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ORIGINAL ARTICLE

Temporal organization among pollination systems in a tropical seasonal forest

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Abstract

Temporal constancy of pollination systems is essential for the maintenance of pollinators through time. Community-level assessment of flowering phenology allows understanding variations across seasons and years and the risks of decoupling flowering and pollinators' activity. We evaluated flowering patterns and temporal diversity of pollination systems in a tropical seasonal forest. We asked whether the temporal organization of flowering times differs among pollination systems; if there is a constancy of pollination systems through the year, since climate and phylogenies constraint flowering time; if there is a prevalent flowering pattern by pollination system, and if the temporal organization of pollination systems by modularity analyses is coherent with grouping by pre-defined seasons. We characterized 10 pollination systems, examined flowering strategies, climate cues and phylogenetic constraints. Pollination by large-to-medium bees dominated (49.2%), followed by diverse insects (22.1%) and flies (14.7%). The remaining systems represented 14% of species. Flowering occurred year-round for most pollination systems, predominating the seasonal flowering strategy. Flowering patterns ranged from aggregated to nested, and random. Climate affected the flowering of most pollination systems, but there was no phylogeny constraint. Modularity grouped pollination systems differently than rainfall seasonality. Contrasting the expectations of reduced temporal constancy, most systems were present year-round, facilitating the exploitation of floral resources by pollinators. Diversity of pollination systems remained constant despite climate seasonality, indicating that several factors influence the optimum flowering time for pollination in seasonally dry vegetations. Global warming may disrupt phenological patterns and the temporal organization of plant communities, a matter for future studies.

Keywords Temporal organization · Climate · Flowering strategy · Flowering patterns · Pollination systems

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Introduction

Among the explanations for the variation in diversity and level of the generalization of pollination systems are geographical location, plant life forms, taxonomic diversity, and suitability of environmental conditions for pollinator activity (Bawa 1990; Devy and Davidar 2003; Kühn et al. 2006). In addition, specific pollination systems may be more advantageous under different ecological conditions (Bawa 1990; Kessler and Krömer 2000; Phillips et al. 2020). For instance, in a study of the distribution of pollination systems among forests with a wide range of environmental conditions, insect-pollinated plants were dominant in dry forest regions, hummingbirds were more associated with high elevations and wetter habitats, and bats were more linked to humid tropical conditions (Kessler and Krömer 2000).

Furthermore, the diversity and frequency of pollination systems may have seasonal variations (Ramirez 2006; Cortés-Flores et al. 2017). Thus, the constancy of pollination systems throughout the year is expected to be more regular in aseasonal than in seasonal environments due to seasonality in flowering phenologies (Ramirez 2006; Cortés-Flores et al. 2017). The influence of seasonality on tropical seasonal forest phenology patterns has been previously reported (van Schaik et al. 1993; Wright 1996; Zimmerman et al. 2007; Morellato et al. 2013, 2016), and the rainfall and day length are considered the main drivers of flowering (Calle et al. 2010; Morellato et al. 2000, 2013, 2016; Wright and van Shaick 1994). However, past evolutionary history is another factor known to shape phenology patterns (Kochmer and Handel 1986; Staggemeier et al. 2010, 2015; Cortés-Flores et al. 2017).

Biotic interactions also influence plant phenology (Elzinga et al. 2007). For example, pollinators and seed dispersers may structure flowering and fruiting onset, duration and synchrony (Bawa et al. 1985, 1990; Cortes-Flores 2017, 2020; Frankie et al. 1974, 1975; Heithaus et al. 1975; Stiles 1977, 1978; Waser 1983). Advantages and disadvantages of shifting flowering times have been addressed from the perspective of the competition and facilitation hypotheses (Aizen and Rovere 2010; Mitchell et al. 2009; Pleasants 1983; Waser 1983; Wheelwright 1985; Staggemeier et al. 2010), a topic that recently has caught a lot of the attention of researchers (Bergamo et al. 2020). According to the former hypothesis, selection favours co-flowering species to shift their blooming times to reduce competition for pollinator services (Armbruster 1986; Armbruster et al. 1994; Feinsinger 1987; Rathcke 1983, 1988; Stone et al. 1998). On the other hand, facilitation for pollinators denotes positive interactions due to resource sharing within a plant guild (Feinsinger 1987; Rathcke 1983 and see Bergamo et al. 2020). In that sense, an aggregated blooming may enhance or facilitate pollination by increasing the conspicuousness of the floral display (Moeller 2004; Schemske 1981) and interactions within temporal modules of species (Albor et al. 2020). Either way, early studies on the temporal organization of co-occurring plant species and pollinator agents are limited to a few species or particular guilds (Augspurger 1981; Feinsinger et al. 1979; Stiles 1977, 1978, but see Heithaus 1974). The recent advances on the interplay of flowering time and pollination, evaluating the facilitation — competition — filtering hypothesis (see Sargent and Ackerly 2007), highlight the importance of taking pollination and associated plant traits into consideration to understand the assembly of plant communities. However, most research still focuses on specific communities or guilds (e.g., hummingbirds; Wolowski et al. 2017). Studies focused on temporal patterns of species sharing the same pollination system, and the seasonal variation of those systems at a whole community scale are still scarce, especially for diverse tropical forests (but see Ramirez 2005, 2006; Cortés-Flores et al. 2017).

Among the causes that may affect the extent of temporal overlap between pollination systems are the number of co-flowering species within each system, the diversity and availability of the pollination agents, and the characteristics of each pollination system (Feinsinger 1987; Ramirez 2005). Plants with different pollination systems may also display flowering strategies that meet their specific pollinator's requirements. For instance, the sequential or extended flowering displayed by plants pollinated by long-lived animals such as hummingbirds and bats has long been hypothesised to be related to the maintenance of these pollinators over time (Aizen and Rovere 2010; Aizen and Vázquez 2006; Feinsinger 1987; Rathcke 1983; Waser 1978). Ultimately, since flowering time is cued by climate, flowering patterns and strategies are likely defined by the pollination system and the integration of pollination effectiveness and reproductive success, which define flower availability and affect the community assembly. The definition of pollination systems, considering different plant traits and pollen vectors (Fenster et al. 2004), approaches the concept of pollination niches (Johnson 2010; Phillips et al. 2020), representing available niches for ecological diversification. That assumption allows a better understanding of the roles of time (phenology) and pollination interactions to the evolution, organization and diversification of plant communities. In this study, we aim to investigate the flowering phenology and the temporal organization of pollination systems in a seasonal forest in south-eastern Brazil. We describe the local diversity of the studied seasonal forest pollination systems and their flowering patterns and strategies. Specifically, we asked: (i) Does the temporal organization of flowering times differ among pollination systems? (ii) Is there a constancy of pollination systems throughout the year since the seasonal climate and phylogenies may constrain flowering times? (iii) Is there a prevalent flowering pattern by pollination system indicating biotic cues to flowering? Furthermore, are the aggregated patterns nested? (iv) Is the temporal organization of pollination systems coherent with pre-defined seasons? To that end, we compared the flowering strategies against null models to determine if phenologies within pollination systems were segregated, random or aggregated and tested for temporal nestedness in the aggregated flowering phenologies. Then, we evaluated the influence of climate and phylogeny on the flowering length and other ecological traits. Finally, we assessed seasonal variation in the diversity of pollination systems throughout the year.

