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INSECT POLLINATORS

Bee-Plant Interaction Networks in a Seasonal Dry Tropical Forest of the Colombian Caribbean

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Abstract

Mutualistic interactions between bees and flowering plants have been widely recognized as one of the most important for the maintenance of these communities throughout ecosystems. Consequently, understanding how these interactions occur is highly important, especially in seasonal dry tropical forest (SDTF), one of the most endangered ecosystems in northern South America. In this study, we analyzed the changes between interaction networks across two well-defined seasons, dry and wet, in a SDTF of the Colombian Caribbean in Taganga, Magdalena. We also determined changes in species composition and their role in interaction networks. To study this system, we compared two approaches: (1) networks constructed with data from direct collections in flowering plants, and (2) networks constructed with pollen data obtained from bees' bodies. A total of 44 species were collected in 18 species of flowering plants; also, we registered 16 additional plants presented in the records only as pollen types. We found that network metrics, connectance, nestedness, specialization (H2′), and interaction strength asymmetry remain stable through seasons. However, when the two types of approximations were compared, there were significant differences. Networks constructed with pollen data are more connected, less specialized, and with lower values of interaction strength asymmetry. The major difference between seasons relied on the interacting species composition, due to a high species turnover. Bee community was more diverse in dry season. Apidae family, mainly eusocial species, persisted in the community, being more abundant and relevant in wet season. For dry season, *Megachile* and other solitary species from Apidae and Halictidae families were better represented and relevant for the community. We found that Fabaceae is an important resource for bees in both seasons. In addition, herbaceous species from Asteraceae and Convolvulaceae were preferred in wet season, while shrub and tree species from Fabaceae and Polygonaceae were the main resource in dry season.

Introduction

Ecological interactions have played an important role shaping the current biodiversity, having plant-pollinator interactions as one of the most important (Bascompte & Jordano 2006). It is estimated that up to 87% of the angiosperm species rely on animal pollination, and this proportion increases in tropical ecosystems, where it is estimated around a 94% (Ollerton *et al* 2011). Therefore, plant-pollinator interactions are fundamental for the reproduction and maintenance of populations (Jordano *et al* 2009).

The role of wild bees as one of the most important pollinators has been widely documented. With little exceptions, bee species depend on the consumption of floral resources, mostly nectar (source of carbohydrates), during their adult life, and pollen (source of proteins) in larval stages (Michener 2007). Besides, a great number of bee larvae feed on microorganisms that grow on pollen (Steffan *et al* 2019). For this high dependence on floral resources, the close relation between plants and bees has driven the diversification of both groups (Cardinal & Danforth 2013).

An approach to visualize the structure of floral visitation interactions at community level is the use of interaction networks, giving an illustrative tool to identify the interacting components of each community (Chacoff *et al* 2012). Besides, this set of interactions has emergent properties. Quantitative network studies provide an idea of the frequency and intensity of these interactions. Moreover, generalism-specialism of each species, dependence of one species to another, and asymmetry level in the specificity of the interactions and other patterns can be measured (Jordano *et al* 2009).

The reconstruction of these networks is the reflection of sampling in a specific place and time (Olesen & Jordano 2002). Several studies have analyzed the changes of these interactions and their properties over time. In those described annual variation, properties as nestedness, connectance, modularity, number of interacting species, and interactions remain constant over years; but the species composition is highly different (Petanidou *et al* 2008, Dupont *et al* 2009, Pradal *et al* 2009, Burkle & Alarcón 2011). In contrast, studies that analyzed variation in smaller periods have shown significant differences in network structure across the day (Baldock *et al* 2011), and across months with differences in connectance, network size, and abundance of interacting species (Basilio *et al* 2006). Burkle and Alarcón (2011) pointed out the importance of network analysis in short periods that are biologically relevant.

In ecosystems with high seasonality, it has been found differences in connectance, modularity, and niche overlap, having dry season networks more connected and less modular and with a higher niche overlap (Santos *et al* 2014). Studies involving bee-plant interactions in these kinds of ecosystems have reported differences in nestedness between seasons, besides a higher diversity of the bee community in dry season (Marques *et al* 2018). Seasonal dry tropical forests (SDTFs) are representative ecosystems characterized by a high seasonality, alternating long dry periods with rainy months (Murphy & Lugo 1986). Despite its notable seasonality, there are always flowering plants, although they can change between seasons (Cortés-Flores *et al* 2017). In Colombia, studies of bee-plant interactions in highly seasonal ecosystems are scarce. SDTFs should be studied, because they are completely fragmented in Colombia, with only 1.5% of their initial coverage remaining; their distribution is related with deforestation and a rapid land transformation (Pizano & Garcia 2014).

Most of bee-plant network studies are plant-based, where samplings are done by recording floral visitors in each plant species; this approach may underestimate the number of interactions, having a wide number of specialists that could be in fact generalists (Bosch *et al* 2009, Jordano *et al* 2009). A way to deal with this biased method is to record pollen grains from bodies of pollinators, giving an extended record of the visitations (Bosch *et al* 2009). However, these methods are uncommon in interaction network studies.

In this study, we have three main goals: (1) determine how bee-plant interactions in a SDTF of the Colombian Caribbean differ between wet and dry seasons, (2) explore if there are differences in the composition of the interacting species and their role in the interaction networks in both seasons, (3) contrast pollen-based and collection-based networks in order to analyze which gives a better resolution of the species interactions.

