Article

POLLINATION FACILITATION AND TEMPORAL CHANGES OF PLANT-FLORAL VISITOR NETWORK IN A SERPENTINE SHRUBWOOD OF CUBA

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Abstract—The stress-gradient hypothesis predicts that in stressful ecosystems, species interactions are facilitative rather than competitive. In Cuba, one of the more stressful environments for plants is serpentinitic shrubwoods (cuabales), which experience intense variations in precipitation and temperature. Plant facilitative mechanisms are reported in this ecosystem, and pollination facilitation could also occur. We hypothesize that in this seasonal ecosystem, characterized by harsh conditions, facilitative pollination interactions prevail accompanied by intense interaction rewiring and species turnover. This research analyzed the temporal variation of the plant-pollinator network of serpentinitic shrubwood in Lomas de Galindo, Mayabeque, Cuba. Data were obtained by monitoring diurnal plant-pollinator interactions for two days each month through one year. The network was composed of 31 plant species and 81 pollinator species, where ten modules of interactions were detected in the network. Nine species were identified as core species; four of them were plants that gathered the majority of interactions. However, plant core species change temporally. The changes in beta-diversity values were higher between the initial and final months of every season, which could be caused by the variations in phenology and changes in pollinators' abundances. Facilitation occurred in six plant species that temporally segregate the pollination interactions and shaped the support of pollination in the community. For this reason, the conservation of pollination services in this ecosystem should be focused on these species.

Keywords—Beta-diversity, core species, interactions, module, serpentinitic shrubwoods

INTRODUCTION

Competition and facilitation are opposite processes of species interactions (Koffel et al. 2021). Environmental conditions influenced both: in benign environments, species frequently compete for resources; while in stressful environments, facilitative interactions between species are more common (Maestre et al. 2009; Holmgren & Scheffer 2010). This postulate is the "stress-gradient hypothesis," and several communities follow this pattern (Callaway et al. 2002; Armas et al. 2011). Usually, harsh conditions for plants include high temperatures and low water availability, which are features of arid and semi-arid environments (Loidi et al. 2022). In these habitats, one common facilitation interaction between plants is "nursing", in which seeds germinate below older plants that facilitate the establishment of seedlings (Oviedo et al. 2013; Filazzola & Lortie 2014). Moreover, facilitation mechanisms are also present in pollination (Ghazoul 2006; Lázaro et al. 2009).

Co-flowering plant species interact via shared pollinators, and this factor influences the assembly of plant communities (Arceo-Gómez et al. 2018). Plant species that do not overlap in flowering and share similar pools of pollinator species can facilitate each other because they jointly offer continuous floral resources to pollinators (Carvalheiro et al. 2014). In this scenario, high species turnover and rewiring of plant-pollinator networks are expected (CaraDonna et al. 2017). However, facilitation or competition among co-flowering plant species not only depends on phenology, but also on similar morphological and physiological traits (Albor et al. 2020). In conclusion, the assembly of co-flowering plant communities is not random and is influenced by facilitative and competitive interactions between species.

The xeromorphic thorny shrubwood formation (or *cuabal*) is a unique vegetation type present in the island of Cuba that combines harsh conditions with high plant richness and endemicity (Capote & Berazaín 1984; Borhidi 1996). This is one of the two vegetal formations over ultramafic soils in Cuba (Capote & Berazaín 1984). Endemic plants of these thorny shrubwood are morphologically and physiologically different from the rest of the species on the island (Borhidi 1996). Low water retention capacity and toxicity of serpentine soils cause reduced growth forms, presence of thorns, sclerophylly, stenophylly, low nectar production, and small flowers (Berazaín 2001; Alameda et al. 2023). Facilitative ("nursing") interactions between plants of thorny shrubwood allow the establishment of seedlings beneath older plants, an eco-evolutionary strategy in harsh environments (Oviedo et al. 2013). Therefore, facilitation may also occur in other ecological processes such as pollination.

Rain strongly influences the ecology of thorny shrubwood in Cuba (Borhidi 1996). In the majority of Cuban territory, there are two seasons during a year: dry season (from November to April) and rainy season (from May to October) (Borhidi 1996). In the rainy season, most flowering plants and insects increase their presence and abundance, which causes temporal changes in plant-pollinator interactions. These interactions can be split into two elements: 1) the interaction rewiring caused by the reorganization of interactions between the same species and 2) the species turnover caused by changes in species identity (CaraDonna et al. 2017). Short-term studies of pollination interactions generally ignore the dynamics of interactions since they are depicted as single structural networks (Trojelsgaard & Olesen, 2016). However, the temporal dynamics of pollination networks are intense both in interaction rewiring and species turnover (Petanidou et al. 2008; Olesen et al. 2011).

This study aimed to characterize the plant-pollinator interactions in a xeromorphic thorny shrubwood formation of Cuba and describe the temporal changes (between seasons). As far as we know, this is the first study that describes the plant-pollinator interactions in semi-desertic environments using a network approach. We hypothesize that in seasonal environments with harsh conditions (low water availability and soil toxicity), facilitative pollination interactions lead to intense interaction rewiring and species turnover.

MATERIALS AND METHODS

STUDY SITE

"Lomas de Galindo" is a protected area of 1,003 ha located in the municipality of Santa Cruz del Norte, in the province of Mayabeque, Cuba (Fig. 1). It is a Floristic Managed Reserve according to the Cuban system of protected areas (CNAP 2013). It is an outcrop of ultramafic rocks that belong to the Canasí-Corral Nuevo serpentinitic group, one of the seven groups of ultramafic outcrops of Cuba (Borhidi 1996). Over these soils, a thorny xeromorphic serpentine shrubwood (cuabal) is distributed (Capote & Berazaín 1984). The rocks that formed the soil have two features that influence the vegetation (Berazaín 2001). The first one is high concentrations of heavy metals (such as iron, nickel, magnesium, chromium, and cobalt) and low concentrations of nutrients (such as phosphorus, potassium, and calcium) (Proctor 1999). The other feature is the low water-retention capacity, which imposes drought all year (Proctor & Woodell 1975). These factors influence the morphology and physiology of the vegetation, which is composed of shrubwoods no more than five meters tall (Berazaín 2001). The weather is similar to the majority of the island, with two seasons (a rainy season between May and October and a dry season between November and April), but with the peculiarities of thorny shrubwood (fast drainage and high concentration of heavy metals) (Borhidi 1996).

STUDY DESIGN

The sampling period spans from October 2018 to September 2019. Monthly, we select two consecutive days with 30 days separating each. On each day, data were recorded in one transect during three consecutive hours, not considering the time for annotations, identification, or collecting. All observations were performed between 09:00 and 14:00, according to the higher

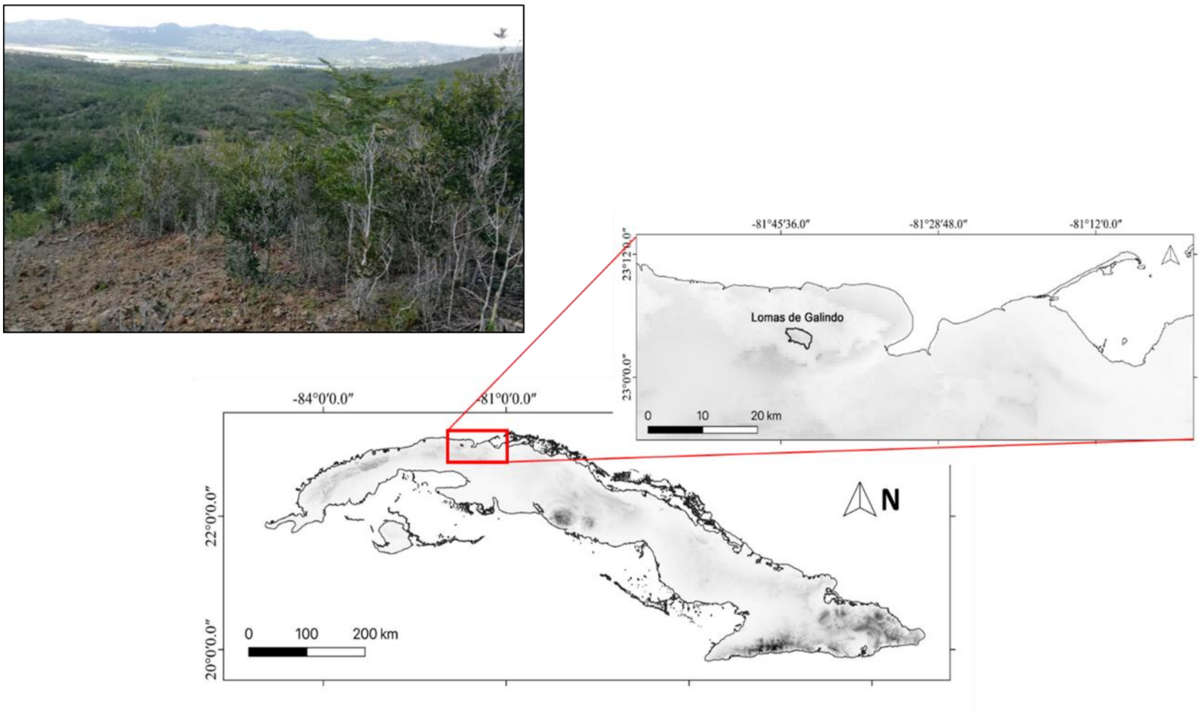

Figure 1. Location of "Lomas de Galindo", the studied thorny xeromorph serpentine shrubwood, in the island of Cuba.

