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Flowering phenology patterns promotes pollination facilitation in coexisting *Anthurium* species from a mountain forest in Colombia

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Abstract

Co-flowering congeneric plant species may either experience competition for the services of shared pollinators or facilitation when together, they attract a higher number and diversity of pollinators. In this study, we evaluate whether temporal segregation in flowering time and temporal partition of shared pollinators operate among sympatric *Anthurium* species as mechanisms to reduce competition to attract potential pollinators. We investigated flowering phenology, the intra-e interspecific synchrony, and the composition of the flower visitor community of seven coexisting *Anthurium* species biweekly for a whole year in Native and Pine forests. We also analyzed the structure of *Anthurium*-flower visitor networks and the functional role of species. Flowering was continuous thorough the year for most *Anthurium* species, but their flowering peaks were segregated significantly in time. Although the flowering periods of these species overlapped, flower visitor communities were very dissimilar among *Anthurium* species, sharing only a tiny fraction of insects that function as connectors among species in the network. The partition of potential pollinators in a fine temporal scale occurred through the rewiring of shared flower visitors to the most abundant flowering *Anthurium* species. On the other hand, a high number of inflorescences attracted larger abundance and richness of insect visitors. Facilitation occurred almost throughout the year, while competition occurred during the flowering peak, where a particular species was the best competitor increasing the constancy of pollinators. This study highlights the role of facilitation and competition as mechanisms that together shape the use of potential pollinator resources between sympatric congeneric plant species.

Keywords Araceae · Co-flowering · Connector species · Curculionidae · Facilitation · Thysanoptera

Introduction

Reproductive success in plants with biotic pollination depends not only on floral traits but on reproductive investment, floral longevity, and the timing of flowering, all of which determine the level of synchrony with conspecific and heterospecific individuals (Conner & Rush 1996; Cardona et al. 2020; Moreno-Betancur & Cuartas-Hernández 2022). It also depends on pollinator density, activity, and foraging behavior (Rymer et al. 2005; Mu et al. 2018).

These pollinators visit multiple plant species; so, co-flowering plants compete for the services of shared pollinators (Willmer 2011; Johnson et al. 2022). The competition may occur not only through reduced visitation of flowers by pollinators but also through changes in the amount and quality of pollen dispersed (Mitchell et al. 2009). These factors can have effects on the fitness of plant species and lead to imbalances that favor one competitor over others, reducing plant coexistence (Johnson et al. 2022).

An expected evolutionary consequence of competition is the partitioning of shared resources. This partitioning reduces the negative impacts of the competition between sympatric plant species (Pianka 1973; Schoener 1983) and can be achieved: (a) through segregation of flowering over the year or growing season (Elzinga et al. 2007; Giorgis et al. 2015; Gurung et al. 2018), (b) through the partition shared pollinators' activity into finer daily timescales (Raine et al. 2007), and (c) through interspecific differences in pollinator guilds, the recruitment of exclusive pollinators, or the

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deposit of pollen on different parts of a shared pollinator's body (Armbruster et al. 1994; Ruchisansakun et al. 2016).

Regarding segregation of flowering time, this not only allows for the temporal partitioning of pollinators, but also reduces the costs of heterospecific pollen deposition or hybridization (Baack et al. 2015; Esposito et al. 2018), and functions as a mechanism of reproductive isolation between sympatric and congeneric species (*i.e*., phenological isolation) (Elzinga et al. 2007; Baack et al. 2015; Ma et al. 2016). The timing of flowering may also play a critical role in plant reproduction since this should coincide with the emergence of pollinators; otherwise, seed production could be pollen-limited (Elzinga et al. 2007; Bennet et al. 2018).

On the other hand, the coexisting plant species might be constrained to co-flower when they show similar responses to environmental signals (e.g., water availability, temperature, etc.) (Bartomeus et al. 2011; Cardoso et al. 2020), or when they are closely related and show limited divergence from ancestral flowering patterns (Wright & Calderon 1995; Mesquita-Neto et al. 2015). As a consequence of flowering periods overlap in sympatric species (*i.e*., interspecific synchronous flowering), the heterospecific flower neighbor density increases. This causes the co-flowering species to either experience competition by shared pollinators (Campbell 1985; Stone et al. 1998) or pollinator facilitation, if they attract a significantly higher number and diversity of pollinators (Johnson et al. 2003), leading to a reduction or increment of reproductive success, respectively (Yang et al. 2007; Grab et al. 2017; Gurung et al. 2018).

In mountain forests in the state of Antioquia, Colombia, several species of *Anthurium* genus grow sympatrically, showing high variation in population abundance (Gómez-Murillo & Cuartas-Hernández 2016; Benavides et al. 2015). The genus *Anthurium* Schott is the largest genera within the Araceae family and contributes significantly to herbaceous/epiphytic biodiversity and biomass in the neotropics (Croat 2015). *Anthurium* species display an enormous variation in growth habit, color, and size of inflorescences (Mayo et al. 1997). Particularly, in the Parque Arví Reserve, ten *Anthurium* species grow in the understory. The Reserve is in the peri-urban area of Medellin, a city which has been transformed by human activity, and has experienced forest fragmentation, pine plantations, and urbanization (Colorado-Zuluaga et al. 2017). There, native forests and pine plantations present differences in vegetation structure and composition, and in abiotic conditions. The latter might influence not only the patterns of flowering of understory herbs but also the composition of insect flower visitor assemblages and their functional roles (Olesen et al. 2007). In fact, multispecies *Anthurium* assemblages commonly co-flower in mountain tropical forests and share some flower visitors (Gómez-Murillo & Cuartas-Hernández 2016). However, little is known about the pollination systems, the reproductive biology, and the spatial and temporal scale at which abiotic and biotic factors operate on these interactions and on the structure of *Anthurium*—flower visitor networks (Hartley & Gibernau 2019).

If co-flowering *Anthurium* species do compete for shared pollinators, we thus hypothesize that (a) temporal segregation in flowering time among species (*i.e*., peaks of flowering to be significantly spaced across species through the year) (Pleasants 1980; Minckley et al. 1994; Waser 1983), and (b) temporal partitioning of shared pollinators (Armbruster et al. 1994; Raine et al. 2007) will be mechanisms operating to reduce competition between these congeneric plant species.

