

**Resistance and Resilience of a Flower-Visitor Network to a Severe Hurricane in an Insular
Tropical Beach Dune System**

By

Nicole A. Martínez-Llaurador

A Dissertation submitted to the

DEPARTMENT OF BIOLOGY

FACULTY OF NATURAL SCIENCES

UNIVERSITY OF PUERTO RICO, RIO PIERDAS CAMPUS

In partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

June 7th 2021

© Nicole A. Martínez-Llaurador

All rights reserve

ACCEPTED BY THE FACULTY OF THE DEPARTMENT OF BIOLOGY OF THE UNIVERSITY OF PUERTO
RICO IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

Dr. James D. Ackerman
Professor of the Department of Biology
Thesis Advisor

Dr. Raymond Tremblay
Professor of the Department of Biology
Committee Member

Dr. Jess Zimmerman
Professor of the Department of Environmental Sciences
Committee Member

Dr. Alberto Sabat
Professor of the Department of Biology
Committee Member

“The great aim of education is not knowledge but action.”

-Herbert Spencer

Acknowledgements

I would like to thank my advisor Dr. James Ackerman for opening the door to his lab and providing me with a unique master's experience. A very special thanks to Dr. Raymond Tremblay for his patience and guidance when teaching me statistics. The rest of my committee Dr. Jess Zimmerman and Dr. Alberto Sabat for their interest in my work, insightful comments, and encouragement. I also want to thank Dr. Elvia Melendez-Ackerman and Dr. Paul CaraDonna for their comments and help with analysis. I want to the Zoology Museum and Herbarium of the University of Puerto Rico for storing the voucher specimens.

I would like to recognize the invaluable support that all my lab mates and friends gave me as well. You have made this into a fun adventure.

A special thanks to my parents and sisters, all of you were always there to support me even when you did not understand what I was doing. I love you all so much.

Lastly, to my beloved partner in life, I cannot thank you enough for encouraging me and believing in me. Going to the field with you and teaching you about plants and insects made me a better scientist.

Table of Contents

Dedication.....	ii
Acknowledgment.....	iii
Table of contents.....	iv
List of tables.....	v
List of figures.....	vi
List of Abbreviations.....	vii
Chapter 1: Resistance and Resilience of a Flower-Visitor Network to a Severe Hurricane in an Insular Tropical Beach Dune System	
1.1 Abstract.....	1
1.2 Introduction.....	2
1.3 Methods.....	5
1.4 Results.....	7
1.5 Discussion.....	10
1.6 Literature cited.....	15
1.7 Tables.....	26
1.8 Figures.....	31
1.9 Appendix.....	45

List of Tables

Table Number	Page
1. Network level metrics for each study year. w.NODF: weighted nestedness, H_2' : specialization index.....	26
2. Species richness in each flower visitor functional group across the four years of study.	
3. T test results of the observed nestedness value by year and null model with 100 randomizations. Using 'r2d' null model ('bipartite' package) since it generates the randomizations with given marginals for the network size.....	27
4. Results of generalized linear mixed models for all species level metrics of the network. The explanatory variables at the visitor level are functional groups and years. Models presented were selected via the AIC criterion.....	28
5. Results of generalized linear mixed models for all species level metrics of the network. The explanatory variable at the plant level is year.....	29
A.1 Values for the species level metrics for each of visitor species by study year.....	45
A.2 Values for the species level metrics for each of the plant species by study year...	48

List of Figures

Figure Number	Page
1. Map of the Piñones network site in Loíza, PR.	31
2. Interaction network visualization by year A (2015), B (2016), C (2018), and D (2019)....	32
3. Species abundance within functional groups by years.....	37
4. Frequency of observations of each plant species by year.....	38
5. Comparison of species level metrics for visitor species.....	39
6. Comparison of species level metrics for plant species.....	42
 A.3 Interaction network visualization with the years combined A (2015-2016) and B (2018- 2019).....	50

List of Abbreviations

wNODEF- Weighted nestedness based on overlap and decreasing fill

H_2' - Interaction specialization index at a network level

d' - Interaction specialization index at a species level

GLM- Generalized linear model

GLMM- Generalized linear mixed model

AIC- Akaike information criterion

**Chapter 1: Resistance and Resilience of a Flower-Visitor Network to a Severe Hurricane in
an Insular Tropical Beach Dune System**

Abstract

Plant-pollinator interactions provide a crucial ecosystem service for which many depend upon. These interactions can be threatened by many different anthropogenic and natural disturbances. While most studies on plant-pollinator interactions have focused on the anthropogenic threats including effects of climate change, fewer studies have evaluated the effects of severe natural disturbances. Hurricanes in the tropics are a natural occurrence that can be catastrophic to communities and ecosystem services. It is common for hurricanes to be responsible for the loss of insect assemblages, which are the most abundant group of pollinators. Here I evaluate how the impact of a category 4 hurricane (Hurricane María) influenced the interactions of plants and their flower visitors in a coastal sand dune ecosystem in Puerto Rico. I used ecological networks and data collected over a five-year period (2015-2019) to assess the effects of the large atmospheric disturbance that passed through in September 2017. After the hurricane, I found a decrease in species abundance and a lower number of interactions, but an increase in species richness. Functional groups of flower visitors responded differently but in general bees were impacted negatively compared to butterflies, flies, and wasps. Overall network had a high dependence on the non-indigenous *Apis mellifera*, but after the hurricane the abundance of the species decreased making it a more generalized network. Other network metrics such as nestedness, connectance, and robustness for plants and flower visitors were consistent across years. Thus, the plant-flower visitor network in the coastal sand dunes of Puerto Rico was largely resistant and resilient against a severe hurricane induced perturbation.

Introduction

For over 350 million years plants and insects have lived together on the planet. They have not only coexisted, but also coevolved, and continue to closely interact with each other (War et al. 2011). Pollination is one of the most important of such interactions and is generally considered mutualistic, being beneficial for both species involved (Ings et al. 2009). As a fundamental ecosystem service, plant-pollinator interactions maintain biodiversity at both global and local scales (Olesen et al. 2007; Hegland et al. 2010). Afterall, reproductive success of 87% of flowering plant species relies on animal pollination, especially by insects (Eckert et al. 2010; Ollerton et al. 2011). Pollination results in biomass production, plant reproduction and food production (Aguado et al. 2019), which in turn benefits society (de Groot et al. 2002). Consequently, pollination services have been studied broadly due to their importance to evolution, ecology, conservation, and human well-being (de Groot et al. 2002; Hegland et al. 2010) .

A new era in community level-pollination ecology began with the development of ecological networks (Jordano, 1987; Bascompte & Jordano, 2007; Vázquez et al., 2009; Baldock et al., 2011). Networks reveal ecological structure and ecosystem function (Hegland et al. 2010). They have properties that can be used to study co-evolution (Carstensen et al. 2016), extinctions (Olesen et al. 2007; Veron et al. 2018), species roles in the communities (Blüthgen et al. 2006; Emer et al. 2016; Coux et al. 2016) and the effects of disturbances (Vanbergen 2014; Soares et al. 2017). They give the opportunity to examine situations such as species coexistence and the community consequences of adding or losing a species (Memmott & Waser 2002; Traveset & Richardson 2006; Bascompte & Jordano 2007; Aizen et al. 2008). For example, Olesen et al. (2007) evaluated the effect of coextinctions of plant-pollinator communities with network analysis by using the compartmentalization of the network. Modules within a network provide information

on which species are highly connected. Furthermore, they can identify key taxa in a community, which may be targeted for management to ameliorate the effects of environmental change (Olesen et al., 2007). Others have focused on using networks to see the effect of anthropogenic disturbances such as invasive species (Memmott & Waser 2002; Traveset & Richardson 2006; Aizen et al. 2008), and landscape alterations and habitat fragmentation on networks (Vanbergen 2014; Traveset et al. 2018). The reason for networks being so useful to study disturbances is because they are meant to be highly structural as they are often described with metrics (heterogeneity, nestedness, and modularity) that may indicate susceptibility to loss of species (Bascompte et al. 2003; Bascompte & Jordano 2007). These characteristics are meant to confer network stability and robustness to lower the probability of cascading effects (Memmott et al. 2004; Fortuna & Bascompte 2006). Network structure is therefore a key tool to study disturbances at the community level (Vanbergen 2014; Soares et al. 2017).

Hurricanes are intense and large-scale storms that can affect the structure and function of ecosystems (Walker et al. 1992). In the wake of such storms vertebrate pollinator populations are reduced (Gannon & Willig 1994; Wunderle 1995; Temeles & Bishop 2019), not only due to the direct effects of the storm but also the abrupt loss of food sources for both nectarivores and frugivores (Askins & Ewert 1991; Lynch 1991; Wunderle et al. 1992; Rathcke 2000). Consequently, plant-pollinator interactions are affected (Rivera-Marchand & Ackerman 2006; Rojas-Sandoval & Meléndez-Ackerman 2011; Pérez et al. 2018; Temeles & Bishop 2019). Invertebrate pollinators are not immune to hurricane effects either (Landry 2013). Villanueva-Gutiérrez et al. (2013) reported that social bee colonies and solitary native bees in Mexico suffered substantial mortality after the passage of Hurricane Sandy. Nevertheless, some mutualistic interactions are resilient, either thriving or appearing stable after a hurricane event, including fig-

wasp and sphingid moth-orchid interactions (Bronstein & Hossaert-McKey 1995; Ackerman & Moya 1996). In Florida, the effect Hurricane Andrew had on pollinator assemblages and pollinator abundance was minimal or even positive (Pascarella 1998). Diaz Infante et al. (2020) compared hummingbird-plant networks in a protected dry forest over a period of 30 years. During this time, the forest experienced two different hurricanes, the most recent was Hurricane Patricia (category 4) in 2015. Overall, they observed that community composition changed, losing generalist plant and pollinator species, and gaining new plant species. Network metrics did not vary much apart from observing an increase in plant robustness and hummingbird niche overlap after hurricanes (Diaz Infante et al. 2020). On the other hand, a recent study showed that pollinator communities of mango (*Mangifera indica*) plantations changed after the passage of hurricanes but returned to pre-hurricane levels after 2 years (Cabrera-Asencio & Meléndez-Ackerman 2021). Thus far, there are no clear patterns as to how hurricanes will affect mutualistic interactions, as it can be variable.

Hurricanes pass through the Caribbean every year. In 2017, many islands were impacted by two consecutive powerful hurricanes, Irma (category 5) and Maria (category 4); Irma skirted Puerto Rico with tropical storm winds, but Maria hit the island two weeks later at full strength. How resistant or resilient are plant-pollinator networks in this hurricane alley? Our focus is to analyze the structure and composition of the networks in Puerto Rico and reveal what impacts hurricanes have had on local networks. I expect to find changes in network nestedness, connectance, and specialization of interactions given that the abundance and composition of plant and insect communities can fluctuate due to habitat degradation caused by the hurricane. I expect that reduced pollinator populations will decrease the level of structure of the network. This network analyses may identify species that are key to the network integrity and determine how they influence resiliency.

Methods

Study site

The study site is the coastal dunes of the Natural Reserve of Piñones, Loíza, Puerto Rico (N18°26.670' W65°55.100', Fig 1). The dunes at this site are dominated by *Ipomoea pes-caprae* (Convolvulaceae), *Scaevola plumieri* (Goodeniaceae), *Bidens alba* (Asteraceae), *Coccoloba uvifera* (Polygonaceae), *Lantana involucrata* (Verbenaceae), and *Canavalia rosea* (Fabaceae). We use dunes as the ecosystem of choice because it is the first barrier against strong winds, ocean surges and big waves, often receiving some of the most severe impacts of hurricanes (Arun et al. 1999). It is also a place where plants and pollinators may be most resilient or resistant to severe natural storms. Furthermore, plant-pollinator interactions are easily observable, being most life forms are either terrestrial vines or short shrubs.

Data collection

Students from the University of Puerto Rico, Río Piedras (J. D. Ackerman laboratory) have been collecting flower visitor data at Piñones for 7 years (2014-2020) all year round. Observations on current flowering plant species located on site were done for 15 min each, recording data on frequency of visits. Only visitors whose size and behavior are likely to contact anthers and stigmas are assumed to be pollinators. Thus, if they appeared to make contact then it is counted as an interaction. We censused flower visitors between 0800 and 1200 on sunny days (< 50% cloud cover) because preliminary studies at Piñones indicated that nearly all flower visiting activity occurred during that time span and under those conditions. The number of observational visits to the site varied across years, but the plot was visited at least 3 times each year. All plant and insect visitors are identified to the lowest taxonomic level possible using available literature (Curran

1928; Grissell 2007; Genaro & Franz 2008; Pérez-Asso et al. 2009; Axelrod 2011; Carpenter & Genaro 2011; Mari Mutt 2015) and comparisons with existing collections. Vouchers are deposited in the entomology collection at the Zoology Museum (MZUPRRP) and the Herbarium of the University of Puerto Rico (UPRRP).