activity period of diurnal pollinators (Baldock et al. 2011; Knop et al. 2017) and our previous experience of 10 years in this area (Alameda et al. 2023). In this time span, the majority of interactions occurred, because after 14:00, the temperature rises and insect activity diminishes significantly. Therefore, a sampling unit consisted of one transect per one day in every month, resulting in 24 transects, two per month. Focal observations of flowering plants during five minutes in a plot of 16 m2 were distributed throughout transects where there were flowers, not considering the time for netting, collecting, or identification. We designed a sampling unit of transects combined with focal observations because transects detect the majority of interactions and important species, while focal points detect rare interactions (Gibson et al. 2011). The length of transects depended on the density of flowers: in the month with higher flower density, transects were shorter, while longer transects were performed in months with scarce flowers. Always transects measured between 500 and 800 meters. We recorded all the interactions observed between flowers and pollinators, considering an interaction as the physical contact of an animal with the reproductive structures (anthers and stigma) of a flower. This sampling design with transects and focal points is the best to obtain a precise description of the interactions (De Aguiar et al. 2019).

Plants and animals were identified in the field or with the help of specialists (see Acknowledgments), or collected for identification in the laboratory. Voucher specimens were deposited in the collection of the research group in the Faculty of Biology of the University of Havana, Cuba. Specimens not identified at the species level were assigned as morphospecies.

Data analysis

The data of monthly interactions was gathered in an adjacency matrix of *i* columns and *j* rows that included the data of the two consecutive days of every month, where columns represented the plant species and rows the pollinators. The cell a_{ij} indicated the frequency of interactions of pollinator *i* with plant *j*. Therefore, 12 matrices composed the basic dataset, one for every month.

General analysis included the data of all the months (12 matrices), but also the general data was divided into two groups for temporal pattern identification. The first group represents the dry season (November 2018 to March 2019) and the second group the wet season (May 2019 to September 2019). For the seasonal analyses, April

2019 data was removed from the dataset to make the data of both seasons independent; also, the data from October 2018 was removed since it was temporally disjointed from the data of the rainy season of 2019.

Sample coverage curves for every season and the entire dataset evaluated whether the sampling effort was sufficient. The expected sample coverage for a hypothetical sample of size *m*, *C(m)*, is calculated with a function developed by Chao & Jost (2012) (Hsieh et al., 2016). Sample completeness is measured by sample coverage, which is the proportion of the total number of individuals (in this case, interactions) that belong to the species (or specific interaction) detected in the sample (Hsieh et al., 2016). Sample coverage curves were performed in the *iNEXT* 2.0.20 package of R. Sample coverage was higher than 90%, both for separate seasons and for all year (Fig. 2). In all situations, the asymptote of the curve included the reference sample. Plants had the higher levels of sample completeness, while interactions required more intense sampling for reaching similar sample coverage values (Fig. 2). However, for all situations, the sampling effort was enough.

Species were classified as either core or peripheral in each season according to their position in the network (Miele et al. 2020), to detect key species that influence pollination in the community. The core-periphery structure is

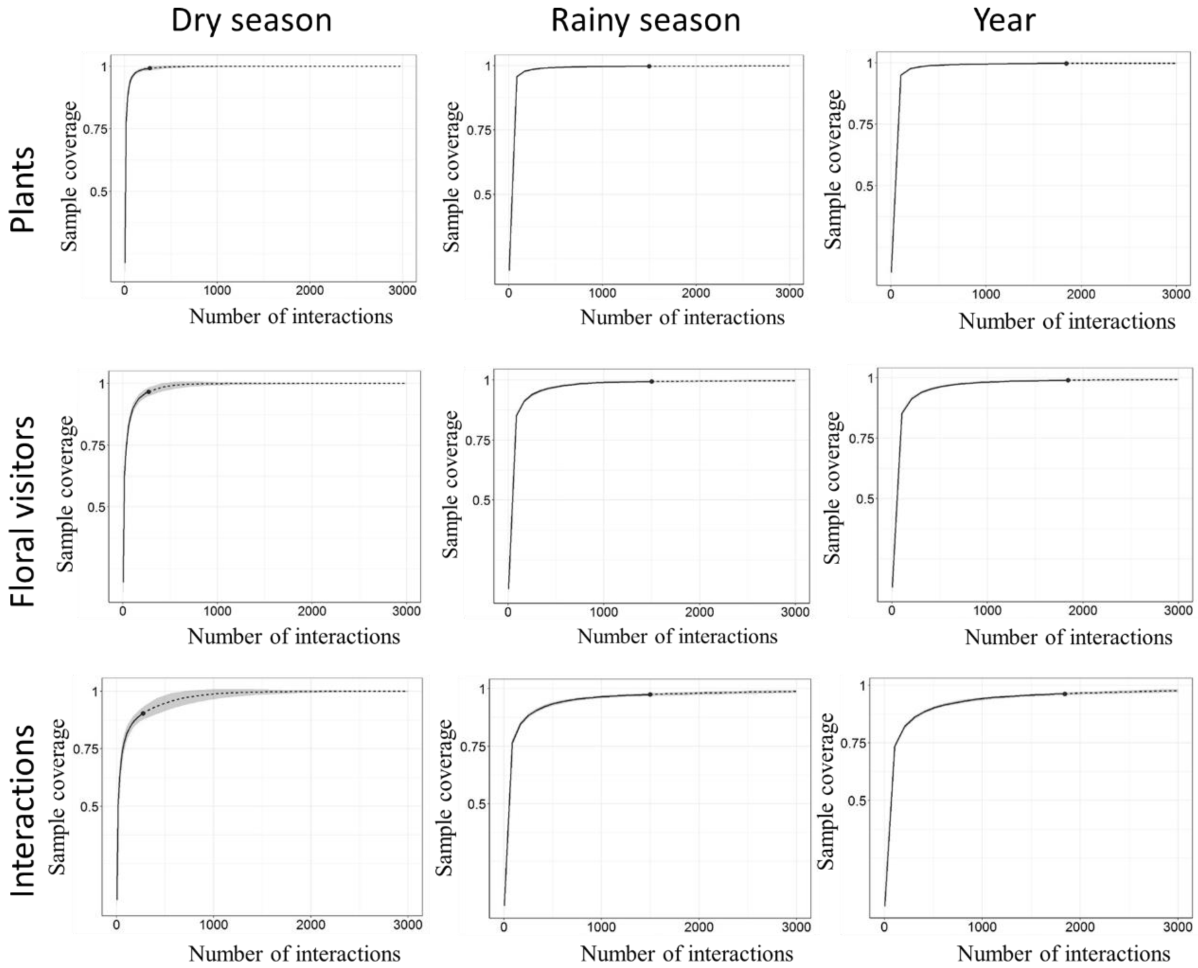

Figure 2. Sample coverage curves of plant-floral visitors' data obtained between October 2018 and Septembre 2019 in the shrubwood of Lomas de Galindo. Curves depicted for plants, floral visitors and interactions in every season and all year. Dry season includes months from November 2018 to March 2019, while rainy season the months between May and September 2019. Dots indicate reference samples; continuous lines indicate rarefaction and dotted lines extrapolation. Reference sample included all interactions of every species (superior and middle rows) or particular interactions (inferior row). Gray shadowed areas of dotted lines indicate 95% confidence intervals.

widespread in many biological networks, where core species exhibit the majority of interactions and form the center of the network (Gallagher et al. 2021). The "stochastic block models" algorithm was used to classify the species as core or peripheral; it is a method to infer statistically similar nodes (Martín González et al. 2020) performed in the econetwork 0.4.1 (Dray et al. 2020) package of R (R Core Team 2022).

The *QuanBiMo* algorithm grouped species of the global dataset in modules. This algorithm is specific to bipartite networks and correctly classifies 70% of links in the proper module (Dormann & Strauss 2014). Modules are groups of species that interact more intensely among themselves than with the rest of the species in the network (Olesen et al. 2007). Moreover, a stacked bar chart in a temporal framework shows the distribution of interactions between months.