To analyze the relationship between co-flowering sympatric *Anthurium* species and their flower insect visitor assemblages through time in the Parque Arví, we examined the annual patterns of flowering and tested for differences in the level of flowering synchrony, and the spatial and temporal variation in the composition of insect flower visitor assemblages in seven *Anthurium* species, based on records of visits every two weeks in Native and Pine forests. We also evaluated the potential for self-fertilization of each *Anthurium* species to determine the level of dependence on pollinators for seed production and the temporal reproductive isolation among co-flowering species. In addition, we described the structure of the *Anthurium*—flower visitor network in each forest type and the plant and insect functional roles within the network. In doing this, we addressed the following questions: (1) Do temporal flowering patterns overlap among *Anthurium* species? (2) What is the level of intra/interspecific flowering synchrony? (3) Is there a facilitative interaction between *Anthurium* species that increases floral visitors (*i.e., potential pollinators)? (4) Does the functional role of *Anthurium* and flower visitor species within the network interaction change spatially (*i.e. among forest types)? We considered that such local-scale detailed studies would help to better understand the nature of plant–flower visitor interactions and their role in the coexistence mechanisms of closely related species in ecologically realistic scenarios.

Materials and methods

Study site

This study was performed in Parque Arví, an area within the Río Nare Reserve, in the Central Mountain Range of Santa Elena, in Medellín, Colombia (6° 15′ 56″ N, 75° 29′ 49″ W). This Reserve comprises an area of 1.761 hectares and has been transformed by anthropogenic activities. The Reserve covers an elevation gradient from 2400 to 2600 m.a.s.l. and has a mean annual temperature of 14 °C (range = 5–28.5 °C). Precipitation exhibits a

bimodal pattern with two rainy periods (March–May and June–August) and two dry periods (Corantioquia 1999). The area presents a mosaic of native forests, pine plantations, orchards, and urban development (Colorado-Zuluaga et al. 2017). The prevailing forest covers in the area are native mountain forests dominated by *Quercus humboldtii* with several vegetation strata, and pine plantations dominated by *Pinus patula,* with two vegetation strata: Pine forming the dosel; and herbaceous plants, in which *Anthurium* is dominant, forming the understory. Both forest types are different in the abiotic environment (*i.e.*, light intensity), which might influence the flowering patterns of the understory plants.

For the purpose of this study, we established a sampling site in each vegetation cover type (Native and Pine forests). Each site included six *Anthurium* species. These sites were selected based on (a) high abundance of *Anthurium* which allowed to observe insect visits to inflorescences, (b) the fact that the area was free from tourist activities, which meant there was no damage to the studied plants, and, (c) easy access. The sites were 1 km apart from each other.

Study system

The genus *Anthurium* belongs to the Araceae family, is strictly neotropical, and is distributed from southern Mexico to northern Argentina. It is the most species-rich genus of all aroids (ca. 1690 species) and the most conspicuous genus in the understory of montane and lowland rain forests (Croat 2015; Mayo et al. 1997). It displays an enormous variation in leaf morphology, growth habit, leaf venation pattern, and size and color of inflorescences, which consist of one cylindrical spadix with protogynous bisexual flowers organized in spirals and a subtended bract called the spathe (Mayo et al. 1997). Besides, it presents a rewarding mutualism with its pollinators (Chartier et al. 2014). These rewards are varied and can be spadix exudates, pollen, or fragrant oils. Despite the immense diversity and the ecological importance that it has in Neotropical forests, the pollination of the genus *Anthurium* remains largely understudied (Hartley & Gibernau 2019).

In the Parque Arví Reserve, where this study was conducted, there are 10 *Anthurium* species (Benavides et al. 2015). The species chosen for the study belong to different sections within the *Anthurium* genus: *A. bogotense*, *A. caramantae* (Cardiolonchium section), *A. caucanum* (Tetraspermium section), *A. cupreum*, *A. longegeniculatum*, *A. microspadix* (Xyalophyllum section), and *A. yarumalense* (Calomystrium section) (Croat & Scheffer 1983). These species differ in plant size, and in inflorescence and infructescence size, color, and aroma (Supplemental Table S1).

Sampling of plant–flower visitor interactions

To carry out the sampling of interactions among inflorescences and insects, one transect of 100×4 m was drawn in Native and Pine forests. Each transect was divided into ten quadrats of 10×4 m, which were randomly sampled in the morning and the afternoon. The sampling of insects visiting inflorescences was performed in each forest from 10:00 to 16:00 h. This period of observation was defined because preliminary records indicated that flower visitors were uncommon before and after those hours. Once determined, the period of observation was divided into 20-min intervals, for a total of 18 intervals per day. The sampling was performed for two consecutive days, one day on each site (Native and Pine forests), and two people per quadrat recorded the interactions. Samplings of open inflorescences of each *Anthurium* species and the insects visiting those inflorescences were performed once every two weeks from August 2020 to August 2021 in each forest type. In total, 864 samples of 20-min interval/quadrat (18 observation periods $\times$ 2 days $\times$ 24 samplings) and 288 h of observation were recorded. The complete sampling period included rainy and dry months, which allowed us to evaluate the effect of precipitation on the composition of the flowering *Anthurium* and flower visitor assemblages.

Interactions were thought to take place when an insect (hereafter flower visitor) visiting an inflorescence contacted the reproductive structures of flowers, regardless of its efficiency as a pollen vector. Most insects were too minute to be identified at a glance, thus, they were collected and deposited in Eppendorf tubes with alcohol 70% for later identification. The insects were identified at the family level, and when it was possible, they were identified to genera. Insects were assigned to morphospecies for the subsequent analyses. Vouchers were deposited at the Entomological Collection of the Universidad de Antioquia (CEUA).

Pooled samples from each sampling and for each quadrat of flowering *Anthurium* and visiting insect species were used as samples of local diversity per forest type. The abundance and richness S (*i.e.*, the total number of species in the sample) of visiting insect species were calculated for each *Anthurium* species, sampling, and forest type.

The differences in insect flower visitor richness among *Anthurium* species were evaluated based on the abundance records of 24 samplings performed during the sampling year using the rarefaction/extrapolation analysis method of the iNEXT package called by R (Hsieh et al. 2016). This method permits to compare the richness of insect flower visitors of different assemblages (*i.e., Anthurium* species) when sample sizes of the assemblages are different. It estimates confidence intervals (95%) for richness estimates for different sample sizes; thus, two assemblages are considered to have significantly different richness when their confidence

intervals do not overlap (Chao et al. 2014). Although in our study the sampling effort was equal for all Anthurium species in terms of sampled area and time, the number of inflorescences from which insects were sampled was variable probably because *Anthurium* species have different densities of individuals as a result of their different competitive abilities in each forest type.