Material and methods

Study site

The study was conducted at the Santa Genebra Reserve (SGR hereafter), a 250-ha remnant of semi-deciduous or seasonal forest, close to an urban area at Campinas (22°49′45″S; 47°06′33″W, 670 m.a.s.l.), São Paulo, south-eastern Brazil. The SGR includes three forest physiognomies: dominant seasonal forest, secondary forest and associated vegetation, and swamp forest (Morellato and Leitão-Filho 1996). The climate at the SGR region is seasonal, with a dry season from May to August, a wet and warm season from November to February (Supplementary Information, Fig. S1) and two transitional periods: March to April (wet-to-dry transition) and September to October (dry-to-wet transition) (Morellato 1991; Morellato and Leitão-Filho 1996). Both transitional seasons are characterized by variations in temperature and rainfall, affecting plant phenology (Morellato 1991; Morellato and Leitão-Filho 1996). The legacy climate data (30 years) used to determine the wet and dry seasons and transitional periods (Morellato and Leitão-Filho 1996) and for the period of this study (1988–1991) were obtained from Fazenda Santa Elisa meteorological station (Campinas, SP), the nearest one to the study site, belonging to the Instituto Agronômico de Campinas (IAC).

Flowering phenology and pollination systems

We report here the phenology and pollination systems of 199 plant species at the SGR seasonal forest. The flowering phenology of trees, treelets, and climbers was recorded weekly to monthly from 1988 to 1991 (Morellato 1991; Morellato and Leitão-Filho 1996). Flowering was defined as the period in which the plant species bear open flowers (Morellato et al. 1989). We grouped species into five flowering strategies (Morellato 1991; adapted from Newstrom et al. 1994a, b): (1) continuous – blooming continuously during the year (10 months or more); (2) episodic – multiple blooming events during the year, separated by non-flowering phases of variable length; (3) brief – short flowerings during a few days up to one month; (4) seasonal – blooming lasts more than one up to four months associated to one season or the transitional periods between two seasons; and (5) extended – blooming of more than four months, associated to more than one season (Supplementary Information, Table S1).

Plant species were characterized by their pollination systems according to the flower morphology and floral biology (Faegri and Pijl 1979; Jones and Little 1983; Real 1983). The flower visitors and their behaviour were observed during the phenological records. On additional days, at least the large taxonomic category (e.g., fly, bee, butterflies, etc.) was noted and whether the visitor behaviour would promote pollen transfer and pollination (Monteiro et al. 2021). The definition of pollination systems, following Bawa et al. (1985), Ollerton et al. (2019) and Monteiro et al. (2021), considered several plant traits and pollen vectors (Fenster et al. 2004), and approaches the concept of pollination niche (Johnson 2010; Phillips et al. 2020). We screened the literature for studies on pollination biology for all the species studied at the SGR to confirm their pollination systems and support the system determination for those few species we were unable to assess based on our field observations (Supplementary Information, Table S1). We kept studies conducted at the SGR or, when absent, those conducted preferably with the same species and vegetation type to confirm the main pollinator and pollination system. Flower characteristics such as colour, smell, the position of flower elements, symmetry, reward to pollinators, time of anthesis, and receptivity of the stigma were recorded by the authors or from the literature survey (Supplementary Information, Table S1) and taken into account to determine the pollination system of each plant species (Morellato 1991; Genini 2011).

The plant species were grouped into the following pollination systems (after Bawa et al. 1985; Ollerton et al. 2019): bats, hummingbirds, large-to-medium bees (larger than 10 mm), small bees (up to 10 mm), beetles, butterflies, moths, flies, wasps and diverse insects (i.e. small bees, butterflies, moths and beetles, wasps, true bugs and other insects), this latter category being composed of agents that visit open flowers with easy access to resources or are not specialized to visit flowers (adapted from Bawa et al. 1985; following Monteiro et al. 2021). Plant species that had a secondary pollinator system (senso Rosas-Guerrero et al. 2014) based on local observation and flower morphology (Supplementary Information, Table S1) were entered in more than one category in our calculations of the proportions of pollination systems.

Niche temporal patterns of pollination systems

To identify the temporal niche of flowering activity for each pollination system (aggregated, segregated or random), we used the phenology data to create an input matrix that contained information of species (rows) vs time (columns). Each cell represented the frequency of flowering of each species (row) in a given month (column). We used a Monte Carlo approach and measured temporal niche overlap via the Pianka (Pianka 1973) and Czechanowski (Feinsinger et al. 1981) indices (Castro-Arellano et al. 2010). Each index is symmetric, approaches zero for species with

non-overlapping activity patterns, and equals 1 for species with identical activity patterns (Castro-Arellano et al. 2010). We employed the randomization algorithm Rosario (Castro-Arellano et al. 2010). This algorithm does not remove the temporal auto-correlation in the data of each species and performs random changes of entire activity patterns within a time extent, thereby restricting randomly generated patterns of activity to be biologically more realistic. In each iteration, Rosario shifts the entire activity pattern of each species a random number of time intervals and calculates the amount of overlap in the randomly generated set of activity patterns (Santos and Presley 2010). We determined the significance of temporal niches by comparing the empirical mean to a frequency distribution of such metrics derived from simulated assemblages for which temporal niches of species were randomized (Castro-Arellano et al. 2010). Rosario used 10,000 iterations to generate the null distributions and determine significance with an α-level of 0.05 (Castro-Arellano et al. 2010).

