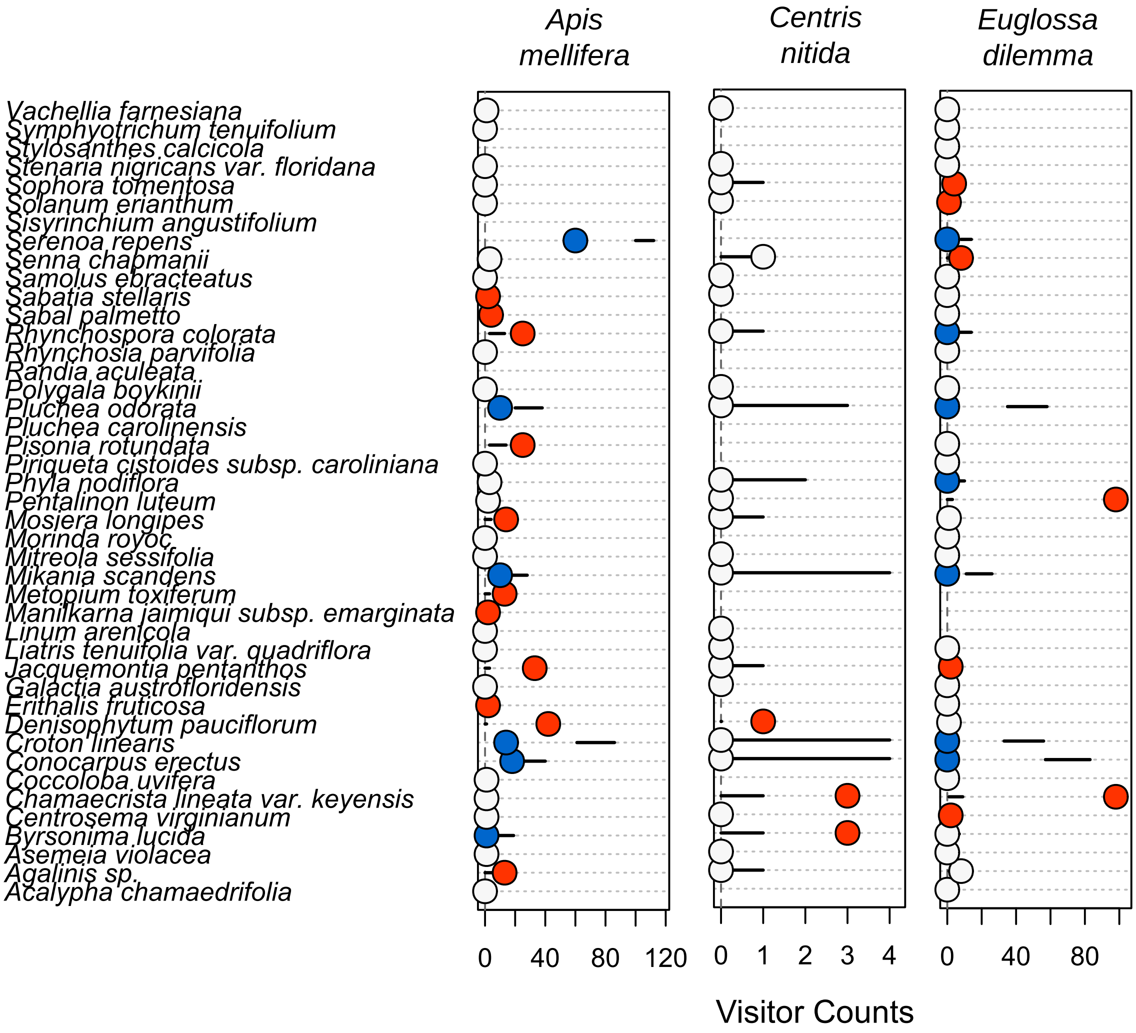

Figure III.6. Observed flower preferences of exotic bees on Big Pine Key, FL compared to 95% confidence intervals of that predicted from a null model of flower abundances. Red dots represent stronger preferences than predicted, blue represent weaker, and white indicates no difference.

Figure IIII.7 Medium to large native and exotic bees visiting flowers in Big Pine Key, FL. A) native locust-berry bee (*Centris errans*) visiting locustberry *(Byrsonima lucida*) B) European honeybee (*Apis mellifera*) visiting skyblue clustervine (*Jacquemontia pentanthos*). C) Southeastern carpenter bee (*Xylocopa micans*) visiting Bahama senna (*Senna mexicana* var. *chapmanii*). D) Male tropical orchid bee (*Euglossa dilemma*) visiting wild allamanda (*Pentalinon luteum*).

IV. ALTERED FIRE REGIMES INFLUENCE NETWORK DYNAMICS AND DIVERSITY OF PLANT-POLLINATOR COMMUNITIES

INTRODUCTION

Fire is a fundamental process that shapes many terrestrial ecosystems across the globe (McLauchlan et al. 2020). When timing and severity of fire is heterogeneous across a landscape, fire can have a positive effect on biodiversity by increasing available niche space and providing refuge (Stein et al. 2014; Kelly and Brotons 2017). Consequently, a landscape of diverse fire-regimes, or “pyrodiversity,” influences the distribution of species diversity (Stein et al., 2014). Indeed, pyrodiversity increases beta-diversity of plants (Potts et al. 2003), bees (Ulyshen et al. 2022), and their interactions (Ponisio et al. 2016).

Pollination systems in fire-prone ecosystems appear to be resilient to and benefit from fire (Potts et al. 2003). A global meta-analysis of pollinator responses to fire regimes suggests that Hymenoptera, an important group of pollinators, respond positively to early fire recovery. (Carbone et al. 2019). Fire enhances nesting habitat for ground and cavity nesting bees, and large flowering events are common shortly after fire (Pyke 2017). As forests regenerate, the composition of plants and flower visitors changes (Ponisio et al. 2016). However, it is less clear how or if community dynamics change over time since fire. Evidence suggests that plant-pollinator communities lack modularity and specialization after a recent fire, but trends across fire-regeneration gradients are less detectable (Peralta et al. 2017). In a naturally burned *cerrado*, pollinator specialization continuously declined with years since the last fire, but plant specialization and other network attributes were not correlated with post-fire age (Baronio et al. 2021). Similarly, changes in flowering plant and pollinator species richness are not always associated with years since fire (Lazarina et al. 2017; Baronio et al. 2021).

Long-term fire suppression may further influence network dynamics. In fire-prone forests, prolonging prescribed burns or suppressing wildfires alters fuel loads over time (O'Brien et al. 2014), and promotes establishment of fire-sensitive species over fire-adapted ones. In the Florida Keys pine rocklands, a few decades of fire suppression can cause stable-state transitions to a fire-sensitive hardwood hammock (Ross et al. 2009). These changes in ecosystem properties may be important in shaping plant-pollinator community dynamics if fire suppression alters floral resources or nesting habitat available. Adaptive foraging suggests that flower visitors readily shift foraging behavior from areas of low resources to areas of high resources, and the ability to shift resources stabilizes pollination networks from species losses (Kaiser-Bunbury et al. 2010; Valdovinos et al. 2016). For example, rapid resource loss, gain, and turnover of floral resources after recent fire may promote flower visitors that are flexible in resource use. Indeed, pollinator interactions after recent fire are often generalized and become more specialized at later fire successional stages (Lazarina et al. 2017; Peralta et al. 2017; da Silva Goldas et al. 2022). High species richness and floral specialization was reported for a fire-suppressed Brazilian *cerrado* (de Deus and Oliveira 2016). However, plant diversity and functional traits decreased in a fire suppressed Mediterranean pine forest (Diaz-Toribio et al. 2020).

I studied the plant-pollinator community of a fire-adapted pine rockland island ecosystem across a chronosequence of years since fire, further termed fire return, in the lower Florida Keys. Historical fire frequency of pine rockland in the Florida Keys is thought to occur 4-15 years on average (Bergh and Wisby 1996). These forests have mostly been managed by prescribed fire, however, and prior to the 1970s suppression was the predominant method for managing fires (Bergh and Wisby 1996). Increasing urbanization on the islands has further challenged the ability to prescribe fire. Consequently, fire return intervals have increased on the island and many burn units remain unburned.

In this study, I aimed to gain a better understanding of how plant-pollinator communities assemble across fire regeneration stages when fire has largely been suppressed across the landscape. Firstly, I will evaluate if changes in species diversity and interaction diversity are correlated with years since fire. Next, I will measure how network dynamics of the plant-pollinator communities shift between early fire recovery years through decades of fire suppression using the chronosequence of fire returns across the island. I expect to find that species richness of flowers, visitors, and their interactions will be highest in recently burned patches and will decline with time since fire. Further, I predict higher generalization in more recently burned sites and increasing specialization and network modularity with more extensive fire suppression.