Flowering phenology and intra/interspecific synchrony

In each transect, every individual *Anthurium* was marked, and open inflorescences were counted at each visit. Each individual of these species produces several inflorescences during the flowering period; however, only one inflorescence is open at one time. Also, each individual plant of each *Anthurium* species was censused within each sampling quadrat to estimate population size. Given that flowering in mountain forests does not present a discrete seasonal flowering period and is almost continuous for most *Anthurium* species throughout the year, it was not possible to identify the onset or duration of flowering. Nonetheless, it was possible to determine the peak of flowering (Giorgis et al. 2015).

The intraspecific synchrony was calculated as the percentage of individuals of the total population that was flowering on the same sampling date in each quadrat. The event was considered asynchronous when 20% or fewer individuals bloomed at the same time. It was considered to have a low synchrony when between 21 and 60% of the population flowered simultaneously, and it was considered to have a high synchrony when more than 60% of the individuals flowered on a specific sampling date (Benckey & Morellato 2002). In addition, the strength of temporal reproductive isolation due to flowering phenology (*i.e.*, asynchrony) between each pair of *Anthurium* species for each forest type was estimated (Martin & Willis 2007).

Given that the variation in the vegetation cover could potentially result in microclimatic differences among sampling sites, which might influence flowering timing in *Anthurium*, precipitation and light intensity were measured in each forest type. The amount of precipitation was recorded once every two weeks and the mean light intensity was obtained based on the illuminance measures in each of the ten quadrats on each site, assuming there were low changes in the vegetation cover through time due to the protected status of the Reserve.

Finally, the potential of self-pollination in 10 inflorescences of each *Anthurium* species on each site was evaluated. The inflorescences were covered with a fine mesh bag prior to the spathe opening to exclude pollinators. They were monitored until they formed infructescences or until they were rotten. A species was considered to be potentially self-pollinating if at least one inflorescence had set fruit (Chouteau et al. 2008).

Similarity between insect flower visitor communities

To assess the dissimilarity of insect visitor species composition between each pair of *Anthurium* species, samplings, and forest types, the Bray–Curtis dissimilarity measure (×100) was estimated on abundance matrices. This dissimilarity is bound between zero and one and reaches its maximum value when there are no shared species between two compared communities. Also, a SIMPER (Similarity Percentage) analysis which allows the detection of shared and exclusive insect visitors to each *Anthurium* species in each sampling was performed using PAST Software (Paleontological Statistic software v. 2.12) (Hammer 2011). Finally, a dendrogram was built based on the similarity in flower visitor composition between *Anthurium* species.

Network analysis and species functional roles

To conduct a network analysis, a cumulative interaction *Anthurium*—flower visitor matrix was built for the Native and Pine forests pooling interactions recorded in 24 samplings. Then, the modularity and nestedness of each network were estimated (Felix et al. 2022). Also, the degree, interaction strength, specialization (d') (Bluethgen et al. 2006), and functional roles of each species within the network were evaluated (Olesen et al. 2007). In modular networks, this functional role is defined by the values of two parameters, c (*i.e.*, among-module connectivity: a measure of how connected a species is to all modules in the network) and z (*i.e.*, within-module degree: the number of links of a species to other species within a module). These parameters group species into peripherals, connectors, module hubs, and network hubs (Olesen et al. 2007). We used the Bipartite package (Dormann et al. 2009) called by R to perform the network analysis and the Circlize package (Gu et al. 2014) called by R to draw the chord diagrams of the network.

Data analysis

The goodness of fit to a normal distribution was evaluated for each variable using a Shapiro–Wilk test. The *Anthurium* and insect species abundance and richness were related to the precipitation in each sampling date and the mean illuminance per site using linear regressions. A *t* test was also performed to investigate whether precipitation and illuminance differed between sites.

To evaluate the interspecific synchrony among *Anthurium* species, the counts of inflorescences per species in the ten quadrats on each forest/sampling were added, and the

whole sampling period (one year) was transformed into a Julian date format. To test whether the time (Julian days) when the flowering peak of each *Anthurium* species (*i.e.*, the highest number of open inflorescences of each species in a sampling) was significantly different among species, a Kruskal–Wallis test was used, since variables did not fulfill the normality or homoscedasticity criterion. In addition, an HSD Tukey test was used to evaluate whether the time when flowering peak occurred was different among pairs of *Anthurium* species in the community (Giorgis et al. 2015).

To evaluate whether flower visitor abundance and richness differed among low, medium, and high abundance of *Anthurium* open inflorescences, a Tukey test was used (Zar 1999). Considering that the number of open inflorescences was very different among forest types, abundance categories were defined based on the difference between the maximum and minimum value (*i.e.*, range) observed in every sampling and the abundance range was divided into three categories that represent the flowering dynamics in each forest type (Native forest: low 0–6, Medium 7–12, High ≥ 13 and Pine forest: low 0–14, Medium 15–27, High ≥ 27). Also, an HSD Tukey test was used to evaluate differences in abundance and richness of flower visitors across flowering abundance categories (Zar 1999). Finally, the relationship between the degree, interaction strength, specialization (*d'*), and the functional role of each species estimated by *c* and *z* values with its abundance in each forest type was evaluated using linear regressions. All analyses were performed using R software (R Development Core Team 2018). The data that support the findings of this study are available from the corresponding author, upon reasonable request.

Results

Anthurium communities

Anthurium communities showed great differences in species abundance and composition among forest types. First, in the Native forest, the total abundance of *Anthurium* individuals was six times lower ($N=156$) than in the Pine forest ($N=941$), and the total number of flowering individuals was four times lower (Native $N=1166$, Pine $N=4597$). Also, in the Native forest, seven species of *Anthurium* were recorded, while in the Pine forest, *A. microspadix* was not present. Second, *A. cupreum* was the dominant species in both sites followed by *A. microspadix* and *A. longegeniculatum* in the Native forest, and by *A. caucanum* and *A. bogotense* in the Pine forest (Table 1).

With respect to the environmental variables, the accumulated precipitation every two weeks was three times higher in the Native forest than in the Pine forest ($t=2.215$, $P=0.037$). However, average illuminance showed the opposite trend ($t=4.679$, $P=0.0001$). In the Pine forest, a carpet of *Anthurium* dominated the understory, while in the Native forest there were other herbs or shrubs belonging to Rubiaceae and Melastomataceae, two typical plant families of tropical mountain forest (Idarraga-Piedrahita et al. 2011) which presented a very sporadic flowering in low abundance.