Network Metrics

All network analysis was done in R studio 3.6.1. using the '*bipartite*' package, which is commonly used to calculate network metrics (Dormann et al. 2008, 2009). Quantitative interaction matrices were done for each year using number of visits per unit time as link weight (Traveset et al. 2018). The metrics that are most commonly used at a network level are weighted nestedness (wNODF), modularity, connectance, interaction specialization at network level (H_2'), and species composition (Tylianakis et al. 2010; Soares et al. 2017). I also included robustness and niche overlap, both of which were also used by Díaz Infante et al. (2020) along with network metrics to provide an overview of the community organization. Lastly, I also evaluated species composition, which can be affected by anthropogenic disturbances (Blüthgen et al. 2006). At the species level, I used the following metrics used by (Traveset et al. 2018): degree, strength, species specialization index (d'), and weighted closeness centrality.

Nestedness relates the connectivity of many specialists to generalists and reduces the possibility of cascading secondary extinctions (Bascompte et al. 2003; Olesen et al. 2006). It is predicted to decrease with a reduction in environmental quality (Vanbergen 2014). Connectance is the proportion of given links over the possible links, which is calculated by multiplying the total number of pollinators and plants (Blüthgen et al. 2008). Another metric that observes a decrease with the reduction of habitat quality is species degree, which is the sum of links per species. Aizen et al. (2008) showed that an increase in species degree for alien species decreases species degree

for native species in the networks. Species strength is the sum of dependencies of each species, it may identify key species, and it can detect changes in species roles (Soares et al. 2017). The interaction specialization (H_2' and d') metric represents “the degree of specialization of elements within an interaction network and the entire network” (Blüthgen et al. 2006). They both decrease when the network has any impacts on it. Closeness centrality describes the centrality of a species by its path length to other nodes in the network (Martín González et al. 2010). I will use these metrics to understand how a major habitat perturbation impacts a plant-pollinator community.

Statistical Analysis

All statistical analyses were done using R ver. 3.6.1. To test the significance of wNODF values, I compared them to 100 randomizations of null models (R package ‘*bipartite*’). Generalized linear models (GLM) were done to compare species richness and flower visitor abundances among years. For species richness a ‘quasipoisson’ distribution was used after testing for overdispersion, while flower visitor abundances used a log normal distribution but not before standardizing the values by hours of observations per year. Lastly, for all species level parameters a generalized linear mixed model (GLMM) was done to compare metrics across years. I used year, and functional group as fixed variables and visitor species as a random factor. For plant species metrics, only year was a fixed variable. I used gamma or log normal distribution for the models based on the best fit. Different models were done for plant, visitors, and each parameter, and chosen following the AIC criterion. For metrics that had values ranging from 0 to 1 and did not exhibit a normal distribution, a beta regression was used (R package ‘*glmmTMB*’ (Brooks et al. 2017).

Results

Community structure

Overall community composition of plants and their visitors did not vary greatly during the four years (Fig 2). There was a total of 26 plant species and 52 visitor species. The most common plant species present varies by year, some of them are *Bidens alba* (Asteraceae), *Coccoloba uvifera* (Polygonaceae), and *Scaevola plumieri* (Goodeniaceae). The most common visitors were *Apis mellifera*, *Centris decolorata* (Hymenoptera: Apidae) and *Agraulis vanillae insularis* (Lepidoptera: Nymphalidae). The abundance of species for each functional group varied significantly for butterflies, wasps, and bees ($\chi^2 = 47.31$, $df = 4$, $P < 0.001$, Fig 3). As for differences among years, a significant decrease in species abundances was observed ($\chi^2 = 8.15$, $df = 3$, $P < 0.05$, Fig 3). The functional group with the most visitor species were butterflies with 19 identified species, and 3 unidentified individuals from the families Hesperidae and Pieridae. The functional group with the most interactions were bees (Fig 2), composed of three generalists: non-indigenous *Apis mellifera*, and the native *Centris decolorata* and *Xylocopa mordax* (Hymenoptera: Apidae). There was a non-significant increase in species richness for the two years post-hurricane ($\chi^2 = 5.07$, $df = 3$, $P = 0.167$). The first year after Hurricane Maria (September 2018) had more visitor species with an increase in fly species (Table 2), but with fewer links (Table 1). Before the hurricane more than half the links to plants were by *A. mellifera*, but after the hurricane the presence of *A. mellifera* decreased significantly affecting the total number of links. Even though *A. mellifera* began to recuperate in 2019, it still had fewer total links compared to the previous year (Fig 2).

As for structural differences in the network, weighted nestedness (wNODF) was consistently low across the years. The closer the wNODF value is to 100 the more nested is the network (Table 1). Null model comparison showed that nestedness values were significantly lower from the expected (Table 3). Modularity analysis was excluded because all networks had only one

module across years. Meanwhile, networks had a consistent connectance of 0.22, except for the 2019 post-hurricane network which saw a slight decrease (Table 1). Before the hurricane, most plant species were visited by *A. mellifera*, but afterwards these interactions were lost causing a decrease in interaction specialization (H2'). Consequently, the network then became more generalized and for plant species niche overlap declined (Table 1). The robustness of the network for all years was high but it showed a slight increase after the hurricane.

Species level metrics

Visitor species

All species level metrics varied but in general whenever bee metrics changed, the other three groups also changed, but not necessarily in the same direction (Fig 5). Species degree declined significantly for bees from pre-hurricane (2016) to post-hurricane (2018) while for butterflies and wasps it increased in those same years (Table 4). Wasps saw a slight increase in species degree, but it did not have as much influence as butterflies and flies (Fig 5). Species strength followed a similar trend for butterflies and flies and by years (Table 4). Flies, butterflies, and wasps all were significantly less connected than bees in 2016 (Table 4). Species specialization index (d') did not vary much among the groups, therefore the model for d' best fit did not include functional groups. Only the year 2015 (pre-hurricane) had significant difference between species specialization (Table 4).

Plant species

Overall plant species metrics did not vary significantly across years. Plant species had an increase in species degree the years after the hurricane (Table 5). As for species strength, weighted closeness, and d' there were not many changes throughout the years, only 2015 showed significant

changes compared to all subsequent years (Table 5). In the case of d' , we saw a slight increase the years after the hurricane. Plant species showed a general trend of low specialization with a few outliers (Fig 6).

Discussion

The Caribbean is a hot spot for hurricanes; thus, it has become a perfect location to study the effects of this natural phenomenon on population, community, and ecosystem levels (e.g., (Askins & Ewert 1991; Lynch 1991; Walker et al. 1992; Wunderle et al. 1992; Bronstein & Hossaert-McKey 1995; Rathcke 2000). Thus far, most studies have focused on plant-pollinator interactions of particular species (Ackerman & Moya 1996; Pascarella 1998; Rivera-Marchand & Ackerman 2006; Rojas-Sandoval & Meléndez-Ackerman 2011; Pérez et al. 2018; Temeles & Bishop 2019; Diaz Infante et al. 2020; Cabrera-Asencio & Meléndez-Ackerman 2021), but none have taken an interaction network perspective. In this study we discuss the changes in the dynamics of plant-visitor communities of coastal dunes after the impact of two strong storms within two weeks of one another, the latter one being very severe (Hurricane María).

According to recent studies (Kishi et al. 2017; Chen et al. 2020; Cabrera-Asencio & Meléndez-Ackerman 2021), insect assemblages show a level of resiliency where they can return to pre-disturbance status in a short time period. I observed similar results with some changes in insect assemblages after Hurricane María and by 2019 the dominant species were back to the top of the interaction network (Fig 2). In 2018 the number of visitor species increased 2-fold, yet this did not increase interactions. After the hurricane, interactions between plants and visitors decreased and continued to decrease two years post hurricane. Originally *A. mellifera* was the most dominating species in the network with more than half of the interactions, but its numbers suffered greatly after the 2017 hurricanes which explains the lower interactions in 2018. By 2019

the abundance of *A. mellifera* recuperated with the bee returning to its role as a supergeneralist, similar to what Cabrera-Asencio & Meléndez-Ackerman (2021) found for pollinators of mango plantations in southern Puerto Rico. The low interactions in 2019 could mean that the communities had not yet fully recovered, or other natural or anthropogenic factors may be involved.

Apis mellifera is one of the most successful pollinator invaders of the world. As a supergeneralist, *A. mellifera* negatively influences pollinator communities and the number of plant-native pollinator interactions. Many native pollinators are outcompeted because of the invader's competitive superiority or because of resource limitation (Traveset & Richardson 2006). Fumero-Cabán (2019) compared the pollinator communities of *Guaiacum sanctum* (Zygophyllaceae) in two dry forest sites, one with *A. mellifera* present (Guánica, Puerto Rico) and one without it (Mona Island). There were more interactions for the Guánica individuals but over 98% of these were solely *A. mellifera*, while in Mona Island there was a larger diversity of visitors for the same tree species, but interactions were fewer among the different visitors. This may indicate that *A. mellifera* has affected native visitors and their interactions (Ackerman 2021). In many cases plant-pollinator networks dominated by an invader shows a level of stability that makes it less likely to switch back to an uninvaded state (Aizen et al. 2008; Tylianakis et al. 2010).

Network structure seemed to be unfazed by the hurricane as most metrics stayed consistent across years which could mean it is a resistant network. Nestedness values were not as expected: overall values had very low nestedness. This may be the consequence of network size. According to Montoya et al. (2006) larger networks tend to have a more nested pattern as there is usually more heterogeneity in their link distribution. Most links in the network at Piñones were with *A. mellifera*, making it a slightly more specialized network with low linkage heterogeneity. The presence of supergeneralist like *A. mellifera* usually influences nestedness positively because they

have a wide range of resources and their extreme foraging gives them the advantage to establish effectively in the network (Olesen et al. 2002; Aizen et al. 2008), but this does not seem to be the case for this network. Therefore, the decrease of *A. mellifera* frequency and its links increased the heterogeneity of links resulting in a low network specialization index after the hurricane. Thus, the flower-visitor network of the beach dune system became more generalized. Plant species also saw a decrease in niche overlap in 2018, which is related to the decrease in visitation frequency of *A. mellifera*. The negative relationship between the abundance of *A. mellifera* and native visitors, and *A. mellifera*'s visitation frequency are among the phenomena associated with resource competition (Aizen & Feinsinger 1994; Thomson 2016). In mainland Neotropics, *A. mellifera* is such a strong competitor that natives must visit alternative resources from those used by *A. mellifera* (Roubik & Villanueva-Gutiérrez 2009). This in turn makes it look like plant species are specialists.

Connectance values also stayed consistent across years which was not as expected considering the increase in the number of species after the hurricane. Connectance is considered a metric of high importance because when used to compare similar size networks (Thébault & Fontaine 2010), higher connectance can mean higher stability due to the redundancy of species interactions (Dunne et al. 2002). Nevertheless, it is highly influenced by the size of the network due to the nature of the metric (Tylianakis et al. 2010).

The hurricanes did not seem to influence species level metrics. For higher-level species (visitors) all metrics except d' experienced some significant changes after the hurricane. There was a negative relationship between bees and the other functional groups. Likely due to the decline in *A. mellifera* after the hurricane, we see an increase in most higher-level metrics for the other functional groups. When a non-indigenous supergeneralist monopolizes resources suppressing native pollinators (Goulson 2003; Dupont et al. 2004; Henry & Rodet 2018; Hung et al. 2018;

Valido et al. 2019), then declines of the species abundance will reduce resource competition with other functional groups. However, Roubik (1992) suggested that in the Neotropics alternative floral resources are not limiting, which in turn means that highly competitive species like *A. mellifera*, and native bees have access to sufficient alternative resources that their abundances will not necessarily be affected by competition. In some cases, the natural disturbance may help native communities by opening up niches and facilitating their occupation (Masciocchi et al. 2013). In the Piñones network the decline of the most abundant and dominant species (*A. mellifera*) leads to the reduction of specialization for other groups like butterflies, flies, and wasps (Table 3). On the other hand, lower-level species (plants) did not exhibit many changes to their metrics. We observed that species degree had an increase in 2018 and it started to go back down in 2019. This is a pattern that is to be expected because of the increase of visitor species that happened in 2018. Species strength had some non-significant variation across years but in 2016 some of the lowest values were observed. Thus, most species of plants that year had very little relevance across all its partners possibly because of the high niche overlap among plants. As a result, that same year weighted closeness showed some variation, but had lower values indicating lack of centrality of the species. Lastly, plant species experience a consistent increase in specialization through the years. Although these values were on the lower end of the scale (closer to 0 is more generalized) this slight increase in specialization could be due to changes in the dynamics of the network. For example, it is expected to see declines in specialization when there is loss of diversity, reduction of specialists and their interactions, and when generalists increase (Burkle & Knight 2012; Grass et al. 2013; Natalie Weiner et al. 2014). Contrary to their observations, we see the diversity of the visitors increase in this network, which could be the result of the addition of specialists.