Materials and Methods

Study area

This study was carried out in Taganga, which is part of the rural area of Santa Marta, in the Magdalena department, Colombia (11°15′46.2″–11°15′40.7″N 74°10′59.0″–74°10′51.9″ W). The study area was a seasonal tropical dry forest with an average annual precipitation of 501 mm and an average temperature of 27.3°C. In addition, this area is characterized by a strong seasonality, where dry season is from December to April, with less than 20 mm per month. Rainy months are September and October, with more than 80 mm per month, and relative humidity is higher in the second semester of the year (IDEAM 2014). Our samplings were conducted in a primary forest with high deforestation rate.

Specimens sampling

We made two samplings for each season (four in total), three days each sampling, between September 2016 and March 2017. We delimited two transects of 180 × 20 m along a trail inside the forest. We sampled only flowering plants inside each transect. Time of sampling was from 6:00 to 13:00, as most bees forage during day (Kelber *et al* 2005), especially at morning hours. The total sampling effort was 42 h per season, with two people collecting bees and one collecting botanical and pollen samples. In each transect, we identified flowering plants and collected botanical samples for taxonomical identification; we also took anthers of these plants into vials with alcohol. Plants were identified in the National Herbarium at the National University of Colombia.

Using insect nets, bees were collected in flowering plants during sampling periods of 5 min for each plant, having continuous samplings in both transects, with approximately two census per plant per day. Bees were transferred to lethal killing jars with potassium cyanide and put into individual vials, then we gathered the contact pollen of each bee using fuchsine-stained glycerinated gelatin. Collected bees were mounted, identified, and deposited in the entomological collection of the Bee Laboratory Research group (LABUN) at the National University of Colombia.

For palynological analysis, flowering plant anthers were collected and the pollen was removed and processed according to the acetolysis method, in order to prepare a reference pollen collection. Contact pollen samples were directly mounted on micro-slides; each slide held the pollen of a single collected bee. We observed pollen grains using a LEICA DM500 with a ×1000 magnification, then we identified pollen types with the reference pollen from the study area, at the palynological collection of the LABUN and with pollen catalogs (Palacios Chávez *et al* 1991, Roubik & Moreno Patiño 1991).

Data analysis

Network analysis

We merged data from the two samples of each season, constructing two quantitative adjacency matrices per season, one collection-based (C.B) and one pollen-based (P.B) (four matrices in total). In collection-based matrices A, a_{ij} = number of bee species *j* collected in each plant species *i*. In pollen-based matrices A, a_{ij} = number of bees *j* that had each pollen type *i*. Then we constructed bipartite networks to illustrate the interactions in wet and dry seasons. We also calculated metrics of these networks using bipartite package (Dormann *et al* 2008); plots were made using circlize (Gu *et al* 2014) package of the R Studio software (R Core Team 2019). Then graphics were edited using CorelDRAW 2017 software.

We calculated network metrics to compare interactions between seasons. One of these was connectance, defined as the number of observed interactions over the number of possible interactions. To explain the dependence of each trophic level, we calculated interaction strength asymmetry, where positive values mean a higher dependence in the higher trophic level, and negative values a higher dependence in the lower trophic level (Blüthgen *et al* 2007). Then we obtained network specialization H2′, in which a totally specialized network has a H2′ value of 1 (Bascompte & Jordano 2006, Dormann *et al* 2008, Jordano *et al* 2009). To determine the organization of networks in both seasons, we calculated nestedness that consists in a core of few generalist species interacting with specialists, in this scenario with the loss of a specialist species the generalist persist in the community (Tylianakis *et al* 2010). Nestedness values were obtained using ANINHADO software (Guimarães & Guimarães 2006), calculating NODF value and comparing it with the null model NODF_Ce using 1000 randomizations. The null model was proposed by Bascompte *et al* (2003), which assumes the probability of an interaction as proportional to the degree of both communities. If NODF is higher than the null model, then the network is nested (Bascompte *et al* 2003). At a species level, for both communities, we obtained values of species strength that refer to the relevance of a species in the network across its partners (Bascompte & Jordano 2006, Dormann *et al* 2008).

Diversity of bee community and Beta diversity of bee-plant interactions

To calculate bee diversity and richness in both seasons, we used asymptotic diversity estimates based on Hill numbers of order *q*. Species richness ($q = 0$), Shannon diversity ($q = 1$, exponential of Shannon entropy), and Simpson diversity ($q = 2$, inverse of Simpson concentration) (Jost 2006) were calculated with a sample size–based rarefaction and extrapolation procedure (Chao *et al* 2014). To determine if the diversity values were different, we compared them by a visual approximation of the superposition of the 95% confidence intervals. The analysis was conducted using the R package iNext R (Chao *et al* 2014).

To determine differences in the interactions between networks of both seasons, we calculated Beta diversity of interactions. Following Poisot *et al* (2012), differences of bee-plant interactions (β_{WN}) have two additive components: turnover in species composition (β_{ST}) and interaction rewiring (βos) between shared species in both seasons. Values for this index range from 0 to 1, where high values denote a high turnover. To conduct the analysis, we used betalink package (Poisot 2016) in R (R Core Team 2019), using Whittaker's beta diversity index (Whittaker 1960).

