

SAZONALIDADE E AS REDES DE INTERAÇÕES PLANTA- POLINIZADOR

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ÍNDICE

ABSTRACT	1
RESUMO	3
INTRODUÇÃO GERAL	5
CAPITULO 1	Long-lasting flowering: temporal nestedness and the aggregation of phenologies
	Julieta Genini, Paulo R. Guimarães Jr. and Leonor Patrícia Cerdeira Morellato
	14
CAPITULO 2	Temporal organization among pollination modes in a Brazilian seasonal Forest
	Julieta Genini, Paulo R. Guimarães Jr., Marlies Sazima, Ivan Sazima and Leonor Patrícia Cerdeira Morellato.....
	31
CAPITULO 3	Temporal dynamic in a plant-hawmoth network and the spatial coupling links
	Julieta Genini, Luis M. Primo, Fransisco de Assis Ribeiro dos Santos, Leonor Patrícia Cerdeira Morellato, Isabel Cristina Sobreira Machado, Jens Olesen and Paulo R. Guimaraes Jr.
	90
CAPITULO 4	Cheaters in mutualisms networks
	Julieta Genini, L. Patrícia C. Morellato, Paulo R. Guimarães, Jr and Jens M. Olesen
	115
CONCLUSOES GERAIS	132

ABSTRACT

Flowering patterns are likely to affect ecological dynamics of plant communities. In that sense, characterization of pollination modes and its flowering patterns at a community level are fundamental to understand the seasonal variation of flowers, pollinators and their temporal organization in different vegetations. Therefore, we examine the flowering patterns at a community level and explored aggregation, segregation and temporal nestedness at the Santa Genebra Reserve, (SGR), a semideciduous forest of Southeastern Brazil. Then, we also evaluate the flowering patterns, diversity and temporal organization of pollination modes within the SGR. Subsequently, we focus on the temporal dynamic of a small sphingophylous flower visitation network. At last, we studied two other flower visitation networks – Malpighiaceae and Bignoniaceae - and evaluated how different types of links (i.e. cheaters and effective pollinators) influence network topology. We found that the flowering pattern of the SGR community is aggregated and nested. We also identified the causes of nestedness in this community by removing the long-lasting flowering plants. In addition, SGR forest present a high diversity of pollination modes, comparable to other tropical systems, and this diversity is represented across the seasons, since climate and phylogeny did not restrict the flowering of most plants regardless the pollination mode. We also find a high temporal dynamic in our small visitation network as well as a spatial component of some links.

Finally, the removal of a particular type of links (cheaters) in one of the visitation networks (Bignoniaceae) completely changed the structure of the network. To conclude, even when the community showed a characteristic temporal pattern (i.e. aggregated and nested) most resources were available for pollinators year round. On the other hand, the high temporal dynamic of the moth small network resulted from the strong seasonality of the mutualists partners and from the spatial component of the network, indicates differences in flowering patterns among local and regional populations. Thus, diversity in flowering phenologies contributes to the maintenance of these populations. Finally, different types of links may maintain the observed structure of flower visitation networks and have an enormous effect on network structure and stability.

Keywords: seasonality, community patterns, ecological networks, temporal dynamics.

RESUMO

Os padrões de floração no nível de comunidade podem afetar a dinâmica dos sistemas ecológicos. Dessa forma a caracterização dos modos de polinização e padrões de floração no nível de comunidade são fundamentais para entender a variação sazonal das flores, polinizadores e sua organização temporal nas diferentes vegetações. Portanto, nos examinamos a floração no nível de comunidade e procuramos identificar padrões agregados, segregados e temporalmente aninhados na Reserva Municipal de Santa Genebra (SGR), uma floresta semidecídua do Sudeste de Brasil. Depois, nós avaliamos os padrões de floração, a diversidade e organização temporal por modos de polinização em SGR. Posteriormente, nos concentramos na dinâmica temporal de uma pequena rede de visitantes florais. Finalmente, estudamos outras duas redes de visitantes florais e avaliamos como diferentes tipos de enlaces (i.e. pilhadores e polinizadores efetivos) afetam a estrutura das redes. Nós encontramos que os padrões de floração em SGR são agregados e aninhados, e identificamos as causas do aninhamento temporal quando removemos as espécies de floração longa. Além do mais, a SGR apresentou uma alta diversidade de modos de polinização, comparável a outras florestas tropicais, e essa diversidade encontra-se representada ao longo das diferentes estações desde que o clima e a filogenia não restringiram a floração da maior parte das espécies. Nós encontramos uma alta dinâmica temporal na nossa pequena rede de visitantes florais junto a um importante componente especial de algumas interações. Por último, a remoção dos pilhadores em uma das

redes de visitantes florais mudou completamente a estrutura da rede. Para concluir, embora a comunidade mostrou um padrão fenológico característico (i.e. agregado e aninhado) a maior parte dos recursos florais estão disponíveis para os polinizadores durante o ano todo. Por outro lado, a alta dinâmica temporal da rede resultou da forte sazonalidade dos mutualistas envolvidos na interação e do componente espacial que indica diferenças nos padrões de floração das espécies entre as populações locais e regionais. Portanto, a diversidade nos padrões de floração contribui a manutenção dessas populações de esfingídeos. Finalmente, diferentes tipos de enlaces podem sustentar a estrutura observada nas redes de visitantes florais e ter um enorme efeito sobre a estabilidade das redes

Palavras-chave: sazonalidade, padrões de floração, redes de interações, dinâmica temporal.