Although the hurricanes proved to be a menacing force that caused much damage to the ecosystem, overall plant-flower visitor network communities proved to be resilient. Pre-hurricane years showed a highly invaded network that largely depended on a supergeneralist species (*A. mellifera*), which are known to seize links previously held by natives (Aizen et al. 2008). Thus, a hurricane may be an event that, to a certain extent, restores the native community of flower visitors. As for the beach dune plant community, most species are likely adapted to survive not only harsh conditions on a daily basis, but also occasional severe atmospheric events. Therefore, changes in plant-flower visitor dynamics were related to the changes in the visitor community.

Ultimately, the overall network was not influenced by the impact of the hurricane as expected. I hypothesized that the loss of species due to the hurricane would have a negative effect on the structure and stability of the network. Contrary to that, I found that networks were quite resistant to the hurricane as metrics did not change much over the years. Although an increase in visitor species was observed after the hurricane, this did not influence network metrics in either a positive or negative way. On the other hand, at a species level it seemed to help native visitors thrive in the community more by reducing the abundance of the highly competitive *A. mellifera*. Network plants proved to be highly resistant, while native flower visitors proved to be more resilient. Thus, the native plant-flower visitor interaction network of Piñones dune vegetation was in fact both resistant and resilient against hurricane damage.

References

- Ackerman JD (2021) Island invasions by introduced honey bees: what can be expected for Puerto Rico and the Caribbean? *Frontiers in Ecology and Evolution* 8: 556744.
- Ackerman JD, Moya S (1996) Hurricane aftermath: resiliency of an orchid-pollinator interaction in Puerto Rico. *Caribbean Journal of Science* 32:369–374.
- Aguado D, Gutiérrez-Chacón C, Muñoz MC (2019) Functional structure and patterns of specialization in plant-pollinator relationships of an agroecosystem in Valle del Cauca, Colombia. *Acta Biologica Colombiana* 24:331–342.
- Aizen MA, Feinsinger P (1994) Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine “Chaco Serrano”. *Ecological Applications* 4:378–392.
- Aizen MA, Morales CL, Morales JM (2008) Invasive mutualists erode native pollination webs. *PLoS Biology* 6:0396–0403.
- Arun A, Beena K, Raviraja N, Sridhar K (1999) Coastal sand dunes-a neglected ecosystem. *Current Science* 77:19–21.
- Askins RA, Ewert DN (1991) Impact of Hurricane Hugo on bird populations on St. John, Virgin Islands. *Biotropica* 23:481–487.
- Axelrod FS (2011) A Systematic vademecum to the vascular plants of Puerto Rico. BRIT Press, Fort Worth, Texas.

- Baldock KCR, Memmott J, Ruiz-Guajardo JC, Roze D, Stone GN (2011) Daily temporal structure in African savanna flower visitation networks and consequences for network sampling. *Ecology* 92:687–698.
- Bascompte J, Jordano P (2007) Plant-animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 38:567–593.
- Bascompte J, Jordano P, Melián CJ, Olesen JM (2003) The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences* 100:9383–9387.
- Blüthgen N, Fründ J, Vázquez DP, Menzel F (2008) What do interaction network metrics tell us about specialization and biological traits? *Ecology* 89:3387–3399.
- Blüthgen N, Menzel F, Blüthgen N (2006) Measuring specialization in species interaction networks. *BMC Ecology* 6:9.
- Bronstein JL, Hossaert-McKey M (1995) Hurricane Andrew and a Florida fig pollination mutualism: resilience of an obligate interaction. *Biotropica* 27:373–381.
- Burkle LA, Knight TM (2012) Shifts in pollinator composition and behavior cause slow interaction accumulation with area in plant-pollinator networks. *Ecology* 93:2329–2335.
- Cabrera-Asencio I, Meléndez-Ackerman EJ (2021) Community and species-level changes of insect species visiting *Mangifera indica* flowers following Hurricane María: “The Devil is in the details.” *Frontiers in Ecology and Evolution* 9:556821.

- Carpenter J, Genaro J (2011) Vespidae (Insecta: Hymenoptera) of Puerto Rico, West Indies. Insecta Mundi Paper 714. [online] URL: <https://digitalcommons.unl.edu/insectamundi/714> (accessed 26 April 2021).
- Carstensen DW, Sabatino M, Morellato LPC (2016) Modularity, pollination systems, and interaction turnover in plant-pollinator networks across space. *Ecology* 97:1298–1306.
- Chen X, Adams BJ, Platt WJ, Hooper-Bùi LM (2020) Effects of a tropical cyclone on salt marsh insect communities and post-cyclone reassembly processes. *Ecography* 43:834–847.
- Coux C, Rader R, Bartomeus I, Tylianakis JM (2016) Linking species functional roles to their network roles. *Ecology Letters* 19:762–770.
- Cribari-Neto F, Zeileis A (2010) Beta regression in R. *Journal of Statistical Software* 34:1–24.
- Curran CH (1928) Scientific Survey of Porto Rico and the Virgin Islands. Insects of Porto Rico: Diptera or two winged flies. New York Academy of Sciences, New York.
- Diaz Infante S, Lara C, Arizmendi C (2020) Temporal dynamics of the hummingbird-plant interaction network of a dry forest in Chamela, Mexico: a 30-year follow-up after two hurricanes. *PeerJ* 8:e8338
- Dormann CF, Fründ J, Blüthgen N, Gruber B (2009) Indices, graphs and null models: analyzing bipartite ecological networks. *Open Ecology Journal* 2:7-24.

- Dormann CF, Gruber B, Fruend J (2008) Introducing the bipartite Package: analysing ecological networks. *R News* 8:8–11.
- Dunne JA, Williams RJ, Martinez ND, Center RT (2002) Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters* 5:558–567.
- Dupont YL, Hansen DM, Valido A, Olesen JM (2004) Impact of introduced honey bees on native pollination interactions of the endemic *Echium wildpretii* (Boraginaceae) on Tenerife, Canary Islands. *Biological Conservation* 118:301–311.
- Eckert CG, Kalisz S, Geber MA, Sargent R, Elle E, Cheptou P-O, Goodwillie C, Johnston MO, Kelly JK, Moeller DA, Porcher E, Ree RH, Vallejo-Marín M, Winn AA (2010) Plant mating systems in a changing world. *Trends in Ecology and Evolution* 25:35–43.
- Emer C, Memmott J, Vaughan IP, Montoya D, Tylianakis JM (2016) Species roles in plant–pollinator communities are conserved across native and alien ranges. *Diversity and Distributions* 22:841–852.
- Fortuna MA, Bascompte J (2006) Habitat loss and the structure of plant-animal mutualistic networks. *Ecology Letters* 9:281–286.
- Fumero-Cabán JJ (2019) Reproductive ecology and population structure of *Guaiacum sanctum* (Zygophyllaceae) in two Caribbean Islands: Implication for Conservation. Doctoral dissertation, University of Puerto Rico, Río Piedras.

- Gannon MR, Willig MR (1994) The effects of Hurricane Hugo on bats of the Luquillo Experimental Forest of Puerto Rico. *Biotropica* 26:320–331.
- Genaro JA, Franz NM (2008) The bees of Greater Puerto Rico (Hymenoptera: Apoidea: Anthophila). *Insecta Mundi* 40:1–24.
- Goulson D (2003) Effects of introduced bees on native ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 34:1–26.
- Grass I, Berens DG, Peter F, Farwig N (2013) Additive effects of exotic plant abundance and land-use intensity on plant-pollinator interactions. *Oecologia* 173:913–923.
- Grissell EE (2007) Scoliid wasps of Florida, *Campsomeris*, *Scolia* and *Trielis* spp. (Insecta: Hymenoptera: Scoliidae) 1. University of Florida Institute of Food and Agricultural Sciences Extension, EENY-409. <http://creatures.ifas.ufl.edu>. (accessed 26 April 2021).
- de Groot RS, Wilson MA, Boumans RMJ (2002) A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecological Economics* 41:393–408.
- Hegland SJ, Dunne J, Nielsen A, Memmott J (2010) How to monitor ecological communities cost-efficiently: the example of plant-pollinator networks. *Biological Conservation* 143:2092–2101.
- Henry M, Rodet G (2018) Controlling the impact of the managed honeybee on wild bees in protected areas OPEN. *Scientific Reports* | 8:9308.

- Hung KLJ, Kingston JM, Albrecht M, Holway DA, Kohn JR (2018) The worldwide importance of honey bees as pollinators in natural habitats. *Proceedings of the Royal Society London B: Biological Sciences* 285:20172140.
- Ings TC, Montoya JM, Bascompte J, Blüthgen N, Brown L, Dormann CF, Edwards F, Figueroa D, Jacob U, Jones JI, Lauridsen RB, Ledger ME, Lewis HM, Olesen JM, van Veen FJF, Warren PH, Woodward G (2009) Ecological networks - beyond food webs. *Journal of Animal Ecology* 78:253–269.
- Jordano P (1987) Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. *American Naturalist* 129:657–677.
- Kishi S, Sakura N, Yoshikawa T, Hiraiwa MK, Katoh K (2017) Interaction between insects and insect-pollinated plants on Miyake Island after a recent volcanic eruption: A comparison between vegetation types. *Journal of Asia-Pacific Entomology* 20:964–970.
- Landry CL (2013) Changes in pollinator assemblages following hurricanes affect the mating system of *Laguncularia racemosa* (Combretaceae) in Florida, USA. *Journal of Tropical Ecology* 29:209–216.
- Lynch JF (1991) Effects of Hurricane Gilbert on birds in a dry tropical forest in the Yucatan Peninsula. *Biotropica* 23:488–496.
- Mari Mutt JA (2015) *Insectos de Puerto Rico*. Ediciones Digitales, Aguadilla, Puerto Rico, 1–112.

- Martín González AM, Dalsgaard B, Olesen JM (2010) Centrality measures and the importance of generalist species in pollination networks. *Ecological Complexity* 7:36–43.
- Masciocchi M, Pereira AJ, Lantschner MV, Corley JC (2013) Of volcanoes and insects: the impact of the Puyehue-Cordon Caulle ash fall on populations of invasive social wasps, *Vespula* spp. *Ecological Research* 28:199–205.
- Memmott J, Waser NM (2002) Integration of alien plants into a native flower-pollinator visitation web. *Proceedings of the Royal Society London B* 269:2395–2399.
- Memmott J, Waser NM, Price MV (2004) Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society London B* 271:2505–2611.
- Montoya JM, Pimm SL, Solé RV (2006) Ecological networks and their fragility. *Nature* 442:259–264.
- Natalie Weiner C, Werner M, Eduard Linsenmair K (2014) Land-use impacts on plant-pollinator networks: interaction strength and specialization predict pollinator declines. *Ecology* 95:466–474.
- Olesen JM, Bascompte J, Dupont YL, Jordano P (2006) The smallest of all worlds: pollination networks. *Journal of Theoretical Biology* 240:270–276.
- Olesen JM, Bascompte J, Dupont YL, Jordano P (2007) The modularity of pollination networks. *PNAS* 104:19891–19896.

- Olesen JM, Eskildsen LI, Venkatasamy S (2002) Invasion of pollination networks on oceanic islands: Importance of invader complexes and endemic super generalists. *Diversity and Distributions* 8:181–192.
- Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? *Oikos* 120:321–326.
- Pascarella' JB (1998) Hurricane disturbance, plant-animal interactions, and the reproductive success of a tropical shrub. *Biotropica* 30:41–47.
- Pérez ME, Meléndez-Ackerman EJ, Monsegur-Rivera OA (2018) Breeding system and pollination of *Gesneria pauciflora* (Gesneriaceae), a threatened Caribbean species. *Flora* 242:8–15.
- Pérez-Asso AR, Genaro JA, Garrido OH (2009) Las mariposas de Puerto Rico. Editorial Cocuyo.
- Rathcke BJ (2000) Hurricane causes resource and pollination limitation of fruit set in a bird-pollinated shrub. *Ecology* 81:1951–1958.
- Rivera-Marchand B, Ackerman JD (2006) Bat pollination breakdown in the Caribbean columnar cactus *Pilosocereus royenii*. *Biotropica* 38:635–642.
- Rojas-Sandoval J, Meléndez-Ackerman E (2011) Reproductive phenology of the Caribbean cactus *Harrisia portoricensis*: rainfall and temperature associations. *Botany* 89:861–871.
- Roubik DW (1992) “Loose niches in tropical communities: why are there so many trees and so few bees?” In: M. D. Hunter, T. Ohgushi, and P. W. Price (ed)

- Resource Distribution and Animal-Plant Interactions. Academic Press, New York pp 327–354.
- Roubik DW, Villanueva-Gutiérrez R (2009) Invasive Africanized honey bee impact on native solitary bees: a pollen resource and trap nest analysis. *Biological Journal of the Linnean Society* 98:152–160.
- Soares RGS, Ferreira PA, Lopes LE (2017) Can plant-pollinator network metrics indicate environmental quality? *Ecological Indicators* 78:361–370.
- Temeles EJ, Bishop GA (2019) A hurricane alters pollinator relationships and natural selection on an introduced island plant. *Biotropica* 51:129–138.
- Thébault E, Fontaine C (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329:853–856.
- Thomson DM (2016) Local bumble bee decline linked to recovery of honey bees, drought effects on floral resources. *Ecology Letters* 19:1247–1255.
- Traveset A, Castro-Urgal R, Rotllàn-Puig X, Lázaro A (2018) Effects of habitat loss on the plant–flower visitor network structure of a dune community. *Oikos* 127:45–55.
- Traveset A, Richardson DM (2006) Biological invasions as disruptors of plant reproductive mutualisms. *Trends in Ecology and Evolution* 21:208–216.
- Tylianakis JM, Laliberté E, Nielsen A, Bascompte J (2010) Conservation of species interaction networks. *Biological Conservation* 143:2270–2279.