We were also interested if pollinators foraged differently across patches of different fire history based on their diet breadth. If pollinators are generalist flower foragers, then preferences for flowers from more recently burned patches may not be different than those from the long-term fire suppressed patches? Introduced honeybees, *Apis mellifera*, are the most generalized of bee foragers on the island and appear to act as networks hubs by reducing modularity and increasing connectance in novel networks (Chapter III). Conversely, exotic *Euglossa dilemma* bees are the most specialized foragers in the community (Chapter III). If networks in more recently burned patches consist of more generalized interactions that become specialized over time, then I would expect *A. mellifera* to forage more frequently in areas recently burned and to forage less frequently in patches long unburned. Conversely, I expect *E. dilemma* to more frequently visit flowers in locally fire suppressed patches.

METHODS

3.1 Site description

I studied the plant and pollinator community within the pine rockland ecosystem on Big Pine Key in the lower Florida Keys (24.699°N, 81.376°W). This site is managed by the US Fish and Wildlife Service National Key Deer Refuge (NKDR). Pine rockland is a globally endangered fire-dependent ecosystem (Snyder et al. 1990) with an average fire return interval of 4-10 years (Bergh and Wisby 1996). It occurs on a few small islands in the Florida Keys of which Big Pine Key is the largest (comprises 5.36 km^2 of the 24.66 km^2 island). When burned regularly with prescribed fire, the plant community consists of a sparse pine canopy (*Pinus elliottii* var. *densa*), a tall palm sub-canopy (predominantly *Leucothrinax morissii* and *Coccothrinax argentata*), and a diverse herbaceous understory (Snyder et al. 1990). Pine rockland soils are shallow with exposed oolitic limestone substrate (Ross et al. 1992). Dead woody and palm debris can be plentiful in areas where prescribed fire is overdue (Ross et al. 2009; Saha et al. 2011). Species composition changes and vegetation becomes dense when fire has long been suppressed (Abrahamson et al. 2021; Harris et al. 2021) in pine rockland. Namely, herbaceous plant diversity wanes, vegetation becomes shrubbier, and heavier fuel loads accumulate with time since burn (O’Brien 1998).

3.2 Site design

I established 21 semi-permanent 30 m x 30 m plots across a time-since-fire chronosequence to sample plant-flower visitor interactions. Using ArcPro (Version 2.9; ESRI 2022), I first delineated contiguous pine rockland habitat patches larger than one hectare within NKDR boundaries using the 2019 Florida Cooperative Landcover map (Version 3.3; FNAI 2019). I used available fire history data maintained by NKDR and the Nature Conservancy (Bergh and Wisby 1996) for years 1969 to 2019. NKDR manages pine rockland with prescribed fires by burn units, so fire history data consisted of yearly polygons of estimated fire perimeters within the burn units. I validated years 2000 to 2016 with available spatial imagery downloaded from the LANDFIRE database (LANDFIRE 2020). LANDFIRE disturbance history consisted of yearly raster images at a 30 m spatial resolution with pixels denoting burn severity (high, medium, low, no fire) of detected fire.

I initially generated 35 simple random points within pine rockland burn units, separated by at least 200 m. Prescribed burning was active in some years and less so in others, so the distribution of fire return was clumped. The most abundant fire return years were patches burned between 15 and 20 years ago or with no recorded fire history within the last 40 years (Fig. IV.1). I trimmed eleven points from overrepresented fire return years to achieve a representative but distributed sample. The only recent fires (< 2 yrs) were from a wildfire in 2018, which occurred across burn units containing some rural housing and adjacent to low-density housing. Most points generated that had no recorded fire history were also within 250 m of low-density housing. Of the 24 sites generated, three additional sites were eventually removed throughout the study due to extensive flooding, homeless encampments, or obstructed access (Table IV.1).

3.3 Plant-flower visitor interaction sampling

Within sites, I conducted timed watches of all open entomophilous flowering plants in each site to quantify interactions between plants and flower visitors. I navigated once through each 900 m^2 site, and when open flowers were encountered, I conducted 5-minute flower visitor watches. Watches included all visible open flowers within $1m^2$. I recorded flower abundances of each plant species, visitor abundances visiting each plant, and counts of flower visits by each species during the timed watches. Only visitors contacting reproductive parts of flowers were included. The sampling effort for each site was dependent on plant abundances, so I limited plant species to 6 watches (i.e., 30 minutes) per site sample campaign to reduce underrepresentation of rare plants in the network. I identified flower visitors to species or genus when possible or collected and preserved them for later identification. Specimens are in the possession of the author, to be deposited as vouchers in the Florida State Museum of Arthropods in Gainesville, FL.

I conducted six sample campaigns, approximately every fifth week from March to early November 2019, to document interactions between plants and flower visitors. Sampling occurred between 07:00 and 17:00. Each sample campaign occurred over 14 days, and site sampling order was randomized so all sites had equal probabilities of being sampled early or later in the day for each campaign. I sampled plant-pollinator interactions throughout the study for 8,585 minutes (143 h) over 62 sample days between March 24 and October 18 of 2019. The average total time among sites was 515 minutes.

The site with the fewest open flowers was sampled for 210 minutes, and the site with the most abundant flowers was sampled for 1,445 minutes.

3.4 Data analysis

3.4.1 Species and interaction diversity

I measured the diversity of plants, flower visitors, and plant-pollinator interactions across the fire return gradient. For each site, I rarefied flowering plant richness based on observed abundances (Hsieh et al. 2016). I performed linear regression analyses on estimated richness values of plants, flower visitors, and interactions of each site, using year-since-last-fire as a continuous independent variable.

To visualize differences in species and interaction diversity at different post-fire years as a non-linear function, I grouped sites into proximal fire ages using the mean of estimated richness values after rarefaction. Though parsing samples can be biased, many of the fire return years were already relatively clumped in time (Table IV.1). Richness values were extrapolated to nearly double the number of individuals observed (Hsieh et al. 2016), and I calculated confidence intervals for comparison of species richness at different stages of fire return (Colwell et al. 2004; Chao et al. 2014).

3.4.2 Foraging specialization

I analyzed flower visitation frequency of select generalist and specialist bees to determine if flower visitors foraged preferentially across habitats of different fire successional stages. I selected the three exotic bees (*Apis mellifera*, *Centris nitida*, and *Euglossa dilemma*), and three common native bees (*Megachile addenda*, *Centris errans.* and *Xylocopa micans*). Bees' diet preferences ranged from specialized to generalized (Chapter III) and values were similar between exotic and native bees. *A. mellifera* and *M. addenda* are the most generalist flower visitors, and *E. dilemma* and *X. micans* have the most specialized diet in the local species pool (Chapter III). For each bee and each site, I aggregated visits to flowers and counts of flowers observed across the six sample campaigns. I modeled visits as count data using generalized linear models with Poisson distributions to evaluate if generalist and specialist exotic and native bees foraged differently across fire-successional stages. Abundances were offset by the log of flowers observed to account for differences in sampling effort. I ran separate models for each of the six flower visitors and assessed model fit using Pearson's χ^2 tests of residuals and residual degrees of freedom. All models resulted in overdispersion, so they were fit with negative binomial distributions. I report back-transformed (i.e., exponentiated) estimates and 95% confidence intervals.

3.4.3 Network indices

I constructed plant-pollinator interaction matrices from the pollinator watch data for each site to quantify network structure. I aggregated interaction data across sample campaigns for each of the 21 sites, resulting in 21 matrices of pollinator abundances at flowering plants. Network size strongly affects network properties, and for networks of one species, some indices are impossible to compute; therefore, I removed one site that had many flower visitors but only a single plant species that was visited.

I computed several indices to describe network specialization and resource partitioning within guilds at different years post-fire regeneration. Network modularity was computed for each site using the DIRTLPAwb+ (Q_W) algorithm (Beckett 2016) implemented in the *bipartite* package (Dormann et al. 2008). This algorithm is derived from Newman's modularity (Newman 2004) and detects modules of two-mode weighted networks. Modularity is highest when subsets of species interactions are closely connected to each other and are isolated from other potential partners in the species pool. I also computed network specialization (H_2'), which estimates the degree of partitioning among interacting partners in the network (Bluthgen et al. 2006).

I measured the degree of niche overlap and weighted link density at the group level. Niche overlap measures the degree of resource partitioning among plants and among flower visitors, which depends on the level of shared cross-trophic partners with others in the same trophic levels. It is calculated as the Bray-Curtis distance and ranges from 0 to 1; higher values indicate high overlap in resource use and low values indicate high partitioning of resources within guilds (i.e., plants or flower visitors). Lastly, generality and vulnerability were used as measures of partner diversity for flower visitors and plants, respectively. Vulnerability was measured for each site as the mean effective number of pollinator species per plant species observed, weighted by the total flowers visited (marginal totals; Bersier et al., 2002). Similarly, generality measures plant links per visitor species.