INTRODUÇÃO GERAL

Existem vários mecanismos potencialmente estruturadores das redes de interações como por exemplo a abundância, a sobreposição espaço-temporal, a filogenia e as variações na fenologia (Bascompte & Jordano, 2007; Vázquez *et al.*, 2009, Rezende *et al.*, 2007). Nas comunidades de plantas tropicais, a diversidade de padrões fenológicos é um dos mecanismos responsáveis da manutenção da biodiversidade (Gentry, 1974). A sazonalidade climática seria um dos principais fatores que condicionam esses padrões fenológicos (Frankie *et al.*, 1974; Wright, 1996). No entanto pressões seletivas bióticas também podem influenciar os padrões de brotamento (Aide, 1992), floração (Appanah, 1985) e frutificação (Kelly, 1994) das espécies. Tradicionalmente, os padrões de floração tem sido classificados como agregados, segregados ou ao acaso (Feinsinger, 1987, Armbruster, 1986). No entanto, recentemente outro tipo de padrão temporal tem sido descrito: o aninhamento temporal. O aninhamento temporal implica que o nicho temporal de algumas espécies é um subconjunto do nicho temporal das espécies com floração mais longa (Elmendorf & Harrison, 2009). O aninhamento temporal poderia ser considerado como outro tipo de padrão agregado (Elmendorf & Harrison, 2009), onde todas as plantas exibem o mesmo tempo ótimo para a reprodução.

Por outro lado, devemos considerar também que a diversidade de padrões de floração também influencia a diversidade e a proporção de modos de polinização em comunidades vegetais (Ramirez, 2006). À

medida que o ambiente torna-se mais sazonal, as épocas de floração são mais restritas aos períodos mais favoráveis e conseqüentemente, a maior diversidade de modos de polinização fica limitada a um período ou estação (Ramirez, 2006). Adicionalmente, cada modo de polinização pode responder diferentemente aos fatores bióticos e abióticos, e dessa forma mostrar distintos padrões de floração.

A estrutura e dinâmica das comunidades vegetais pode ser melhor detectada por meio da análise das redes de interações. A análise de redes complexas procura reconhecer quais são os princípios organizadores da evolução e formação das redes (Albert e Barabási, 2002; Barabási & Oltvai, 2004). As redes de interações podem ser representadas por um grafo, ou seja, um conjunto de nós ou vértices (espécies) conectados por interações que representam as interações entre eles (Barabási & Oltvai, 2004).

As redes de interações entre animais e plantas podem apresentar dois tipos principais de padrões topológicos: *aninhado* e *modular*. Apesar do padrão aninhado prevalecer em grande parte das redes mutualistas (Bascompte *et al.*, 2003), as redes de polinização e dispersão aninhadas também podem ser modulares (Olesen *et al.*, 2007; Donatti *et al.*, 2011). Portanto esses padrões não são mutuamente excludentes.

Na topologia *aninhada* (Bascompte *et al.*, 2003; Guimarães *et al.*, 2006), as plantas com muitas interações interagem com animais com muitas interações, enquanto plantas e animais com poucas interações raramente interagem entre si, mas sim com espécies com muitas

interações (Bascompte *et al.*, 2003; Guimarães, 2006). O aninhamento confere duas características: primeiro um padrão altamente coesivo que oferece respostas alternativas às perturbações e, segundo um padrão assimétrico que assegura, por exemplo, a subsistência de espécies raras (Bascompte *et al.*, 2003). Por outro lado, o padrão *modular* apresenta subgrupos de plantas e animais que interagem de modo que as espécies apresentam mais interações dentro dos subgrupos do que entre eles (Lewinsohn *et al.*, 2006).

Em sistemas ecológicos, existe uma sucessão temporal das espécies que interagem (Jordano *et al.*, 2007; Olesen *et al.*, 2008) e uma mudança nas características das comunidades à medida que chegam as espécies de animais e/ou começam os períodos de floração ou de frutificação das espécies de plantas. Entretanto, as redes mutualísticas usualmente estudadas são redes estáticas, que refletem as interações resultantes da coleta de dados durante longos períodos de tempo e que desconsideram a influência da variação temporal. Portanto uma descrição adequada das redes de interações mutualísticas por meio do uso de redes sequenciais, que representam os padrões de interações durante períodos discretos de tempo, permite descrever as interações entre espécies com fenologias coincidentes e revelar as oscilações no número de interações e espécies (Basílio *et al.*, 2006).

Por outro lado as interações entre plantas e animais não são todas iguais e essa variação afeta a estrutura das redes (Guimarães *et al.*, 2007). No entanto, em quase todos os estudos as interações são

unicamente de um tipo (mas veja Melián *et al.*, 2008). Por exemplo, nos estudos de polinização todas as interações são consideradas como mutualistas (Elberling & Olesen 1999). No entanto, os visitantes florais utilizam os recursos florais para muitos motivos: herbívoros florais, predação de ovulo/semente, sítio de acasalamento, roubo de néctar e pólen, “turismo”, e, é claro, forrageio de recursos como néctar, pólen e óleos (Inouye, 1983; Simpson & Neff, 1983; Frame, 2003, Strauss & Whittall, 2006). Portanto, a influência do tipo de interações na topologias de redes de visitantes florais precisa ser avaliada.

Dessa forma, este estudo teve como objetivos (i) avaliar os padrões de floração no nível de comunidade na Reserva Municipal de Santa Genebra (RSG) assim como caracterizar seus modos de polinização, (ii) avaliar a dinâmica temporal e a influencia do tipo de interação na topologia das redes de visitantes florais.

Nos capítulos 1 e 2 avaliamos os padrões de floração para uma floresta tropical com uma sazonalidade acentuada no Sudeste do Brasil (SGR). No capítulo 1 investigamos quais são os padrões de floração no nível da comunidade e avaliamos o aninhamento temporal. Posteriormente discutimos a importância das espécies de floração longa no surgimento do aninhamento temporal e as implicações desse padrão para a coexistência das espécies na comunidade. No capítulo 2, avaliamos a diversidade de modos de polinização na comunidade de SGR, os padrões e estratégias de floração para cada modo de polinização, assim como a variação temporal na diversidade de modos

de polinização. Finalmente, discutimos como os padrões de floração, a diversidade dos modos de polinização e a sua variação temporal influenciam a oferta de recursos para polinizadores ao longo do ano.