- Valido A, Rodríguez-Rodríguez MC, Jordano P (2019) Honeybees disrupt the structure and functionality of plant-pollinator networks. *Scientific Reports* 9:4711.
- Vanbergen AJ (2014) Landscape alteration and habitat modification: Impacts on plant-pollinator systems. *Current Opinion in Insect Science* 5:44–49.
- Vázquez DP, Blüthgen N, Cagnolo L, Chacoff NP (2009) Uniting pattern and process in plant-animal mutualistic networks: a review. *Annals of Botany* 103:1445–1457.
- Veron S, Fontaine C, Dubos N, Clergeau P, Pavoine S (2018) Predicting the impacts of co-extinctions on phylogenetic diversity in mutualistic networks. *Biological Conservation* 219:161–171.
- Villanueva-Gutiérrez R, Roubik DW, Colli-Ucán W, Gumez-Ricalde FJ, Buchmann SL (2013) A critical view of colony losses in managed Mayan honey-making bees (Apidae: Meliponini) in the heart of Zona Maya. *Journal of The Kansas Entomological Society* 86:352–362.
- Walker LR, Voltzow J, Ackerman JD, Fernandez DS, Fetcher N (1992) Immediate impact of Hurricane Hugo on a Puerto Rican rain forest. *Ecology* 73:691–694.
- War AR, Paulraj MG, War MY, Ignacimuthu S (2011) Jasmonic acid-mediated-induced resistance in groundnut (*Arachis hypogaea* L.) against *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae). *Journal of Plant Growth Regulation* 30:512–523.
- Wunderle JM (1995) Responses of bird populations in a Puerto Rican forest to Hurricane Hugo: the first 18 months. *The Condor* 97:879–896.

Wunderle JM, Lodge DJ, Waide RB (1992) Short-term effects of Hurricane Gilbert on terrestrial bird populations on Jamaica. *The Auk* 109:148–166.

Table 1. Network level metrics for each study year. w.NODF: weighted nestedness, H_2' : specialization index.

Metrics	2015	2016	2018	2019
No. species of visitors	14	16	37	24
No. species of plants	8	15	15	12
No. of links	1,375	4,910	1,061	597
connectance	0.22	0.22	0.22	0.19
w.NODF	28.29	26.59	26.1	24.91
H_2'	0.54	0.56	0.36	0.46
niche.overlap.visitors	0.31	0.18	0.17	0.26
niche.overlap.plants	0.72	0.41	0.24	0.19
robustness.visitors	0.71	0.75	0.82	0.75
robustness.plants	0.57	0.70	0.66	0.63

Table 2. Species richness in each flower visitor functional group across the four years of study.

	2015	2016	2018	2019
bee	3	3	3	3
butterfly	7	8	13	7
wasp	3	3	5	3
fly	1	2	13	0
beetle	0	0	1	1
other	0	0	2	0

Table 3. T test results of the observed nestedness value by year and null model with 100 randomizations. Using ‘r2d’ null model (‘bipartite’ package) since it generates the randomizations with given marginals for the network size.

Year	null mean	lower CI	upper CI	t	P-value
2015	63.59	62.51	64.67	65.05	<0.001
2016	77.78	77.37	78.20	245.12	<0.001
2018	50.58	50.14	51.02	109.99	<0.001
2019	56.90	56.22	57.57	94.23	<0.001

Table 4. Results of generalized linear mixed models for all species level metrics of the network.

The explanatory variables at the visitor level are functional groups and years. Models presented were selected via the AIC criterion.

Indice	Explanatory fixed variable	Estimate	SE	t-value	P-value
Degree (AIC= 390.5)	Intercept	0.926	0.346	2.679	< 0.01
	Butterflies	-0.930	0.350	-2.656	<0.01
	Flies	-1.183	0.371	-3.190	<0.01
	Others	-0.977	0.449	-2.175	<0.05
	Wasps	-0.524	0.399	-1.314	0.189
	year2016	0.521	0.162	3.229	<0.01
	year2018	0.867	0.151	5.739	<0.001
	year2019	0.331	0.166	1.996	<0.05
Strength (AIC= -4.1)	Intercept	-0.807	0.811	-0.995	0.320
	Butterflies	-2.345	0.845	-2.777	<0.01
	Flies	-2.850	0.870	-3.277	<0.01
	Others	-0.919	1.322	-0.695	0.487
	Wasps	-1.276	1.002	-1.273	0.203
	year2016	1.172	0.429	2.731	<0.01
	year2018	0.727	0.371	1.961	<0.05
	year2019	0.874	0.382	2.290	<0.05
Weighted Closeness (AIC=-534)	Intercept	-2.854	0.366	-7.788	<0.001
	Butterflies	-1.635	0.394	-4.153	<0.001
	Flies	-1.509	0.414	-3.646	<0.001
	Others	-0.747	0.587	-1.273	
	Wasps	0.986	0.440	-2.238	<0.05
	year2016	-0.744	0.268	-2.775	<0.01
	year2018	-0.117	0.222	-0.530	0.596
	year2019	-0.112	0.229	-0.488	0.625
d' (AIC=-43.9)	Intercept	-0.544	0.239	-2.276	<0.05
	year2016	0.404	0.293	1.378	0.168
	year2018	-0.432	0.271	-1.592	0.112
	year2019	-0.095	0.291	-0.327	0.744

Table 5. Results of generalized linear mixed models for all species level metrics of the network.

The explanatory variable at the plant level is year.

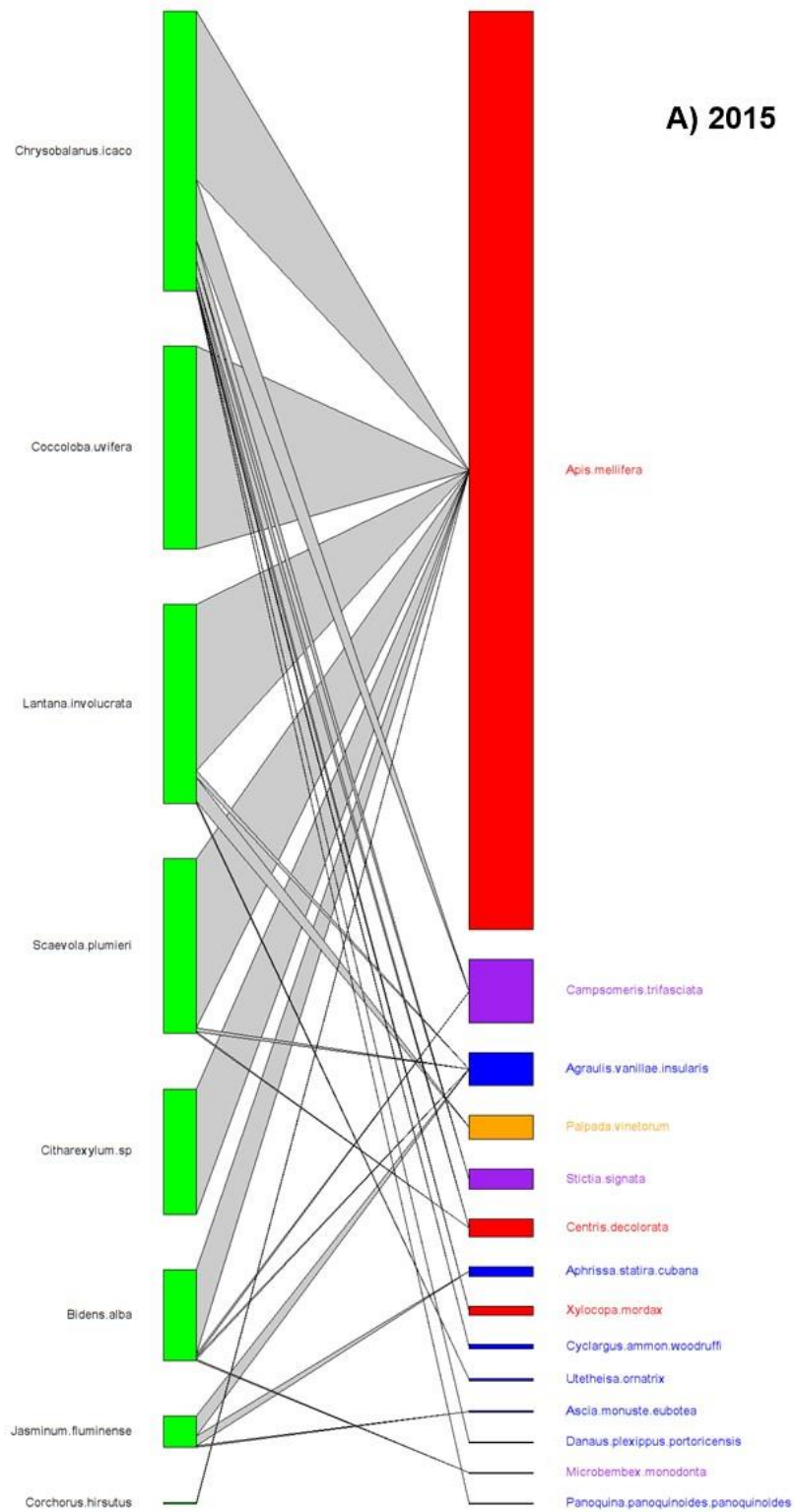
Indice	Explanatory fixed variable	Estimate	SE	t-value	P-value
Degree (AIC= 161.0)	Intercept	0.247	0.180	1.367	0.172
	year2016	0.241	0.169	1.431	0.152
	year2018	0.758	0.140	5.432	<0.001
	year2019	0.446	0.150	2.980	<0.01
Strength (AIC= 56.5)	Intercept	-2.054	0.583	-3.523	<0.001
	year2016	0.204	0.640	0.319	0.750
	year2018	0.357	0.424	0.843	0.399
	year2019	0.620	0.425	1.459	0.145
Weighted Closeness (AIC=-184.7)	Intercept	-3.224	0.413	-7.801	<0.01
	year2016	0.169	0.410	0.412	0.680
	year2018	0.138	0.404	0.342	0.732
	year2019	0.130	0.397	0.328	0.743
d' (AIC=-73.9)	Intercept	-1.665	0.352	-4.736	<0.001
	year2016	-0.614	0.403	-1.524	0.127
	year2018	-0.069	0.372	-0.186	0.852
	year2019	0.153	0.376	0.406	0.684