3.4.4 Null models

Most network indices, like modularity, are dependent on the number of species and the number of links in the network (Dormann and Strauss 2013); therefore, direct comparisons of indices are not valid (Beckett 2016). I compared each observed index for each site to those generated from null models to evaluate standardized effect sizes (Dormann and Strauss 2013). For each site network, I generated an ensemble of 1000 null networks consisting of random two-way tables, given the marginal sums (species abundances) provided in each network (Patefield 1981). I computed indices for the null network ensemble and calculated z-scores from the observed and expected null model distribution to evaluate the direction and degree of deviation of the index values from the null. I used linear models to evaluate if the standard effect sizes of network structural properties changed linearly with increasing time since fire. I conducted separate tests for each network index using the z-scores as response variables and years since fire as the predictor variable. I evaluated model fit by plotting residuals.

RESULTS

I surveyed 84,204 flowers of 74 plant species. Of the surveyed flowers, 10,293 were visited by 1,832 individual insects composed of 48 species. I did not observe any flower visitors at 24 of the 74 plant species, many of which were infrequent at sites. Observed interactions resulted in 264 unique links between plants and flower visitors. The most abundant visitors were bees, particularly *Megachile* spp., *Lasioglossum surianae*, and *Apis mellifera*. The next most abundant flower visitors were wasps, followed by syrphid flies, and then skipper butterflies.

Estimates of plant diversity after rarefaction were highest in the sites most recently burned and diversity decreased with time since fire ($F_{19} = 8.53$ $P < 0.01$, $R^2 = 0.31$) by a factor of 0.32 species per unit increase in time. Similarly, interaction diversity decreased with time since fire, but the relationship was marginally significant ($F_{19} = 4.26$, $P = 0.05$, $R^2 = 0.18$). In contrast, pollinator diversity was not correlated with time since fire ($F_{19} = 0.25$, $P > 0.5$, $R^2 = 0.01$). After grouping sites into proximal fire return classes, I see that estimated and extrapolated flower diversity values are highest in the first 4 years after fire and lowest in the longest fire return class (> 40 years; Fig. IV.2a). Confidence intervals of intermediate fire returns all overlap each other and are positioned between the youngest and oldest fire return classes (Fig. IV.2a). Estimates for interaction diversity were also highest in sites experiencing the most recent fire, but confidence intervals overlapped with sites not burned in 30 to 35 years (Fig IV.2c). Pollinator diversity overlapped for all fire return classes (Fig IV.2b).

Generalist and specialist flower visitors did not forage differently across fire successional stages. Flower visitation rates of exotic *Apis mellifera* (honeybees) decreased by 1.37% (95% C.I. = -3.48% to 0.7%) with each year since fire but was not significant ($Z_{19} = -1.25$, $P > 0.1$; Fig. IV.3; Table IV.2). Similarly, *Euglossa dilemma* (orchid bees) visited flowers 4.82% (95% C.I. = - 11.7% to 4%) less frequently per increasing year since fire, and this too was not significant ($Z_{19} = - 1.55$, $P > 0.1$; Fig. IV.3; Table IV.2). The exotic oil-collecting bee, *Centris nitida*, was infrequent (n = 8 individual visitors) at flowers in the study but all observed visits were distributed randomly across the fire-successional stages ($Z_{19} = 0.77$, $P > 0.1$; Fig. IV.3). Visitation frequency did not differ across fire returns for native bees either (Fig. IV.3).

Most of the resulting 21 plant-pollinator networks were significantly more modular (Q_w) than expected by the null model distribution (Table IV.3). Sites more recently burned had the highest observed modularity. Deviations between observed modularity and null values decreased by 0.27 with every unit increase in fire age ($F_{18} = 7.66$, $p < 0.05$, $R^2 = 0.3$; Fig. IV.3a). Similarly, all networks were composed of more specialized interactions (H_2’) than expected (Table IV.3). Plant and pollinator interactions became less specialized with time since fire (Fig. III.3b). Network specialization (H2’) decreased by 0.34 (s.e. = 0.14) with each unit increase in fire age ($F_{18} = 5.96$, $P < 0.05$, $R^2 = 0.25$).

Plant and flower visitors in most sites exhibited high resource partitioning and high linkage diversity within trophic groups. Overlap of floral resources used by flower visitors were all lower than expected from the null model and most were significantly lower (Table IV.4). Flower visitor niche overlap at one 15-year site, one 18-year site, and two sites greater than 40 years since fire, were not different from random. However, the general trend was that the effect size decreasingly deviated from random by 0.04 (s.e. = 0.02) with each unit increase in fire return ($F_{18} = 5.07$, $P < 0.05$, $R^2 = 0.22$; Fig. IV.3c). Similarly, overlap in visitors shared by flowering plants were significantly lower in most sites than expected (Table IV.5) and was lowest in the earliest fire-successional stages. The effect size decreased by a factor of 0.07 (s.e. = 0.14) with increasing fire return, ($F_{18} = 5.6$, $P < 0.05$, $R^2 = 0.24$). Trends were similar for pollinator generality and plant vulnerability, which indicate the average number of links per guild, weighted by abundances of the guild. Effect size for generality and vulnerability were estimated at -10.2 and -10.1, respectively, for the youngest fire successional stages, and decreased by a factor of 0.18 (s.e. 0.08) and 0.19 (s.e. = 0.08; Table IV.4 & IV.5).

DISCUSSION

Time since fire was an important factor in structuring plant-pollinator communities in pine rockland forests of the lower Florida Keys. Interaction networks, in general, were more modular and specialized than expected, and modularity and specialization decreased monotonically with time since fire. Resource partitioning in plants and flower visitor guilds also decreased with increasing time since fire, suggesting that plants and visitors shared more resources and were less specialized in fire suppressed sites compared to those burned more recently. Network indices for most sites were significantly different than values predicted by resource abundances; therefore, non-neutral processes were important in shaping the plant-pollinator communities of nearly all fire-successional stages on the island, particularly those more recently burned.

These findings on network dynamics across the time since fire chronosequence differ from findings in other systems, however, few studies have aimed to understand these relationships, particularly in fire-suppressed pinelands. One common conclusion in other studies is that network dynamics are resistant to change over time after fire (Baronio et al. 2021; da Silva Goldas et al. 2022). Although monotonic changes are not frequently observed, some studies suggest that plant-pollinator communities lack modularity and specialization after recent fire (Lazarina et al. 2017; da Silva Goldas et al. 2022). However, in a naturally burned *cerrado* with a short fire return, pollinator interactions were most specialized after fire and decreased with increasing time since fire (Baronio et al. 2021), mirroring our findings.

Generalization in flower foraging is often associated with the ability of flower visitors to shift floral resources. To be a generalist suggests some level of tolerance to disturbances or resource variability across space or time (Resasco et al. 2021). Generalization could be expected in areas recently burned if floral abundances are high and flower diversity is low. On the contrary, specialization may be favored after a recent burn if diversity of flower resources available increases (Potts et al. 2003; Pyke 2017). In the latter, flower visitors may specialize on preferred floral resources if available, as opposed to those most abundant.

In this study, floral richness was highest after fire and lowest in the most fire suppressed sites; however, flower abundances were highest in sites with the lowest diversity. Flowering hardwood trees and large shrubs were more prevalent at sites with longer fire returns than the forbs common in recently burned sites, and flower abundances per plant were much larger for trees and shrubs compared to forbs. Large richness of flowers and floral rewards are common in Mediterranean forests after fire, and lower in subsequent years (Potts et al. 2003). For flower visitors foraging in fire suppressed areas, species may converge on the most abundant resources available. Similar relationships were found for flowering plant diversity in fire suppressed pine savannas in north Florida (Diaz-Toribio et al. 2020). In that study, flowering richness was lower for sites where fire was suppressed between 10 and 40 years than those recently burned, and functional traits of plants became more homogenous with prolonged fire exclusion (Diaz-Toribio et al. 2020). Conversely, flower diversity increased after 20 years of fire suppression in a Brazilian *cerrado* (de Deus and Oliveira 2016).

An increase in bee diversity is often associated with recent fires (van Nuland et al. 2013; Brown et al. 2017; Carbone et al. 2019) but in this study, pollinator diversity was not correlated with fire age. In some fire-prone open forests, bee richness increases with floral richness (Grundel et al. 2010). In this study, flowering richness was highest in recently burned sites, but flower visitor richness was not. Nesting resources can also be important for shaping bee communities (Potts et al. 2005). Bare ground and nesting cavities for bees are generally more abundant after fire, but this relationship with time since fire was not monotonic in a Mediterranean fire-prone landscape (Potts et al. 2005). Relationships between pollinator diversity and time since fire may not be consistent for all pollinator groups and should be considered. For example, Lepidoptera mortality is generally high after fire, and therefore butterflies and moths are often most associated with fire suppressed habitats (Swengel and Swengel 2007). Lepidopterans were not very abundant in this study, but perhaps separating out insect visitors by phylogenetic relatedness may provide more insight. Further, interaction diversity between plants and flower visitors was only moderately correlated with year since fire, but this may be the result of mixed relationships between plant and pollinator diversity in this study.