Nos capítulos 3 e 4 trabalhamos com dois estudos de caso em redes de interações de visitantes florais. No capítulo 3 avaliamos a dinâmica temporal em uma rede de visitantes florais utilizando o conceito da diversidade beta aditiva e identificamos interações com um componente espacial. Nós evidenciamos uma alta dinâmica temporal devida a sazonalidade climática que influencia as espécies presentes nas redes mensais e sazonais tanto nas plantas quanto nos visitantes florais (i.e. esfingídeos). Devemos considerar também a importância das interações espaciais, que demonstra como as diferenças nos padrões de floração entre diferentes áreas sustentam as populações de esfingídeos que se deslocam de uma área a outra. No capítulo 4 estudamos duas redes de visitantes florais em relação ao tipo de enlace. As redes de visitantes florais variam no seu nível de antagonismo, dessa forma as interações podem ser mutualistas (i.e. polinizadores efetivos) ou antagonistas (pilhadores de néctar e/ ou pólen). Nós evidenciamos que diferentes redes de visitantes florais diferem no seu grau de antagonismo e que redes mais antagonistas mostram um padrão modular. Nós evidenciamos que a presença dos enlaces antagonistas (i.e. pilhadores) determina a estrutura modular em uma das redes.

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Capítulo 1

Long-lasting flowering: temporal nestedness
and the aggregation of phenologies

**Long-lasting flowering: temporal nestedness and the
aggregation of phenologies**

Short title: Temporal nestedness in phenologies

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1 SUMMARY

2 Patterns of flowering phenology at the community level might affect
3 ecological dynamics, influencing the persistence of pollinators. Aggregation and
4 segregation in flowering have been investigated in distinct tropical communities, but
5 these patterns are just two of the possible non-random patterns of flowering. Here we
6 examine flowering patterns at a community level and explore the potential of
7 temporal nestedness. Temporal nestedness indicates that some plant species have
8 flowering seasons that include other species' flowering periods. We applied temporal
9 niche analyses to characterise the pattern of flowering phenologies in a Brazilian
10 semi-deciduous forest. Then, we tested the influence of environmental factors on
11 community flowering and assessed phylogenetic conservatism in ecological traits.
12 Community flowering occurred throughout the year, with a decrease of species in the
13 dry season. Environmental factors influenced the percentage of species blooming, but
14 we did not find a phylogenetic signal for flowering length. We detected an aggregated
15 and temporal nestedness flowering pattern for the entire community. Nestedness
16 emerged as a consequence of a few long-lasting flowering species. Thus, nestedness
17 analysis revealed the crucial role of a small set of species (3.5% of all species) in
18 shaping the temporal organisation of plant communities.

19 **Keywords:** temporal nestedness, temporal niche patterns

20

1 1. INTRODUCTION

2 Time is a major niche dimension and many organisms show seasonal
3 synchronization in their activity periods [1]. Partitioning of time to reduce niche
4 overlap is a mechanism responsible for species coexistence [2]. Nevertheless, some
5 seasons are more suitable for species activities than others owing to the temporal
6 variation in the conditions affecting species activity patterns [3]. The activity of these
7 organisms is usually restricted to particular periods, whereas during the rest of the
8 year they are either inactive or engage in another part of their life cycle [4].
9 Consequently, time partitioning among species might be favoured by competitive
10 interactions or limited by physiological constraints.

11 In plant species, activity periods include leafing, flowering and fruiting times.
12 Thus, temporal patterns among co-occurring plants are classified as segregated,
13 aggregated or random. Environmental conditions and phylogeny are the key factors
14 affecting flowering times [5,6], although biotic factors may also influence
15 phenologies [7]. Segregated flowering times increase reproductive fitness through
16 decreased competition for pollinators, whereas aggregated patterns might be related to
17 limiting physiological constraints and an increasing conspicuousness of the floral
18 display that facilitates pollination [8]. Thus, traditional niche temporal analyses are
19 focussed on detecting whether phenologies exhibit random, segregated or aggregated
20 temporal patterns [9]. However, aggregated and segregated flowerings are only two of
21 the candidate theoretical patterns that might be observed in ecological communities.
22 Temporal nested patterns represent one of these alternative outcomes [10].

23 Temporal nested patterns [11] occur if some plant species have a flowering
24 season that includes other species' flowering periods. The flowering of the other
25 species then represents a subset of the flowering period occupied by the long-lasting

1 flowering species (Fig. 1). Thus, nestedness primarily reflects whether a community is
 2 characterised by broadly similar or differing responses to environmental variation
 3 [10]. Temporal nested aggregated patterns are expected if the optimum flowering time
 4 is the same for all species and some species have broader temporal niches (Fig. 1).
 5 Conversely, different optima may result from varying environmental conditions
 6 within the reproductive season that influence plants in divergent ways.

7 We characterised the flowering patterns of a semi-deciduous tropical forest as
 8 segregated, random and aggregated using a traditional approach. We then compared
 9 these results with those obtained using temporal nested analyses. We also evaluated
 10 the influence of climate and shared evolutionary history as constraints on plant
 11 flowering times. We used a temporal niche analysis to detect whether the entire plant
 12 community and the community without the long-lasting flowering species exhibited
 13 segregated (sequential flowering and reduced temporal overlap) (Fig. 1a), random (no
 14 particular trend in flowering phenologies) (Fig. 1b), or aggregated temporal patterns
 15 (species overlap greatly) (Fig. 1c). Finally, we applied nestedness analysis, previously
 16 used to characterise biogeographical patterns of species composition [11], species
 17 interactions [12], and niche variation within populations [13,14], to characterise
 18 temporal variation in species niches (Fig 1d).

19 2. MATERIAL AND METHODS

20 a) *Study site, phenology, seasonality and phylogeny*

21 The study was conducted at the Santa Genebra Reserve (SGR), a 250-ha semi-deciduous forest, near
 22 Campinas, SE Brazil. The climate is seasonal, with one rainy and one dry season [15] (Fig 2). The
 23 flowering phenology (open flowers) of trees, treelets, and climbers was recorded from 1989 to 1991
 24 [15]. The data analysed here are from [15].

25 We used principal component analysis (PCA) based on six environmental variables (rainfall, mean
 26 temperature, daylength, relative humidity, cloud cover and solar irradiation). The PCA components
 27 accounting for most of the variance were regressed against the percentage of species flowering in the

community.