Results

A total of 364 bee specimens were collected, belonging to three families and 44 species: Apidae (27), Megachilidae (12), and Halictidae (4) (Table 1), of which 11 species (25%) were found in both seasons. Based on the confidence intervals, we found significant differences in richness and diversity values between wet and dry season (Fig 1). Species richness was greater in dry season (33 species) compared to wet season (22 species). Also, diversity was higher in dry season (Shannon = 24.063, Simpson = 18.070) than wet season

Table 1 Number of specimens of each bee species collected in wet and dry seasons in a seasonal seasonal dry tropical forest of the Colombian Caribbean in Taganga, Magdalena.

Family		Species	Number of specimens	
			Wet season	Dry season
Apidae	1	*Ancylocelis* sp.	5	–
	2	*Apis mellifera*	10	9
	3	*Centris analis*	1	–
	4	*Centris fascialis*	–	3
	5	*Centris geminata*	–	3
	6	*Centris nitens*	2	–
	7	*Centris tarsata*	–	3
	8	*Centris trigonoides*	1	4
	9	*Centris niveofasciata*	–	13
	10	*Ceratina* (*Ceratinula*) sp. 1	–	3
	11	*Ceratina* (*Ceratinula*) sp. 2	–	2
	12	*Ceratina* (*Crewella*) sp. 1	–	7
	13	*Ceratina* (*Crewella*) sp. 2	–	3
	14	*Diadasia* sp. 1	6	–
	15	*Diadasia* sp. 2	4	–
	16	*Frieseomelitta* sp.	8	3
	17	*Geotrigona joearroyoi*	18	13
	18	*Melipona favosa*	36	6
	19	*Melitomella schwarzii*	11	–
	20	*Mesocheira bicolor*	–	2
	21	*Thygater analis*	6	–
	22	*Trigona nigerrima*	26	21
	23	*Trigonisca* sp.	12	6
	24	*Xylocopa fimbriata*	–	1
	25	*Xylocopa mordax*	2	1
	26	*Xylocopa muscaria*	–	3
	27	*Xylocopa transitoria*	–	1
Megachilidae	28	*Heriades tayrona*	–	6
	29	*Megachile* (*Chelostomoides*) sp.	–	26
	30	*Megachile* (*Chrysosarus*) sp.	–	3
	31	*Megachile* (*Neochelynia*) sp.	–	5
	32	*Megachile* (*Pseudocentron*) sp.	–	2
	33	*Megachile* (*Sayapis*) sp.	3	–
	34	*Megachile* (*Tylomegachile*) sp.	4	7
	35	*Megachile* sp. 5	–	5
	36	*Megachile* sp1.	3	–
	37	*Megachile* sp2	2	9
	38	*Megachile* sp3	–	6
	39	*Megachile* sp4	2	–
Halictidae	40	*Augochlora* sp.	–	5
	41	*Augochlorella* sp.	–	2
	42	*Halictus ligatus*	3	–
	43	*Halictus* sp.	–	6
	44	*Lasioglossum* sp	3	7
	Total		168	196