We calculated beta-diversity between consecutive months using the method proposed by Poisot et al. (2012) to analyze the temporal replacement of interactions and species. This method splits the global beta-diversity (β_{WN}) into two additive components: species turnover (β_{ST}) and species rewiring (β_{OS}). Species turnover (β_{ST}) is the dissimilarity of species composition between months and depends on the incorporation or loss of a species in the monthly networks. Otherwise, species rewiring (β_{OS}) depends on the change of the links formed or lost between species present in consecutive months. Beta-diversity measures (β_{WN}, β_{ST}, and β_{OS}) vary between 0 and 1, where 0 indicates high similarity between months, while 1 indicates dissimilarity. When the value of β_{WN} was 1 (all interactions and species are different), it was assigned a value of 0.5 to every component β_{ST} and β_{OS}. R package betalink 2.2.1 (Poisot 2016) was used for these analyses.

Network robustness to the loss of interactions was measured with attack-tolerance curves (Memmott et al. 2004; Burgos et al. 2007). These curves are built by the progressive elimination of species of one trophic level (pollinators or plants) and analyzing the number of species of the counterpart trophic level that are eliminated from the network because they lost all their interactions (Memmott et al. 2004). Attack-tolerance curves were built for every season and the global network. We built extinction curves for both plants and pollinators. In every case, we used three methods of elimination: random elimination, eliminating first core species, and eliminating first peripheral species. Using this method, we obtained 18 curves from the combination at 3 temporal scales (one comprehending the global network and two from seasonal networks) x 2 kinds of nodes (plants or pollinators) x 3 methods of elimination. The area under the attack-tolerance curves (R) was the measure of robustness used (Burgos et al. 2007). When $R \rightarrow 0$, the attack-tolerance curve decreases abruptly and the system is not robust; when $R \rightarrow 1$, the curve decreases mildly and the system is robust (Burgos et al. 2007). These analyses were performed in the bipartite 2.17 package (Dormann et al. 2022) of R using the function second.extinct with 100 replicates in every extermination scenario. We calculated the area under the curve (R) in every replicate and compared them using Kruskal-Wallis tests because assumptions of data normality and homogeneity of variances were not fulfilled. For the graphics, we used the package ggplot2 3.3.5 (Wickham et al. 2021).

RESULTS

The plant-pollinator network of the entire year consisted of 1,844 interactions from 112 species (31 plants and 81 pollinators; Supporting information, Tab. S1). The majority of interactions concentrated in the rainy season, with 1500 interactions between 22 plants and 64 pollinators, compared with 271 interactions in the dry season between 16 plants and 35 pollinators (Fig. 3). The majority of pollinators were insects, and only two bird species (*Chlorostilbon ricordii* and *Icterus melanopsis*). Hymenoptera (34 species) and Lepidoptera (24 species) were the orders with higher species richness. Among hymenopterans, 15 species were bees belonging to the families Apidae and Halictidae.

Plant core species changed between seasons (Fig. 3). *Agave offoyana* was the only core species in the dry season, while *Coccoloba praecox*, *Bourreria havanensis*, and *Croton origanifolius* formed the core in the rainy season. For pollinators, *Apis mellifera* and *Melipona beecheii* were core species in both seasons, while *Aellopos blaini*, *Megachile poeyi*, and *Centris poecila* were observed as core species only during the rainy season (Fig. 3).

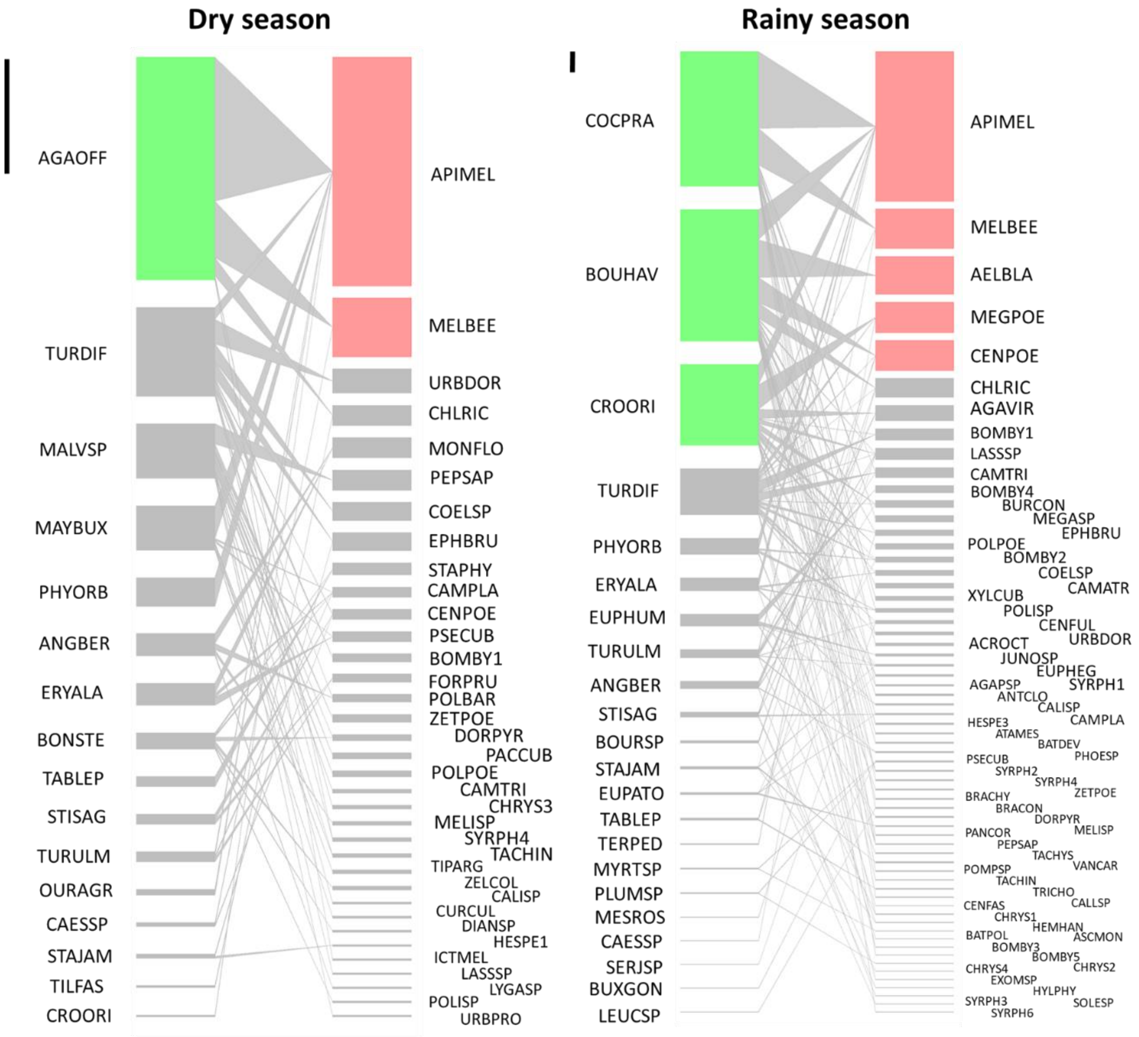

Figure 3. Interaction networks formed between plants and pollinators in the dry and rainy seasons of the shrubwood of Lomas de Galindo. In every network, the plants are depicted in left boxes while pollinators in the right ones. Green and red boxes indicate the plant and pollinator core species of each network. Black bars in the left sides of each season indicate the scale for 50 interactions. Full names of species are in Table S1.

Species were grouped into 10 modules for the pooled data, with four main modules including most pollinators (Fig. 4). All species of the plant-pollinator network maintain most of their interactions inside the module, except for *Apis mellifera*, which also established interactions with plants outside of its module. Core plant species were separated into different modules, except *Agave offoyana* and *Coccoloba praecox*, which integrated the same module. Core plant species maintained the majority of interactions in different months (Fig. 5). *Agave offoyana* during the dry season, particularly in March. The bulk of interactions grouped around *Coccoloba praecox*, *Bourreria havanensis* and *Croton origanifolius* in the rainy season, but not at the same time. At the beginning, in May, they gathered in *Coccoloba praecox*, while during June and July in *Bourreria havanensis*. Finally, at the end of the rainy season, gathered around *Croton origanifolius*, particularly in August and September (Fig. 5). Therefore, there is a pattern of temporal replacement between *Agave offoyana*, *Coccoloba praecox*, *Bourreria havanensis* and *Croton origanifolius* in that particular order (Fig. 5).