Flowering phenology and intra/interspecific synchrony

In both study sites, a constant and simultaneous flowering was evidenced and the flowering peak of each *Anthurium* species was significantly temporarily segregated, as indicated by the results of the Tukey test (Fig. 1; Table 2). The average values of the intraspecific flowering synchrony of each *Anthurium* species showed that in general, the species had asynchronous flowering events (less than 20%), regardless of their population abundance, with few exceptions of low synchrony, as is the case of populations of *A. yarumalense* (30%) and *A. microspadix* (34%) in the Native forest (Supplemental Table S2). Moreover, reproductive isolation values (*RI*) were higher than 70% in most of the comparisons between most pairs of *Anthurium* species which suggests that flowering phenology may function as a reproductive isolation barrier among the *Anthurium* species studied. In

Table 1 Total number individuals, mean number of flowering individuals, and standard deviation (SD) of each *Anthurium* species through the year in Native and Pine forests, and Kruskal–Wallis test results for comparison between the mean abundance of flowering individuals from 24 samplings in the Native and the Pine forests

| *Anthurium* Species	Abundance						Kruskal–Wallis test		
	Native forest			Pine forest			χ^2	DF	*P*
	Total	Mean	SD	Total	Mean	SD			
A. bogotense	9	2	1.42	71	10	4.66	33.89	1	< 0.0001
A. caramantae	2	0.33	0.70	15	2	1.21	22.28	1	< 0.0001
A. caucanum	5	–	–	150	38	12.38	40.31	1	–
A. cupreum	40	10	4.56	693	132	49.64	35.32	1	< 0.0001
A. longegeniculatum	36	10	2.62	9	2	1.06	35.55	1	< 0.0001
A. microspadix	38	22	5.58	0	–	–	40.35	1	–
A. yarumalense	26	8	2.29	3	3	1.69	32.27	1	< 0.0001
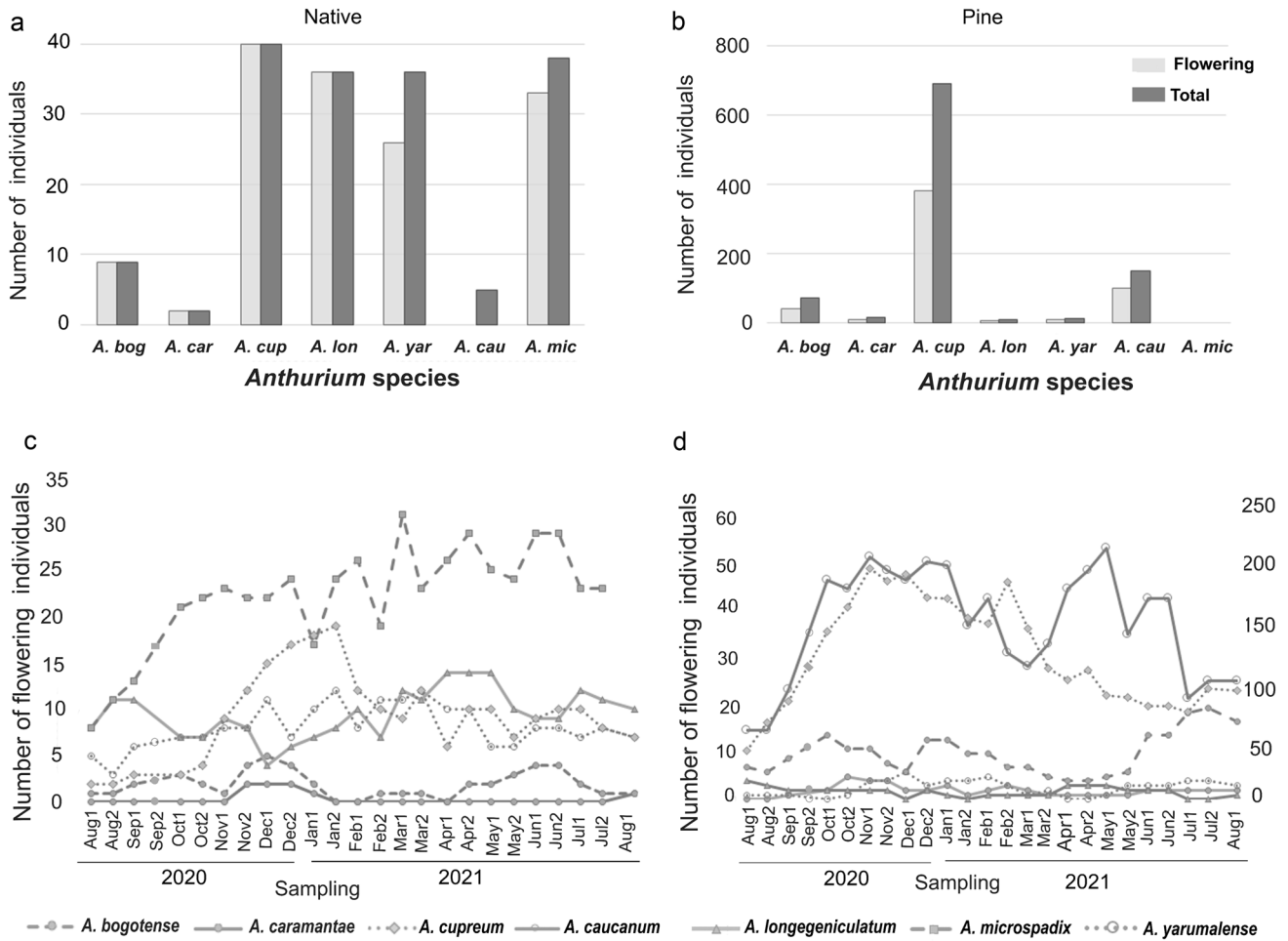
Fig. 1 Flowering phenology of seven *Anthurium* species in Parque Arví (Antioquia, Colombia) in Native and Pine forest. **a** Population size and total number of flowering individuals of each *Anthurium* species during the whole sampling period in Native forest, and **b** in Pine forest. Note that the Y-axes have different scales. **c** Number of flowering individuals in each of the 25 samplings performed every two weeks from August 2020 to August 2021 in the Native forest and **d** in the Pine forest. Due to the great differences in the number of flowering individuals between *Anthurium* species in the Pine forest, a second Y-axis in panel d was added, and it represents the number of flowering individuals for *A. cupreum* and *A. caucanum*

Table 2 Post hoc Tukey test results of the comparison of flowering peaks (Julian days) between pairs of *Anthurium* species in the Native and the Pine forests