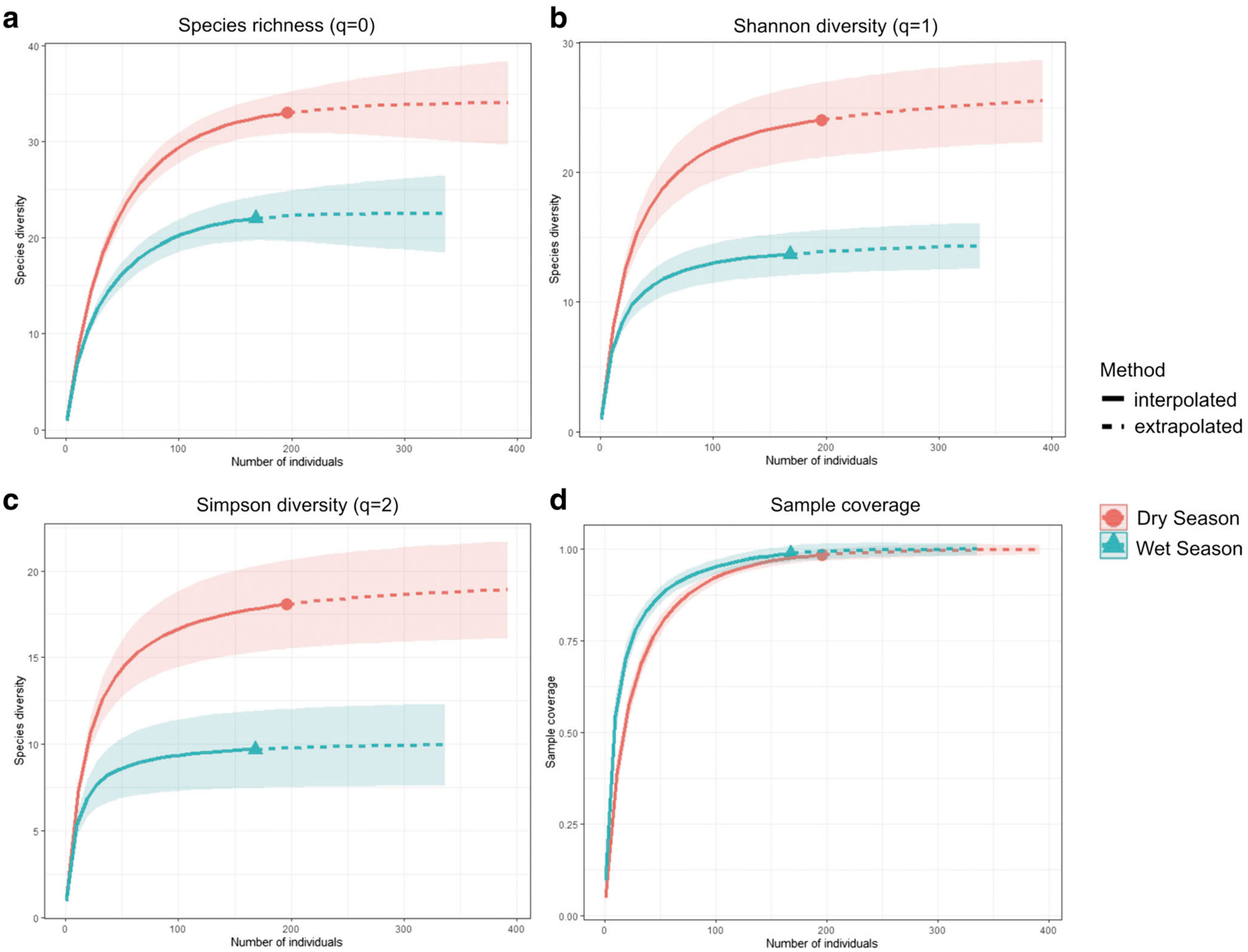

Fig 1 Diversity of bee species in wet and dry seasons in a seasonal dry tropical forest of the Colombian Caribbean in Taganga, Magdalena. Plots show (A) species richness (Hill number for $q = 0$), (B) equally abundant species ($q = 1$), (C) dominance ($q = 2$), and (D) sample coverage curve. Diversity curves were constructed using rarefied (solid lines) and extrapolated nectar samples (dashed lines) with sample size–based estimations. Color-shaded regions represent the 95% confidence intervals.

(Shannon = 13.711, Simpson = 9.706). For the plant community, we recorded 34 plant species; 16 species were registered only as contact pollen (Table 2), and six species were found in both seasons. We found 18 families, and Fabaceae was the best represented, with 10 species registered.

Wet season networks

The interaction networks for wet season (Fig 2A, Fig 3A) showed 22 interacting bee species and 18 plant species for the pollen-based network (P.B) and 11 plant species for the collection-based (C.B) (P.B matrix size = (22, 18), C.B matrix size = (22, 11)).

Network metrics values are presented in Table 3. Connectance was low but pollen-based networks had higher values than collection-based networks (P.B = 0.3, C.B = 0.21). Interaction strength asymmetry value was positive, indicating that bees (higher trophic level) depend more on the plant community than vice versa. Networks showed a nested pattern, as the NODF_total values were higher when compared with the null model NODF_Ce; however, P.B networks were more nested than C.B networks. Specialization values H2′of this season were lower in pollen-based network (P.B = 0.27, C.B = 0.45).

At species level, more relevant bee species (with higher species strength values) were mostly Apidae species; those were *Melipona favosa* (Fabricius), *Geotrigona joearroyoi* (Gonzalez & Engel), *Trigona nigerrima* (Cresson), and *Thygater analis* (Lepeletier). For the plant community, species with higher values were Heliantheae (Asteraceae), *Senna atomaria*, *Merremia umbelata*, and Faboideae Type 1 (Fig 4).

Dry season networks

The interaction networks for dry season (Fig 2B, Fig 3B) showed 33 interacting bee species and 20 plant species for

Table 2 Flowering plants and pollen types found in wet and dry seasons in a seasonal dry tropical forest of the Colombian Caribbean in Taganga, Magdalena. Abundance refers to number of bee specimens in which each pollen type was found. Plants with symbol (*) are those that were observed only in the palynological analysis. Species with (**) were observed in pollen and flowering in field.

			Abundance	
Family		Species/pollen type	Wet season	Dry season
Fabaceae	1	*Senna atomaria* (**)	16	21
	2	*Senna* sp. (*)	29	–
	3	Faboideae type 1 (*)	49	34
	4	Faboideae type 2 (*)	29	20
	5	*Prosopis juliflora* (**)	7	–
	6	*Gliricidia sepium*(**)	–	20
	7	*Platymiscium pinnatum* (**)	–	34
	8	*Parkinsonia aculeata* (**)	–	5
	9	*Haematoxylum brasiletto* (**)	–	73
	10	*Dioclea* sp. (*)	6	–
Polygonaceae	11	*Coccoloba coronata* (**)	55	–
	12	*Coccoloba acuminata* (**)	–	57
Convolvulaceae	13	*Merremia umbelata* (**)	46	–
	14	*Merremia aegyptia* (**)	23	–
	15	*Ipomoea* sp. (*)	14	–
Asteraceae	16	Heliantheae (**)	62	–
Malvaceae	17	Type Malvaceae (*)	8	–
	18	*Sida cordifolia* (**)	–	19
Melastomataceae	19	Melastomataceae (*)	14	
Bignoniaceae	20	*Tecoma stans* (**)	5	1
	21	*Arrabidea* sp. (*)	–	3
Cucurbitaceae	22	*Cucurbita* sp. (*)	8	–
Meliaceae	23	*Melia azederach* (**)	9	5
Capparaceae	24	*Capparidastrum pachaca* (**)	–	11
Scrophulariaceae	25	*Leucophyllum frutescens* (**)	–	6
	26	Scrophulariaceae type 1 (*)	–	9
	27	Scrophulariaceae type 2 (*)	–	12
Bombacaceae	28	*Pseudobombax septenatum* (*)	–	4
Nyctaginaceae	29	*Boerhavia erecta* (**)	6	3
Arecaceae	30	Arecaceae 1 (*)	–	2
Sapotaceae	31	*Chrysophyllum* sp. (*)	–	9
Zygophyllaceae	32	*Guaiacum officinale* (**)	11	–
Rubiaceae	33	Rubiaceae type (*)	–	4
Malpighiaceae	34	Malpighiaceae type (*)	–	4

the pollen-based network and 12 plant species for the collection-based (P.B matrix size = (33, 20), C.B matrix size = (33, 12)).