Temporal nestedness

Temporal nestedness occurs if, on average, the narrower flowering periods of some species are a subset of the broader flowering periods of other species. Temporal nestedness is expected when plants display similar responses and share the same optimal time for reproduction (Genini 2011). As aggregation is a prerequisite for temporal nestedness, we only ran this analysis for the pollination systems that displayed aggregated flowering patterns. We used the NODF metric (Almeida-Neto et al. 2008) to calculate temporal nestedness. We built a presence-absence (1/0) matrix with plant species (rows) and months (columns), presences (ones) indicate if a plant species flowers in a given month. We used the null model 2 (Bascompte et al. 2003) to test for the significance of NODF. In null model 2, the probability of observing a plant species in flower in a given month is a function of the number of months in which it is flowering and the number of plants flowering in that given month (Bascompte et al. 2003; Guimarães and Guimarães 2006).

Climate

To assess the influence of environmental factors on the phenology of each pollination system, we carried out a principal component analysis (PCA). We used six environmental variables (rainfall, mean temperature, day length, relative humidity, cloud cover, and sun irradiation). We employed the components of the PCA that accounted for most of the variance and regressed them against the percentage of species flowering in each pollination system.

Phylogeny

Names of plant species, genera and families follow the International Plant Names Index (http://www.inpi.org:80/ipni/plantsnamesearchpage.do) and Tropicos Names database (http://www.tropicos.org/NameSearch.aspx). We constructed the phylogeny of the species using Phylomatic, a phylogenetic toolkit for the assembly of phylogenies (Webb and Donoghue 2005). The node ages of families were estimated from the APG3-derived megatree. We assigned branch lengths to genera and species of the phylogenetic tree using the BLADJ (Branch Length Adjustment) averaging algorithm of the Phylocom software package (version 4.0.1, http://www.phylodiversity.net/phylocom/). The BLADJ spaces undated nodes evenly between dated nodes in the tree.

We tested for a phylogenetic signal (i.e., the tendency for evolutionarily related organisms to resemble each other) of the pollination system, floral reward, habit, and flowering length using the statistic K (Blomberg et al. 2003). We categorized pollination systems, rewards and habits and assigned the corresponding category to each genus. We used four categories for reward: pollen, nectar, oil, and resin, and four categories for habit: vine, climber, tree, and treelet. Flowering length is the number of months a given plant genus is blooming. The statistic K gives the strength of the phylogenetic signal observed in a set of comparative data divided by the amount expected under a Brownian motion character evolution along the specified tree topology and branch lengths (Blomberg et al. 2003). A K less than one implies that relatives resemble each other less than expected under Brownian motion evolution along the candidate tree (Blomberg et al. 2003). $K > 1$ implies that close relatives are more similar than expected under Brownian conditions (Blomberg et al. 2003). K was calculated by the R package ''picante'' (Kembel et al. 2010). The statistical significance of the phylogenetic signal was evaluated by comparing observed patterns of the variance of independent contrasts of the trait to a null model based on shuffling species across the tips of the phylogenetic tree using 999 permutations (Kembel et al. 2010).

Seasonal variation in the diversity of pollination systems

To assess seasonal variation of the diversity of pollination systems, we used two approaches: grouping the species flowerings periods by seasons defined by rainfall and using a modularity analysis. We grouped the blooming of plant species according to the four previously defined local seasons: dry (D), wet (W), wet-to-dry (W-D) and dry-to-wet (D-W) transitional periods (Morellato and Leitão-Filho 1996) and classified species by their pollination system.

Then, we calculated the proportion of species in each pollination system every season. We did not group species monthly since most of the species in the community display a seasonal flowering strategy (Table 2). Species were scored in all the seasons encompassing their blooming period.

Modularity is a network-based pattern that describes cohesive groups of species (Guimarães 2020). We used a modularity analysis to obtain an independent grouping of plants apart from the seasons defined by rainfall. We aimed to identify groups of plants and months of the year that are associated with each other. We pooled the two-year phenology data of plant species as an adjacency matrix of a network depicting the relationships (links) between the time slices (months) and the flowering phenology of the plants. Each matrix element was $r_{ij} = 1$, if plant species i flowered in the month j and zero otherwise (Bascompte et al. 2003). We used Netcarto software to characterize for modularity (Guimerà and Amaral 2005). The program employs Guimerà's algorithm, which is based on simulated annealing to identify the modules and estimate modularity. Modularity M ranges from 0 to 1 (1–1/*number of modules*), according to increasing modularity (for further details, see Guimerà and Amaral 2005; Olesen et al. 2007). We ran 100 randomizations of the empirical network and calculated the significance level of the observed M (following Olesen et al. 2007).

Results

Pollination systems, flowering phenology and strategies

Pollination by large-to-medium bees predominated at the RSG seasonal forest (49.2%), followed by diverse insects (22.1%), flies (14.7%) and moths (8%) (Table1). The blooming of most systems was seasonal, with a reduced proportion of species in the dry season (June–July), but with species flowering throughout the year (Fig. 1). Plants pollinated by large-to-medium bees flowered mainly in the wet season, from October to March, decreasing from April to July (Fig. 1a), and included all flowering strategies, although seasonal flowering was the prevalent one (Table 2). Plants pollinated by diverse insects, the second most frequent pollination system at the SGR seasonal forest, displayed a well-defined flowering peak in the dry season (August) and a minor increase in the rainy season (Fig. 1b). Similar to large-to-medium bees, seasonal flowering was the predominant strategy of plants pollinated by diverse insects, encompassing 70% of species (Table 2). Fly-pollinated flowers displayed a peak from November to January, in the wet season, a minor increase from March to May, in the wet-to-dry season transition (Fig. 1c), and most species also presented a seasonal strategy (Table 2). All flowering strategies were represented in the previous three pollination systems (large-to-medium bees, diverse insects, and flies), regardless of whether the flowering was less or more concentrated at a specific time of the year, followed by plants with brief and continuous strategies (Table 2). Plants pollinated by butterflies and moths flowered mainly in the wet season (Fig. 1d–e). However, moth-pollinated plants presented a pronounced peak in the dry-to-wet season transition, whereas the blooming peak of butterfly-pollinated species was less pronounced, lasting from December to March, during the wet season (Fig. 1d–e). The seasonal flowering strategies prevailed again among 70% of species within butterfly and moth pollination systems; however, no continuous or episodic strategies were recorded (Table 2). Plants pollinated by small bees flowered irregularly along the year, increasing from May to July in the dry season (Fig. 1f). Hummingbird, wasp and bat pollination systems displayed a similar pattern, with species blooming year-round (Fig. 1g-h-i). Nevertheless, vertebrate-pollinated plants displayed a flowering peak in the dry season (August). Wasp-pollinated species showed continuous, extended, and episodic flowering strategies, although seasonal flowerings were still present (Table 2). Most hummingbird-pollinated plants also displayed a seasonal flowering strategy (Table 2). The bat-pollination system was the only one in which the extended flowering strategy was prevalent, followed by seasonal and brief strategies (Table 2). Beetle pollination is not graphically represented here, as the only two species flowered in the rainy season, from October to December.