All three of the exotic bees on the island (*Apis mellifera, Centris nitida,* and *Euglossa dilemma)* were equally likely to forage in sites of any fire-successional stage. Native generalist and specialist bees also foraged evenly across habitats of different fire return years. As expected, the generalist exotic *A. mellifera* and the native *Megachile addenda* (Chapter 2) were equally abundant at all sites, but I had expected the specialized orchid bees, *E. dilemma,* and equally specialized native *Xylocopa micans* to selectively forage more frequently in areas recently burned. *Euglossa dilemma*'s preferred flower resources are most abundant in the few years after fire, such as *Chamaecrista lineata* var *keyensis* (Liu et al. 2005; Hodges and Bradley 2006) and *Agalinis* spp. However, *E. dilemma* are also avid visitors of *Pentalinon luteum* flowers (Chapter III), and flowers of this woody vine were abundant at various fire successional stages, particularly between 15 and 35 years. In a Brazilian grassland, *Apis mellifera* switched network roles from a network hub to a connector between recently burned and long unburned grasslands (da Silva Goldas et al. 2022); however, results of that study may not be directly comparable as they considered 'long-unburned' as only two years since fire, an interval that in pine savannas is consider recently burned. Interestingly, exotic plants are rare in the interior pine rocklands of the Florida Keys. Only one exotic flowering plant was observed in the sites, *Alysicarpus vaginalis* (White moneywort), but it only occurred at one site and in small abundances.

The lack of consistent evidence for network attributes and species diversity across recent and fire suppressed ecosystems suggests that perhaps other variables may be at play. Primarily, research in different fire-prone ecosystems is needed to better understand and compare how altered fire regimes influence diversity measures of plants and flower visitors as well as network dynamics. Other attributes of fire regimes can also affect habitat quality and should be investigated. For example, fire severity, frequency, or fire season can alter successional processes by influencing factors like species survival, demography, and seed bank quality (Keeley and Fotheringham 2000; Pausas and Keeley 2014). For large wildfires, local fire severity positively influences nesting quality and flowering richness (Galbraith et al. 2019). Factors other than fire history can also impact site conditions, particularly hurricanes and coastal storm surge. Lower Keys pine rockland occurs on low-lying islands, and pine trees are salt intolerant. Pine mortality near coastal and low-lying areas on the island can disrupt future fuel loads resulting in rapid state transitions and habitat loss for fire-adapted species (Ross et al. 2009). Many sites could have been more impacted by salt-water intrusion and pine mortality than by the absence of fire. These factors warrant further investigation into their effects on plant-pollinator communities.

In this study, increasing fire suppression appeared to disassemble complex network attributes. More recently burned pine rockland had higher floral and interaction richness and higher levels of resource partitioning among plants and flower visitors. Furthermore, pollinator networks in earlier fire age sites were more modular than those where fire was suppressed, and increasingly so with prolonged fire management. Although I have a good understanding of positive relationships between pyrodiversity and beta-diversity (Ponisio et al. 2016; McLauchlan et al. 2020; Ulyshen et al. 2022), links between time since fire and dynamics of pollinator networks have not been explored in pine forests and may be important for understanding how fire management influences diversity and resiliency of networks to perturbations. For example, modularity and high resource partitioning in networks is thought to increase network resilience (Olesen et al. 2007). In modular networks, disturbances are likely to affect subsets of the community interacting more with each other rather than disassembling the whole network. As prescribed burning is delayed, floral richness diminishes, flower visitors share more resources, and networks become more generalized and less modular. Because altered fire regimes is a global issue, understanding how prolonged fire affects network resiliency is critical for fire management and increasing biodiversity.

LITERATURE CITED

Abrahamson WG, Abrahamson CR, Keller MA (2021) Lessons from four decades of monitoring vegetation and fire: maintaining diversity and resilience in Florida’s uplands. *Ecol Monogr* 91:1–20. https://doi.org/10.1002/ecm.1444

Baronio GJ, Souza CS, Maruyama PK, Ros M (2021) Natural fire does not affect the structure and beta diversity of plant-pollinator networks , but diminishes floral-visitor specialization. *Flora* 281:1–8. https://doi.org/10.1016/j.flora.2021.151869

Beckett SJ (2016) Improved community detection in weighted bipartite networks. R Soc Open Sci. https://doi.org/10.1098/rsos.140536

Bergh C, Wisby J (1996) Fire History of Lower Keys Pine Rocklands. 296–3880

Bersier L-F, Banasek-Richter C, Cattin M-F (2002) Quantitative descriptors of food-web matrices. *Ecology* 23:2394–2407. https://doi.org/https://doi.org/10.1890/0012-9658(2002)083[2394:QDOFWM]2.0.CO;2

Bluthgen N, Menzel F, Blüthgen N (2006) Measuring specialization in species interaction networks. *BMC Evol Biol* 12:. https://doi.org/10.1186/1472-6785-6-9

Brown J, York A, Christie F, Mccarthy M (2017) Effects of fire on pollinators and pollination. *Journal of Applied Ecology* 54:313–322. https://doi.org/10.1111/1365-2664.12670

Carbone LM, Tavella J, Pausas JG, Aguilar R (2019) A global synthesis of fire effects on pollinators. *Global Ecology and Biogeography* 28:1487–1498. https://doi.org/10.1111/geb.12939

Chao A, Gotelli NJ, Hsieh TC, et al (2014) Rarefaction and extrapolation with Hill numbers : a framework for sampling and estimation in species diversity studies. *Ecol Monogr* 84:45–67

Colwell RK, Chang XM, Chang J (2004) Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology*. https://doi.org/10.1890/03-0557

da Silva Goldas C, Podgaiski LR, Veronese Corrêa da Silva C, et al (2022) Structural resilience and high interaction dissimilarity of plant–pollinator interaction networks in fire-prone grasslands. *Oecologia* 198:179–192. https://doi.org/10.1007/s00442-021-05071-x

de Deus FF, Oliveira PE (2016) Changes in floristic composition and pollination systems in a “Cerrado” community after 20 years of fire suppression. *Revista Brasileira de Botanica* 39:1051–1063. https://doi.org/10.1007/s40415-016-0304-9

Diaz-Toribio MH, Carr S, Putz FE (2020) Pine savanna plant community disassembly after fire suppression. *Journal of Vegetation Science* 31:245–254. https://doi.org/10.1111/jvs.12843

Dormann CF, Gruber B, Fründ J (2008) Introducing the bipartite package: analysing ecological networks. R News 8:8–11

Dormann CF, Strauss R (2013) A method for detecting modules in quantitative bipartite networks. *Methods Ecol Evol* 5:90–98. https://doi.org/10.1111/2041-210X.12139

Galbraith SM, Cane J, Moldenke AR, Rivers J (2019) Wild bee diversity increases with local fire severity in a fire prone landscape. *Ecosphere* 10(4): e02668 https://doi.org/10.1002/ecs2.2668

Grundel R, Jean RP, Frohnapple KJ, et al (2010) Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. *Ecological Applications*. https://doi.org/10.1890/08-1792.1

Harris BM, Freidenreich A, Betancourt E, Jayachandran K (2021) Short-term vegetation responses to the first prescribed burn in an urban pine rockland preserve. *Fire Ecology* 17:1–9. https://doi.org/https://doi.org/10.1186/s42408-021-00116-1

Hodges SR, Bradley KA (2006) Distribution and population size of five candidate plant taxa in the Florida Keys: *Argythamnia blodgettii*, *Chamaecrista lineata* var. *keyensis, Indigofera mucronata* var. *keyensis, Linum arenicola, and Sideroxylon reclinatum* subsp. *Austrofloridense*. USFWS.

Hsieh TC, Ma KH, Chao A (2016) iNEXT : an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol Evol* 7:1451–1456. https://doi.org/10.1111/2041-210X.12613

Kaiser-Bunbury CN, Muff S, Memmott J, et al (2010) The robustness of pollination networks to the loss of species and interactions: A quantitative approach incorporating pollinator behaviour. *Ecol Lett* 13:442–452. https://doi.org/10.1111/j.1461-0248.2009.01437.x

Keeley JE, Fotheringham CJ (2000) Role of fire in regeneration from seed. In: Seeds The Ecology of Regeneration in Plant Communities. pp 311–330

Kelly LT, Brotons L (2017) Using fire to promote biodiversity. *Science* (1979) 355:1264–1265

LANDFIRE (2020) Landfire Remap 2016 Historical Disturbance. U.S. Department of Interior, Geological Survey, and U.S. Department of Agriculture

Lazarina M, Sgardelis SP, Tscheulin T, et al (2017) The effect of fire history in shaping diversity patterns of flower-visiting insects in post-fire Mediterranean pine forests. *Biodivers Conserv*. https://doi.org/10.1007/s10531-016-1228-1

Liu H, Menges ES, Quintana-Ascencio PF (2005) Population Viability Analysis of *Chamaecrista keyensis*: Effects of Fires Season and Frequency. *Ecological Applications* 15:210–221

McLauchlan KK, Higuera PE, Miesel J, et al (2020) Fire as a fundamental ecological process: Research advances and frontiers. *Journal of Ecology* 108:2047–2069

Newman MEJ (2004) Analysis of weighted networks. *Phys Rev E Stat Nonlin Soft Matter Phys*. https://doi.org/10.1103/PhysRevE.70.056131