We constructed the phylogeny using Phylomatic [16]. We assigned branch lengths to genera and species of the phylogenetic tree using the BLADJ averaging algorithm of the Phylocom software package. We tested for a phylogenetic signal in flowering length using the statistic K [17] (details in ESM).

b) *Temporal niche overlap*

We assessed temporal patterns of flowering for all plant species at the SGR and for the community without the long-lasting flowering species (more than ten months' flowering per year). We used a matrix in which cells represented the frequency of flowering of each species (rows) in a given month (columns). We applied a Monte Carlo approach and estimated temporal niche overlap using Pianka and Czechanowski indices [18]. Each index is symmetric and ranges from zero (no species overlap) to one (complete species overlap) [18]. We used the Rosario randomisation algorithm to shift the entire activity pattern of each species a random number of time intervals and calculate the amount of overlap in the randomly generated set of activity patterns [18]. We determined the significance level of the temporal niche pattern by comparing the empirical mean to a frequency distribution ($N = 10,000$ iterations) of such metrics derived from simulated assemblages for which the temporal patterns of species had been randomised [18].

c) *Temporal nestedness*

We calculated nestedness using the NODF metric [19]. We built a presence-absence matrix in which cells with ones indicated that a plant species (rows) flowers in a given month (column) and zeros indicated otherwise. To test the significance of the NODF values, we used a null model in which the probability of observing a plant species flowering in a given month was a function of the number of months in which the plant was flowering (null model 2, [12]). We ran the analyses for the whole community and for the community without the long-lasting flowering species.

3. RESULTS

Flowering in the community ($N=199$) occurred throughout the year, decreasing in the dry season (June-July) (Fig. 2). The first two PCA components explained 59% and 21% of the total variance, respectively, and were used in the regression analyses. Cloud cover, daylength, rainfall and temperature contributed most to the variation of

1 the first component and the relative humidity of the second component. We detected a
 2 significant effect of the two components on the proportion of plants flowering each
 3 month ($R^2 = 0.86$, $F=65.89$, $p < 0.001$).

4 Flowering length showed a weaker phylogenetic signal than expected by chance, that
 5 is, $K < 1$ ($K = 0.37$, $p = 0.025$).

6 The two indices of temporal overlap gave similar estimates, indicating aggregation,
 7 i.e., the distributions overlapped significantly. Accordingly, we found similar results
 8 for the entire community (Pianka Index=0.21, $p<0.0421$; Czekanowski Index= 0.15,
 9 $p<0.0008$), and without the long-lasting flowering species (Pianka Index=0.20,
 10 $p<0.0145$; Czekanowski Index= 0.15, $p<0.0003$).

11 The flowering pattern of the entire community was significantly nested (NODF =
 12 0.31, $p = 0.001$). The nested pattern emerged as a consequence of seven continuously
 13 flowering species (3.5% of all species). After these species were removed from the
 14 analysis, no evidence of significant nestedness remained (NODF = 0.27, $p = 0.073$).

15 **4. DISCUSSION**

16 Flowering occurred year-round but peaked during the wet season. The
 17 percentage of species flowering was positively influenced by the combined effect of
 18 cloud cover, daylength, rainfall, and temperature. For most Southeastern Brazilian
 19 forests, flowering is primarily related to daylength [20]. We found that the flowering
 20 of the entire community is organised in a particular type of aggregated pattern, the
 21 nested pattern.

22 Aggregation is expected owing to phylogenetic constraints because closely
 23 related species may exhibit similar environmental needs and concentrate reproduction
 24 in the same period as a result of physiological similarities [5]. Nevertheless, even
 25 when phylogeny constrains phenologies, flowering may be more related to climatic

1 variation throughout the year than to species relatedness [6]. We found no evidence
2 for effects of a shared evolutionary history on flowering patterns. This result indicates
3 that the similar flowering phenologies result from environmental conditions rather
4 than phylogenetic constraints [5,6].

5 Synchronous flowering has been associated with seasonal variation in
6 environmental conditions, such as irradiance [22], daylength and temperature [20,23].
7 Nevertheless, the flowering pattern of the SGR community is not just aggregated; it is
8 also nested. By removing the long-lasting flowering plants from our analysis, we were
9 able to identify the causes of nestedness in this community. Nestedness resulted from
10 the long phenologies of a small set of species in the community. These species show
11 flowering periods that include the shorter phenologies of all the other species in the
12 community, leading to nestedness.

13 Nestedness implies asymmetrical niche overlap and indicates that whereas
14 some species are restricted to narrow temporal windows, others occupy the whole
15 temporal niche. Asymmetrical overlap in the temporal niche could generate
16 asymmetrical competition interactions if pollinators are limiting resources. For
17 example, nestedness in trophic niche patterns was associated with asymmetrical
18 competitive interactions within populations [13,14]. The flowering phenology of the
19 more temporally restricted species is confined within the flowering span of the less
20 temporally restricted species. The latter species are not entirely confined to any other
21 species' flowering period.

22 Alternatively, nestedness could also reduce effective interspecific competition
23 and enhance the number of coexisting species [23]. For example, temporal nestedness
24 could facilitate the maintenance of pollinators over time. Facilitation is likely to occur
25 at the SRG if we consider that long-lasting flowering species belong to different

1 pollination modes (Fig. 2). Therefore, theoretical studies are needed to clarify the
 2 relationship between nestedness, competition, and facilitation. Independently of the
 3 ecological consequences of nestedness, the fact that long-lasting flowering species,
 4 which constitute <10% of tropical species [24,20], generated the nested pattern
 5 indicates a disproportionate role of these species in the temporal organisation of plant
 6 communities.

7 **ACKNOWLEDGEMENTS**

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1

1 Figure Legends

2 Fig. 1. Theoretical flowering scenarios of niche temporal patterns: a) segregated
3 pattern; b) random pattern; c) aggregated non-nested pattern; d) aggregated
4 nested pattern. Modified from [13].

5 Fig. 2. Climate (1956-1988), community pattern and flowering strategies of some
6 species and their pollination mode in the Santa Genebra Reserve
7 semideciduous forest, Campinas, Brazil. Data source: [20]. Bars indicate
8 rainfall and the red line the temperature.