Temporal niche patterns and temporal nestedness of the pollination systems' flowering phenologies

Large-to-medium bees, diverse insects, moths, and butterflies displayed an aggregated temporal flowering pattern, whereas flowering of the remaining pollination systems showed no difference of temporal niche patterns from random (Table 3).

In the tests for temporal nestedness for those pollination systems that showed aggregated flowerings (i.e., large-to-medium bees, diverse insects, moths and butterflies), we only found a significant nested pattern for large large-to-medium bee pollination (NODF = 0.33, p = 0.012). In contrast, the other aggregated pollination systems were not nested ($NODF_{Div.Insects} = 0.235$, $p = 0.125$; $NODF_{Moths} = 0.243$, $p = 0.78$; $NODF_{Butterflies} = 0.15$, $p = 1.00$).

Climate and flowering

The two first components of the PCA explained 79% of the total variation (58.5% and 20.5%, respectively) and were used in the regression. The variables cloud cover, day length, and mean temperature contributed most to the first principal

Table 1 Comparison of pollination systems of woody species from tropical forests. Symbols: * = large-to-medium bees, ** sunbirds, *** small bees are with diverse insects, §includes small insects, diverse small insects, others

Vegetation	Country	N	Bee Large-medium	Diverse insects§	Fly	Moth	Humming bird	Bee small	Butterfly	Bat	Wasp	Beetle	Reference
Cerrado woodland	Brazil	184	23.9	45.6	0.5	9.3	1.7	10.3	0.5	2.2		4.4	Gottsberger & Silberbauer-Gottsberger (2018)
Cerrado	Brazil	178	83.1*	-	2.3	3.4	3.4	***	2.3	3.9		1.7	Silva et al. (2012)
Cerrado	Brazil	59	32*	44	-	12	2	***	0	3		2	Oliveira & Gibbs (2000)
Forest (gallery)	Brazil	102	23.0	45.0	-	12.0	0.0		2.0	4.0		6.0	Oliveira and Gibbs (2002)
Dry forest (Caatinga)	Brazil	142	30.5	12.4	-	8.5	15.0	12.6	3.9	13.1	1.3	0.7	Machado & Lopes (2004)
Dry forest	Mexico	154	46.0	14.0	1.5	9.0	7.5	11.0	2.5	4.0	-	0.5	Cortés-Flores et al. (2017)
Seasonal forest	**Brazil**	**199**	**49.2**	**22.1**	**13.6**	**8.0**	**4.5**	**10.1**	**5.0**	**3.0**	**2.5**	**1.0**	**This study**
Seasonal forest	Colombia	80	38.6	21.8	5.9	4.0	5.9		6.9	3.0	5.9	5.9	Van Dulmen (2001)
Rainforest (upland)	Colombia	77	41.9	32.6	0.0	2.3	7.0		3.5	1.2	4.7	7.0	Van Dulmen (2001)
Rainforest	Costa Rica	145	23.9	45.6	0.5	4.9	2.2	10.3	0.5	2.2	-	4.4	Kang & Bawa (2003)
Rainforest	Costa Rica	320	38.3	13.0	1.8	7.5	16.2		2.5	2.9	2.5	12.3	Kress & Beach (1994)
Rainforest	Venezuela	175	73.1*	-	2.8	8.3	2.8	-	4.2	2.8	0.0	2.8	Ramirez 2004
Rainforest	India	86	18.0	25.0	6.0	10.0			5.0	3+	2.0	17.0	Devy & Davidar (2003)
Dipterocarp forest	Malaysia	41	26.7	2.4	7.3	2.4	9.8**	44.0	2.4	0.0	2.4	2.4	Kato (1996)
Dipterocarp forest	Malaysia	270	50.4	13.7	3.9	1.1	7.0**		2.2	1.9	0	20.7	Momose et al. (1998)