Species	A. bogotense	A. caramantae	A. cupreum	A. longegeniculatum	A. yarumalense
Native					
A. caramantae	$3.6*10^{-5}$				
A. cupreum	$1.5*10^{-7}$	$1.3*10^{-8}$			
A. longegeniculatum	$3.7*10^{-8}$	$1.3*10^{-8}$	0.76		
A. yarumalense	$6.1*10^{-8}$	$1.3*10^{-8}$	0.59	0.19	
A. microspadix	$2.9*10^{-8}$	$1.3*10^{-8}$	$1.5*10^{-7}$	$8.2*10^{-8}$	$3.9*10^{-8}$
Pine					
A. caramantae	$4*10^{-8}$				
A. cupreum	$3.8*10^{-8}$	$3.80*10^{-8}$			
A. longegeniculatum	$3.8*10^{-8}$	1	$3.8*10^{-8}$		
A. yarumalense	$7*10^{-8}$	1	$3.8*10^{-8}$	$5.5*10^{-1}$	
A. caucanum	$3.8*10^{-8}$	$3.80*10^{-8}$	$7*10^{-8}$	$3.8*10^{-8}$	$3.8*10^{-8}$

The values in the table are probabilities. The flowering peaks differ significantly when $P < 0.05$

the case of *A. caramantae*, the estimated reproductive isolation with all other *Anthurium species* was low (33%) in the Native forest; however, due to the low number of individuals of this species, this result should be interpreted prudently (Supplemental Table S3).

The total number of flowering *Anthurium* individuals per sampling in the Native forest did not show any relationship with precipitation levels ($R^2 = 0.02$, $\beta = -0.02$, $F = 0.47$, $P = 0.4900$). In contrast, in the Pine forest, the number of flowering individuals increased with precipitation ($R^2 = 0.20$, $\beta = 0.95$, $F = 5.85$, $P = 0.0200$). Besides, the total number of flowering individuals per quadrat did not show a relationship with illuminance in any site. In general, these trends were observed when analyzing individual species, with some exceptions (Supplemental Table S4). Similarly, the abundance and richness of visiting insects in each sampling or quadrat did not depend on the two-week period average rainfall in either Native or Pine forests, or on the average illuminance of each transect (Supplemental Table S4). Regarding the bagged inflorescences of each *Anthurium* species, none of these produced infructescence, which indicates that seed production depends on pollinators.

Insect flower visitor communities

A total of 2059 individual insects of 123 morphospecies visiting the inflorescences of *Anthurium* were recorded. The most abundant orders were Thysanoptera (63%), with *Frankliniella* as the only genus of this order; Hymenoptera (11%), with Formicidae and Platygastridae as the most abundant families; Coleoptera (9%) with Curculionidae as the most abundant family; and Diptera (5%), with Drosophilidae as the most abundant family. The remaining 12% of the insect morphospecies was composed of individuals of other insect orders.

The abundance and composition of insect visitor assemblages differed among forest types (Pine forest: N = 1471, Native forest: N = 659, Bray–Curtis dissimilarity = 0.49) and among samplings in both study sites (~40%), with some exceptions of higher values (Supplemental Table S5). It also differed among *Anthurium* species. In both Native and Pine forest, *A. yarumalense* and *A. cupreum* had a higher abundance of insects visiting their inflorescences: 328 and 1257 insect individuals, respectively. Based on the rarefaction/extrapolation analysis, in the Native forest, *A. caramantae* showed a significantly lower insect richness compared to the other *Anthurium* species. In the Pine forest, *A. cupreum* had a higher richness than the other *Anthurium* species only when insect abundance was higher than 400 individuals (Supplemental Fig. S1, Table S6).

The composition of flower visitor assemblages showed high levels of dissimilarity (> 70%) among *Anthurium*
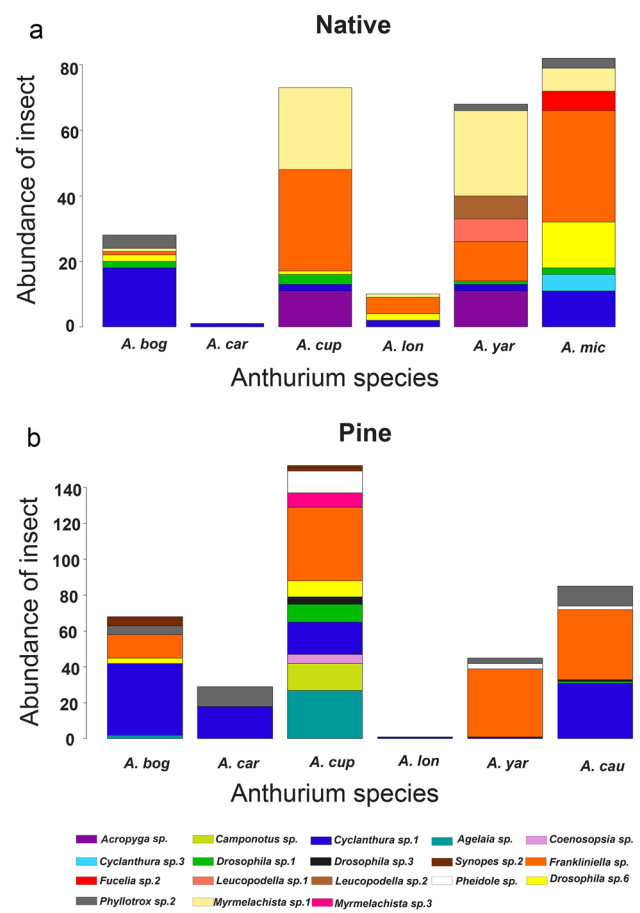

Fig. 2 Abundance and composition of flower visitor assemblages for each *Anthurium* species in **a** Native forest and **b** Pine forest. Only insects with an abundance equal to or greater than 5 individuals were included in the figure. Each color represents an insect morphospecies

species for most paired comparisons (Fig. 2; Supplemental Table S5, Table S6). However, three groups of *Anthurium* species which were related to spadix color and size were obtained: dark and medium size spadix (*A. bogotense*, *A. caucanum* and *A. caramantae*), green and small spadix (*A. longegeniculatum* and *A. microspadix*), and reddish/green and large spadix (*A. cupreum* and *A. yarumalense*) (Supplemental Fig. S2).

The shared fraction of insect visitors was variable among pairs of *Anthurium* species (0–0.48%) and was composed mainly of the most abundant morphospecies which visited between four and six species of *Anthurium* in each forest type (Fig. 2). In the Native forest, those species were *Cyclanthura sp1, Frankliniella,* and *Myrmelachista sp.1*. In the Pine forest, they were *Cyclanthura sp.1, Frankliniella,* and *Phyllotrox sp.2*. Some of these common insect morphospecies were observed shifting to the most abundant *Anthurium* flowering species in consecutive samplings (Supplemental Fig. S3).