Figure 1

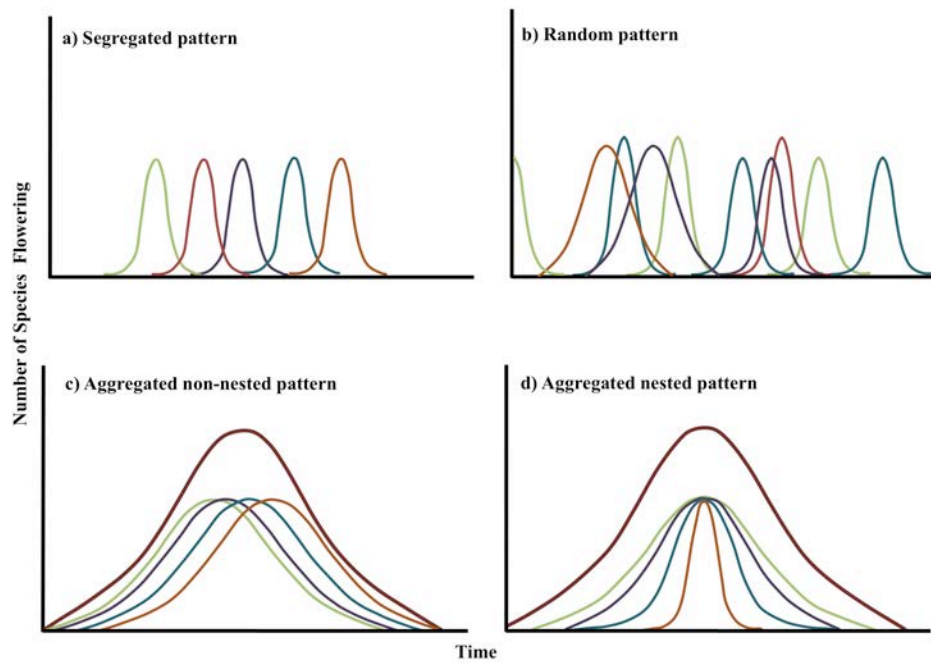
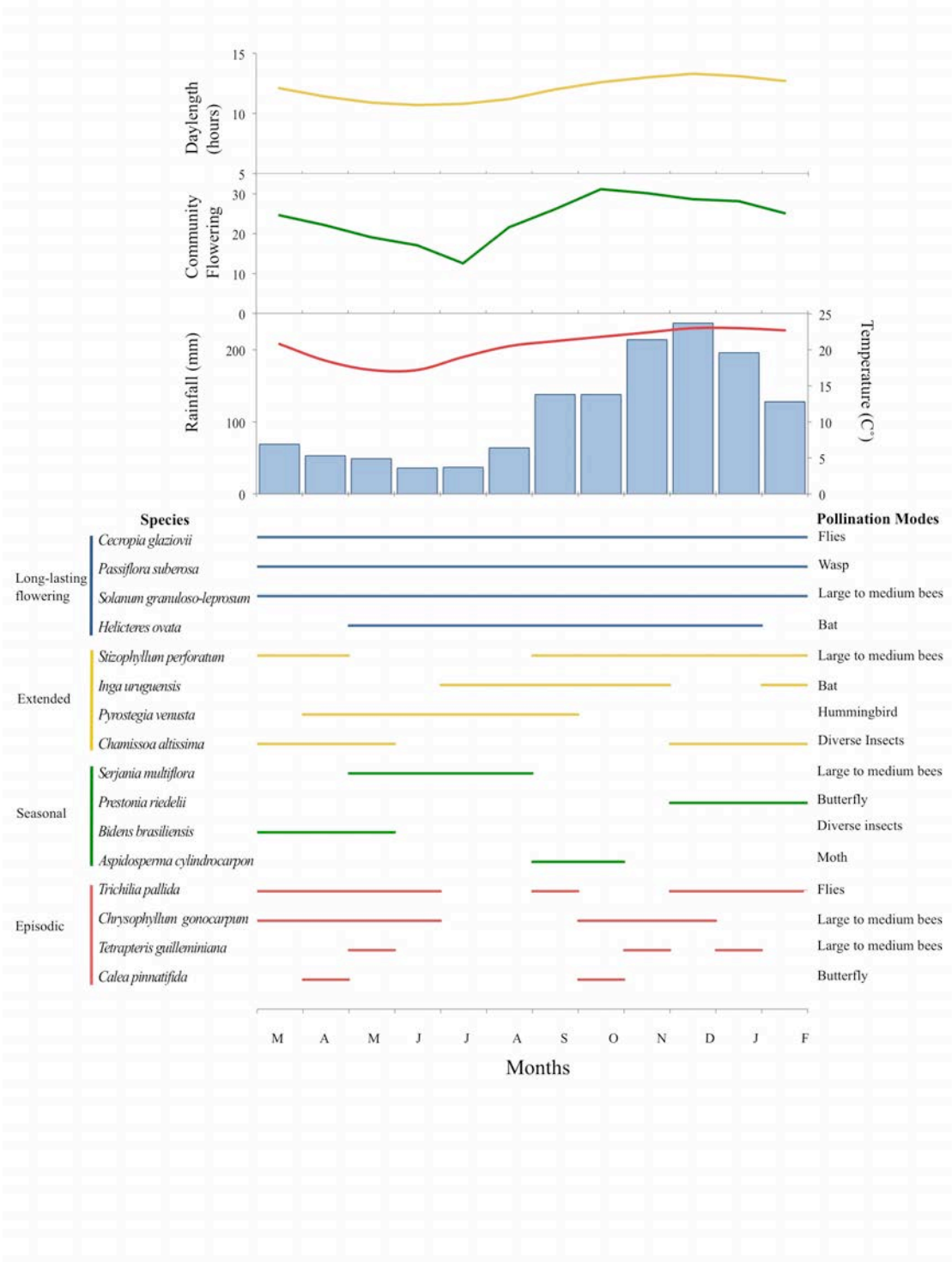


Figure 2



ELECTRONIC SUPPLEMENTARY MATERIAL*Phylogeny*

The names of plant species, genera and families are in accordance with the International Plant Names Index (<http://www.inpi.org:80/ipni/plantsnamesearchpage.do>) and the Tropicos Names database (<http://www.tropicos.org/NameSearch.aspx>). We constructed the species phylogeny using Phylomatic, a phylogenetic toolkit for the assembly of phylogenies [1]. 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) with respect to pollination mode, floral reward, habit and flowering length using the statistic K [2]. We took the categorised pollination modes, reward and habit of the species from [3] and assigned the corresponding category to each genus. We used four categories for reward (pollen, nectar, oil, and resin), and four habit categories (vine, climber, tree, and treelet, [3, 4]). Flowering length was the number of months a given plant genus was 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 [3]. A K of less than one implies that relatives resemble each other less than expected under Brownian motion evolution along the candidate tree [3]). $K > 1$ implies that close relatives are more similar than expected under Brownian conditions [3]. K was calculated by the R

package “picante” [5]. 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 [5].