O’Brien JJ (1998) The distribution and habitat preferences of rare *Galactia species* (Fabaceae) and *Chamaesyce* (Euphorbiaceae) native to Southern. *Natural Areas Journal* 18:208–222

O’Brien JJ, Butler B, Loudermilk E, Ross MS (2014) Fuels, ecological state transitions, and management: tipping points as trigger points

Olesen JM, Bascompte J, Dupont YL, Jordano P (2007) The modularity of pollination networks. *Proc Natl Acad Sci* 104:19891–19896. https://doi.org/10.1073/pnas.0706375104

Patefield WM (1981) AS159 An efficient method of generating random “R” x “C” tables with given row and column totals. *Appl Stat* 30:81

Pausas JG, Keeley JE (2014) Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytologist* 204:55–65

Peralta G, Stevani EL, Chacoff NP, et al (2017) Fire influences the structure of plant–bee networks. *Journal of Animal Ecology* 86:1372–1379. https://doi.org/10.1111/1365-2656.12731

Ponisio LC, Wilkin K, M’Gonigle LK, et al (2016) Pyrodiversity begets plant-pollinator community diversity. *Glob Chang Biol* 22:1794–1808. https://doi.org/10.1111/gcb.13236

Potts SG, Vulliamy B, Dafni A, et al (2003) Response of plant-pollinator communities to fire: changes in diversity, abundance and floral reward structure. *Oikos* 101:103–112. https://doi.org/10.1034/j.1600-0706.2003.12186.x

Potts SG, Vulliamy B, Roberts S, et al (2005) Role of nesting resources in organising diverse bee communities in a Mediterranean. *Ecol Entomol* 30:78–85

Pyke GH (2017) Fire-Stimulated Flowering: A Review and Look to the Future. *CRC Crit Rev Plant Sci* 36:179–189. https://doi.org/10.1080/07352689.2017.1364209

Resasco J, Chacoff NP, Vázquez DP (2021) Plant–pollinator interactions between generalists persist over time and space. *Ecology* 0:1–7. https://doi.org/10.1002/ecy.3359

Ross MS, O’Brien JJ, Flynn LJ (1992) Ecological Site Classification of Florida Keys Terrestrial Habitats. *Biotropica* 24:488–502

Ross MS, O’Brien JJ, Ford RG, et al (2009) Disturbance and the rising tide: The challenge of biodiversity management on low-island ecosystems. *Front Ecol Environ* 7:471–478. https://doi.org/10.1890/070221

Saha S, Bradley KA, Ross MS, et al (2011) Hurricane effects on subtropical pine rocklands of the Florida Keys. *Clim Change*. https://doi.org/10.1007/s10584-011-0081-1

Snyder JR, Herndon A, Robertson Jr. WB (1990) South Florida rockland. In: Myers R, Ewel J (eds) Ecosystems of Florida. University of Central Florida Press, Orlando, FL, pp 230–277

Stein A, Gerstner K, Kreft H (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecol Lett* 17:866–880

Swengel AB, Swengel SR (2007) Benefit of permanent non-fire refugia for Lepidoptera conservation in fire-managed sites. *J Insect Conserv* 11:263–279. https://doi.org/10.1007/s10841-006-9042-9

Ulyshen MD, Hiers JK, Pokswinksi SM, Fair C (2022) Pyrodiversity promotes pollinator diversity in a fire-adapted landscape. *Front Ecol Environ* 20:78–83. https://doi.org/10.1002/fee.2436

Valdovinos FS, Brosi BJ, Briggs HM, et al (2016) Niche partitioning due to adaptive foraging reverses effects of nestedness and connectance on pollination network stability. *Ecol Lett* 19:1277–1286

van Nuland ME, Haag EN, Bryant JAM, et al (2013) Fire promotes pollinator visitation: Implications for ameliorating declines of pollination services. PLoS One 8(11): e79853 https://doi.org/10.1371/journal.pone.0079853

Table IV.1. Site fire history. The number of years since the last fire (Fire age), the number of fires recorded for each site since 1970, and the grouped categorical age class of each site used in species and interaction diversity measurements.

Site	Fire age (years)	Age class	Fires (1970)
1	18	20	1
2	5	10	5
3	32	35	1
4	8	10	2
5	18	20	2
6	40	40	0
7	33	35	1
8	1	5	1
9	15	15	3
10	40	40	0
11	1	5	1
12	8	10	5
13	15	15	4
14	15	15	3
15	40	40	0
16	18	20	1
17	40	40	0
18	1	5	1
19	15	15	3
20	15	15	3
21	18	20	2

Table IV.2. Pollinator visitation frequency across habitat of increasing time since burn on Big Pine Key, FL pine rockland using generalized linear models with negative binomial error distributions (θ dispersion parameter and standard error). Differences in visitation rates across fire returns of three native and three exotic bees with different levels of specialization (d') on the island.

Pollinator	d'	Status	Est.	2.5%	97.5%	θ (s.e.)	Z	P-value
Apis mellifera	0.10	Exotic	-0.01	-0.04	0.01	3.29 (1.4)	-1.25	0.21
Centris nitida	0.28	Exotic	0.03	-0.06	0.11	0.33 (0.2)	0.77	0.44
Euglossa dilemma	0.40	Exotic	-0.05	-0.12	0.04	0.30 (0.1)	-1.55	0.12
Megachile addenda	0.12	Native	0.05	-0.01	0.11	0.59 (0.3)	1.80	0.07
Centris errans	0.26	Native	0.03	-0.03	0.09	0.44(0.2)	1.08	0.28
Xylocopa micans	0.39	Native	0.01	-0.03	0.05		0.54	0.60

Table IV.3. Network-level modularity (Q_w) and specialization (H_2’) observed scores and standard effect size from expected null model distribution (1000 simulations) of each site at different fire ages. Significance of P-value calculated from two-tailed Z-scores (N.S. = not significant; * = < 0.05; ** = < 0.01; *** = < 0.001; **** = < 0.0001).

Fire age	Q_w	Z-score		H_2'	Z-score	
1	0.45	0.45	****	0.45	10.23	****
1	0.45	0.45	****	0.39	41.12	****
1	0.50	12.51	****	0.52	15.40	****
5	0.49	4.29	****	0.74	4.40	****
8	0.63	19.49	****	0.77	22.53	****
8	0.64	17.41	****	0.68	18.95	****
15	0.52	6.15	****	0.57	4.81	****
15	0.53	7.41	****	0.66	8.45	****
15	0.34	4.52	****	0.52	7.88	****
15	0.62	13.08	****	0.78	13.79	****
15	0.06	1.64	*	1.00	2.34	*
18	0.57	8.17	****	0.68	8.95	****
18	0.56	5.31	****	0.52	5.87	****
18	0.62	9.61	****	0.58	9.98	****
32	0.49	7.59	****	0.66	7.47	****
33	0.32	3.86	****	0.40	5.14	****
40	0.68	5.53	****	0.92	5.74	****
40	0.50	2.16	*	1.00	2.60	**
40	0.44	1.84	*	0.50	2.20	*
40	0.57	10.08	****	0.88	10.72	****

Table IV.4. Pollinator group level niche overlap and generality observed index scores and standard effect size from expected null model distribution (1000 simulations) of each site at different fire ages. Significance of P-value calculated from two-tailed Z-scores (N.S. = not significant; * = < 0.05; ** = < 0.01; *** = < 0.001; **** = < 0.0001).

Fire age	**Niche overlap**	Z-score		**Generality**	Z-score	
1	0.09	-4.65	****	6.20	-9.24	****
1	0.15	-3.59	***	3.99	-22.04	****
1	0.13	-2.27	*	3.72	-6.23	****
5	0.14	-2.29	*	1.53	-3.04	**
8	0.10	-5.05	****	1.50	-14.02	****
8	0.10	-4.25	****	1.78	-12.71	****
15	0.19	-4.37	****	1.56	-8.80	****
15	0.16	-4.09	****	1.76	-6.54	****
15	0.12	-4.09	****	1.87	-5.59	****
15	0.35	-2.97	**	1.00	-2.60	**
15	0.24	-1.37	N.S.	1.75	-3.24	***
18	0.12	-3.79	****	1.98	-6.85	****
18	0.11	-3.00	**	2.01	-6.30	****
18	0.18	-1.17	N.S.	1.93	-4.52	****
32	0.13	-2.74	**	1.45	-5.01	****
33	0.17	-2.68	**	2.12	-4.14	****
>40	0.16	-3.01	**	1.19	-4.72	****
>40	0.10	-2.27	*	1.65	-7.09	****
>40	0.38	-1.66	*	1.00	-2.58	**
>40	0.34	-0.04	N.S.	1.84	-1.95	*

Table IV.5. Plant group level niche overlap and vulnerability observed index scores and standard effect size from expected null model distribution (1000 simulations) of each site at different fire ages. Significance of P-value calculated from two-tailed Z-scores (N.S. = not significant; * = < 0.05; ** = < 0.01; *** = < 0.001; **** = < 0.0001).