Relationship between number of flowering individuals and insect visitor abundance and richness

In the Native forest, there was an increase in the abundance of flower visitors at medium floral abundance, and an increase in richness of visitors at medium and high floral abundance (Abundance floral visitor: $\chi^2 = 17.69$, $P = 0.0001$; Richness floral visitor: $\chi^2 = 14.27$, $P = 0.0007$, Supplemental Table S7). Contrastingly, in the Pine forest, the increase in both the abundance and richness of flower visitors occurred at medium or high floral abundance (Abundance floral visitor: $\chi^2 = 15.34$, $P = 0.0004$; Richness floral visitor: $\chi^2 = 14.05$, $P = 0.0008$) (Fig. 3; Supplemental Table S7).

Network structure and functional role of species

A significant modular structure was detected in *Anthurium*—flower visitor networks in both forests. One or two *Anthurium* species formed a module, which suggests that certain insect morphospecies visit predominantly one *Anthurium* species and few insects function as connectors among species (modules). The species degree and interaction strength increased with species abundance in the Pine forest but not in the Native forest. The species connectivity within and between modules (z and c values) was positively related to species abundance, except the z value in the Pine forest (Supplemental Table S8). The connector species were *Frankliniella,* in the Native forest; and *Cyclanthura sp.1,* in the Pine forest (Fig. 4; Supplemental Table S8). These species functioned as non-hubs connectors ($z < 2.5$) with links across several modules ($c > 0.62$). The rest of species were peripheral ($c \leq 0.62$), with most links inside their own module (Olesen et al. 2007).
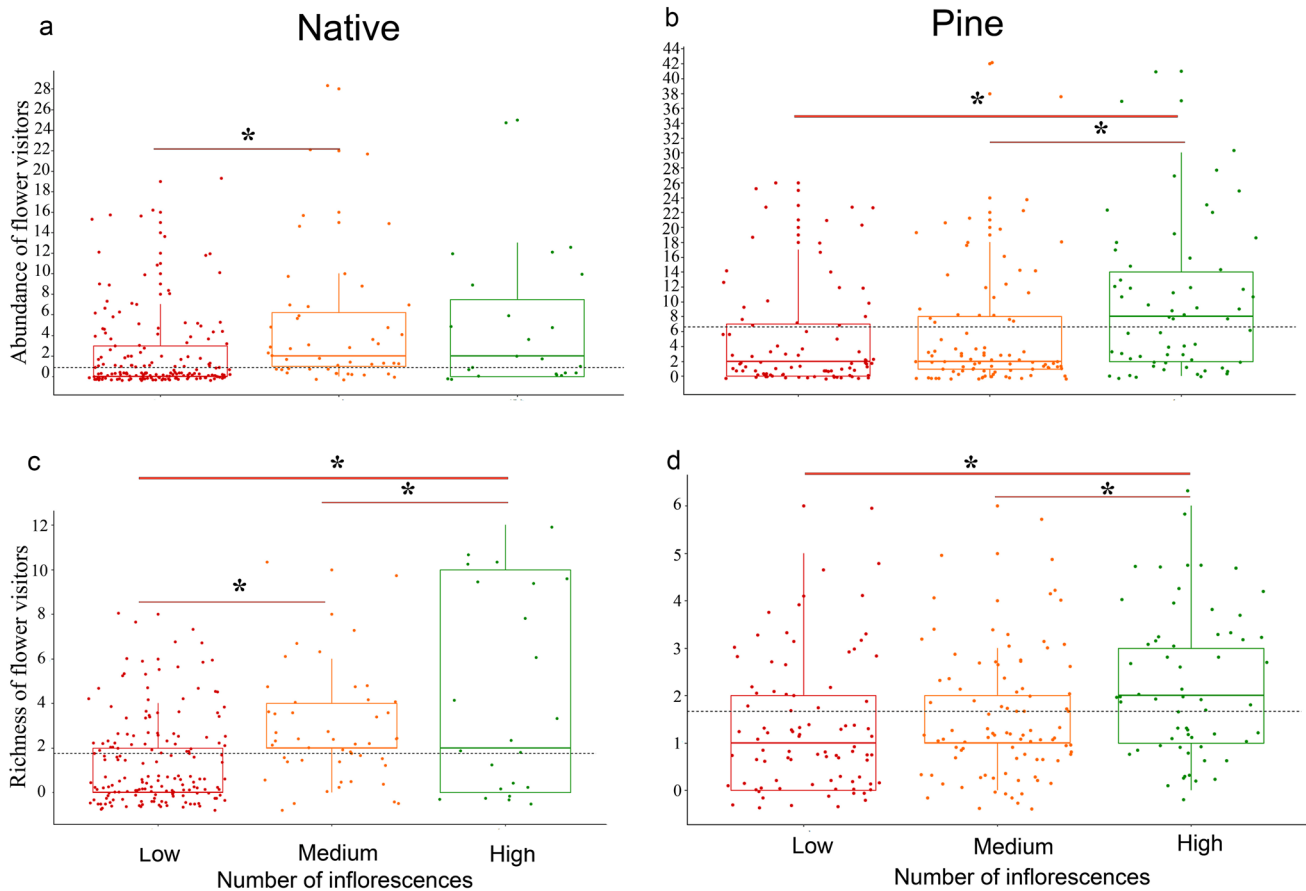

Fig. 3 Abundance of floral visitor assemblages to low, medium, and high abundance categories of flowering *Anthurium* individuals **a** in Native forest and **b** in Pine forest. Richness of flower visitor assemblages to low, medium, and high abundance categories of flowering *Anthurium* individuals **c** in Native forest and **d** Pine forest. Dotted lines in each panel represent the average abundance and richness of flower visitors in each forest type, and asterisks represent significant statistical differences among flowering abundance categories