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Capítulo 2

Temporal organization among pollination
modes in a Brazilian seasonal Forest

Temporal organization among pollination modes in a Brazilian seasonal forest

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Running title: Temporal organization among pollination modes

1 **ABSTRACT**

2 **Background and aims** Characterization of pollination modes and flowering patterns at a
 3 community level are fundamental to understand the seasonal variation of flowers, pollinators
 4 and their temporal organization in different vegetation types. Traditionally, temporal patterns
 5 are evaluated within one pollination mode albeit community level assessments are scarce.
 6 Therefore, this study aims to evaluate flowering patterns, diversity of pollination modes and
 7 their temporal organization in a semi-deciduous forest in south-eastern Brazil.

8 **Methods** We characterized pollination modes, and examined their flowering phenology and
 9 strategies. We identified climate factors and phylogenetic effects that may cue flowering. We
 10 compared flowering patterns against null models to determine if the phenologies of each
 11 pollination mode were segregated, random or aggregated; then, for the aggregated flowerings,
 12 we tested temporal nestedness. We grouped species pollination by flowering season (dry, wet,
 13 wet-to-dry and dry-to-wet transitions); we applied modularity analysis to independently group
 14 the proportion of species by pollination mode throughout the year.

15 **Key Results** Of the ten pollination modes described, large to medium bees (49.2 %) were
 16 dominant, followed by diverse insects (22.1 %), flies (14.7 %) and moths (10%). The
 17 remaining pollination modes accounted for the 4% species left (butterflies, hummingbirds,
 18 bats, wasps, and beetles). Flowering occurred year-round for almost all pollination modes.
 19 The predominant flowering strategy was seasonal but at least three types were found in every
 20 pollination mode. Large to medium bees, diverse insects, moth and butterfly pollination
 21 modes were aggregated, and only large to medium bees displayed temporal nestedness.
 22 Flowering of wasp, fly, small bees and vertebrate-pollinated species were random. Climate
 23 affected flowering of most pollination modes, except for diverse insects, small bees and bat-
 24 pollinated species and there was no effect of phylogeny on the evaluated traits. Finally, the

modularity analyses grouped the pollination modes into different periods compared to the four pre-established seasons.

Conclusions The diversity of pollination modes at the studied forest is comparable to other tropical forests and confirmed the importance of insect pollination. We demonstrated that each pollination mode displayed a particular flowering pattern, encompassing a diversified number of flowering strategies, and that most pollination modes are present throughout the year inspite ot climate seasonality, indicating a continuous resource supply for pollinators throughout the year.

1 INTRODUCTION

2 Among the explanations for the variation in diversity and level of the generalization of
 3 pollination modes are geographical location, vegetation life forms, taxonomic diversity, and
 4 suitability of environmental conditions for pollinator's activity (Bawa, 1990, Devy and
 5 Davidar, 2003; Kühn *et al.*, 2006). In addition, specific pollination modes may be more
 6 advantageous under different ecological conditions (Bawa, 1990; Kessler and Krömer, 2000).
 7 For instance, in a study of the distribution of pollination modes among forests with a wide
 8 range of environmental conditions, insect pollinated plants were dominant in dry forest
 9 regions, hummingbirds were more associated to high elevations and wetter habitats, whereas
 10 bats were more linked to humid tropical conditions (Kessler and Krömer, 2000).

11 In addition, the diversity and frequency of pollination modes may have seasonal
 12 variations (Ramirez, 2006). Thus, constancy of pollination modes throughout the year is
 13 expected to be more regular in aseasonal than in seasonal environments due to seasonality in
 14 flowering phenologies (Ramirez, 2006). The influence of seasonality on phenology patterns
 15 has been previously reported (van Schaik *et al.*, 1993; Wright, 1996; Zimmerman *et al.*,
 16 2007), and the effect of rainfall, light, temperature, and day length was confirmed (Wright and
 17 Van Shaick, 1994; Morellato *et al.* 2000; Calle *et al.*, 2010). Moreover, phylogeny is another
 18 factor known to influence phenology patterns (Kochmer and Handel, 1986; Staggemeier *et*
 19 *al.*, 2010).

20 Furthermore, biotic interactions influence phenology as well (Elzinga *et al.*, 2007).
 21 For example, pollinators and seed dispersers may structure flowering and fruiting onset,
 22 duration and synchrony (Frankie *et al.*, 1974; Heithaus *et al.*, 1974; Frankie, 1975; Stiles,
 23 1977, 1978; Waser, 1983; Bawa *et al.*, 1985; Bawa, 1990). Advantages and disadvantages of
 24 shifting flowering times have been addressed from the perspective of the competition and
 25 facilitation hypotheses (Pleasants, 1983; Waser, 1983; Wheelwright, 1985; Aizen and Rovere,

2010, Mitchell *et al.*, 2009). According to the former hypothesis, selection favours co-flowering species to shift their blooming times to reduce competition for pollinator services (Rathcke, 1983; 1988; Feinsinger, 1987; Armbruster, 1986; 1994; Borchsenius, 2002; Stone *et al.*, 1998). On the other hand, facilitation for pollinators denotes positive interactions due to resource sharing within a plant guild (Rathcke, 1983, Feinsinger, 1987). In that sense, an aggregated blooming may enhance or facilitate pollination by increasing the conspicuousness of the floral display (Schemske, 1981; Moeller, 2004).