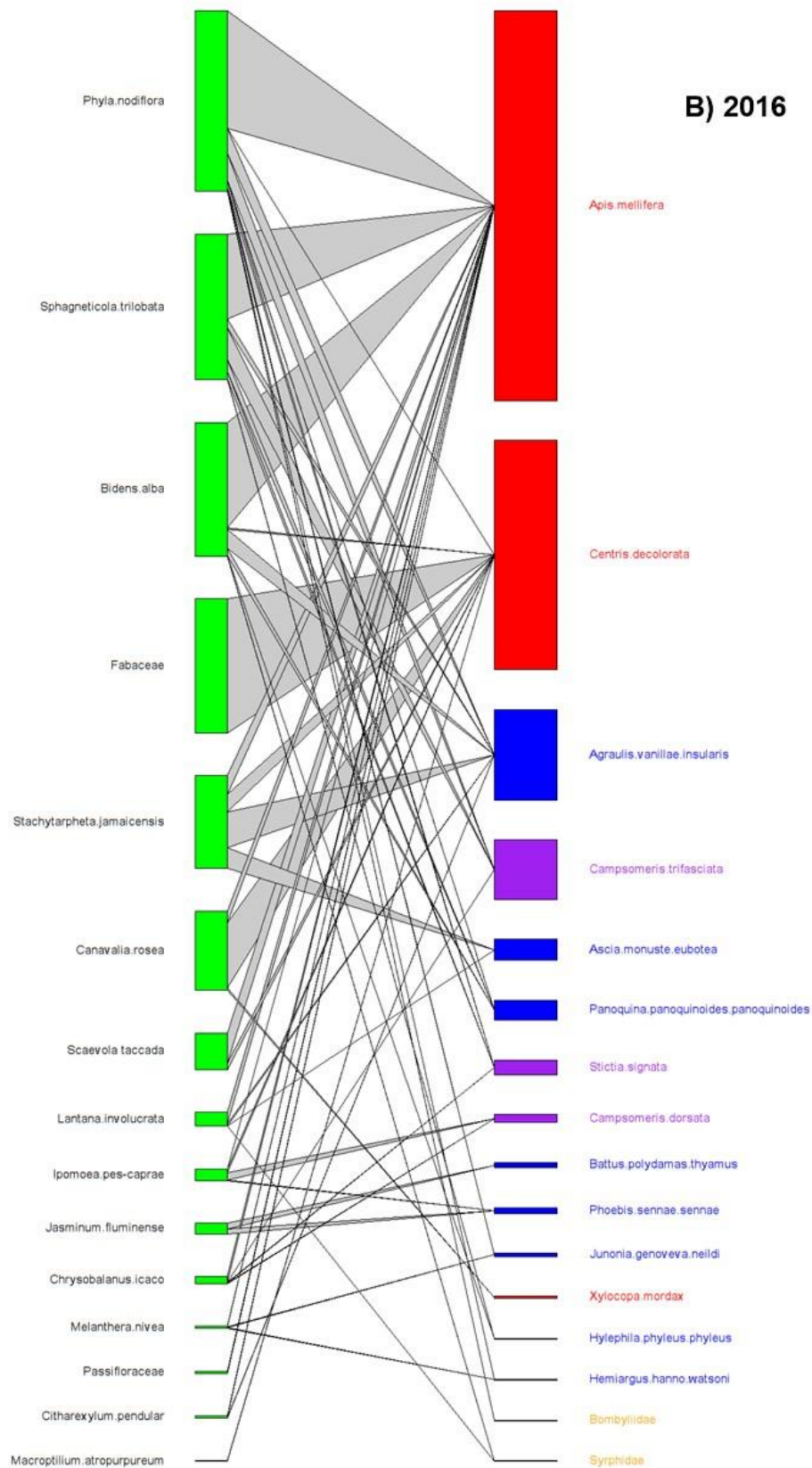
Fig 1. Piñones network site in Loíza, PR. Study area is represented by the yellow area. Examples of common plants found in the coastal dune: top picture- *Ipomoea pes-caprae*, bottom left- *Canavalia rosea*, bottom right- *Scaevola plumieri*.

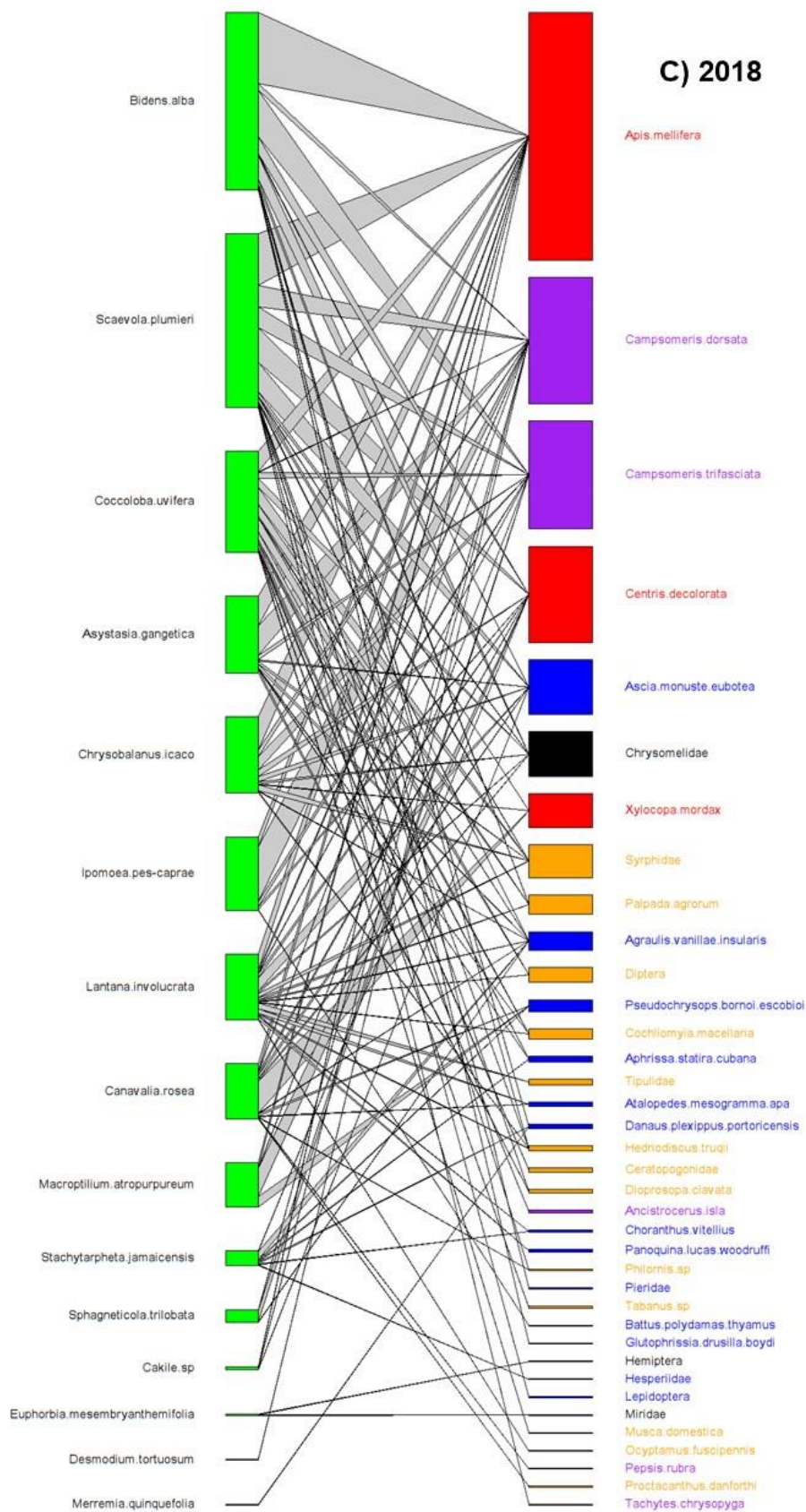


Figure 2. Interaction network visualization by year **A** (2015), **B** (2016), **C** (2018), and **D** (2019).

Species on the left (green) represent plants and on the right visitor species. Visitors are colored by functional group (Red = bees, Blue = butterflies, Purple = wasps, Orange = flies, and Black = others). Size of the vertical bars represents the abundance of the species, and the lines connecting between the groups represents the links between the species. The size of the links is proportional to the number of interactions of the species.







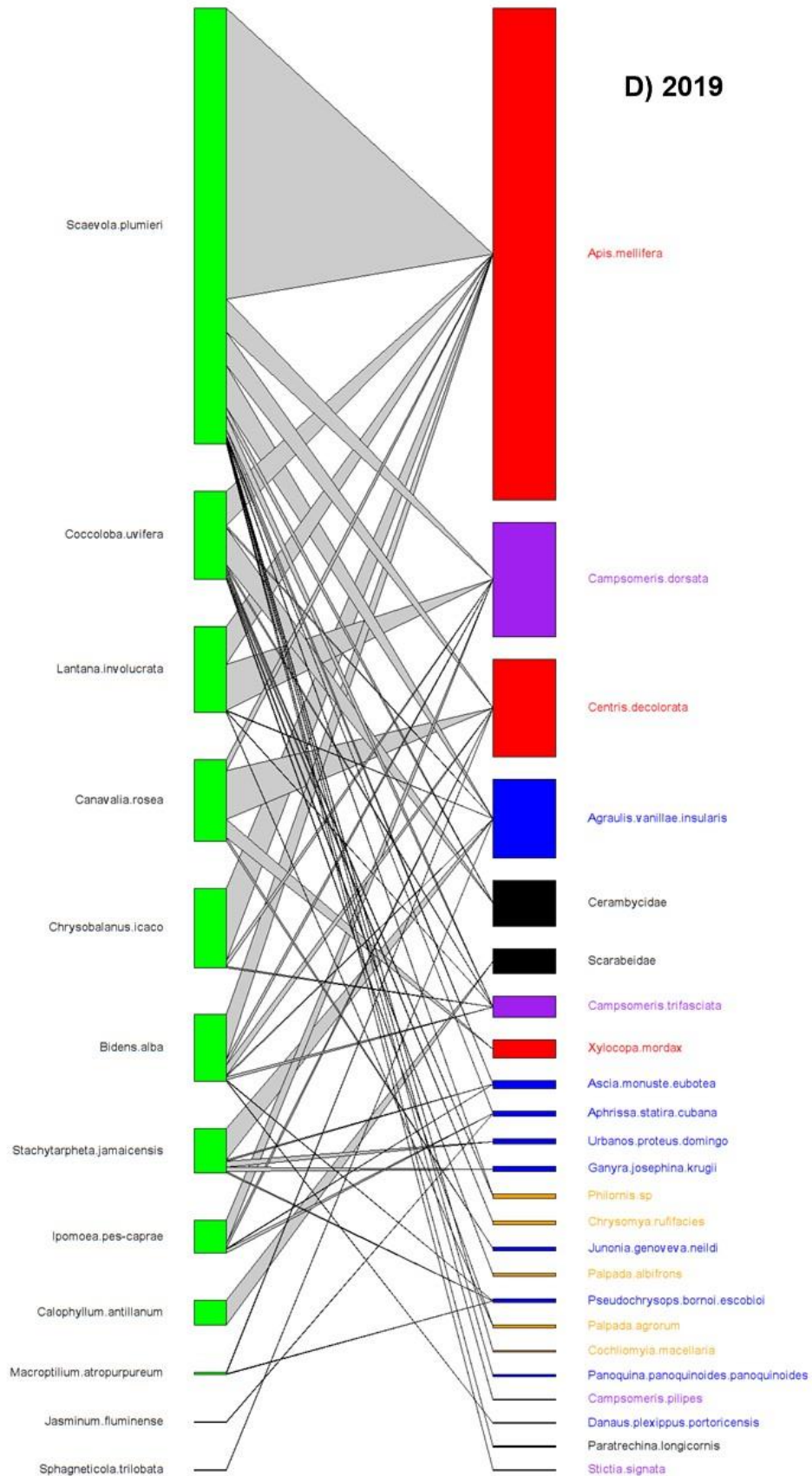


Fig 3. Species abundance within functional groups by years. The abundance of each species is adjusted to the hours of observation per year. The year 2017 was excluded because no observations could be made after the hurricane mid-September.

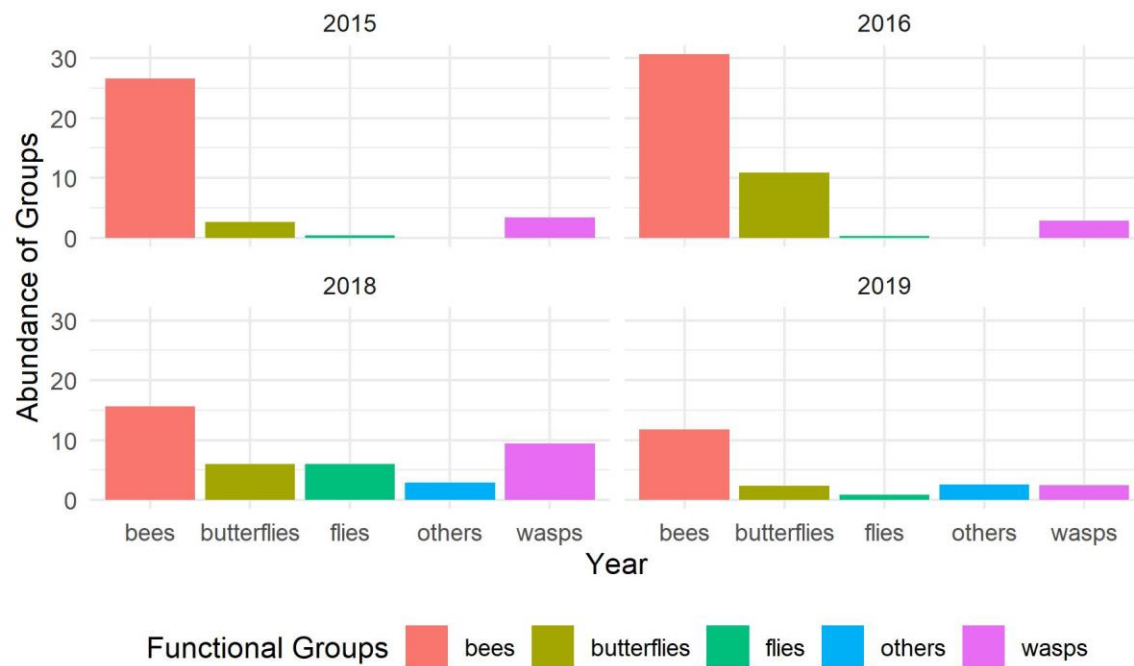


Fig 4. Frequency of observations of each plant species by year. The frequency is adjusted by hours of observation per year. Plants with the highest frequency were the most predominant and common of the coastal sand dunes.