Fig. 4 *Anthurium*—flower visitor networks for **a** Native and **b** Pine forest. Insect orders and *Anthurium* species are represented by different colors
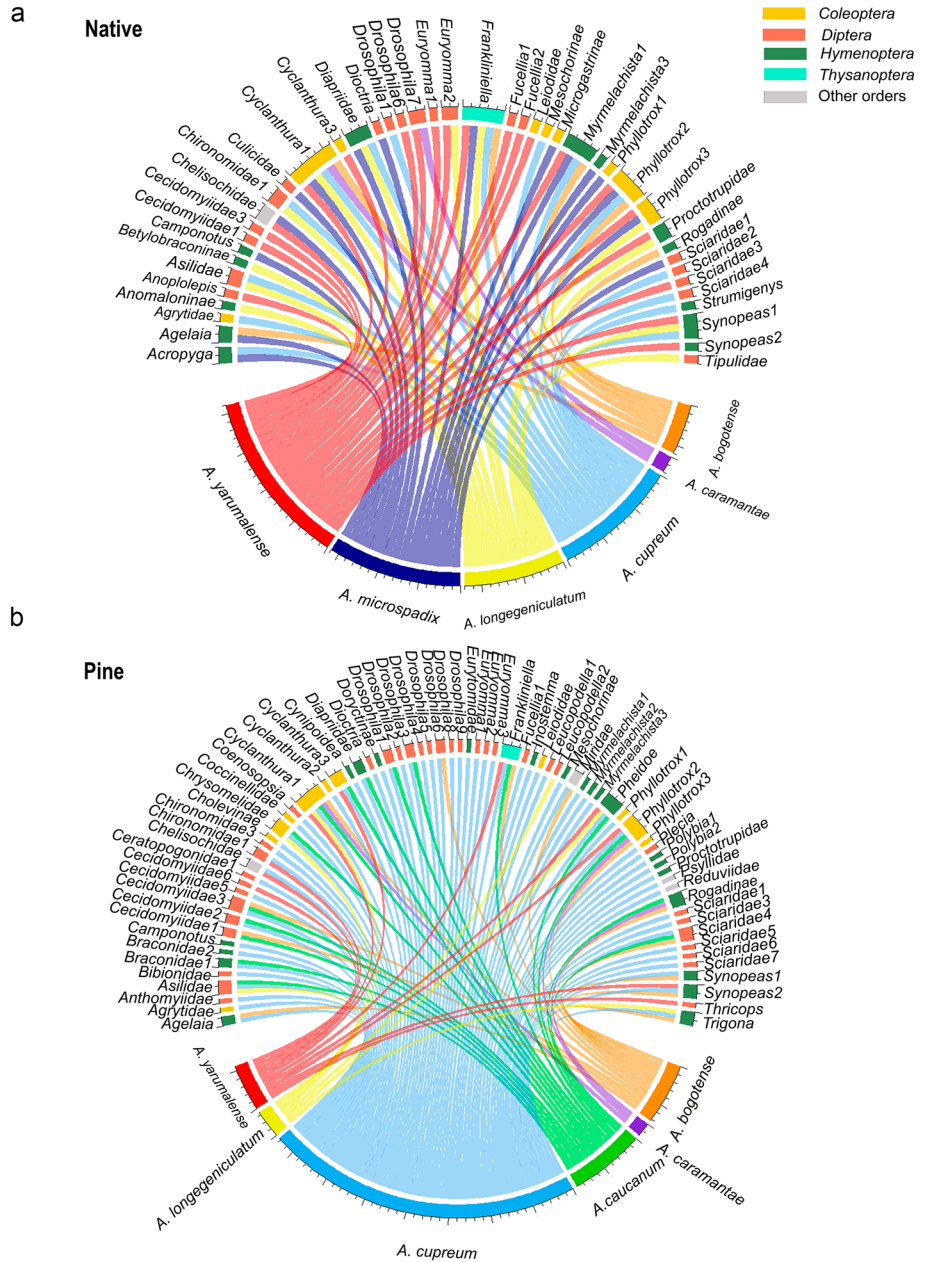
Discussion

Results from the study of Native and Pine forests showed differences in composition and abundance of *Anthurium* species, which reflected the contrasting environmental conditions and successional patterns in both forest types. As a consequence of these contrasting conditions, insect flower visitor communities also showed differences. However, a high resemblance in processes such as *Anthurium* flowering patterns and the temporal organization of interactions with insects visiting inflorescences was observed in both forest types.

Another important finding was that low precipitation and high illuminance promoted flowering in most *Anthurium* species, and therefore, the intensity of flowering was higher in the Pine forest than in the Native forest. However, the flowering in *A. longegeniculatum*, *A. yarumalense*, and *A. microspadix* was high in the Native forest where the illuminance intensity was low. These differences in flowering intensities suggest that signals that trigger flowering differ among species within the same genus and that the species flowering patterns obey to specific environmental cues, probably due to differences in evolutionary history, life strategies, and ecological adaptations (Kochmer & Handel [1986]).

The results also revealed the occurrence of temporal segregation of flowering peaks and the high dissimilarity in the assemblage of flower visitors among *Anthurium* species in both forest types which might function to reduce competition. Moreover, they indicate that the continuous and overlapping flowering pattern of most *Anthurium* species forms a more attractive pool of flower resources for insects visiting flowers all year, which might function a facilitative mechanism of pollination through overlapping flowering. Finally, they evidenced that the differential use of shared flower visitors on fine time scales reduces competition in coexisting *Anthurium* species. Together, these strategies ensure the permanence of the flower visitor populations and the reproductive isolation among the *Anthurium* species.

In general, the study established that the flowering of *Anthurium* species can be categorized as continual according to Newstrom et al.'s (1994) classification, which means that there is a continuous flowering throughout the year, interrupted only by a few short breaks. This continuous flowering of several *Anthurium* species leads to overlapping flowering phenologies, with low levels of intraspecific synchrony and significant temporal segregation of the flowering peaks.

The above-mentioned phenomenon, called partial asynchrony, allows temporary segregation in the use of a shared resource such as pollinators, and reduces competition (Henderson et al. 2000; Husband & Sabara 2004; Gurung et al. 2018). The temporal segregation of flowering peaks may also limit the transfer of heterospecific pollen and act as an effective reproductive isolation mechanism between pairs of *Anthurium* species (Martin & Willis 2007). Besides, each *Anthurium* species may become a stronger competitor during its flowering peak, increasing the probability of massive and successful pollination due to a visitor moving sequentially and reliably among conspecific inflorescences (Willmer 2011; Gurung et al. 2018). Furthermore, continuous and asynchronous flowering promotes outcrossing in plant species with temporarily separated sexual phases (*i.e.*, dichogamy) and self-incompatibility, such as *Anthurium.* This is due to the fact that it prevents all individuals within the population from being in the same sexual phase simultaneously and increases the probability of outcrossing by forcing pollinators to disperse pollen between plants (Rathcke & Loncey 1985; Bronstein et al. 1990).