Fire age	Niche overlap	Z-score		Vulnerability	Z-score	
1	0.12	-6.53	****	5.53	-25.14	****
8	0.05	-5.36	****	2.68	-12.91	****
8	0.08	-8.70	****	2.48	-10.25	****
1	0.16	-5.95	****	2.67	-9.57	****
15	0.06	-3.74	****	2.95	-7.82	****
>40	0.06	-3.52	***	1.69	-7.35	****
18	0.08	-4.50	****	2.94	-7.26	****
15	0.09	-3.84	****	2.63	-5.91	****
15	0.05	-3.04	***	2.98	-5.81	****
1	0.12	-3.98	****	3.46	-5.76	****
18	0.09	-4.65	****	2.25	-5.55	****
32	0.05	-1.33	*	2.86	-5.45	****
>40	0.04	-3.39	***	2.51	-3.69	***
18	0.08	-2.40	**	3.59	-3.60	***
33	0.09	-2.27	**	4.11	-3.52	***
15	0.08	-1.46	*	3.18	-3.19	***
5	0.08	-0.90	N.S.	3.37	-3.00	**
15	0.00	-2.98	***	2.97	-2.30	*
>40	0.00	-2.37	**	3.77	-2.18	*
>40	0.15	-1.40	*	2.73	-1.22	N.S.

Figure IV.1. Images of representative sites across the fire-return chronosequence on Big Pine Key, FL. a) a recent fire less than 1 year old b) 8 fire-return c) 18 fire return d) 32-year fire return e) No recorded fire history within forty years (since 1979).

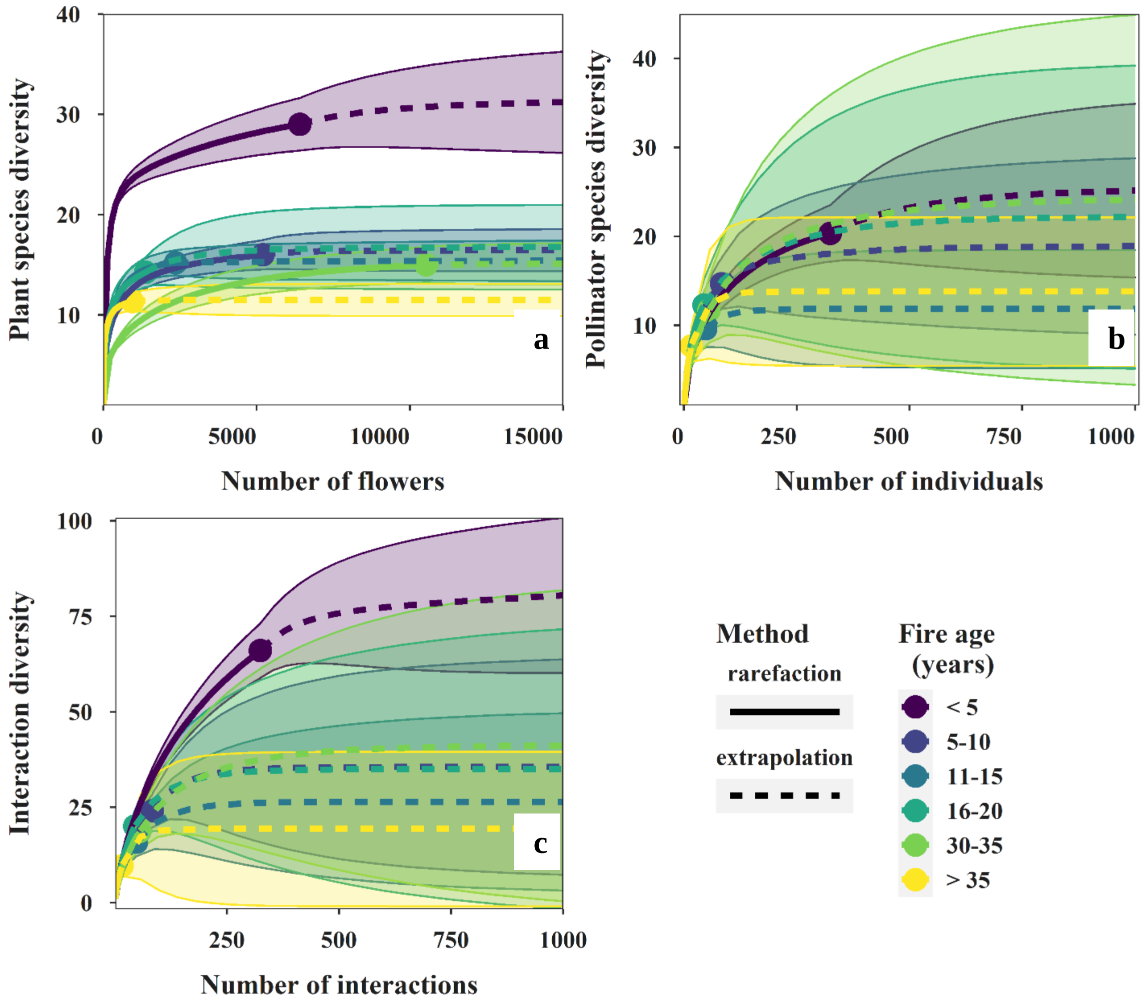

Figure IV.2. Species diversity curves and confidence intervals, rarefied and extrapolated to equal sample size. a) Flower abundance-based plant richness b) Richness of visitors observed at flowers c) Interaction richness based on unique interactions between plants and flower visitors.

Figure IV.3. Flower visitors at flowers in different fire return sites across the pine rockland in Big Pine Key, FL a*) Apis mellifera* and *Syntomeida epilais* at *Pithecellobium bahamense* flowers in an 18-year fire return site b) *Megachile bahamensis* at *Pisonia rotundata* flowers in a 32-year fire return c) *Strymon istapa* at *Asemeia violacea* flowers in a 1-year fire return d) *Euglossa dilemma* at *Sephora tomentosa* flowers in an 8-year fire return site.

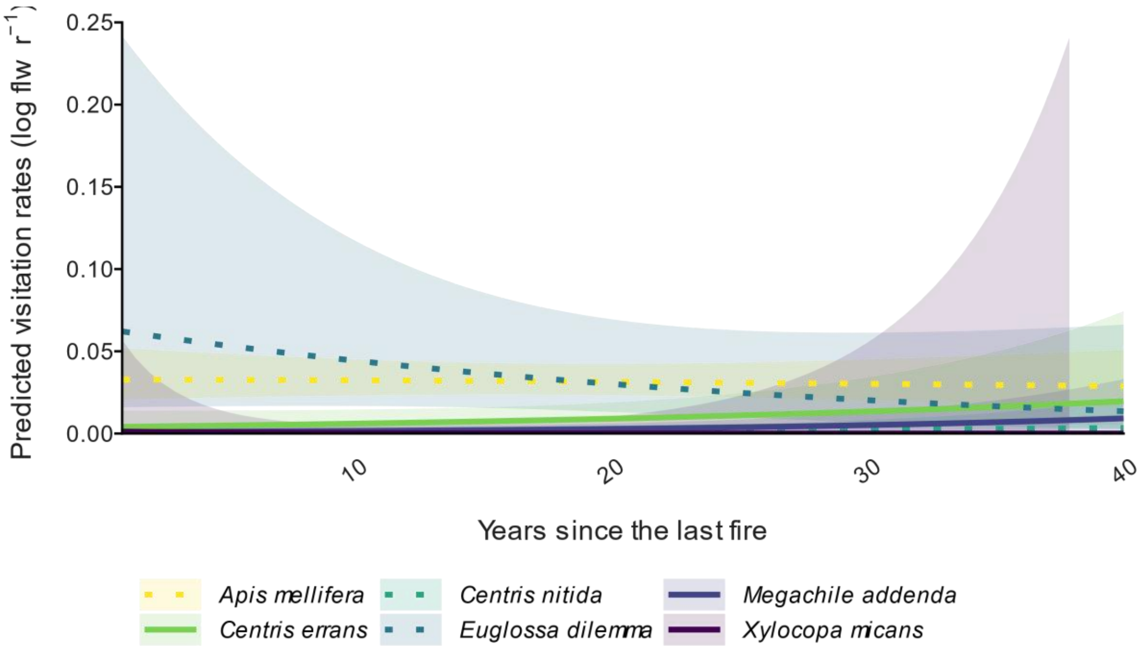

Figure IV.4. Predicted pollinator visitation rates to flowers (pollinator visits/log of flowers observed) across a pine rockland time since fire chronosequence in Big Pine Key, FL. Solid lines indicate native bees and dashed lines indicate introduced bee. Native and exotic, generalists and specialists did not forage differently across patches of different fire returns (P > 0.05).