Beta-diversity values were high between all months because all global values (β_{WN}) were closer to 1 (Fig. 6). The components of rewiring and species turnover also had high values in most months. However, the component of species turnover was the only one present in the beta-diversity value between December-January and

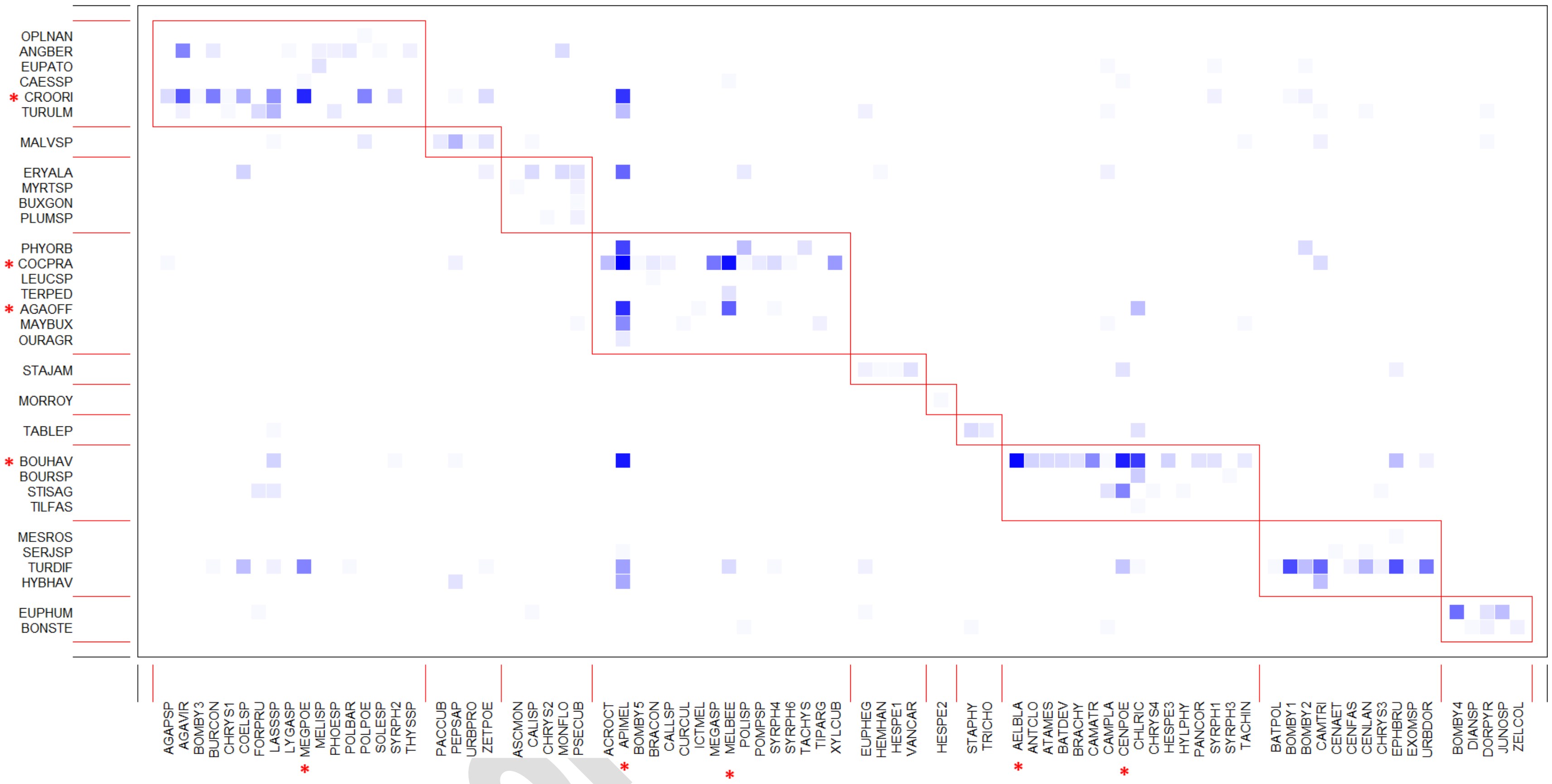

Figure 4. Modules formed from the interactions between plants (rows) and pollinators (columns) in the shrubwood of Lomas de Galindo. Blue squares indicate the interaction between a plant and a pollinator, while the color intensity indicates the frequency of each interaction. Red boxes delineate the formed modules. Red asterisks indicate core species. Full names of species are in Table S1.

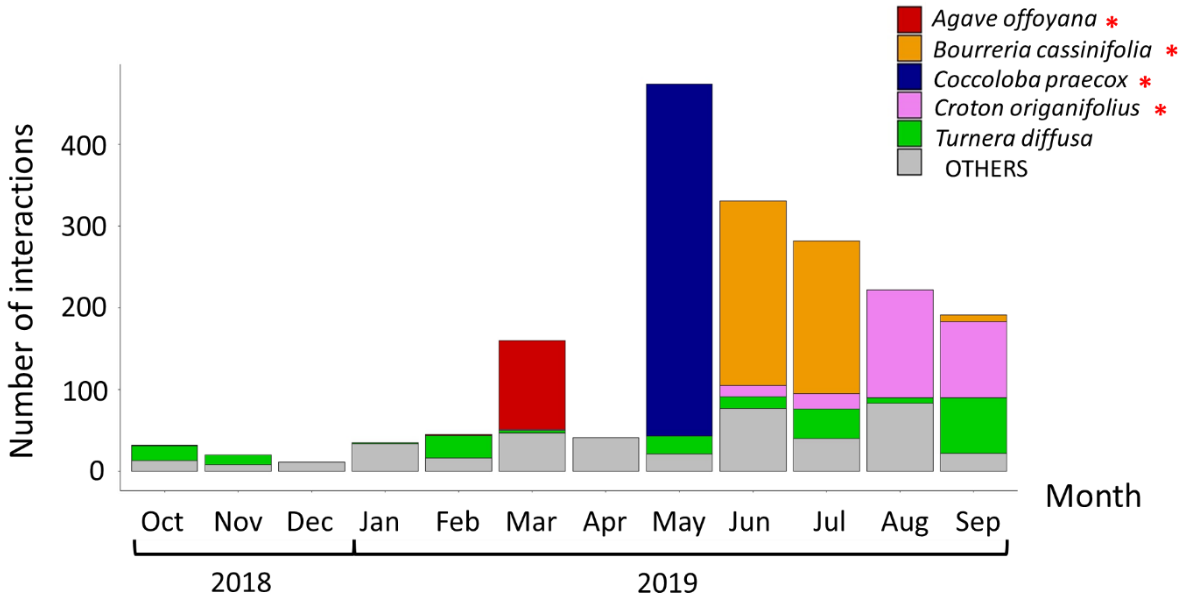

Figure 5. Stacked bar chart of temporal distribution of interactions between plant species in the shrubwood of Lomas de Galindo, between October 2018 and September 2019. The label "OTHERS" includes the plant species with fewer interactions. Red asterisks (*) identify core plant species.

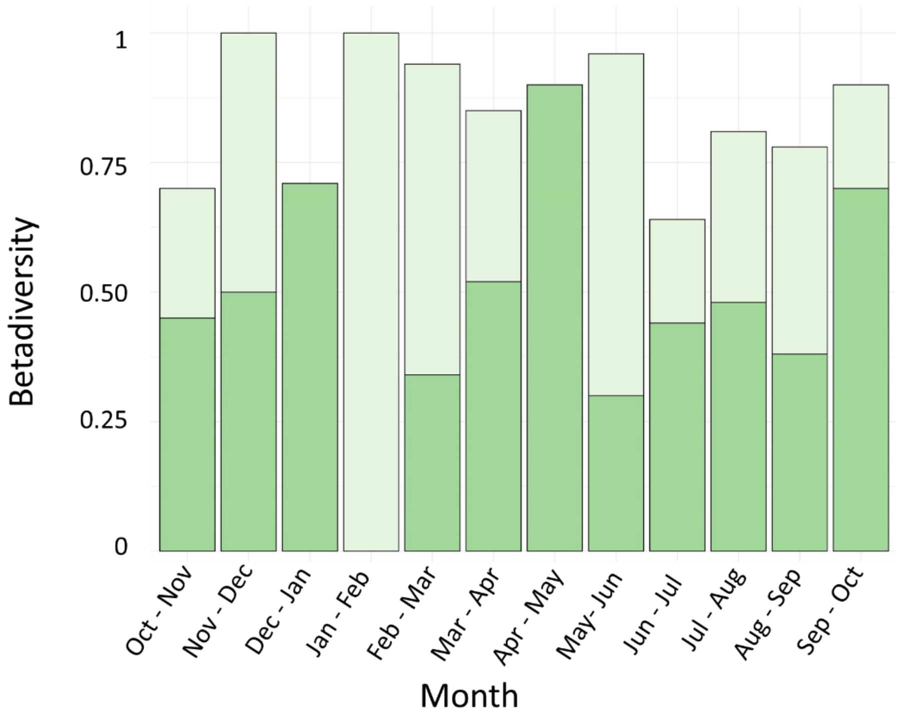

Figure 6. Temporal variation of beta-diversity (β_{WN}) and its components of species rewiring (β_{OS}) and species turnover (β_{ST}) in the shrubwood of Lomas de Galindo between October 2018 and September 2019. The bars depict the total beta-diversity value (β_{WN}), while the species rewiring (β_{OS}, light green) and species turnover (β_{ST}, dark green). The dry season spans from October 2018 to April 2019 and the wet season from May 2019 to September 2019.

April-May. In contrast, rewiring was the only component of beta-diversity between January-February, where the species reordered all the interactions. The change of beta-diversity value between June and July was the lowest and was mainly due to species turnover.