At the same time, intraspecific asynchronous flowering events result in low flower density, making it hard to maintain pollinator assemblages and lowering the chances of reproductive success, as flower visitors leave patches when resources are scarce (Augspurger 1981). In this community, this might be prevented due to the co-flowering of several *Anthurium* species over time, which guarantees permanent resources for the maintenance of potential pollinators that depend on the flowering of *Anthurium* for the permanence of their populations and ecological functions. This co-flowering of *Anthurium* species may be related to a facilitation mechanism evidenced by the significant increase in the abundance and richness of insect visitors when the density of open inflorescences was high. Thus, a continuous and aggregated floral display in a specific time attracted more potential pollinators from more different taxa, which might improve the reproductive success of the coexisting *Anthurium* species. These mechanisms allowed the species with low population density (*i.e.,* rare) and low investment in flower production to be visited by pollinators and reproduce (*i.e.*, increase in fitness) on account of other flowering species (Valladares et al. 2015). Each *Anthurium* species contributed throughout the year to the maintenance of the floral display in higher or lower proportion. For example, *A. cupreum* invested in more and larger inflorescences compared to the other *Anthurium* species in the community which present medium to small inflorescences in lower numbers. In consequence, the fitness gain could be asymmetric among *Anthurium* species since some species obtain higher benefits (*i.e.*, insect visits), which mitigates the adverse effects of low density for pollination (Moeller 2004). Evidence of this is, *A. caramantae,* a species with high ornamental value which has been extracted from the forest, leading to a very small population size, small number of inflorescences, and low probability of insect visits. However, it received few visits when co-flowering with other *Anthurium* species. Such great differences in *Anthurium* species densities have also been recorded in other mountain forests in the state of Antioquia, where *A. cupreum* was also dominant (Gómez-Murillo & Cuartas-Hernández 2016).

We hypothesized that facilitation for pollination services could be a mechanism to ensure seed production in *Anthurium* species, which in general, present low reproductive success, related to an inefficient pollination (Uemura et al. 1993; Moreno-Betancur & Cuartas-Hernández 2022), or short viability of pollen grains (Albre & Gibernau 2008). Although we did not examine fruit or seed production, which limits our conclusions about the facilitation as a mechanism operating among the studied *Anthurium* species, the shown increase in abundance and richness of flower visitors when there were more available flower resources is a first insight for this assumption. The reproductive success of *Anthurium* species is a matter to research in the future. Most studies describing the mechanism of facilitation for pollination in congeneric species have not associated such mechanism with fitness estimates (Gross et al. 2000; Gurung et al. 2018; Bergamo et al. 2020). In studies on communities of congeneric species of *Clarkia* and grassland plant species, for example, facilitation has been described based on the increase on pollen deposition and number of pollen tubes as estimates of fitness related to the presence of multiple congeners or to flowering synchrony and floral trait similarity, respectively (Moeller et al. 2004, Bergamo et al. 2020). The positive

effect on the abundance and diversity of flowers on pollinator visitation in congeneric species of *Primula* in the Himalayas was considered an argument for pollination facilitation, as in our case (Gurung et al. 2018). Facilitation has also been described in studies on species from different genus with different floral morphologies (Gross et al. 2000, Ghazoul et al. 2006, Bergamo et al. 2020).

Other relevant finding of the study was that more than half of the interactions between plants and insect occurred once or twice, both in the Pine forest (79%) and the Native forest (79%), reflecting the erratic use of flower resources. However, a small fraction of interactions (12% for both forest types) were frequent and performed by four insect morphospecies (*Frankliniella, Cyclanthura* sp.1, *Myrmelachista* sp.1, *Phyllotrox* sp.2) that were the most abundant and that visited five or six *Anthurium* species throughout the year, functioning as connector species that link modules together and are thus important to network coherence. Although networks of both forest types presented modular structures, the functional role of species changed spatially. *Frankliniella* functioned as a connector species in the Native forest ($c = 0.72$, $z = 1.93$), while this role was played by *Cyclanthura* sp.1 in the Pine forest ($c = 0.67$, $z = 1.5$).

On the other hand, the interactions changed over time due to the rewiring of shared and frequent insect taxa (*i.e.,* connectors) to the most abundant flower resource in a specific sampling date, due not only to the higher availability but to more intense attraction signals of inflorescences (*i.e.*, aroma, color) (Levin & Anderson 1970; Bergamo et al. 2020).

Another interesting result finding is that the studied *Anthurium* species could be grouped into a generalist pollination syndrome (Willmer 2011) with all *Anthurium* species being visited by a diverse array of small insects representing four to five orders (Bawa et al. 1985). The generalist pollination syndrome can be related to the open morphology of inflorescences which do not limit the spectra of visitors, which has also been described for several species within the genus *Anthurium* (Díaz Jiménez et al. 2019). Although specialized relationship of some *Anthurium* species with Euglossine bees has been described in other ecosystems (Hentrich et al. 2010), we did not observe bees visiting inflorescences of the studied *Anthurium* species. Nevertheless, the differences in the composition of flower visitors among the three groups of *Anthurium* species obtained seem to be related to differences in spadix color and size. In grassland communities in Brazil, co-flowering plants possessing similar floral color flowered synchronously, and also shared pollinators. In addition, those co-flowering plants had higher fitness via joint pollinator attraction, suggesting that facilitative mechanisms act favoring flowering synchrony and trait similarity (Bergamo et al. 2020).

On the other hand, there were also certain tighter interactions between *A. cupreum – Frankliniella,* and *A.*

*bogotense—Cyclanthura sp.*1 which were constant during the year and in both forest types, highlighting the importance of small insects of Thysanoptera and Coleoptera orders as potential pollinators in *Anthurium* (Wardhaugh 2015; Sayers et al. 2019).

This study contributes to understanding the mechanisms underlying the coexistence of sympatric *Anthurium* species (Vogt 2009). Facilitation and competition seem to shape the use of floral visitor resources and operate at different temporal scales (Valladares et al. 2015). Facilitation occurs through almost the whole year, while competition occurs in a temporal recruitment window in which exogenous temporal variability (*e.g*., precipitation and illuminance intensity) determines which species is the best competitor (*i.e*., has more intense flowering) in each habitat type during specific periods, limiting the use of the resource by other species (Barot 2004). Faegri & van der Pijl (1966) called this the Arnell´s dominating flower phenomenon.

Thus, facilitation might occur through pollination service sharing in *Anthurium* species, which might be an advantageous strategy in the cold environment of the mountain forest, where plant reproduction can be limited (Valladares et al. 2015) due to low insect abundance (Blionis & Vokou 2001; Barrios et al. 2010; Cuartas-Hernández & Gómez-Murillo 2015).

Shifts from competition to facilitation have been demonstrated in stressful and milder environments highlighting the importance of positive interactions on species coexistence and maintenance of diversity in plant communities (Holmgren & Scheffer 2010; Gross et al. 2013).

Lastly, differences in insect composition in both forest types highlight the relevance of continuing the conservation efforts of several vegetation cover types resulting from different successional processes to maintain the insect diversity and ensure the pollination services in the understory plants in the Parque Arví Reserve.

Declarations

Competing interests The authors have no competing interests to declare that are relevant to the content of this article.

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