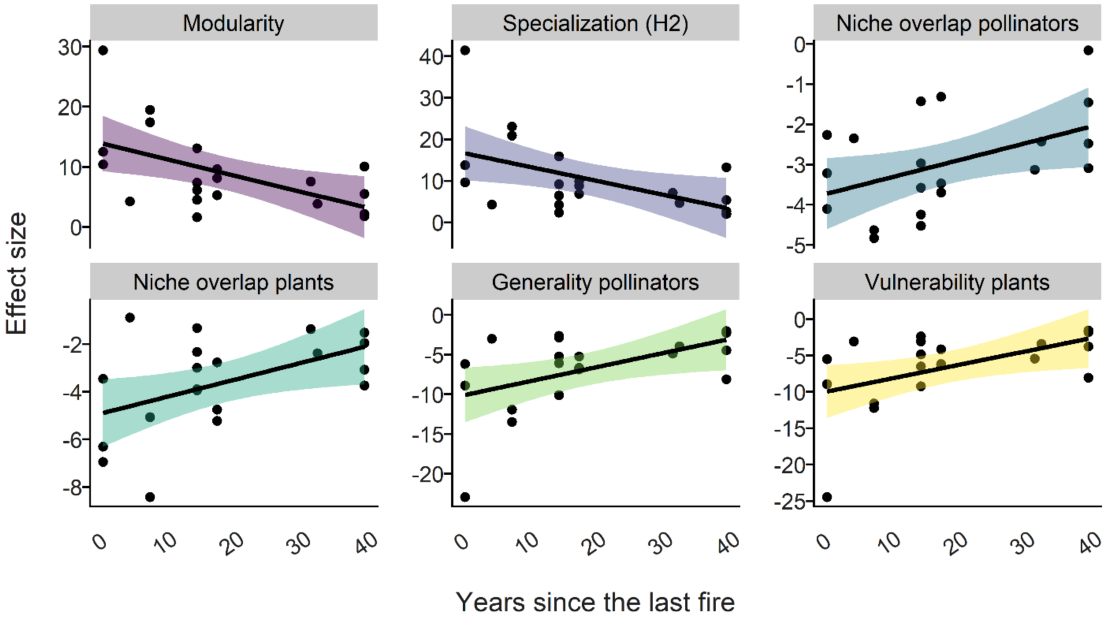

Figure IV.5. The distribution of z-scores from observed and null model generated network (1000 simulations) metrics for each site across the fire-return chronosequence in pine rockland on Big Pine Key, FL.

V. CONCLUSION

In this study, biotic and abiotic anthropogenic change influenced the structure and composition of plant-pollinator communities. Despite the potential for strong competitive effects in species with shared attributes, partitioning floral resources across seasons appeared to promote co-existence between naturalized bees and other abundant native buzz-bees, like *Centris errans* and *Melissodes communis*.

Specialization appears to play a strong role in how *Euglossa dilemma* integrated into the system. Indeed, high visitation frequency and specialization on plants with poricidal anthers may have contributed to the successful buzz-pollination of Big Pine partridge pea, despite that its most important pollinator had been displaced after naturalization of orchid bees on the island. Exploitative competition for pollen resources on the island may have caused displacement of carpenter bees from the pollinator assemblage. In other words, when resources are limited, and species exhibit similar functional traits and resource use, competition exceeds facilitation and coexistence is unlikely (Koffel et al., 2018).

On the contrary, coexistence is apparent in nearly all documented pollinator invasions (Downing & Liu, 2012; Vanbergen et al., 2013), apart from managed *Bombus* bees (Morales et al., 2013), even if native populations are slightly reduced (Graham et al., 2019; Taggar et al., 2021; Vanbergen et al., 2013). However, species saturation and limiting similarity may be more apparent on islands where resources are limited (Elton, 1958) refuge habitat is sparse, and functional redundancy is generally low (Denslow, 2003). Indeed, invasions are frequent on islands (Moser et al., 2018). Although extinctions of some vertebrates from islands is common, extinctions of insects are rarely documented (Sax & Gaines, 2008).

In a study of two invaded island communities, native endemic species were mostly supergeneralists, while native non-endemic and exotic species were less generalized (Olesen et al., 2002). These authors suggest that because species density is low on islands, generalization may prevail. Similarly, *Apis mellifera* (honeybees) are commonly documented as generalist hubs that connect modules together (Aslan et al., 2019), reducing network specialization and modularity. However, the plant-pollinator network in our study was highly specialized and modular.

Drivers of network modularity and resource partitioning in flower visitors varied at the scale of the community considered. Phenology was the primary driver of structure in the buzz-bee subnetwork, in which pollinators shared similar functional attributes. In other words, when morphology was held constant, phenology explained how species partition resources and subdivide into modules. When morphology was not contained, as in the whole flower-visitor community, phenology was only slightly important for pollinator niche overlap and largely underpredicted network modularity. The idea that network attributes are scale-dependent is not new; this trend has been detected in almost all mutualistic networks, including plant-pollinator (Chacoff et al., 2012), seed-dispersal (Costa et al., 2016), and ant-extrafloral nectary networks (Falcão et al., 2016). However, these studies investigated differences in sampling method (Gibson et al., 2011), sampling size, or type of network type (quantitative or qualitative). To our knowledge, this is the first study to evaluate differences in drivers of network dynamics in a hierarchical network consisting of a whole community and a specialized subset. The relatively simple community of flowering plants and flower visitors of pine rocklands invaded by several different bees provided an excellent opportunity to examine these differences.

Network dynamics were also dependent on fire regimes in the fire-prone pine rockland. Time since fire was an important factor in structuring plant-pollinator communities in pine rockland forests of the lower Florida Keys. Interaction networks, in general, were more modular and specialized than expected, and modularity and specialization decreased monotonically with time since fire. Particularly, networks of fire suppressed sites were more generalized and overlap in resource use was high for plants and flower visitors.

Flowering diversity was lowest but flowering abundances were highest in fire suppressed sites, owing to the small number of large flowering trees and shrubs in these sites. In chapter two, we see that many of these flowering trees common in fire suppressed sites produce flower in early spring in short bursts. Common trees like poisonwood (*Metopium toxiferum*) and large clumping palms like Saw palmetto (*Serenoa repens*) commenced and concluded flowering within a month. Indeed, the silver thatch palm (*Leukothrinax morissii*), the most common palm on the island, flowered so abruptly that we missed the flowering event between campaigns. On the contrary, recently burned sites are composed of a high diversity of small herbaceous flowers that flower throughout the year.

Seasonal differences in flowering between large trees in fire suppressed sites and high temporal turnover of flowers in more recently burned sites may contribute to the overall stability of the plant-pollinator community. Chapter two demonstrated that modularity and network specialization in the buzz-bee network was driven by phenology.

Despite niche partitioning among buzz-pollinators by seasons, non-native buzz-pollinators, *Euglossa dilemma* and *Centris nitida* did not partition niches by fire age. I find this absence of habitat selection to be perplexing. Flowering resources and buzz-pollinators vary across seasons and flowering in fire suppressed sites were mostly of large flowering trees early in the season with few flowers later in the season. However, these bees were as likely to forage for flowers in recently burned sites as they were in those suppressed by fire.

Increasing fire suppression appeared to disassemble complex network attributes. More recently burned pine rockland had higher floral and interaction richness and higher levels of resource partitioning among plants and flower visitors. Although positive relationships between pyrodiversity and beta-diversity are well accepted (McLauchlan et al., 2020; Ponisio et al., 2016; Ulyshen et al., 2022), links between time since fire and dynamics of pollinator networks have not been explored in pine forests and may be important for understanding how fire management influences diversity and resiliency of networks to perturbations. For example, modularity and high resource partitioning in networks is thought to increase network resilience (Olesen et al., 2007). In modular networks, disturbances are likely to affect subsets of the community interacting more with each other rather than disassembling the whole network. As prescribed burning is delayed, floral richness diminishes, flower visitors share more resources, and networks become more generalized and less modular. Because altered fire regimes is a global issue, understanding how prolonged fire affects network resiliency is critical for fire management and increasing biodiversity.

Spatio-temporal analyses may lend insight into why species partition niches by phenology but not by fire age, despite that modularity and niche partitioning were high in both instances. In my Chapter 2 temporal study, space was static, and in my Chapter 3 fire age study, intra-annual variability was ignored. It is possible that seasonal differences in combination with spatial differences may interact and influence pollinator movement. Measures of beta-diversity and temporal turnover across space (Dupont et al., 2009; Dupont & Olesen, 2012) could illustrate that plant-polliantor communities are more dynamic than they appear in single static studies.

LITERATURE CITED

Aslan, C. E., Shiels, A. B., Haines, W., & Liang, C. T. (2019). Non-native insects dominate daytime pollination in a elevation Hawaiian dryland ecosystem. *American Journal of Botany*, *106*(2), 313–324. https://doi.org/10.1002/ajb2.1233

Chacoff, N. P., Vázquez, D. P., Lomáscolo, S. B., Stevani, E. L., Dorado, J., & Padrón, B. (2012). Evaluating sampling completeness in a desert plant-pollinator network. *Journal of Animal Ecology*, *81*(1), 190–200. https://doi.org/10.1111/j.1365-2656.2011.01883.x

Costa, J. M., da Silva, L. P., Ramos, J. A., & Heleno, R. H. (2016). Sampling completeness in seed dispersal networks: When enough is enough. *Basic and Applied Ecology*, *17*(2), 155–164. https://doi.org/10.1016/j.baae.2015.09.008

Denslow, J. (2003). Weeds in Paradise : Thoughts on the Invasibility of Tropical Islands. *Annals of the Missouri Botanical Garden*, *90*(1), 119–127.