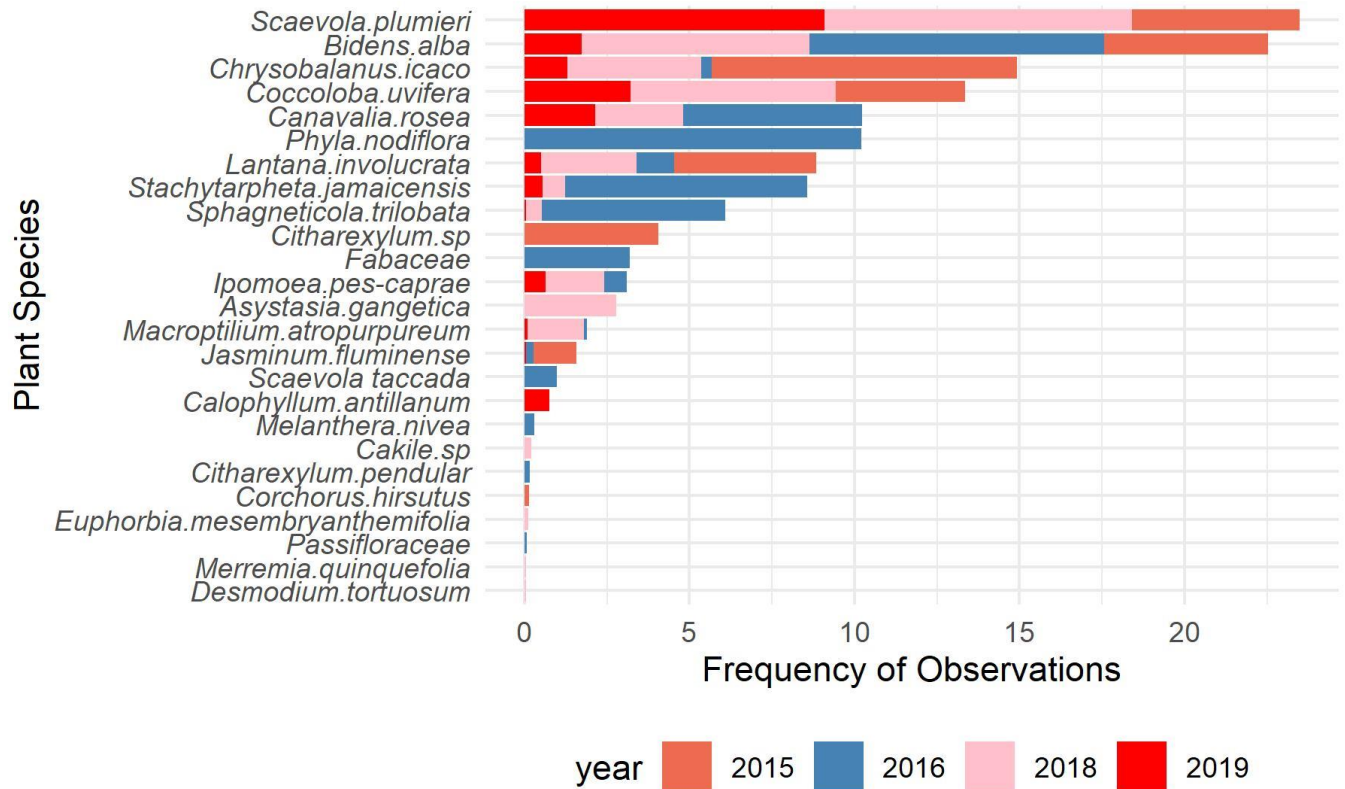
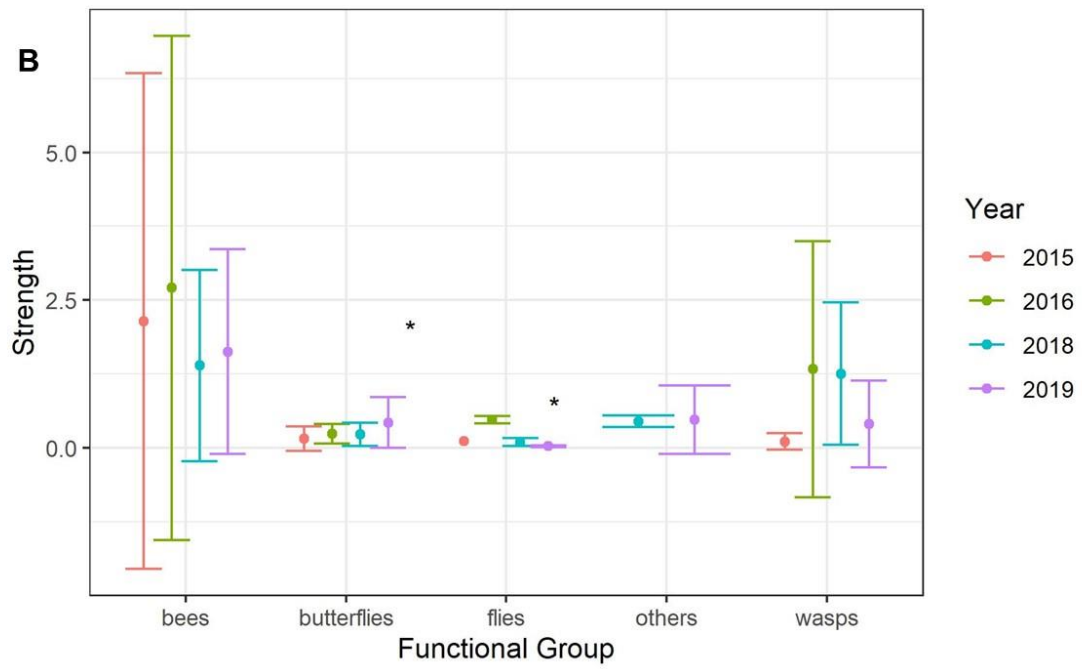
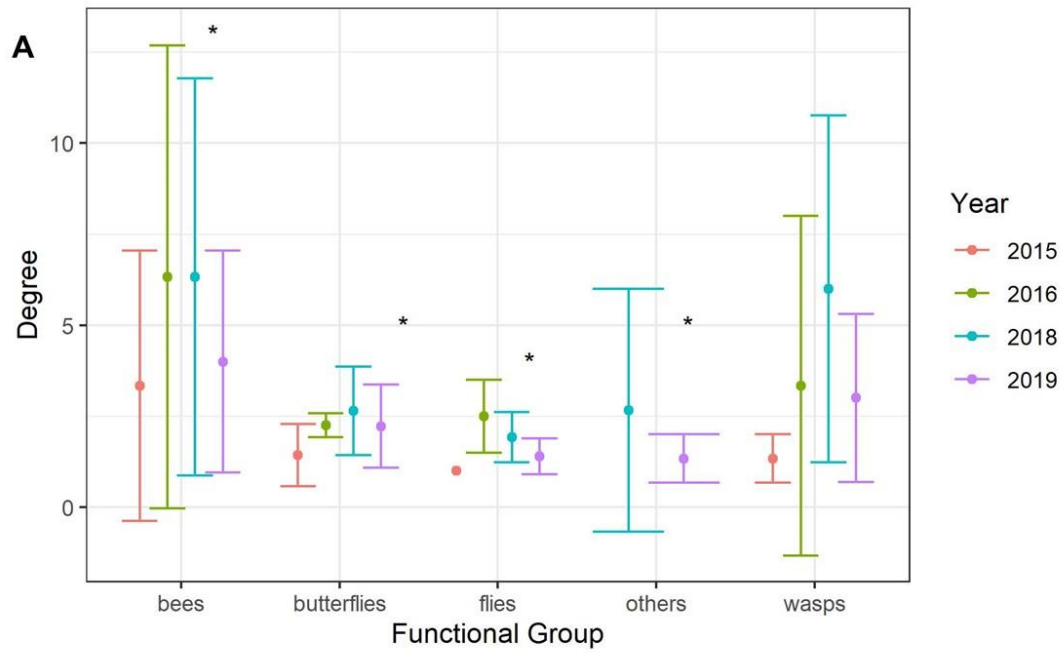
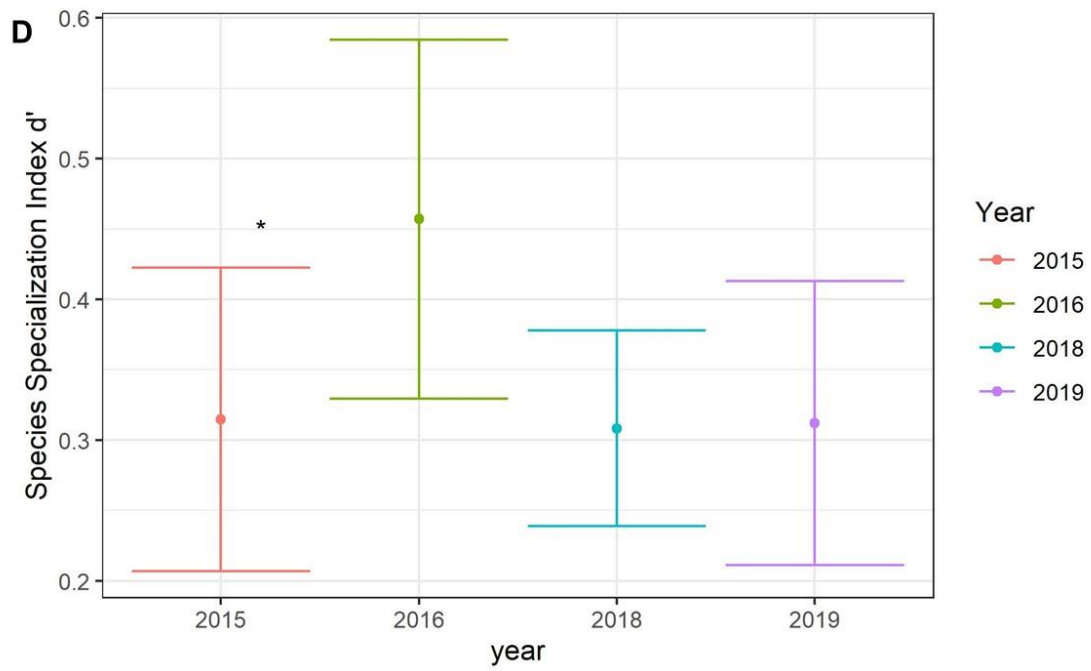
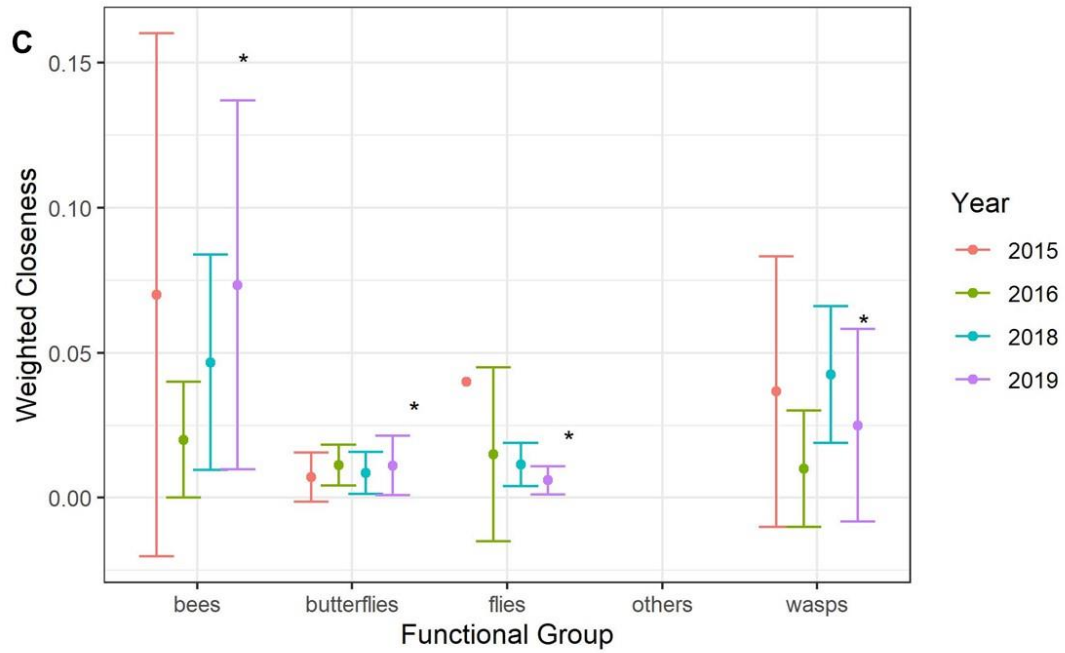