Similar to wet season, connectance was low and pollen-based networks had higher values than collection-based networks (P.B = 0.26, C.B = 0.19). We found that bee community relies more on plant community than inversely, based on the positive value of interaction strength asymmetry. Regarding specialization values H2′, pollen-based networks had lower specialization values (P.B = 0.31, C.B = 0.49). Networks of this season were nested, but P.B network had a higher value than C.B reconstruction (Table 3).

In contrast with the wet season, species with higher species strength values from the bee community belong to Apidae, Halictidae, and Megachilidae families: *Ceratina* (*Crewella*) sp., *Lasioglossum* sp., *G. joearroyoi*, *Megachile* sp. 3, and *Apis mellifera* (Linnaeus). For plant community, more relevant species were *Haematoxylum brasiletto*, *Coccoloba acuminata*, *Gliricidia sepium*, and *Platymiscium pinnatum*.

When interaction networks of both seasons were compared using Beta diversity values, we found a high turnover of interactions between seasons ($\beta_{WN} = 0.89$), differences in species composition and interaction rewiring contribute similarly to the turnover of the interactions ($\beta_{ST} = 0.48$, $\beta os = 0.41$).

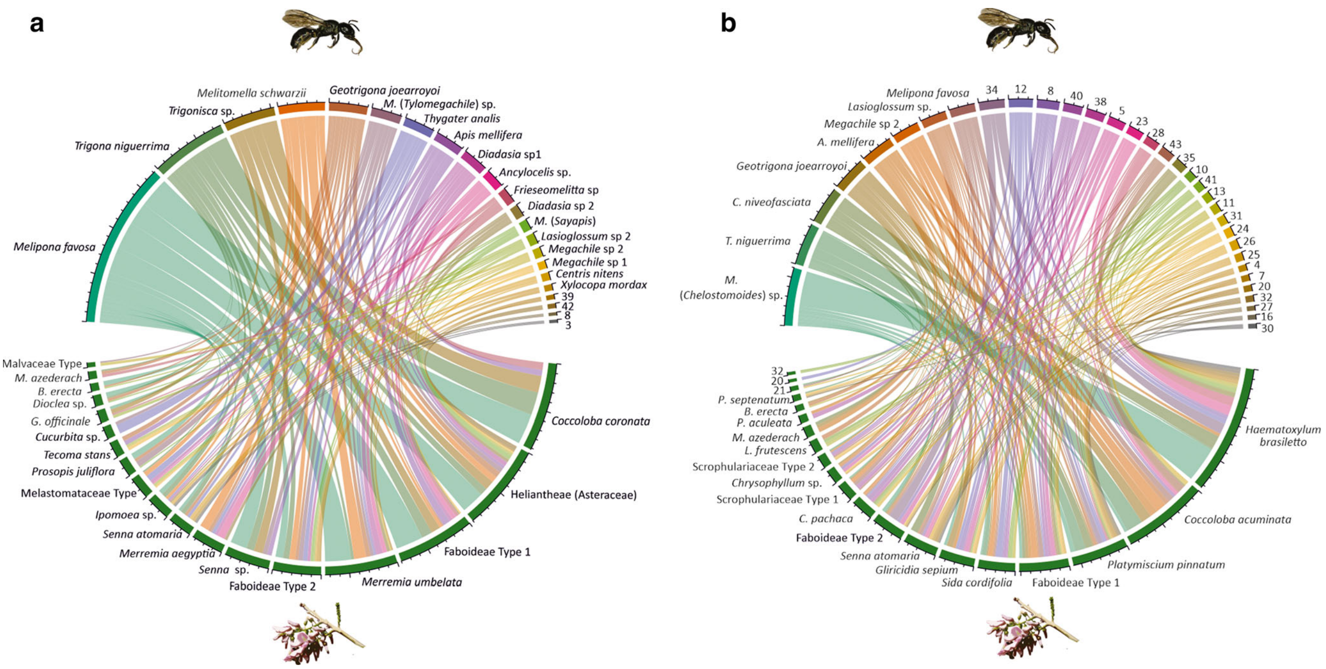

Fig 2 Bee-plant interaction networks in a seasonal dry tropical forest of the Colombian Caribbean for wet season (a) and dry season (b) constructed with pollen-based matrices. Numbers correspond to species according to the Table 1 for bee species, and Table 2 for plant species

Discussion

Our study revealed differences in interaction networks between wet and dry seasons. These differences were mainly due to a turnover in the interacting species. However, network metrics remained constant through seasons. Small variations in metrics were related to changes in diversity and richness between seasons, which were higher in dry season. Moreover, we found differences between the types of network reconstruction, where pollen-based networks gave a better resolution of interactions than collection-based networks.