Network robustness was statistically different in all extermination scenarios (Figs. 7, 8). In the majority of simulations, the dry season was less robust than the rainy season, except when pollinator peripheral species were eliminated first (Figs. 7, 8). However, the removal of plant

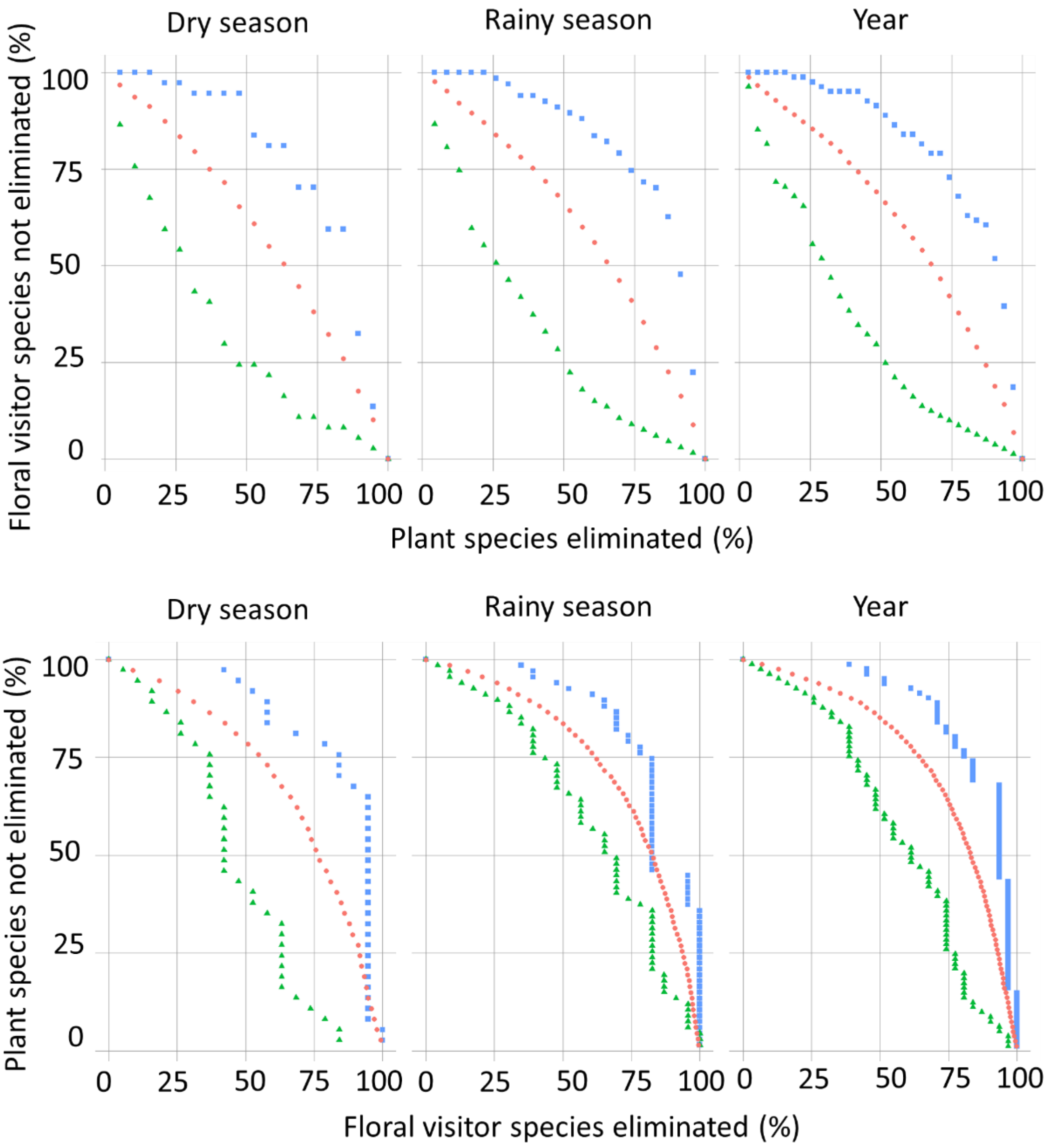

Figure 7. Attack-tolerance curves simulated from plant-pollinator interaction networks in the shrubwood of Lomas de Galindo. Top panels show the curves obtained when plants are eliminated, while the bottom shows the elimination of pollinators. Green triangles indicates the curves with elimination of core species, red dots means elimination of peripheral species, and blue squares random species.

peripheral species does not cause this pattern. Moreover, the loss of core plant species caused the fastest collapse of the network because R values were the lowest, hence the importance of core plants for network cohesiveness (Fig. 8). In all scenarios, the loss of core species (plants or pollinators) triggers the collapse of the entire network (Fig. 7). The opposite happened with peripheral species, which its loss do not cause a rapid collapse. Only when approximately 75% of peripheral plant species or more than 80% of peripheral pollinators were removed did the cohesiveness of the network decrease substantially (Fig. 7).

DISCUSSION

COMPOSITION OF POLLINATION NETWORK

The datasets obtained are good representations of reality, as sampling completeness was higher for both seasons and throughout the year (Hsieh et al. 2016). However, the present study had one limitation: it only analyzes diurnal pollination interactions, and therefore, conclusions could only be applied to diurnal pollination interactions. Core

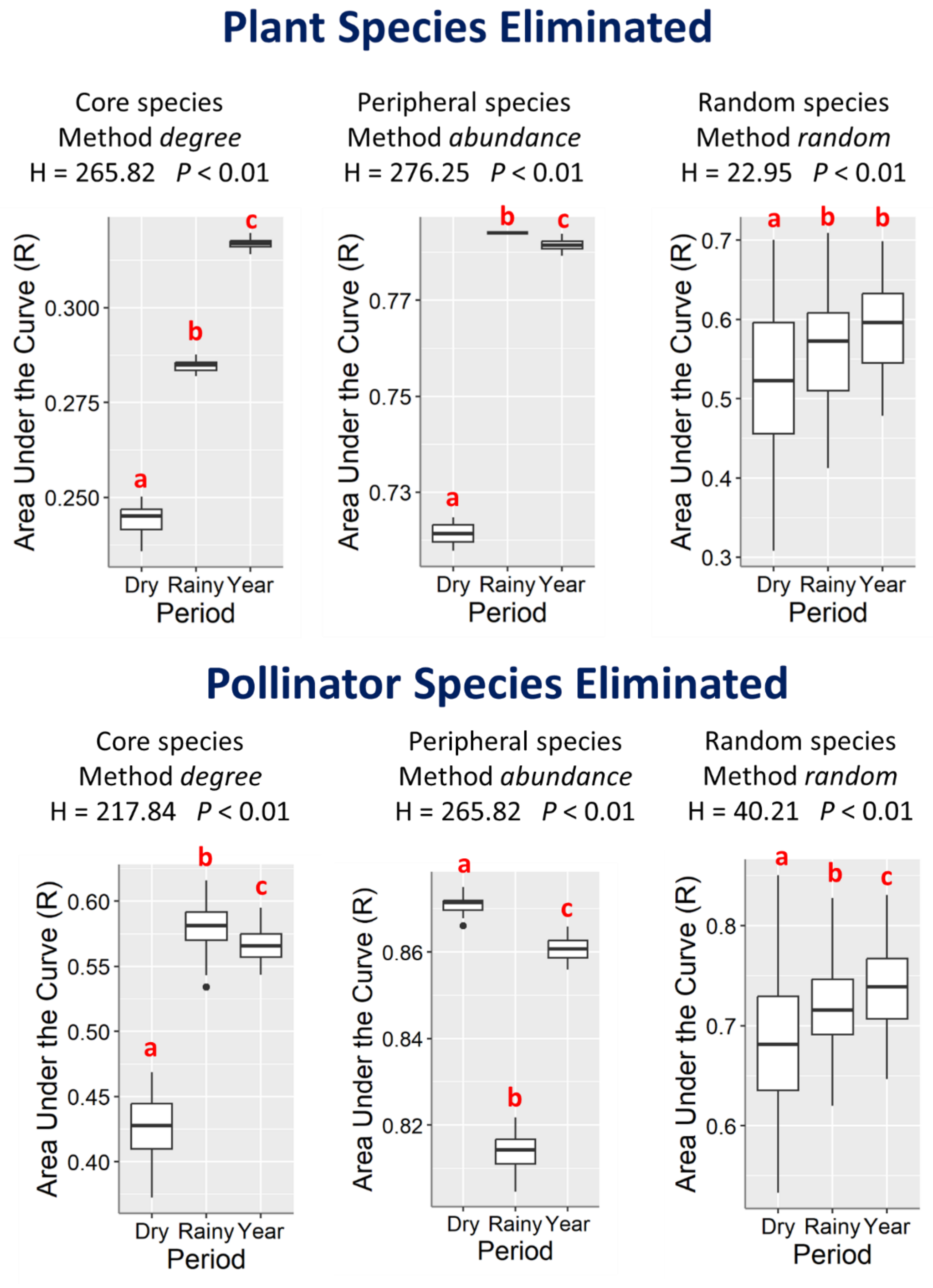

Figure 8. Robustness (*R*, Area Under the Curve) differences between dry season, rainy season and all year after 100 replicates. Kruskall-Wallis tests performed in every scenario and boxes depicted mean, 25th and 75th percentiles, minimum and maximum. Dots indicate outliers. Top panels show the curves obtained when plants are eliminated, while the bottom row shows the elimination of pollinators.

pollinator species include *Apis mellifera* and *Melipona beecheii*, which established the majority of interactions in both seasons. This could be due to the social nature of these bees, which are the only social bee species in Cuba (Genaro & Lóriga 2018).