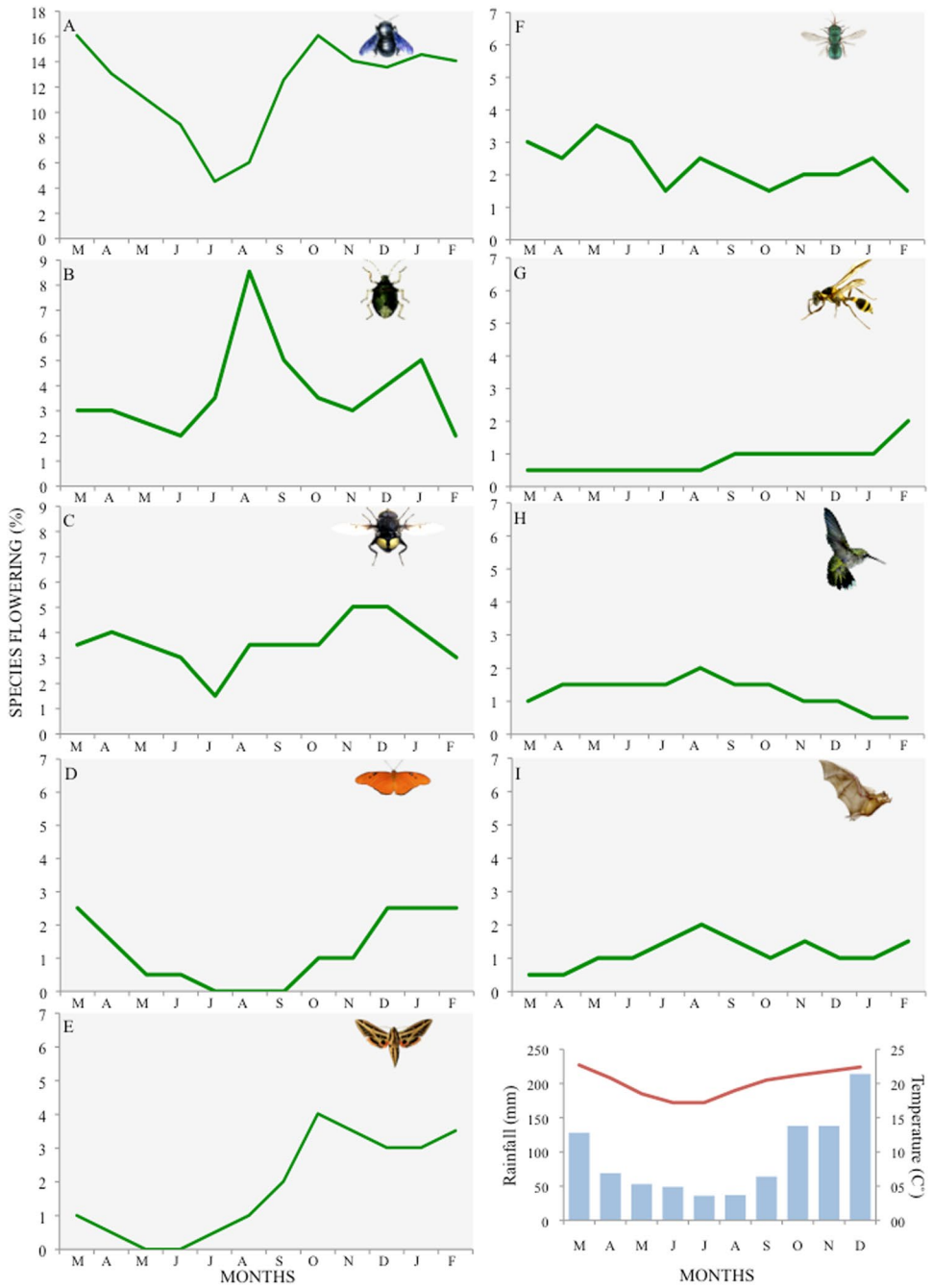

Fig. 1 Percentage of plant species flowering in each pollination system throughout the year at the SGR seasonal forest, south-eastern Brazil. **A** = large-to-medium bees, **B** = diverse insects, **C** = flies, **D** = butterflies, **E** = moths, **F** = small bees, **G** = wasps, H = hummingbirds and **I** = bats. Note the different scale for A-C and D-G. Bottom right: climate during the study period: blue bars = rainfall, red line = mean temperature

component, whereas relative humidity, sun irradiation, and day length contributed most to the second component. We found a significant relationship between the two PCA components with the percentage of plant species flowering for fly, hummingbird and moth pollination systems. For large-to-medium bees, wasp and butterfly pollination systems, only the first component of the PCA was significant (Table 4). Consequently, the flowering of plants within the large-to-medium bees, wasp, and butterfly-pollination systems was positively affected by the combined effect of cloud cover, day length, and mean temperature, whereas hummingbird, fly and moth-pollination systems were also influenced by relative humidity and irradiation. No effect of environmental variables was found for bat, small bees and diverse insects pollination systems (Table 4).

Phylogeny

All traits showed a weaker phylogenetic signal than expected, that is, $K < 1$ (Pollination system: $K = 0.34$, $p = 0.001$; Reward: $K = 0.56$, $p = 0.001$; Habit: $K = 0.38$, $p = 0.001$; and Flowering length: $K = 0.37$, $p = 0.025$). Thus,

Table 2 Number of plant species (N) by pollination system and the percentage (%) of distribution according to the flowering strategy at the SGR seasonal forest, south-eastern Brazil

Pollination systems		Flowering strategy				
	N	Continuous	Extended	Seasonal	Episodic	Brief
Large-to-medium bees	98	3.1	11.2	65.3	4.1	16.3
Diverse insects	44	0	2.3	70.4	9.1	18.2
Flies	28	7.1	7.1	60.7	3.6	21.5
Moths	17	0	23.5	70.6	0	5.9
Hummingbirds	9	0	33.3	55.6	0	11.1
Small bees	20	0	10.0	70.0	5.0	15.0
Butterflies	10	0	20.0	70.0	0	10.0
Bats	6	16.7	50.0	33.3	0	0
Wasps	5	20.0	20.0	40.0	20.0	0
Beetles	2	0	0	50.0	0	50.0

Table 3 Niche temporal flowering pattern for Czechanowski and Pianka Index for each pollination system at the SGR seasonal forest, south-eastern Brazil

Pollination systems	Pianka Index	P	Czechanowski Index	P
Large-to-medium bees	0.22	$p < 0.0225$	0.16	$p < 0.0036$
Diverse insects	0.18	$p < 0.0028$	0.14	$p < 0.0018$
Flies	0.22	n.s	0.16	n.s
Moths	0.27	$p < 0.0055$	0.22	$p < 0.0016$
Hummingbirds	0.21	n.s	0.18	n.s
Small bees	0.19	n.s	0.15	n.s
Butterflies	0.27	$p < 0.0442$	0.20	n.s
Bats	0.3	n.s.	0.22	n.s
Wasps	0.38	n.s.	0.26	n.s
Beetles	---	---	---	---

All significant temporal patterns are aggregated. n.s., not significant; --- not calculated due to small sample size

Table 4 Results of multiple regression analyses between the two main components of the PCA for environmental variables by pollination systems and the percentage of plant species flowering at the SGR seasonal forest, south-eastern Brazil

Pollination systems	Regression summary		ß Explanatory variables	
	R^2	$F_{2,21}$	Component 1	Component 2
Large-to-medium bees	0.65	19.88 ***	−0.78 ***	0.23 n.s
Diverse insects	0.07	0.82 n.s	0.76 n.s	0.26 n.s
Flies	0.44	8.31 ***	−0.49 ***	0.45 ***
Moths	0.81	44.41 ***	−0.67 ***	0.59 ***
Hummingbirds	0.67	21.33 **	0.76 ***	0.31 *
Small bees	0.73	0.83 n.s	0.19 n.s	−0.19 n.s
Butterflies	0.60	15.85 ***	−0.78 ***	0.03 n.s
Bats	0.19	2.61 n.s	0.31 n.s	0.31 n.s
Wasps	0.32	5.04 *	−0.56 **	−0.10 n.s
Beetles				

Statistical significance: *$P < 0.05$; **$P < 0.001$; and ***$P < 0.0001$. n.s., not significant; and ß, standard partial regression coefficient

species were more different than could be explained by the neutral evolution of these traits.