Either way, most studies on temporal organization of co-occurring plant species and pollinator agents are limited to a few species or to particular guilds (Heithaus, 1974; Stiles 1977, 1978; Feinsinger *et al.* 1979, 1987, Augspurger, 1981). Studies focused on temporal patterns of species sharing the same pollination mode (i.e. same pollinator agent), as well as on the seasonal variation of pollination modes at a community scale are scarce (but see Ramirez, 2005; 2006).

Among the causes that may affect the extent of temporal overlap between pollination modes are the number of co-flowering species within each pollination mode, the diversity and availability of the pollination agents, and the characteristics of each pollination mode (Ramirez, 2005; Feinsinger, 1987). Besides, plants belonging in different pollination modes may display flowering strategies that meet their specific pollination agent's requirements. For instance, the sequential or extended flowering displayed by long lived animals such as hummingbirds and bats are hypothesised to be related to the maintenance of pollinators over time (Feinsinger, 1987; 1991; Aizen and Rovere, 2010; Waser, 1978; Aizen and Vázquez 2006; Rathke, 1983; Faria, 1996). On the other hand, seasonal or cornucopia flowering has been associated with large bees and/or butterfly-pollinated Bignoniaceae (Gentry, 1974).

Therefore, in this study we aim to analyse pollination diversity, flowering strategies and temporal organization in a semi-deciduous forest in south-eastern Brazil. First, we

describe the diversity of pollination modes, their flowering patterns and strategies. Second, we compare the species flowering against null models to determine if phenologies within pollination modes were segregated, random or aggregated, and test temporal nestedness for the aggregated flowerings. Then, we evaluate the influence of climate and phylogeny on flowering length and other ecological traits. Finally, we assess seasonal variation on the diversity of pollination modes throughout the year. Thus, we intent to answer: 1) does the temporal organization of flowering times differ among pollination modes? 2) is there any constancy of pollination modes along the year, since the seasonal climate would restrict flowering time and pollinator activity, and phylogenies may constraint flowering times? 3) is there a prevalent flowering pattern (aggregated, segregated or random) within each pollination mode indicating biotic cues to flowering at a community level, and are the aggregated patterns nested? 4) does the temporal organization of pollination modes differ if the species were arranged by the independent modularity grouping instead of grouping by seasonality?

MATERIAL AND METHODS

Study site

The Santa Genebra Reserve (SGR hereafter), is a 250-ha fragment of semi-deciduous forest, close to an urban area in Campinas (22°49'45"S; 47°06'33"W, 670 m.a.s.l.), São Paulo, south-eastern Brazil. The reserve includes three main types of vegetation: semi-deciduous forests, secondary vegetation, and swamp forest (Morellato and Leitão Filho, 1996; Sigrist 2004). 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 and two transitional periods or seasons, from March to April (wet-to-dry) and from September to October (dry-to-wet) (see Morellato, 1991; Morellato and Leitão- Filho, 1996, Figure 1 Supplementary Information). Both transitional seasons are characterized by variations in temperature and rainfall which affects plant phenology (Morellato 1991; Morellato and Leitão- Filho, 1996).

1 We report here the phenology and pollination modes of 199 plant species at SGR. The
 2 flowering phenology of trees, treelets, and climbers was recorded from 1988 to 1991
 3 (Morellato 1991; Morellato and Leitão Filho, 1996). Flowering was defined as the period in
 4 which the plant species bear open flowers (Morellato *et al.*, 1989). Plant species were
 5 characterized by their pollination modes according to Faegri and Pijl (1979), Jones and Little
 6 (1983) and Real (1983). Flower visitors and their behaviour were observed during the
 7 phenological records and on additional days. We also screened the literature for studies in
 8 pollination biology of all the species studied at the SGR to confirm the pollination modes of
 9 the species we observed and to determine the pollination mode of those species we were
 10 unable to assess based on our field observations [Table 1, Supplementary Information]. Other
 11 flower characteristics such as: colour, smell, position of flower elements, symmetry, reward
 12 to pollinators, time of anthesis, and receptivity of the stigma were also recorded and take into
 13 account to determine the pollination mode of each plant species. The plants were grouped in
 14 ten pollination modes [Table 1, Supplementary Information], which include the following
 15 agents: bats, hummingbirds, medium to large bees (larger than 10 mm), small bees (up to 10
 16 mm), beetles, butterflies, moths, flies, wasps and diverse insects (i.e. small bees, butterflies,
 17 moths and beetles, wasps, true bugs and other insects), this latter category is composed by
 18 generalist flowers visited by a wide variety of agents (adapted from Bawa *et al.*, 1985). Plant
 19 species that have more than one pollinator agent enter more than once in our calculations. We
 20 grouped species into five flowering strategies (Morellato 1991, adapted from Newstrom *et al.*
 21 1994): 1) continuous – blooming continuously along the year (10 months or more); 2)
 22 episodic – multiple blooming events during the year, separated by non-flowering phases of
 23 variable length; 3) brief – short flowerings during a few days up to four weeks; 4) seasonal –
 24 blooming lasts more than one up to four months associated to one season or the transitional
 25 periods between two seasons; and 5) extended – blooming of more than four months usually

associated to more than one season.

Niche temporal patterns of pollination modes

To identify the niche temporal patterns of flowering activity for each pollination mode 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 that have non-overlapping activity patterns, and equals 1 for species that have identical activity patterns (Castro-Arellano *et al.*, 2010). We employed the newly developed randomization algorithm Rosario (Castro-Arellano *et al.*, 2010). This algorithm does not remove the temporal autocorrelation in the data and perform random shifts 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 niche pattern by comparing the empirical mean to a frequency distribution of such metrics derived from simulated assemblages for which temporal patterns of species were randomized (Castro-Arellano *et al.*, 2010). Rosario used 10000 iterations to generate the null distributions and determine significance with a α -level of 0.05 (Castro-Arellano *et al.*, 2010).