The social structure implies that they maintain colonies with many individuals all year, one or more queens, and many foragers (Michener 2007). Moreover, social bees store food as honey, which is used when floral resources are scarce. Notably, *Apis mellifera* is a widespread species that has been introduced to Cuba and many ecosystems worldwide (Goulson 2003).

Apis mellifera colonies are both feral and maintained by humans for crop pollination and honey production. This and the extensive use of floral resources of honeybees caused a high abundance in almost all ecosystems around the world (Goulson 2003). Therefore, just because of the abundance and generalization of *Apis mellifera*, the effect of honeybees in native pollination networks is high and includes the reduction in the diversity of wild pollinators and rewiring of the interaction links (Valido et al. 2019). The invasion of this species causes significant changes in the structure of native pollination networks and frequently occupies a central position, monopolizing the majority of interactions (Santos et al. 2012). In the studied ecosystem, the effect could be the same, and further research should measure it, mainly the effect on plant reproductive success.

Another 13 species of bees integrate the pollination network, where some of them are rare and endemic to Cuba (Alayo 1976; Genaro 2008). Among them, two species (*Centris poecila* and *Megachile poeyi*) function as core pollinators in the rainy season. Bee diversity and its function within pollination networks are higher in arid ecosystems of the Caribbean (Martín González et al. 2009), mainly because the high temperatures of the soil do not allow nest infection with fungi or bacteria. In Cuba, the highest diversity of bees may be concentrated in these shrubwoods over ultramafic soils.

Core pollinators of the rainy season include the hawkmoth *Aellopos blaini*. The majority of species of the genus *Aellopos* are hawkmoths adapted for diurnal pollination (Amorim 2020). These species converge with hummingbirds and share similar traits: fast-flight behavior and visit short-tubed plants with mixed pollination systems (Amorim 2020). In this case, *Aellopos blaini* visited mainly the flowers of *Bourreria havanensis*, a plant with these flower traits (Alameda et al. 2023).

The majority of pollinators were insects, similar to other shrubwoods of Cuba over ultramafic soils (Faife-Cabrera et al. 2012; Alameda et al. 2020). Plants in these ecosystems are adapted to insect pollination (Faife-Cabrera et al. 2012), maybe because these animals consume low quantities of nectar and pollen, compared to other pollinators such as birds. Plants adapted to bird pollination produce high amounts of nectar that is highly diluted (Nicholson & Fleming 2003), which could be a constraint for the plant species of thorny shrubwood with low water availability (Brady et al. 2005).

Plant species that maintain the highest number of interactions are native; none of them are reported as invasive or introduced (Oviedo & González-Oliva 2015). Particularly, *Agave offoyana* bloomed in a short period during the dry season, between February and March 2019. This species, similar to other species of Agavaceae, is adapted to bat and bird pollination (Good-Ávila et al. 2006). However, a wide array of insect pollinators visited these species, which contribute to pollination with the same effectiveness as vertebrates (Slauson 2000; Molina-Freaner & Eguiarte 2003). In the shrubwood studied, *A. offoyana* represents a key resource in the dry season due to its abundance and high production of nectar (Álvarez 1986). High nectar production in the dry season can be possible because the leaves store water for years that the plant uses to produce a single, massive inflorescence, and after that, the individual dies (Rocha et al. 2006). This is not particular to *Agave offoyana* in Cuba; it also happens in the 166 species of *Agave* in semi-desertic areas of Mexico, which could function as a core species in pollination networks (Rocha et al. 2006).

STRUCTURE AND TEMPORAL VARIATION OF POLLINATION NETWORK

The separation of core plant species into different modules and the temporal replacement in the interactions between them and *Turnera diffusa* could imply a mechanism of niche segregation. Moreover, there could occur temporal facilitation between core plant species and *Turnera diffusa*, which together fill the year with floral resources that maintain the populations of pollinators, as the initial hypothesis suggested. The majority of interactions move from *Turnera diffusa*, *Agave offoyana*, *Coccoloba praecox*, *Bourreria havanensis* to *Croton origanifolius*, in that particular order. The frequency of facilitative interactions is higher in ecosystems with high abiotic stress, according to the stress-gradient hypothesis (Maestre et al. 2009). Thorny shrubwoods over the ultramafic soils of

Cuba are under stress due to abiotic conditions, and facilitative interactions could be an evolutionary advantage to ameliorating this stress and increasing the fitness of these plant species (Maestre et al. 2009). Moreover, there is evidence that facilitative interactions in these ecosystems not only occurred in pollination but also in coexistence by plant nursing (Oviedo et al. 2013).

The temporal dynamic of pollination networks occurs at different scales. The smallest scale includes the differences between day and night, where the networks are strikingly different (Knop et al. 2017). This study did not include nocturnal interactions, which could add more precision to the structure and dynamics of the network. Bigger scales include seasonal changes, mainly caused by changes in temperature and rain. In semi-desert ecosystems, the influence of rain and temperature triggers the flowering of plants and therefore the interactions with pollinators (Kigel et al. 2011). This also happens in the network of Lomas de Galindo, where the seasonal dynamic is high. Temporal changes are intense in seasonal communities with a high diversity of species (Dáttilo & Rico-Gray, 2018), as in the studied shrubwood. However, although intra-annual changes are high, temporal changes between years only occur in the periphery of the network, while the core of species and interactions remains stable (Olesen et al. 2008; Fang & Huang 2012).

Generally, both components of beta-diversity values: species turnover and interaction rewiring influence temporal changes (Marques et al. 2018; Cappellari et al. 2019; Flórez-Gómez et al. 2020). Particularly, the identity of species that integrate the network of Lomas de Galindo changed markedly between December and January (the dryest period in this area) and between April and May (beginning of the wet season). In these periods, the rain dynamics and temperature influence the flowering of plants and the abundance and presence of pollinator populations, which indicate a high intra-annual dynamic. Although this network is temporally highly variable, due to both the presence of different species and interaction reordering, the core plant species replace each other during the year. This ecological mechanism maintains stable floral resources to the pool of pollinators and is indicative of temporal facilitation among plants (Moore & Elmendorf 2011).

Robustness analysis indicates that core plant species are extremely important for the maintenance of the structural stability (Rohr et al. 2014). Pollination networks are not very sensitive to the loss of peripheral species but are highly sensitive to the extinction of core species (Memmott et al. 2004; Kaiser-Bunbury et al. 2010). These core plant species should receive special conservation priority, although they are not in threatened categories (González-Torres et al. 2016), but their effect on the functionality of the ecosystem is essential (Elle et al. 2012; Biella et al. 2020). Specifically, the elimination of core plant species in the dry season caused the lowest values of robustness. This highlights the importance of *Agave offoyana* for the functionality of the pollination service. Future research should focus on the ecology of core species, such as the one performed with *Agave offoyana* in Lomas de Galindo (Toledo & García-Beltrán 2020). The mechanism of facilitation among core plants implies that the local extinction of one of them could collapse the entire system, because it creates a temporal gap if not filled with other plant species. Moreover, the introduction of an invasive species that functions as a core and overlaps its flowering with the flowering of a native species can cause the decoupling of the network. In the shrubwood of Lomas de Galindo, core plant species are the most important nodes for the maintenance of the pollination service in the community; in fact, the temporal segregation is a key factor for the robustness of the network (Ramos-Jiliberto et al. 2018).

In conclusion, the intra-annual dynamic of the pollination network of the shrubwood of Lomas de Galindo is intense both in species turnover and interaction rewiring. Interactions were established mainly around nine species of plants and pollinators, which formed a core. These species offer robustness to the network, and their extinction could cause a collapse of the system. Moreover, there is a temporal replacement between core plant species, which could be the result of niche segregation and temporal facilitative interactions. In this arid ecosystem, facilitative interactions are common and are a mechanism to increase the survival of plant species. Therefore, the conservation in this protected area should include these core species, because they maintain the pollination service in the entire ecosystem.

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AUTHOR CONTRIBUTION

Concept and design DA, AB & CAMA, data collection DA & AB, data analysis DA & CAMA, writing DA, edits and approval for publication DA, AB & CAMA.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

DATA AVAILABILITY STATEMENT

The data used to write this article are available as in the Appendices.