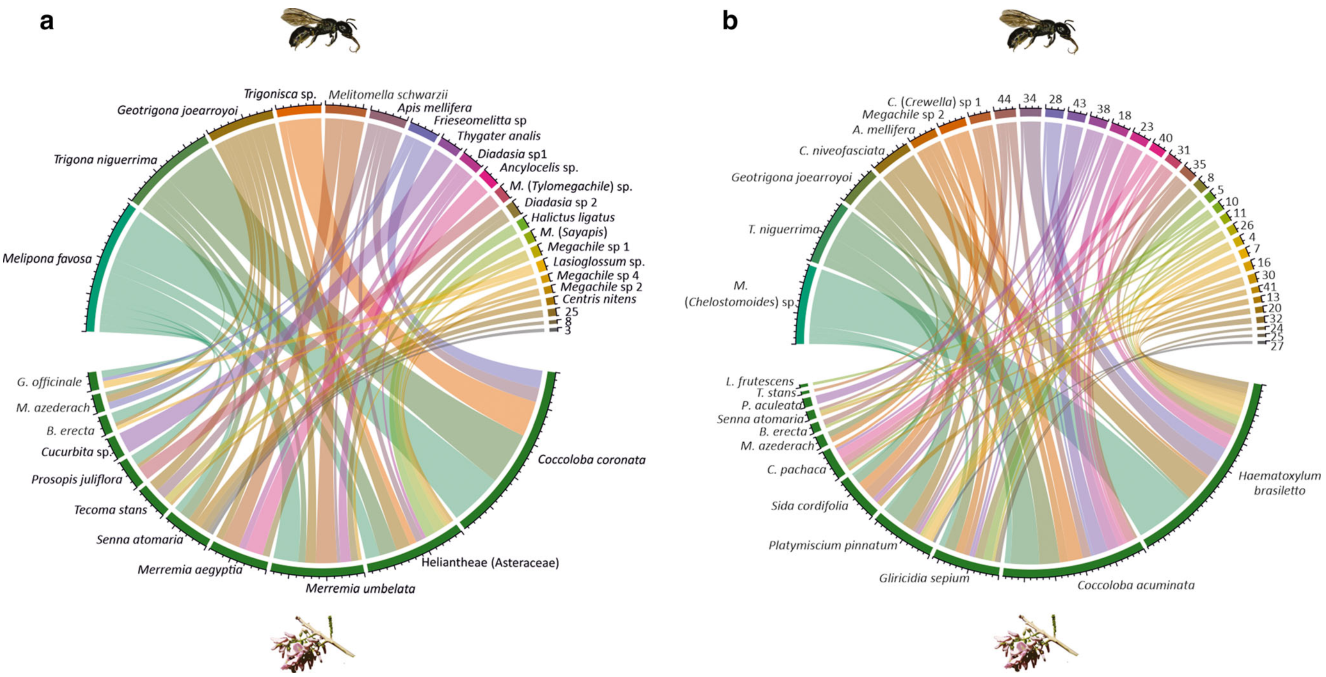

Fig 3 Bee-plant interaction networks in a seasonal dry tropical forest of the Colombian Caribbean for wet season (a) and dry season (b) constructed with collection-based matrices. Numbers correspond to species according to the Table 1 for bee species, and Table 2 for plant species.

Table 3 Values for connectance, nestedness (NODF), nestedness null model (NODF_Ce mean), interaction strength asymmetry, and specialization (H2′) of interaction networks for wet and dry seasons of a seasonal dry tropical forest of the Colombian Caribbean.

	Wet season		Dry season	
	Pollen-based	Collection-based	Pollen-based	Collection-based
Connectance	0.3	0.21	0.26	0.19
Interaction strength asymmetry	0.013	0.14	0.039	0.18
H2′	0.27	0.45	0.31	0.49
NODF	47.68	31.16	42.32	32.11
NODF_Ce mean	37.63	28.19	33.26	26.29

Dry and wet season: interaction networks and diversity

We corroborated what similar studies have found; network properties remain quite constant through time (Alarcón *et al* 2008, Olesen *et al* 2008, Petanidou *et al* 2008, Marques *et al* 2018). Low connectance is an excepted property of pollination networks (Jordano 1987), and obtained networks had a low connectance, being lower in dry season; this season had a higher species richness and connectance has a negative relation with this value (Jordano *et al* 2009). Reconstructed networks also showed a nested pattern, meaning that interactions between sampled communities are resilient if some interactions disappear; this is a distinctive property of pollination and flower visitation networks (Bascompte & Jordano 2006). Given the interaction strength asymmetry values, for both seasons, we found a higher dependence of the bee