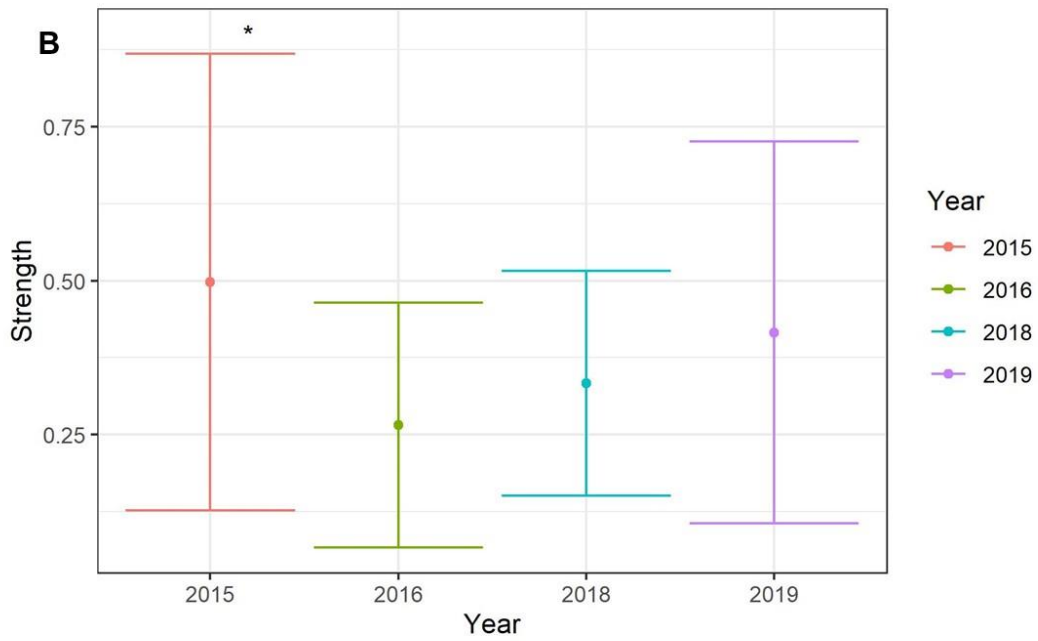
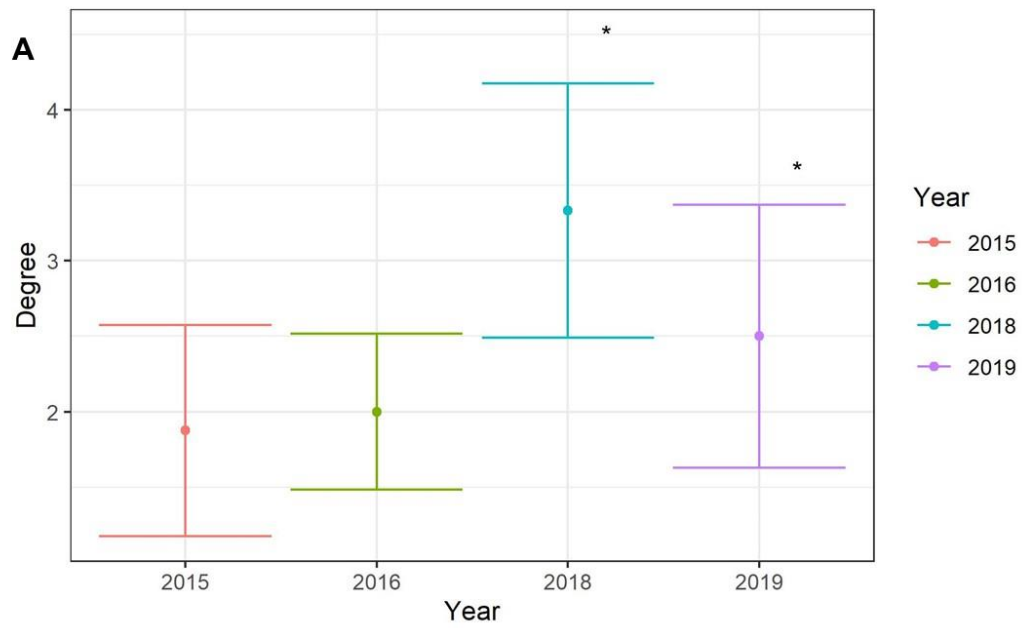
Fig 5. Comparison of species level metrics for visitor species. A) Species degree values represent the sum of links per species. B) Species strength values represent the sum of dependencies of each species. C) Weighted closeness values represent the centrality of the species; values go from 0-1 the closer to one more central the species. D) Specialization index (d') determines how much of a specialist or generalist is the species; values go from 0-1 the closer to one the more specialist is the species.

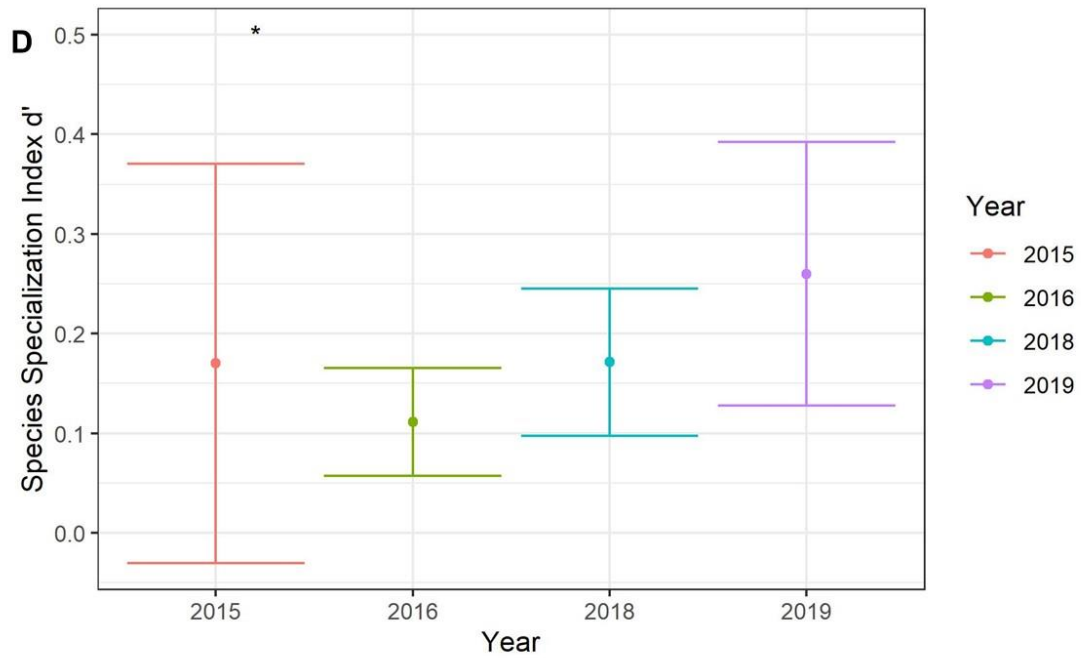
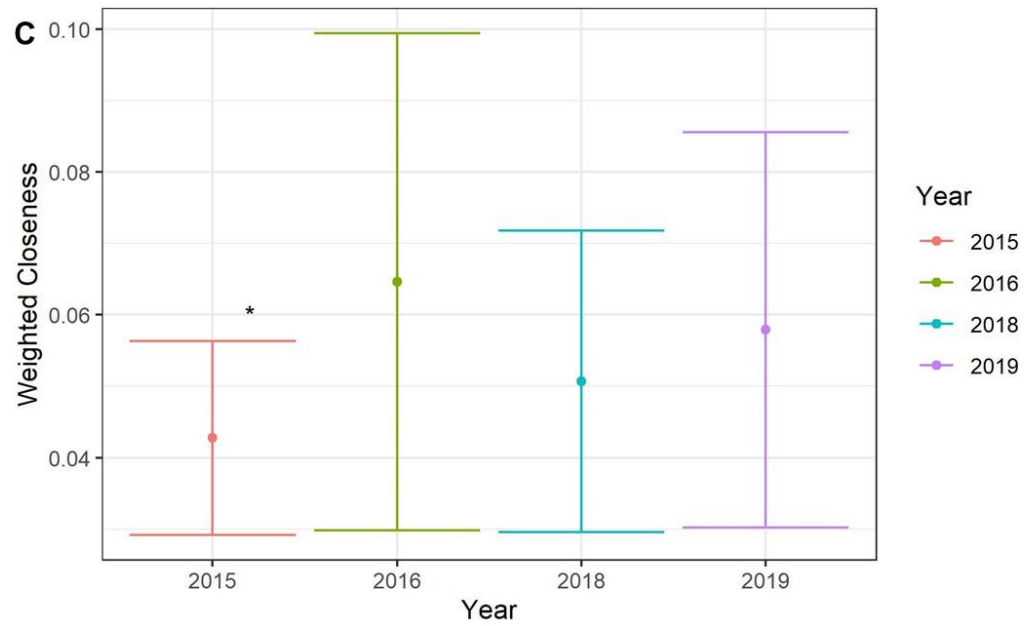




*Significant P-values (0.05). Specialization index does not include the functional group variable according to the best model selection following AIC criterion.

Fig 6. Comparison of species level metrics for plant species. A) Species degree values represent the sum of links per species. B) Species strength values represent the sum of dependencies of each species. C) Weighted closeness values represent the centrality of the species; values go from 0-1 the closer to one more central the species. D) Specialization index (d') determines how much of a specialist or generalist is the species; values go from 0-1 the closer to one the more specialist is the species.





*Significant P-values (0.05).

Appendix

Appendix 1. Values for the species level metrics for each of visitor species by study year.

Year	Visitor Sp	Functional Group	degree	strength	wcloseness	d
2015	<i>Agraulis vanillae insularis</i>	butterflies	4	0.72	0.03	0.53
2015	<i>Aphrissa statira cubana</i>	butterflies	1	0.31	0.01	0.75
2015	<i>Apis mellifera</i>	bees	7	6.34	0.16	0.25
2015	<i>Ascia monuste eubotea</i>	butterflies	1	0.05	0.00	0.48
2015	<i>Campsomeris trifasciata</i>	wasps	2	0.25	0.08	0.43
2015	<i>Centris decolorata</i>	bees	2	0.07	0.03	0.27
2015	<i>Cyclargus ammon woodruffi</i>	butterflies	1	0.01	0.01	0.22
2015	<i>Danaus plexippus portoricensis</i>	butterflies	1	0.00	0.00	0.00
2015	<i>Microbembex monodonta</i>	wasps	1	0.01	0.00	0.19
2015	<i>Palpada vinetorum</i>	flies	1	0.12	0.04	0.45
2015	<i>Panoquina panoquinoides panoquinoides</i>	butterflies	1	0.00	0.00	0.00
2015	<i>Stictia signata</i>	wasps	1	0.07	0.03	0.34
2015	<i>Utetheisa ornatrix</i>	butterflies	1	0.01	0.00	0.22
2015	<i>Xylocopa mordax</i>	bees	1	0.03	0.02	0.28
2016	<i>Apis mellifera</i>	bees	6	1.17	0.03	0.27
2016	<i>Centris decolorata</i>	bees	12	6.92	0.03	0.39
2016	<i>Agraulis vanillae insularis</i>	butterflies	2	0.24	0.02	0.59
2016	<i>Stictia signata</i>	wasps	1	0.52	0.00	0.87
2016	<i>Campsomeris trifasciata</i>	wasps	1	0.00	0.00	0.20
2016	<i>Ascia monuste eubotea</i>	butterflies	2	0.73	0.02	0.88
2016	Syrphidae	flies	3	0.45	0.03	0.36
2016	<i>Campsomeris dorsata</i>	wasps	8	3.48	0.03	0.78
2016	<i>Panoquina panoquinoides panoquinoides</i>	butterflies	2	0.31	0.00	0.56
2016	<i>Hylephila phyleus phyleus</i>	butterflies	2	0.01	0.00	0.15
2016	<i>Phoebis sennae sennae</i>	butterflies	2	0.32	0.01	0.35
2016	<i>Hemiargus hanno watsoni</i>	butterflies	3	0.14	0.02	0.26
2016	Bombyliidae	flies	2	0.51	0.00	0.82
2016	<i>Battus polydamas thymus</i>	butterflies	3	0.16	0.02	0.23
2016	<i>Junonia genoveva neildi</i>	butterflies	2	0.02	0.00	0.22
2016	<i>Xylocopa mordax</i>	bees	1	0.03	0.00	0.39
2018	<i>Agraulis vanillae insularis</i>	butterflies	8	0.74	0.02	0.39