Temporal variation in the diversity of pollination systems

Plants from all the pollination systems were blooming every season, except for beetle-pollinated plants, which flowered in the dry-to-wet season transition and the rainy season; all pollination systems were present in the wet season (Fig. 2). In general, the best-represented pollination systems in the community (large-to-medium bees, diverse insects, flies and small bees) were also the best-represented in each season (Fig. 2) (Supplementary Information, Table S2). Accordingly, the less common pollination systems were poorly represented in each season (Table 1, Fig. 2). Nevertheless, the proportion of plants flowering in each pollination system varied seasonally (Supplementary Information, Table S3). For instance, more plant species from the large-to-medium bees, butterfly and wasp-pollination systems bloomed in the wet-to-dry transition; most moth and all beetle-pollinated plants were in flower during the wet season, and the majority of hummingbird-pollinated plants were flowering in the dry-to-wet transition. The other pollination systems displayed a higher proportion of species flowering in the dry season (Fig. 2) (Supplementary Information, Table S3). Thus, even when the whole diversity of pollination systems is present year-round, flowering seasonality influences the abundance of each pollination system in every season.

We obtained four modules of three months each ($M = 0.44$; $p < 0.001$), grouping plants that flowered in particular months. The first module corresponded to April to June (M1), the second January to March (M2), the third

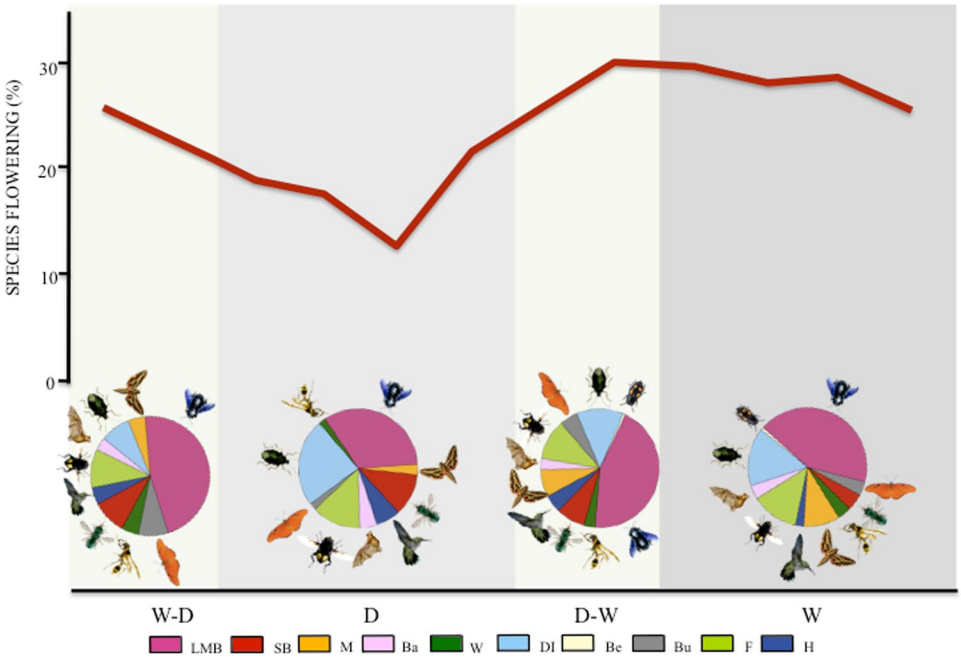

Fig. 2 Percentage of plant species flowering in the community (red line) and their proportion by pollination system according to the seasons (W-D = wet-to-dry transition, D = dry season, D-W = dry-to-wet transition, W = wet season) at the SGR seasonal forest, south-eastern Brazil. LMB = large-to-medium bees, DI = diverse insects, SB = small bees, Be = beetles, M = moths, Bu = butterflies, W = wasps, F = flies, Ba = bats and H = hummingbirds