Downing, J. L., & Liu, H. (2012). Friend or foe? Impacts of the introduced tropical oil bee Centris nitida on a threatened and specialized native mutualism in Southern Florida. *Biological Invasions*, *14*, 2175–2185. https://doi.org/10.1007/s10530-012-0223-z

Dupont, Y. L., & Olesen, J. M. (2012). Stability of modular structure in temporal cumulative plant-flower-visitor networks. *Ecological Complexity*, *11*, 84–90. https://doi.org/10.1016/j.ecocom.2012.03.004

Dupont, Y. L., Padro, B., Olesen, J. M., & Petanidou, T. (2009). *Spatio-temporal variation in the structure of pollination networks*. *February*. https://doi.org/10.1111/j.1600-0706.2009.17594.x

Elton, C. S. (1958). *The ecology of invasions by animals and plants*. Methuen.

Falcão, J. C. F., Dáttilo, W., & Rico-Gray, V. (2016). Sampling effort differences can lead to biased conclusions on the architecture of ant – plant interaction networks. *Ecological Complexity*, *25*, 44–52. https://doi.org/10.1016/j.ecocom.2016.01.001

Gibson, R. H., Knott, B., Eberlein, T., & Memmott, J. (2011). Sampling method influences the structure of plant-pollinator networks. *Oikos*, *120*(6), 822–831. https://doi.org/10.1111/j.1600-0706.2010.18927.x

Graham, K. K., Eaton, K., Obrien, I., & Starks, P. T. (2019). Anthidium manicatum , an invasive bee , excludes a native bumble bee , Bombus impatiens , from floral resources. *Biological Invasions*, *21*(4), 1089–1099. https://doi.org/10.1007/s10530-018-1889-7

Koffel, T., Boudsocq, S., Loeuille, N., & Daufresne, T. (2018). Facilitation- vs. competition-driven succession: the key role of resource-ratio. *Ecology Letters*, *21*(7), 1010–1021. https://doi.org/10.1111/ele.12966

McLauchlan, K. K., Higuera, P. E., Miesel, J., Rogers, B. M., Schweitzer, J., Shuman, J. K., Tepley, A. J., Varner, J. M., Veblen, T. T., Adalsteinsson, S. A., Balch, J. K., Baker, P., Batllori, E., Bigio, E., Brando, P., Cattau, M., Chipman, M. L., Coen, J., Crandall, R., … Watts, A. C. (2020). Fire as a fundamental ecological process: Research advances and frontiers. *Journal of Ecology* 108(5): 2047–2069). Blackwell Publishing Ltd. https://doi.org/10.1111/1365-2745.13403

Morales, C. L., Arbetman, M. P., Cameron, S. A., & Aizen, M. A. (2013). Rapid ecological replacement of a native bumble bee by invasive species. *Frontiers in Ecology and the Environment*, *11*(10), 529–534. https://doi.org/10.1890/120321

Moser, D., Lenzner, B., Weigelt, P., Dawson, W., Kreft, H., Pergl, J., Pyšek, P., van Kleunen, M., Winter, M., Capinha, C., Cassey, P., Dullinger, S., Economo, E. P., García-Díaz, P., Guénard, B., Hofhansl, F., Mang, T., Seebens, H., & Essl, F. (2018). Remoteness promotes biological invasions on islands worldwide. *Proceedings of the National Academy of Sciences*. https://doi.org/10.1073/pnas.1804179115

Olesen, J. M., Bascompte, J., Dupont, Y. L., & Jordano, P. (2007). The modularity of pollination networks. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(50), 19891–19896. https://doi.org/10.1073/pnas.0706375104

Olesen, J. M., Eskildsen, L. I., & Venkatasamy, S. (2002). Invasion of pollination networks on oceanic islands: Importance of invader complexes and endemic super generalists. *Diversity and Distributions*, *8*(3), 181–192. https://doi.org/10.1046/j.1472-4642.2002.00148.x

Ponisio, L. C., Wilkin, K., M'Gonigle, L. K., Kulhanek, K., Cook, L., Thorp, R. W., Griswold, T., & Kremen, C. (2016). Pyrodiversity begets plant-pollinator community diversity. *Global Change Biology*, *22*, 1794–1808. https://doi.org/10.1111/gcb.13236

Sax, D. F., & Gaines, S. D. (2008). Species invasions and extinctions: The future of native biodiversity on islands. *Proceedings of the National Academy of Sciences*, *105*(1), 11490–11497. https://doi.org/https://doi.org/10.1073/pnas.0802290105

Taggar, A. K., McGrath, E., & Despland, E. (2021). Competition between a native and introduced pollinator in unmanaged urban meadows. *Biological Invasions*, *23*(6), 1697–1705. https://doi.org/10.1007/s10530-021-02465-z

Ulyshen, M. D., Hiers, J. K., Pokswinksi, S. M., & Fair, C. (2022). Pyrodiversity promotes pollinator diversity in a fire-adapted landscape. *Frontiers in Ecology and the Environment*, *20*(2), 78–83. https://doi.org/10.1002/fee.2436

Vanbergen, A. J., Garratt, M. P., Vanbergen, A. J., Baude, M., Biesmeijer, J. C., Britton, N. F., Brown, M. J. F., Brown, M., Bryden, J., Budge, G. E., Bull, J. C., Carvell, C., Challinor, A. J., Connolly, C. N., Evans, D. J., Feil, E. J., Garratt, M. P., Greco, M. K., Heard, M. S., … Wright, G. A. (2013). Threats to an ecosystem service: Pressures on pollinators. *Frontiers in Ecology and the Environment*, *11*(5), 251–259. https://doi.org/10.1890/120126

VITA

BRITTANY HARRIS

	Born, New Orleans, Louisiana, USA
2007-2009	Associate of Science Pellissippi State Technical Community College Oak Ridge, Tennessee
2010-2012	Bachelor of Science, Biological Sciences University of New Orleans New Orleans, Louisiana
2012	Americorp Research Intern, Jean Lafitte National Historic Park and Preserve, Barataria Preserve, Marrero, Louisiana
2013-2014	Conservation Research and Records Intern Fairchild Tropical Botanic Garden, Miami, Florida
2014-2016	Master of Science, Environmental Studies, Agroecology Florida International University, Miami, Florida
2016-2022	Doctoral Candidate, Biology Florida International University Miami, Florida
2016-2019	Research Assistant, GIS & Remote Sensing Center Florida International University, Miami, Florida
2017	Tropical Biology: An Ecological Approach Field Course Organization for Tropical Studies, Costa Rica
2018	Bee Course, Southwestern Biological Research Station, Arizona
2019-2020	UGS Dissertation Evidence Acquisition Fellowship (2) Florida International University, Miami, Florida
2021	UGS Dissertation Year Fellowship Florida International University, Miami, Florida
2022	UGS Excellence Award for Outstanding Graduate Teaching Assistant, Florida International University, Miami, Florida

PUBLICATIONS AND PRESENTATIONS

Harris, B., Lui, H., Koptur, S. (August, 2022) *Displacement and replacement of buzz-pollination by an exotic solitary bee on a sub-tropical island*. Paper presented at the meeting of the Ecological Society of America, Montreal, Canada.

Koptur, S., J. Clayborn, B. Harris, I. Jones, M. Pimienta, A. Salas, P. Oliveira. (2022). Caterpillar Responses to Ant Protectors of Plants. In B. Marquis & S. Koptur (Eds.), *Caterpillars in the Middle*: *Tritrophic interactions in a changing world.* Springer Publishing.

Harris, B. & S. Koptur. (2022). Facilitated fecundity in sand flax: pollination in an endangered herb of pine rocklands. *Flora*. 152041.

Harris, B. (June 2021). *Plant-pollinator networks in pine Rockland of the Florida Keys*. Florida Native Plant Society (FNPS) Miami, Florida

Harris B., Freidenreich A., Jayachandran K. (2021) Short-term vegetation responses to the first prescribed burn in an urban pine rockland preserve. *Fire Ecology*, 17, 1–9.

Freidenreich, A., B. Harris, S. Dattamudi, E. Betancourt, M. Reis, K. Jayachandran (2020). Effects of prescribed fire on soil properties in a pine rockland ecosystem. *Agricultural and Environmental Letters.*

D. Gann, J. Richards, B. Harris. 2019. Vegetation change along ENP boundary areas of Northeast Shark River Slough between 2010/13 and 2016/17. Miami, FL: Florida International University, GIS Center. *84:* 1-62. Report National Park Service

Zona, S. & B. Harris (2018). Heterocarpy in *Salvia roemeriana* (Lamiaceae). *Plant Species Biology*.