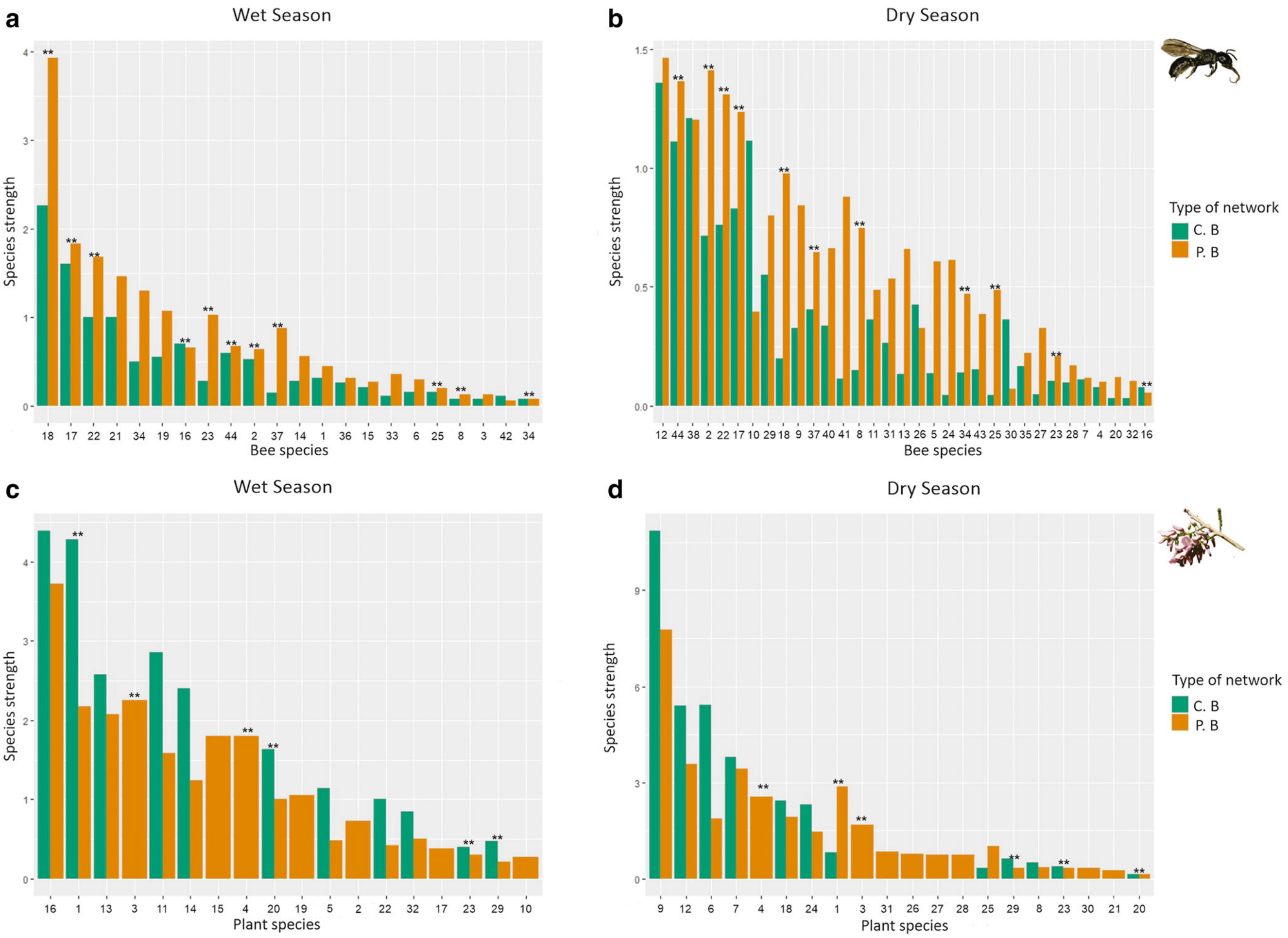

Fig 4 Species strength values for bee and plant species in the constructed networks for wet and dry season in a seasonal dry tropical forest of the Colombian Caribbean. Bee species for wet season (a) and dry season (b). Plant species for wet season (c) and dry season (d). Species marked with (**) were present in both seasons. Yellow bars correspond to values for pollen-based networks (P.B) and green bars to collection-based networks (C.B). Numbers in the *x*-axis correspond to species according to the Table 1 for bee species, and Table 2 for plant species.

community on plant community. This indicates that plant community is more likely to receive a greater number of bee species visitors than bee species to visit a wide variety of plants. Similar studies with butterflies have shown that these insects depend more on the plant community, because of their relying on floral resources, while plants can have other floral visitors more than one specific taxonomic group (Martínez-Adriano *et al* 2018).

We recorded a high turnover in plant and bee species, having a small percentage of shared species in both seasons; for the bee community, most of them were eusocial groups. This strong seasonality may be caused by life history traits of bees and plant phenology (Ogilvie & Forrest 2017) that may be adapted to the typical conditions of the SDTF.

We found 44 of the 128 species (33%) registered for the Colombian Caribbean region (Gonzalez *et al* 2012), most of them occurring during the dry season. It is possible that megachilids and other groups found mainly in this season have synchronized their life cycles to the availability of preferred flowers, having immature stages during the wet season and emergence in dry season as reported in previous studies (Roubik 1989, Marinho *et al* 2018). Another factor that may have an effect on the bee activity in this season is nesting preference. For example, Megachilidae family that was more abundant and diverse in dry season has been reported a preference of nidification in dry seasons (Marques & Gaglianone 2013). A similar pattern could occur in *Ceratina*, a genus that constructs their nests in dry twigs, and also found only in this season, despite that tropical species tend to be multivoltine (Rehan *et al* 2015). Previous studies have reported a preference of nesting in sunny and warmer sites (Vickruck & Richards 2012), and this scenario is more probable in dry season. During the wet season, Apidae family was more abundant and the majority of these species were eusocial. Eusocial species take advantage of higher diversity and number of flowering plants in the wet season; thus, they invest more resources in brooding and increase the number of foraging workers, allowing the nest to store as many resources in preparation for the dry season (Nunes-Silva *et al* 2010, Maia-Silva *et al* 2014).

It is well known that floral resources, floral availability, and abiotic factors influence the temporal patterns of foraging activity of bees (Wojcik *et al* 2008, Aleixo *et al* 2017). Bee groups that were active through the seasons experienced a higher turnover in the composition of floral species they used, than those that were active in a single season. The first ones tend to be social bees, with several generations of workers and therefore necessarily polylectic, while the second ones are typically solitary, and more likely to be oligolectic (Ogilvie & Forrest 2017). Species with short periods of activity forage only when the preferred resource is available (Lattke & Rangel-Ch 2015).