APPENDICES

Additional supporting information may be found in the online version of this article:

Table S1. Plant species and floral visitors recorded in the plant-pollinator network of Lomas de Galindo.

Table S2. Dataset for the plant–floral visitors of the global network

Table S3. Dataset for the plant–floral visitors of the dry season

Table S4. Dataset for the plant–floral visitors of the rainy season

REFERENCES

Alameda D, Falcón B, Rijo G, de Vales D, Castañeda A, Leyva LM (2020) Diurnal pollination network of "Cuabales de Cajálbana", a serpentine shrubwood in western Cuba. Revista del Jardín Botánico Nacional 41:25-30.

Alameda D, Corso AJ, González AP, Tejeda A, Rodríguez AL, Carralero MF, Barro A (2023) *Bourreria havanensis*: a nectar oasis in the serpentine shrubwood of Lomas de Galindo? Revista del Jardín Botánico Nacional 44:1-8.

Alayo P (1976) Introducción al estudio de los himenópteros de Cuba. Superfamilia Sphecoidea. Serie Biológica 67:1-46.

Albor C, Arceo-Gómez G, Parra-Tabla V (2020) Integrating floral trait and flowering time distribution patterns help reveal a more dynamic nature of co-flowering community assembly processes. Journal of Ecology 108:2221-2231. https://doi.org/10.1111/1365-2745.13486

Álvarez A (1986) Las inflorescencias de *Agave*. Revista del Jardín Botánico Nacional 7(2):3-14.

Arceo-Gómez G, Kaczorowski RL, Ashman TL (2018) A network approach to understanding patterns of coflowering in diverse communities. International Journal of Plant Sciences 179(7):569-582. https://doi.org/10.1086/698712

Armas C, Rodríguez-Echeverría S, Pugnaire FI (2011) A field test of the stress-gradient hypothesis along an aridity gradient. Journal of Vegetation Science 22:818-827. https://doi.org/10.1111/j.1654-1103.2011.01301.x

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(3):687-698. https://doi.org/10.1890/10-1110.1

Berazaín R (2001) The influence of ultramafic soils on plants in Cuba. South African Journal of Science 97:510-512.

Biella P, Akter A, Ollerton J, Nielsen A, Klecka J (2020) An empirical attack tolerance test alters the structure and species richness of plant-pollinator networks. Functional Ecology 34:2246-2258. https://doi.org/10.1111/1365-2435.13642

Borhidi A (1996) *Phytogeography and vegetation ecology of Cuba*. Budapest: Akademia Kiado.

Brady KU, Kruckeberg AR, Bradshaw HD (2005) Evolutionary ecology of plant adaptation to serpentine soils. Annual Review of Ecology, Evolution and Systematics 36:243-266. https://doi.org/10.1146/annurev.ecolsys.35.021103.105730

Burgos E, Ceva H, Perazzo RPJ, Devoto M, Medan D, Zimmermann M, Delbue AM (2007) Why nestedness in mutualistic networks? The Journal of Theoretical Biology 249:307-313. https://doi.org/10.1016/j.jtbi.2007.07.030

Cappellari S, Lim JL, Tidon R, Neff JL, Simpson BB, Pawar S (2019) Seasonal variation of a plant-pollinator network in the Brazilian Cerrado: implications for community structure and robustness. PLoS ONE 14(12):e0224997. https://doi.org/10.1371/journal.pone.0224997

CaraDonna PJ, Petry WK, Brennan RM, Cunningham JL, Bronstein JL, Waser NM, Sanders NJ (2017) Interaction rewiring and the rapid turnover of plant-pollinator networks. Ecology Letters 20:385-394. https://doi.org/10.1111/ele.12740

Capote R, Berazaín R (1984) Clasificación de las formaciones vegetales de Cuba. Revista del Jardín Botánico Nacional 5(2):27-75.

Callaway RM, Brooker RW, Choler P, Kikvidze Z, Lortie CJ, Michalet R, Paolini L, Pugnaire FI, Newingham B, Aschehoug ET, Armas C, Kikodze D, Cook BJ (2002) Positive interactions among alpine plants increase with stress. Nature 417:844-848. https://doi.org/10.1038/nature00812

Carvalheiro LG, Beismeijer JC, Benadi G, Fründ J, Stang M, Bartomeus I, Kaiser-Bunbury CN, Baude M, Gomes SIF, Merckx V, Baldock KCR, Bennett ATD, Boada R, Bommarco R, Cartar R, Chacoff N, Dänhardt J, Dicks LV, Dormann CF, Ekross J, Henson KSE, Holzschuh A, Junker RR, Lopezaraiza-Mikel M, Memmott J, Montero-Castaño A, Nelson IL, Petanidou T, Power EF, Rundlöf M, Smith HG, Stout JC, Temitope K, Tscharntke T, Tscheulin T, Vilá M, Kunin WE (2014) The potential for indirect effects between co-flowering plants via shared pollinators depends on resource abundance, accesibility and relatedness. Ecology Letters 17:1389-1399. https://doi.org/10.1111/ele.12342

Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93:2533-2547. https://doi.org/10.1890/11-1952.1

CNAP (Centro Nacional de Áreas Protegidas) (2013) Plan del Sistema Nacional de Áreas Protegidas 2014-2020. Ministerio de Ciencias, Tecnología y Medio Ambiente, La Habana, Cuba.

Dáttilo W, Rico-Gray V (eds) (2018) Ecological Networks in the Tropics. An Integrative Overview of Species Interactions from Some of the Most Species-Rich Habitats on Earth. Springer International Publishing. https://doi.org/10.1007/978-3-319-68228-0

De Aguiar MAM, Newman EA, Pires MM, Yeakel JD, Boettiger C, Burkle LA, Gravel D, Guimaraes Jr. PR, O´Donnel JL, Poisot T, Fortin MJ, Hembry DH (2019) Revealing biases in the sampling of ecological interaction networks. PeerJ 7:e7566. https://doi.org/10.7717/peerj.7566

Dormann CF, Strauss R (2014) A method for detecting modules in quantitative bipartite networks. Methods in Ecology and Evolution 5:90-98. https://doi.org/10.1111/2041-210X.12139

Dormann CF, Freund J, Gruber B, Beckett S, Devoto M, Felix GMF, Iriondo JM, Opsahl T, Pinheiro RBP, Strauss R, Vázquez DP (2022) *bipartite* 2.17: Visualising bipartite networks and calculating some (ecological) indices. URL: https://github.com/biometry/bipartite

Dray S, Matias C, Miele V, Ohlmann M, Thuiller W (2020) *econetwork* 0.4.1: Analyzing ecological networks. URL: https://plmlab.math.cnrs.fr/econetproject/econetwork

Elle E, Elwell SL, Gielens GA (2012) The use of pollination networks in conservation. *Botany* 90:525-534. https://doi.org/10.1139/b11-111

Faife-Cabrera M, Díaz-Álvarez E, Cañizares-Morera M, Torres-Roche EM (2012) Síndromes de polinización y dispersión de endemismos en las serpentinas al suroeste de Santa Clara, Cuba. Centro Agrícola 39(2):61-66.

Fang Q, Huang SQ (2012) Relative stability of core groups in pollination networks in a biodiversity hotspot over four years. PLoS ONE 7(3):e32663. https://doi.org/10.1371/journal.pone.0032663

Filazzola A, Lortie CJ (2014) A systematic review and conceptual framework for the mechanistic pathways of nurse plants. Global Ecology and Biogeography 23:1335-1345. https://doi.org/10.1111/geb.12202

Flórez-Gómez NA, Maldonado-Cepeda JD, Ospina-Torres R (2020) Bee-plant interaction networks in a seasonal dry tropical forest of the Colombian Caribbean. Neotropical Entomology 43:533-544. https://doi.org/10.1007/s13744-020-00804-8

Gallagher RJ, Young JG, Welles BF (2021) A clarified topology of core-periphery structure in networks. Science Advances 7:eabc9800. https://doi.org/10.1126/sciadv.abc9800

Genaro J (2008) Origin, composition and distribution of the bees of Cuba (Hymenoptera: Apoidea: Anthophila). Insecta Mundi 0052:1-16.

Genaro J, Lóriga W (2018) *Melipona beecheii* Bennett (Hymenoptera: Apidae): origen, estudios y meliponicultura en Cuba. Insecta Mundi 0643:1-18.

Ghazoul J (2006) Floral diversity and the facilitation of pollination. Journal of Ecology 94:295-304. https://doi.org/10.1111/j.1365-2745.2006.01098.x

Gibson RH, Knott B, Eberlein, 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

González-Torres LR, Palmarola A, González-Oliva L, Bécquer ER, Testé E, Barrios D (eds.) (2016) Lista roja de la flora de Cuba. Bissea 10(1):1-352.

Good-Ávila S, Souza V, Gaut BS, Eguiarte LE (2006) Timing and rate of speciation in *Agave* (Agavaceae).