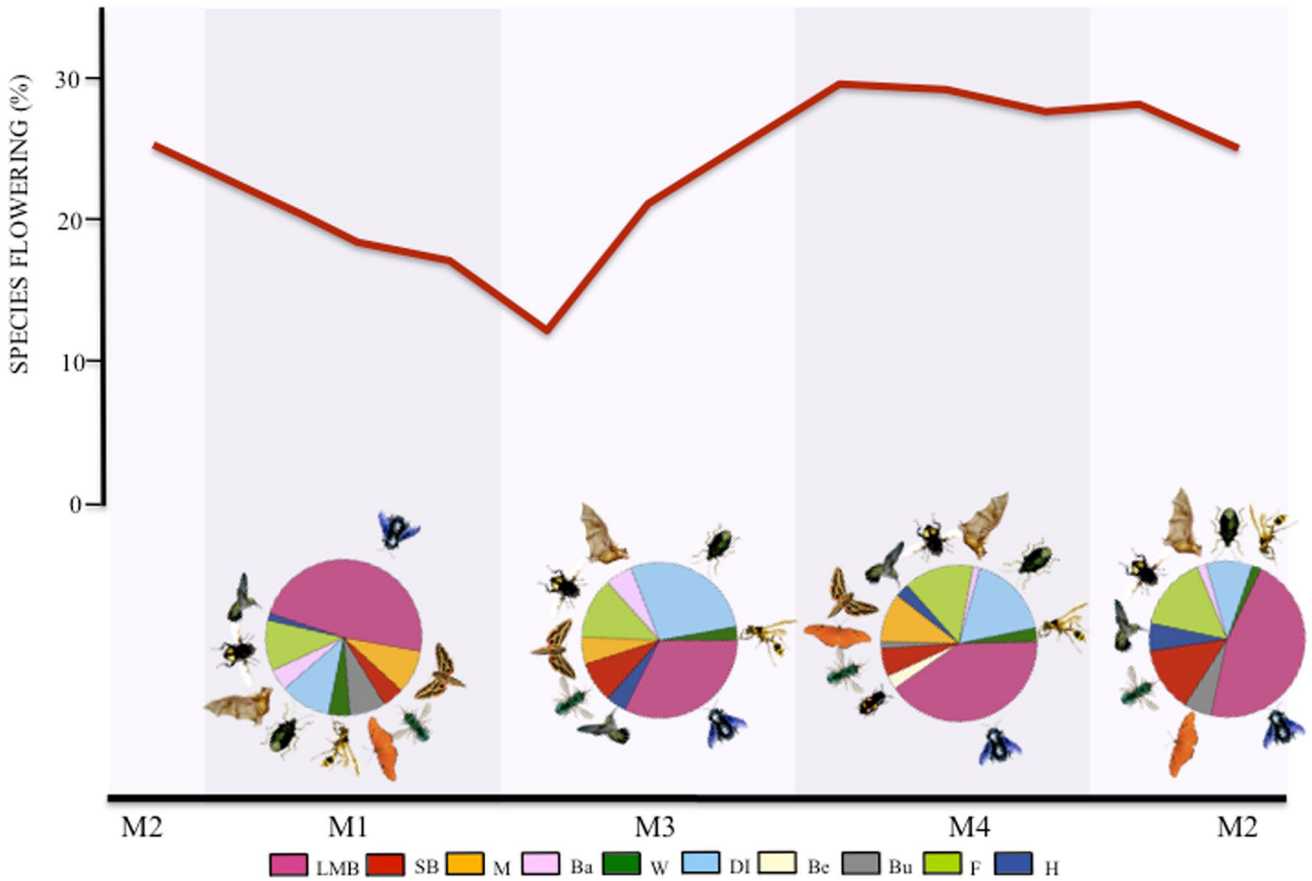

Fig. 3 Percentage of plant species flowering in the community (red line) and their proportion by pollination system according to the independent modules (M1 = module1 January to March; M2 = module2 April to June; M3 = module3 July to September, M4 = module4 October–November) at the SGR semi-deciduous forest, south-eastern Brazil. LMB = large-to-medium bees, DI = diverse insects, SB = small bees, Be = beetles, M = moths, Bu = butterflies, W = wasps, F = flies, Ba = bats and H = hummingbirds

July to September (M3) and the fourth October to December (M4). The proportion of plant species from each pollination system in each module is shown in Fig. 3. Similar to when we grouped species by seasons, most pollination systems were present in all modules, although proportions also varied from one period to the other (Supplementary Information, Table S3). Large-to-medium bees, diverse insects, flies, and small bees were the best-represented pollination systems in each period. Beetles were restricted to one module (M4 = October–December), which coincided with the end of the dry-to-wet transition and the onset of the rainy season. Butterflies were absent from July to September (M3) and moths from April to June (M1).

Discussion

Our study showed that the SGR tropical seasonal forest has a high diversity of pollination systems comparable to other tropical forests and that this diversity is represented across the seasons. Accordingly, the best-represented pollination system was large-to-medium bees, followed by the generalist diverse insects and fly pollination systems. Overall, the flowering times of plant species from the different pollination systems were not equally affected by climate, and phylogeny did not affect flowering. We found that although seasonal flowering strategy predominated, the flowering periods differed among pollination systems, which indicates that the conditions of some seasons favoured blooming of different species and habits. Additionally, just four out of the 10 pollination systems showed aggregated temporal patterns and only large-to-medium bees had significant temporal nestedness. Finally, the modularity analysis grouped the flowering periods in different seasons as those defined only by climate seasonality, indicating that other factors rather than weather may define the optimum flowering time of some pollination systems.

The proportion of pollination systems at the SGR seasonal forests agreed with those found in other tropical forests (Table 1): large-to-medium bee pollination prevailed, followed by diverse insects, flies, and moths, whereas vertebrate pollination was poorly represented. Tropical forests are dominated by bee-pollination, whereas pollination by vertebrates is relatively uncommon (Bawa 1990; Devy and Davidar 2003, 2006; Kato 1996; Kato et al. 2008; Selwyn and Parthasarathy 2006; Table 1). In our study, the dominance of large-to-medium bee-pollinated plants was also associated with the high proportion of climber species, which are mostly bee-pollinated (Morellato 1991; Morellato and Leitão-Filho 1996). The SGR seasonal forest presented an unprecedented proportion of fly pollination (~ 14%), much above any other tropical forest or system (Table 1). The fly pollination system is recognized as important in mountains and temperate vegetations (Freitas and Sazima 2006; Lefebvre et al. 2018; Monteiro et al. 2021). We suggest that careful studies on flowers initially regard as "generalists" or pollinated by diverse insects will reveal flies as the primary pollinators, as seen in our study (Table S1 Supplementary Information and related references). On the other hand, moth-pollinated species were underrepresented compared to other tropical rainforests studies, including understory species (Bawa et al. 1985) but were comparable to those of the other forests and seasonal cerrado savannah vegetation (Table 1). The proportion of the remaining pollination systems at SGR seasonal forest was similar to other tropical forests (Table 1). However, the low proportion of beetle-pollination may be related to the absence or the reduced number of species belonging to cantharophilous families such as Araceae, Lauraceae, Myristicaceae, Arecaceae, and Annonaceae (Bawa 1990; Momose et al. 1998; Morellato 1991).

The highest diversity of flowering strategies at SGR occurred in species within large-to-medium bees and fly pollination systems, yet at least three types of flowering strategies were present in any system. The high diversity of phenological strategies emphasizes the importance of considering the temporal organization of communities (Estes et al. 2018) and the fine organization of flower resources within the dominant large-to-medium bee system. The seasonal strategy predominated among species within all pollination systems but bats. Despite that, pollination by large-to-medium bees was dominant over the whole year, suggesting a broad temporal niche structuring the pollination community (Phillips et al. 2020). Plant species pollinated by large-to-medium bees whose flowers include resources such as oil, resin, and odoriferous substances besides dominant nectar and pollen, embraced a large diversity of pollination strategies (Supplementary Information, Table S1). The bee-pollination system is the most abundant one in the Venezuelan Central Plain and is also related to the highest diversity of pollination strategies and vectors (Ramirez 2005). The occurrence of bee-pollinated plants flowering all year round in our study is likely associated with the variety of flowering strategies displayed by different species and life forms within this pollination system, as recorded for other communities as well (Kato et al. 2008; Ramirez 2005). For instance, at the SGR, lianas bloomed mainly during the wet-to-dry season transition and dry season, whereas trees and treelets concentrated flowering in the dry-to-wet season transition (Morellato and Leitão-Filho 1996).

We found aggregated temporal patterns for large-to-medium bees, diverse insects, butterfly, and moth-pollination, supporting the dominant seasonal flowering strategy. Besides being aggregated, the flowering of the plants within the large-to-medium bee pollination system was nested, which suggests a unique optimum time for reproduction.