Taking a closer look to the bee species recorded in our study, we found uncommon reported species like *Mesocheira bicolor* (Fabricius), rarely sampled due to its cleptoparasitic habits. We also found endemic ones to the Caribbean Colombian region, as *Heriades tayrona* (Gonzalez & Griswold) and *Geotrigona joearroyoi*, and one vulnerable species *Melipona favosa* (Amat-Garcia *et al* 2007), although none of these allegedly endemisms or vulnerable statuses are corroborated by formal research. This supports the idea that the Colombian Caribbean region has an interesting bee fauna that deserves more study (Gonzalez *et al* 2012) and might have some unique interactions with the flora in this particularly seasonal ecosystem. Interestingly, we found that introduced species *A. mellifera* played a secondary role in both seasons, suggesting little or no displacement of native bees in the presence of *A. mellifera*. This result contrasts previous studies, where this species tends to have high species strength values, hence an important role in interaction networks (Giannini *et al* 2015).

For the plant community, flowering species during the wet season were mainly herbaceous, but in dry season trees and shrubs were better represented. This is consistent with previous studies on plant phenological patterns in SDTF, where herbaceous plants tended to flower during the wet season; meanwhile, trees did it during the dry season, due to differences in the radicular system (Cortés-Flores *et al* 2017). Differences in flowering patterns explain the floral resources usage by bee community according to seasons. In our results, Asteraceae and Convolvulaceae (herbaceous species) were the most visited in wet season, and shrub species like *Haematoxylum brasiletto* and *Platymiscium pinnatum* were preferred during the dry season. Species from the Fabaceae and Polygonaceae (genus *Coccoloba*) families were an important floral resource for the bee community since they were present in both seasons and had high species strength values. Studies from other SDTFs have proven that Fabaceae, Convolvulaceae, and Asteraceae families are important for bee communities (Pacheco Filho *et al* 2015, Alvarado-Ospino *et al* 2020). Looking in detail, some plant families are important for specific bee groups, as Fabaceae for Meliponini species (Gaona *et al* 2019), Convolvulaceae for Emphorini tribe (represented in our study by *Melitomella schwarzii* (Michener)*, Diadasia* and *Ancyloscelis* genera), and Asteraceae for Eucerini (represented by *T. analis*) (Pacheco Filho *et al* 2015).

Network reconstruction comparison: pollen-based vs. collection-based

Our results reveal that pollen-based and collection-based networks have consistent differences. The inclusion of pollen data increased the number of interacting plant species, giving a better understanding of the flowering species richness and the resource relative importance in the study area. Besides, the number of interactions per sampled bee also increased; in some cases, species that were registered once could have more than one visited plant, having as a result, networks with higher connectance. Specialization H2′ also varied depending on the reconstruction. We obtained higher values in collection-based networks; hence, a phytocentric approach overestimates the specialization (Dorado *et al* 2011, Vizentin-Bugoni *et al* 2018). This result is also related to the differences in interaction strength asymmetry values. We found lower values with the inclusion of pollen data, suggesting that an approach based only in visitation records could overestimate this network parameter. Our results corroborate Bosch *et al*'s (2009) and Dorado *et al*'s (2011) findings, where networks constructed with pollen data are more connected and less specialized, as rare interactions may be detected.

Pollen-based approximation has some limitations that should be taken into account. First, there is a lower taxonomic resolution for the plant community when compared with collection-based approximations, since pollen identification is difficult, especially in diverse tropical ecosystems (Vizentin-Bugoni *et al* 2018). For this reason, in our study, most of the plant morphospecies, registered only as pollen types, were identified to a family or genus level. Second, pollen-based networks based on presence-absence of a pollen type might underestimate the importance magnitude of the resource per individual in contrast with pollen type–counting approximations (Novella-Fernandez *et al* 2019).

It is important to take into account that constructed networks evaluate the interactions as flower visitation, but not the quality of interactions. Not all bee visitors are effective pollinators, de Santiago-Hernández *et al* (2019) reported that 59% of floral visitors in an interaction network are effective pollinators in a Mexican SDTF. On the other hand, pollen-based approach could underestimate the number of plant species that are important for the bee community maintenance. This approximation ignores the importance of the non-pollen resources offered by plants, like nectar and nesting substrate, which are resources of major importance for bee species (Dailey & Scott 2006, Jha & Vandermeer 2010), hence possibly underestimating the importance of non-pollen providing plant species and adding bias to the interaction strength asymmetry index. For further studies, it is important to consider the inclusion of pollen abundance data, besides observations of plants that bring other resources for bee community (e.g., nectar, resins, or nesting sites), in order to have a better approximation of the relation between bee and plant communities.

Given the strong seasonality of SDTFs and importance of the bee community in the pollination of neotropical flora, it is necessary to maintain pollen sources for their survival. In our study, we found that these resources are provided by a wide variety of plants, from herbs to trees. These flowering species contribute distinctively in each season, and are used by different bee species through time. For further studies, it is important to consider in network reconstruction other approaches that include plant species which provide nesting substrate and food resources, and contribute to the maintenance of the bee community in these endangered ecosystems.

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Data Accessibility All data are fully available without restriction. All files are available from the Harvard Dataverse database (https://doi.org/10.7910/DVN/CKRVKA).

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