2018	<i>Ancistrocerus isla</i>	wasps	1	0.02	0.01	0.28
2018	<i>Aphrissa statira cubana</i>	butterflies	3	0.15	0.01	0.32
2018	<i>Apis mellifera</i>	bees	10	2.87	0.07	0.08
2018	<i>Ascia monuste eubotea</i>	butterflies	7	0.79	0.05	0.28
2018	<i>Atalopedes mesogramma apa</i>	butterflies	2	0.08	0.01	0.38
2018	<i>Battus polydamas thymus</i>	butterflies	1	0.01	0.00	0.16
2018	<i>Campsomeris dorsata</i>	wasps	11	2.76	0.06	0.39
2018	<i>Campsomeris trifasciata</i>	wasps	9	1.64	0.06	0.20
2018	<i>Centris decolorata</i>	bees	8	1.22	0.06	0.27
2018	Ceratopogonidae	flies	1	0.04	0.01	0.35
2018	<i>Choranthus vitellius</i>	butterflies	2	0.08	0.00	0.34
2018	Chrysomelidae	others	6	0.35	0.04	0.17
2018	<i>Cochliomyia macellaria</i>	flies	3	0.11	0.02	0.36
2018	<i>Danaus plexippus portoricensis</i>	butterflies	3	1.13	0.01	0.41
2018	<i>Dioprosopa clavata</i>	flies	2	0.05	0.01	0.27
2018	Diptera unknown sp	flies	2	0.15	0.02	0.48
2018	<i>Glutophrissia drusilla boydi</i>	butterflies	1	0.00	0.00	0.00
2018	<i>Hedriodiscus truqii</i>	butterflies	4	0.06	0.01	0.11
2018	Hemiptera unknown sp	others	1	0.50	0.00	0.87
2018	Hesperiidae	butterflies	1	0.06	0.00	0.46
2018	Lepidoptera unknown sp	butterflies	1	0.00	0.00	0.00
2018	Miridae	others	1	0.50	0.00	0.87
2018	<i>Musca domestica</i>	flies	1	0.01	0.00	0.10
2018	<i>Ocyptamus fuscipennis</i>	flies	1	0.01	0.00	0.19
2018	<i>Palpada agrorum</i>	flies	3	0.19	0.03	0.30
2018	<i>Panoquina lucas woodruffi</i>	butterflies	1	0.04	0.01	0.37
2018	<i>Philornis sp</i>	flies	1	0.01	0.00	0.22
2018	Pieridae	butterflies	2	0.02	0.00	0.11
2018	<i>Proctacanthus danforthi</i>	flies	1	0.01	0.00	0.13
2018	<i>Pseudochrysops bornoi escobioi</i>	butterflies	1	0.01	0.00	0.22
2018	Syrphidae	flies	3	0.31	0.02	0.56
2018	<i>Tabanus sp</i>	flies	5	0.36	0.04	0.26
2018	<i>Tachytes chrysopyga</i>	flies	1	0.02	0.00	0.23
2018	Tipulidae	flies	1	0.00	0.00	0.00
2018	<i>Xylocopa mordax</i>	bees	1	0.09	0.01	0.49
2018	<i>Pepsis rubra</i>	wasps	3	0.60	0.04	0.77
2019	<i>Agraulis vanillae insularis</i>	butterflies	6	1.85	0.05	0.35
2019	<i>Aphriss statira cubana</i>	butterflies	3	1.11	0.01	0.48

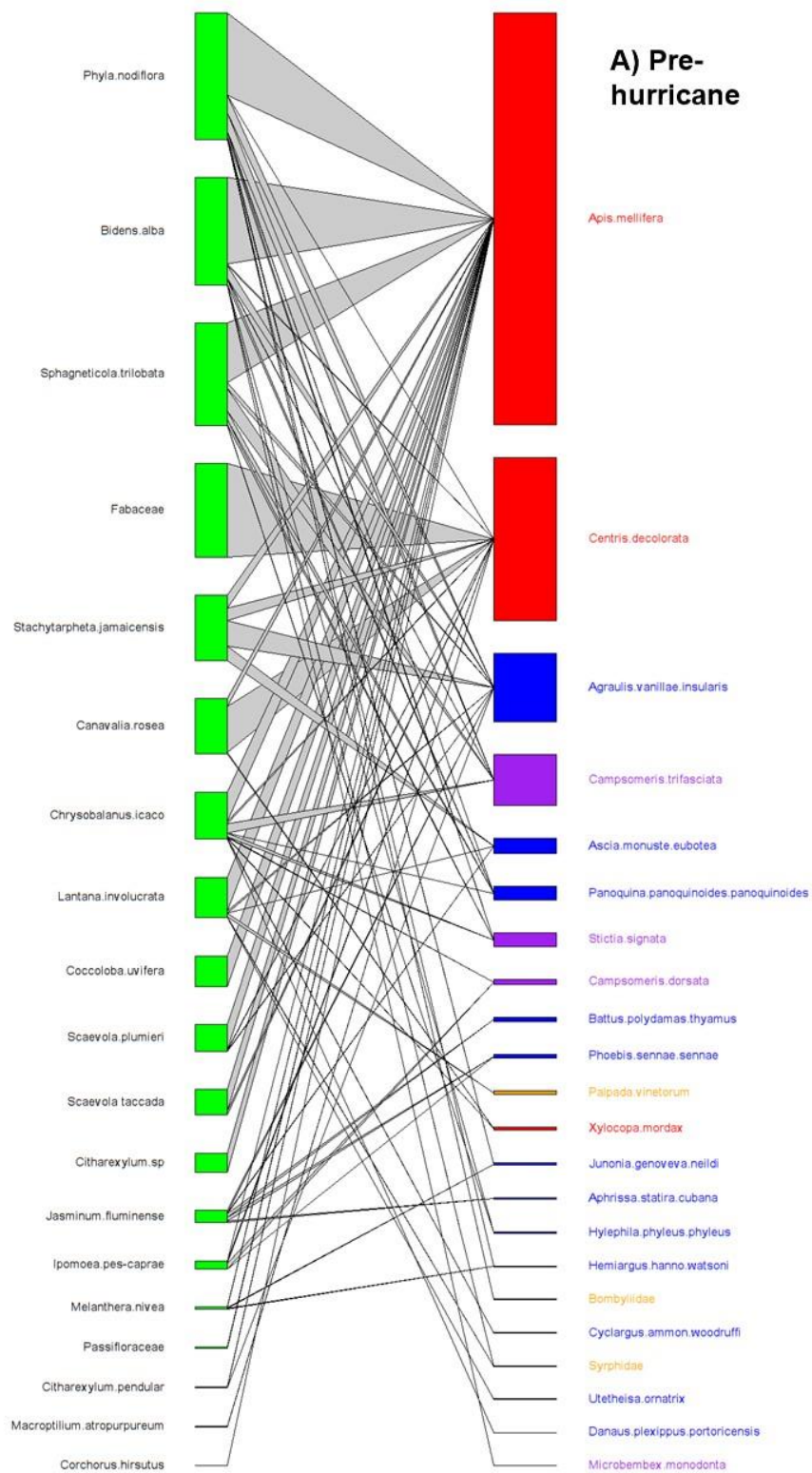
2019	<i>Apis mellifera</i>	bees	6	3.21	0.13	0.29
2019	<i>Ascia monuste eubotea</i>	butterflies	3	0.08	0.01	0.13
2019	<i>Campsomeris dorsata</i>	wasps	5	1.50	0.07	0.37
2019	<i>Campsomeris pilipes</i>	wasps	1	0.00	0.00	0.00
2019	<i>Campsomeris trifasciata</i>	wasps	5	0.12	0.03	0.07
2019	<i>Centris decolorata</i>	bees	5	1.46	0.07	0.37
2019	Cerambycidae	others	2	0.44	0.05	0.53
2019	<i>Chrysomya rufifacies</i>	flies	1	0.04	0.01	0.36
2019	<i>Cochliomyia macellaria</i>	flies	1	0.00	0.00	0.00
2019	<i>Danaus plexippus portoricensis</i>	butterflies	1	0.01	0.00	0.30
2019	<i>Ganyra josephina krugii</i>	butterflies	1	0.10	0.01	0.53
2019	<i>Junonia genoveva neildi</i>	butterflies	1	0.04	0.01	0.38
2019	<i>Palpada agrorum</i>	flies	2	0.03	0.00	0.21
2019	<i>Palpada albifrons</i>	flies	1	0.04	0.01	0.36
2019	<i>Panoquina panoquinoides panoquinoides</i>	butterflies	1	0.00	0.00	0.00
2019	<i>Paratrechina longicornis</i>	others	1	0.00	0.00	0.00
2019	<i>Philornis sp</i>	flies	2	0.03	0.01	0.13
2019	<i>Pseudochrysops bornoi escobioi</i>	butterflies	3	0.55	0.00	0.43
2019	Scarabeidae	others	1	1.00	0.00	1.00
2019	<i>Stictia signata</i>	wasps	1	0.00	0.00	0.00
2019	<i>Urbanos proteus domingo</i>	butterflies	1	0.12	0.01	0.56
2019	<i>Xylocopa mordax</i>	bees	1	0.22	0.02	0.62

Appendix 2. Values for the species level metrics for each of the plant species by study year.

Year	Plant Sp	degree	strength	wcloseness	d
2015	<i>Bidens alba</i>	3	0.18	0.04	0.01
2015	<i>Chrysobalanus icaco</i>	3	1.26	0.06	0.16
2015	<i>Citharexylum</i>	1	0.13	0.05	0.07
2015	<i>Coccoloba uvifera</i>	1	0.21	0.05	0.09
2015	<i>Corchorus hirsutus</i>	1	0.002	0.002	0.0001
2015	<i>Jasminum fluminense</i>	1	0.6	0.03	0.86
2015	<i>Lantana involucrata</i>	3	1.34	0.06	0.11
2015	<i>Scaevola plumieri</i>	2	0.26	0.05	0.06
2016	<i>Bidens alba</i>	3	0.68	0.16	0.05
2016	<i>Canavalia rosea</i>	1	0.13	0.11	0.13
2016	<i>Chrysobalanus icaco</i>	2	0.03	0.01	0.05
2016	<i>Citharexylum pendular</i>	2	0.005	0.002	0.02
2016	Fabaceae unknown sp	1	0.21	0.17	0.17
2016	<i>Ipomoea pes-caprae</i>	3	0.1	0.02	0.21
2016	<i>Jasminum fluminense</i>	1	0.07	0.02	0.4
2016	<i>Lantana involucrata</i>	3	0.14	0.02	0.03
2016	<i>Macroptilium atropurpureum</i>	1	0.002	0.001	0.04
2016	<i>Melanthera nivea</i>	2	0.01	0.003	0.09
2016	<i>Passifloraceae</i>	1	0.004	0.003	0.05
2016	<i>Phyla nodiflora</i>	4	1.34	0.17	0.02
2016	<i>Scaevola taccada</i>	1	0.06	0.05	0.1
2016	<i>Sphagneticola trilobata</i>	3	0.76	0.13	0.07
2016	<i>Stachytarpheta jamaicensis</i>	2	0.44	0.1	0.24
2018	<i>Asystasia gangetica</i>	4	0.34	0.07	0.05
2018	<i>Bidens alba</i>	5	1.08	0.12	0.09
2018	<i>Cakile</i>	3	0.01	0.005	0.002
2018	<i>Canavalia rosea</i>	5	0.24	0.06	0.12
2018	<i>Chrysobalanus icaco</i>	5	0.37	0.07	0.01
2018	<i>Coccoloba uvifera</i>	5	0.91	0.08	0.32
2018	<i>Desmodium tortuosum</i>	1	0.003	0.001	0.07
2018	<i>Euphorbia mesembryanthemifolia</i>	1	0.04	0.003	0.43
2018	<i>Ipomoea pes-caprae</i>	3	0.3	0.08	0.28
2018	<i>Lantana involucrata</i>	5	0.48	0.06	0.13
2018	<i>Macroptilium atropurpureum</i>	3	0.18	0.05	0.16
2018	<i>Merremia quinquefolia</i>	1	0.007	0.001	0.19
2018	<i>Scaevola plumieri</i>	5	0.86	0.12	0.03

2018	<i>Sphagneticola trilobata</i>	2	0.06	0.02	0.26
2018	<i>Stachytarpheta jamaicensis</i>	2	0.12	0.02	0.43
2019	<i>Bidens alba</i>	3	0.18	0.07	0.05
2019	<i>Calophyllum antillanum</i>	1	0.35	0.03	0.71
2019	<i>Canavalia rosea</i>	2	0.16	0.08	0.14
2019	<i>Chrysobalanus icaco</i>	2	0.17	0.08	0.11
2019	<i>Coccoloba uvifera</i>	5	1.34	0.08	0.3
2019	<i>Ipomoea pes-caprae</i>	3	0.22	0.04	0.29
2019	<i>Jasminum fluminense</i>	1	0.008	0.001	0.26
2019	<i>Lantana involucrata</i>	4	0.46	0.08	0.21
2019	<i>Macroptilium atropurpureum</i>	2	0.01	0.003	0.03
2019	<i>Scaevola plumieri</i>	5	1.68	0.17	0.06
2019	<i>Sphagneticola trilobata</i>	1	0.01	0.001	0.26
2019	<i>Stachytarpheta jamaicensis</i>	1	0.4	0.06	0.7

Appendix 3. Interaction network visualization with the years combined **A** (2015-2016) and **B** (2018-2019). Species on the left (green) represent plants and on the right visitor species. Visitors are colored by functional group (Red = bees, Blue = butterflies, Purple = wasps, Orange = flies, and Black = others). Size of the vertical bars represents the abundance of the species, and the lines connecting between the groups represents the links between the species. The size of the links is proportional to the number of interactions of the species.



B) Post-hurricane