The apparent contradiction between this result and our above statement of broad temporal niches is explained by the continuous flowering strategy of five species within this pollination system (see Table S1, Supplementary Information). We suggest that a few long-lasting flowering species have a disproportional effect on SGR plant community blossoming patterns and that nestedness arises due to their influence, a matter deserving further investigation. Four out of these five long-lasting species are dominant lianas, reinforcing their role as resources year-round at the studied forest (Morellato and Leitão-Filho 1996) and overall importance in tropical forests (see Vargas et al. 2021 for review).

On the other hand, lack of temporal nestedness for moth, butterfly and diverse insects' pollination systems suggests that, despite their aggregated patterns, they may have different optimal times for reproduction. At the SGR, moth- and butterfly-pollinated plants flowered during the rainy season when these pollen vectors are more abundant, similarly to the records for other seasonal forests (Brown and Freitas 2002; Frankie 1975; Kato et al. 2008; Ramirez 2006). Butterfly and moth population dynamics in the tropics usually face extremely seasonal environments with marked wet and dry seasons, and their abundance and survival are expected to decrease in the dry season due to scarcity of water, nectar, and fresh new leaves (Bonebrake et al. 2010; Brown and Freitas 2002). The flowering of beetle-pollinated plants was also restricted to the rainy season, as already recorded for other seasonal vegetations (Gottsberger 1989; Ramirez 2006). Conversely, the seasonal flowering strategy of diverse insect-pollinated plants was not affected by the environmental variables evaluated in our study since it includes various pollination agents that may respond in different ways to environmental cues.

At the SGR seasonal forest, the blooming of fly, small bee, wasp, and vertebrate-pollinated plants was recorded in all the seasons, without a prominent peak of activity, resulting in a broad temporal niche that is neither segregated nor aggregated. The irregular and uncertain patterns of fly-pollinated plants have been related to the behaviour of these insects, which do not use flower resources to feed their offspring, and to the fact that these plants are visited by a great variety of other insects (Pombal and Morellato 1995, 2000; Proctor et al. 1996). The aseasonal flowering of wasp-pollinated plants may be related to the predominance of *Ficus* species since the typical phenological pattern of *Ficus* is annual or supra-annual at the individual level, integrated into a continuous pattern at the population level (Figueiredo and Sazima 1997; Sakai et al. 1999).

Finally, hummingbird-and bat-pollinated plants displayed seasonal and extended flowering strategies that resulted in a sequential flowering in the SGR seasonal forest, similarly to what has been found for rainforest plant communities in south-eastern Brazil (Buzato et al. 2000; Sazima et al. 1996, 1999; Wolowski et al. 2017). In the Venezuelan Central Plain, Ramirez (2006) reported non-seasonal, continuous flowering for hummingbird- and bat-pollinated plants and suggested a sequential replacement of bird- and bat-flowers throughout the year. Sequential patterns have been associated with avoiding competition for pollinators or avoiding interspecific pollen transfer (Aizen and Rovere 2010; Aizen and Vázquez 2006; Feinsinger 1987; Stiles 1977, 1978). In bat-pollinated species, extended flowering strategies prevailed, and such a pattern is related to the trapline foraging of bats that may benefit from extended blooming (Heithaus et al. 1975).

So far, we have detected a strong temporal organization within and among pollination systems, likely driven by the plant-pollinator interactions. The four pollination modules derived from independent modularity grouping encompassed the traditional dry (M2 and M3 including April to June and July to September) and wet (M4 and M1 October–November and January to March) seasons. The independent modularity grouping captured better the flowering periods of the moths, butterflies, and beetles plant pollination systems than the pre-defined grouping by rainfall seasonality. The appearance and abundance of certain pollination systems are influenced by flowering phenology since some pollinators may change their behaviour in response to the availability of flowering species, becoming more opportunistic or even migrating elsewhere when resources are scarce (Devy and Davidar 2003; Kato et al. 2008; Maruyama et al. 2013; Ramirez 2006; Sazima et al. 1999). In seasonal forests, a higher diversity of pollination systems is expected during peak flowering periods and, consequently, as the diversity of resources increases, consumer diversity increases as well (Cortés-Flores et al. 2017; Ramirez 2006). In our study, most pollination systems were evenly represented in conjunction with the seasons even when their abundances were variable. The constancy of pollination systems during the year may be related to differences in flowering peaks among plant life forms and promotes the coexistence of various pollination systems (Cortés-Flores et al. 2017; Ramirez 2006). Further studies should address floral trait similarity among co-flowering species sharing the same pollination systems and pollinators, pollination rewiring during periods of reduced flower offer, and the potential influence of long-last flowering and flower abundance on the synchronicity and temporal organization of resources in tropical forests (Albor et al. 2020; Bergamo et al. 2020; Sargent and Ackerly 2008).

In conclusion, our study addressed different phenological aspects of the pollination systems of a tropical plant community and its ecological and evolutionary constraints. We demonstrated that the diversity of pollination systems remained constant despite climate seasonality which may facilitate the exploitation of diverse floral resources by the pollinator agents. The temporal organization of our

flowering plant community is triggered by climate and dominated by seasonal flowering strategies finely shaped by the plant-pollinator interactions. Our observations are 30-years-old, and over the last three decades, we have faced a steep increase in global warming (IPCC 2014), with widely documented effects of rising temperatures causing shifts plant in phenology, mostly from temperate regions (Abernethy et al. 2018; Chambers et al. 2013). One of the consequences of early flowering due to climate change is the disruption of plant-animal interactions, decoupling the time of flowering and pollinators' activity and other mutualistic and antagonistic interactions (Burkle and Alarcon 2011; Memmott et al. 2007). We do not have long-term or flowering data or present phenology information from our site to test for such shifts and the likely effects on plant-pollinator synchrony. However, we expect that the increasing temperatures and dry season length and intensity in our region due to global warming are likely affecting species' flowering time and disrupting the pollination interactions, with significant effects on biodiversity conservation and ecosystems services (Morellato et al. 2016). That topic is of utmost importance for future studies for tropical areas, especially those areas where legacy phenological and plant-animal interaction information were collected in the past (e.g., Miller-Rushing and Primack 2008).

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Author contribution JG, PG and LPCM design the study, LPCM, MS and IS collected the data, JG and PG analysed the data, JG wrote the first draft and all authors contributed and approved the final version.

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Data and materials availability Data is available as Supplementary Information.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare no competing interests.

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