PNAS 103(24):9124-9129. https://doi.org/10.1073/pnas.0603312103

Goulson D (2003) Effects of introduced bees on native ecosystems. Annual Review of Ecology, Evolution and Systematics 34:1-26. https://doi.org/10.1146/annurev.ecolsys.34.011802.132355

Holmgren M, Scheffer M (2010) Strong facilitation in mild environments: the stress gradient hypothesis revisited. Journal of Ecology 98:1269-1275. https://doi.org/10.1111/j.1365-2745.2010.01709.x

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

Kaiser-Bunbury CN, Muff S, Memmott J, Müller CB, Caflisch A (2010) The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behavior. Ecology Letters 13:442-452. https://doi.org/10.1111/j.1461-0248.2009.01437.x

Kigel J, Konsens I, Rosen N, Rotem G, Kon A, Fragman-Sapir O (2011) Relationships between flowering time and rainfall gradients across Mediterranean-desert transects. Israel Journal of Ecology and Evolution 57(1-2):91-109. https://doi.org/10.1560/IJEE.57.1-2.91

Knop E, Gerpe C, Ryser R, Hofmann F, Menz MHM, Trösch S, Zoller S, Fontaine C (2017) Rush hours in flower visitors over a day-night cycle. Insect Conservation and Diversity 11(3):267-275. https://doi.org/10.1111/icad.12277

Koffel T, T Daufresne, CA Klausmeier (2021) From competition to facilitation and mutualism: a general theory of the niche. Ecological Monographs 91(3):e01458 https://doi.org/10.1002/ecm.1458

Lázaro A, R Lundgren, Totland O (2009) Co-flowering neighbors influence the diversity and identity of pollinator groups visiting plant species. Oikos 118:691-702. https://doi.org/10.1111/j.1600-0706.2008.17168.x

Loidi J, G Navarro-Sánchez, D Vynokurov (2022) Climatic definitions of the world's terrestrial biomes. Vegetation Classification and Survey 3:231-271. https://doi.org/10.3897/VCS.86102

Maestre FT, Callaway RM, Valladares F, Lortie CJ (2009) Refinig the stress-gradient hypothesis for competition and facilitation in plant communities. Journal of Ecology 97:199-205. https://doi.org/10.1111/j.1365-2745.2008.01476.x

Marques MF, Deprá MS, Gaglianone MC (2018) Seasonal variation in bee-plant interactions in an Inselberg in the atlantic forest in Southeastern Brazil. Sociobiology 65(4):612-620. https://doi.org/10.13102/sociobiology.v65i4.3473

Martín González AM, Dalsgaard B, Ollerton J, Timmermann A, Olesen JM, Andersen L, Tossas A (2009) Effects of climate on pollination networks in the West Indies. Journal of Tropical Ecology 25:493-506. https://doi.org/10.1017/S0266467409990034

Martín González AM, Vázquez DP, Ramos-Jiliberto R, Hoom S, Miele V (2020) Core-periphery structure in mutualistic networks: an epitaph for nestedness? bioRxiv 2020.04.02.021691. https://doi.org/10.1101/2020.04.02.021691

Martínez-Adriano CA, Díaz-Castelazo C, Aguiire-Jaimes A (2018) Flower-mediated plant-butterfly interactions in an heterogeneous tropical coastal ecosystem. PeerJ 6:e5493 https://doi.org/10.7717/peerj.5493

Memmott J, Waser NM, Price MV (2004) Tolerance of pollination networks to species extinctions. Proceedings of the Royal Society, Biological Sciences 271:2605-2611. https://doi.org/10.1098/rspb.2004.2909

Michener CD (2007) The bees of the world, Second Edition. The Johns Hopkins University Press. https://doi.org/10.56021/9780801885730

Miele V, Ramos-Jiliberto R, Vázquez DP (2020) Core-periphery dynamics in a plant-pollinator network. Journal of Animal Ecology 89:1670-1677. https://doi.org/10.1111/1365-2656.13217

Molina-Freaner F, Eguiarte LE (2003) The pollination biology of two paniculate Agaves (Agavaceae) from northwestern Mexico: contrasting roles of bats as pollinators. American Journal of Botany 90(7):1016-1024. https://doi.org/10.3732/ajb.90.7.1016

Moore KA, Elmendorf SC (2011) Plant competition and facilitation in systems with strong environmental gradients. In: Harrison S, Rajakaruna (eds) Serpentine. The evolution and ecology of a model system. University of California Press, United States of America, pp 223-236. https://doi.org/10.1525/9780520948457-013

Nicolson SW, Fleming PA (2003) Nectar as food for birds: the physiological consequences of drinking dilute sugar solutions. Plant Systematics and Evolution 238:139-153. https://doi.org/10.1007/s00606-003-0276-7

Olesen JM, Bascompte J, Dupont YL, Jordano P (2007) The modularity of pollination networks. PNAS 104(50):19891-19896. https://doi.org/10.1073/pnas.0706375104

Olesen JM, Bascompte J, Elberling H, Jordano P (2008) Temporal dynamics in a pollination network. Ecology 89(6): 1573-1582. https://doi.org/10.1890/07-0451.1

Olesen JM, Stefanescu C, Traveset A (2011) Strong, long-term temporal dynamics of an ecological network. PLoS ONE 6(11): e26455. https://doi.org/10.1371/journal.pone.0026455

Oviedo R, Faife-Cabrera M, Noa-Monzón A, Arroyo J, Valiente-Banuet A, Verdú M (2013) Facilitation allows plant coexistence in Cuban serpentine soils. Plant

Biology 16(4):711-716. https://doi.org/10.1111/plb.12116

Oviedo R, González-Oliva L (2015) Lista nacional de plantas invasoras y potencialmente invasoras en la República de Cuba. Bissea 9(2):1-88.

Petanidou T, Kallimanis AS, Tzanopoulos J, Sgardelis SP, Pantis JD (2008) Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. Ecology Letters 11:564-575. https://doi.org/10.1111/j.1461-0248.2008.01170.x

Poisot T, Canard E, Mouillot D, Mouquet N, Gravel D (2012) The dissimilarity of species interaction networks. Ecology Letters 15:1353-1361. https://doi.org/10.1111/ele.12002

Poisot T (2016) betalink 2.2.1: Beta-diversity of species interactions. URL: http://poisotlab.io/software

Proctor J (1999) Toxins, nutrient shortages and droughts: the serpentine challenge. TREE 14(9):334-335. https://doi.org/10.1016/S0169-5347(99)01698-5

Proctor J, Woodell SRJ (1975) The ecology of serpentine soils. Advances in Ecological Research 9:225-366. https://doi.org/10.1016/S0065-2504(08)60291-3

R Core Team (2022) R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. URL: http://www.R-project.org/

Ramos-Jiliberto R, Moisset P, Franco-Cisterna M, Petanidou T, Vázquez D (2018) Phenology determines the robustness of plant-pollinator networks. Scientific Reports 8:14873. https://doi.org/10.1038/s41598-018-33265-6

Rocha M, Good-Ávila SV, Molina-Freaner F, Arita HT, Castillo A, García-Mendoza A, Silva-Montellano A, Gaut BS, Souza V, Eguiarte LE (2006) Pollination biology and adaptive radiation of Agavaceae, with special emphasis on the genus *Agave*. Aliso 22:329-344. https://doi.org/10.5642/aliso.20062201.27

Rohr RP, Saavedra S, Bascompte J (2014) On the structural stability of mutualistic systems. Science 345(6195):1253497. https://doi.org/10.1126/science.1253497

Santos GMM, Aguiar CML, Genini J, Martins CF, Zanella FCV, Mello MAR (2012) Invasive africanized honeybees change the structure of native pollination networks in Brazil. Biological Invasions 14:2369-2378. https://doi.org/10.1007/s10530-012-0235-8

Slauson LA (2000) Pollination biology of two chiropterophilous Agaves in Arizona. American Journal of Botany 87(6):825-836. https://doi.org/10.2307/2656890

Toledo S, García-Beltrán JA (2020) Population structure and recruitment microsites of *Agave offoyana* (Asparagaceae: Agavoidea/Agavaceae) at two locations in western Cuba with different plant communities. Bradleya 38(38):254-267. https://doi.org/10.25223/brad.n38.2020.a24

Trojelsgaard K, Olesen JM (2016) Ecological networks in motion: micro- and macroscopic variability across scales. Functional Ecology 30:1926-1935. https://doi.org/10.1111/1365-2435.12710

Valido A, Rodríguez-Rodríguez MC, Jordano P (2019) Honeybees disrupt the structure and functionality of plant-pollinator networks. Scientific Reports 9:4711 https://doi.org/10.1038/s41598-019-41271-5

Wickham H, Chang W, Henry L, Pedersen TL, Takahashi K, Wilke C, Woo K, Yutani H, Dunnington D (2021) ggplot2 3.3.5: Create Elegant Data Visualizations Using the Grammar of Graphics. URL: https://github.com/tidyverse/ggplot2