Temporal nestedness

Temporal nestedness is expected when plants display similar responses and share the same optimum time for reproduction (Genini *et al.*, unpublished). As aggregation is a prerequisite for temporal nestedness we only run this analysis for the pollination modes that displayed aggregated patterns. We employed 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 CE (Bascompte *et al.*, 2003) to test for the significance of *NODF*. In CE, 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 (Bascompte *et al.*, 2003; Guimarães and Guimarães, 2006).

Climate

To assess the influence of environmental factors on the phenology of each pollination mode we carried out a principal components 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 dependent variable (i.e. percentage of species flowering in each pollination mode).

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, which is a phylogenetic toolkit for the assembly of phylogenies (Webb & 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 mode, floral reward, habit, and flowering

length using the statistic K (Blomberg *et al.*, 2003). We categorized pollination modes, reward and habit 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 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 of the diversity of pollination modes

To assess seasonal variation of the diversity of pollination modes we used two approaches: grouping by season and using modular analysis.

Season grouping

We grouped 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 seasons and classified species in relation to their pollination mode. Then, we calculated the proportion of species in each pollination mode 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 the blooming period.

Modularity grouping

To obtain an independent grouping of plants apart from pre defined seasons we used a modular analysis. We aimed to identify groups of plants and months that are associated with each other. We pooled the 2yr phenology data of plant species as an adjacency matrix depicting the relationships between the time slices (months) and the flowering phenology of the plants. Each matrix element $r_{ij} = 1$, if plant species i flowers in the month j and zero otherwise (Bascompte *et al.* 2003). We used netcarto software to test for modularity (Guimerà and Amaral, 2005). The program employs Guimerà's algorithm, which is based on simulated annealing to identify the modules and to compute modularity. Modularity M range from 0 to 1 ($1 - 1/\text{number of modules}$), 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 significance level of the observed M .

RESULTS

Pollination modes, flowering phenology and strategies

Pollination by large to medium bees was the dominant mode at the RSG (49.2%), followed by diverse insects (22.1%), flies (14.7%) and moths (8%) (Table1). Blooming of most modes was seasonal but occurred throughout the year, with a reduced proportion of species in the dry season (June-July). 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 mode at the SGR, displayed a well-defined flowering peak in the dry season and a minor peak in the rainy season (Fig. 1b). Similarly to large to medium bees, seasonal flowering was the predominant strategy of plants pollinated by diverse insect, encompassing 70% of species (Table 2). Fly-pollinated flowers displayed a minor peak from March to May and a major peak from November to January (Fig. 1c), and most species also presented seasonal strategy (Table 2).

All flowering strategies were represented in the previous pollination modes, regardless if the flowering was less or more concentrated in a specific time of the year, followed by plants with brief and continuous strategies (Table 2). Plants pollinated by butterflies and moths were flowering mainly in the wet season, (Fig. 1d-e). However, moth-pollinated plants presented a pronounced peak in the dry-to-wet season transition, whereas blooming peak of butterfly-pollinated species was less pronounced, lasting from December to March (Fig. 1d-e). The seasonal flowering strategies prevailed again for both pollination modes with 70% of species; 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 modes 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 plants showed continuous, extended, and episodic flowerings, although seasonal strategies were still dominant (Table 2). Most hummingbird-pollinated plants also displayed a seasonal flowering strategy (Table 2). Bat-pollination mode 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.

Niche temporal patterns of the pollination modes

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

Temporal nestedness

In the tests for temporal nestedness for those pollination modes that showed aggregated flowerings (i.e. large to medium bees, diverse insects, moths and butterflies), we only found a

significant nested pattern for large to medium bees pollination mode ($\text{NODF}=0.33$, $p=0.012$) whereas the other aggregated pollination modes were not nested ($\text{NODF}_{\text{Div.Insects}}=0.235$, $p=0.125$; $\text{NODF}_{\text{Moths}}=0.243$, $p=0.78$; $\text{NODF}_{\text{Butterflies}}=0.15$, $p=1$).

Seasonality

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

Phylogenetic signal

All traits showed a weaker phylogenetic signal than expected, that is, $K < 1$ (Pollination mode: $K= 0.34$, $p = 0.001$; Reward: $K = 0.56$, $p = 0.001$; Habit: $K = 0.38$, $p = 0.001$; and Flowering length: $K = 0.37$, $p = 0.025$). Thus, species were more different than could be explained by phylogeny alone.

Seasonal variation in the diversity of pollination modes

Plants from all the pollination modes were blooming every season, except for beetle-pollinated plants, which flowered in the dry-to-wet season transition and in the rainy season; all pollination modes were present in the wet season (Figure 2). In general, the best

represented pollination modes in the community (large to medium bees, diverse insects, flies and small bees) were also the best represented in each season (Fig 2) [Table 1, Supplementary Information]. Accordingly, the less represented pollination modes were poorly represented in each season (Table 1, Figure 2). Nevertheless, the proportion of plants flowering in each of the pollination modes varied seasonally [Table 2, Supplementary Information]. For instance, more plant species from the large to medium bees, butterfly and wasp-pollination modes 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 modes displayed higher proportion of species flowering in the dry season (Fig 2) [Table 2, Supplementary Information]. Thus, even when the whole diversity of pollination modes is present year round, flowering seasonality influences the abundance of each pollination mode in every season.

We obtained four modules of three months each ($M = 0.44$; $p < 0.001$) grouping plant species' flowering time by their affinity with months (i.e. plants that flowered in particular months). The first module corresponded to April-June, the second to January-March, the third to July-September and the fourth to October-December. The proportion of plant species from each pollination mode in each module is shown in Figure 3. Similarly, when we grouped species by seasons, most pollination modes were present in all modules, although proportions also varied from one period to the other [Table 3 Supplementary Information]. Large to medium bees, diverse insects, flies and small bees were the best represented pollination modes in each period. Beetles were restricted to one module ($M4 =$ October-December), which coincided with the end of dry-to-wet transitional period and the onset of rainy season. Butterflies were absent from July to September ($M3$), and moths from April to June ($M1$).

DISCUSSION

Our study demonstrated that the SGR tropical semi-deciduous forest has a high

diversity of pollination modes, comparable to other tropical systems, and that this diversity is represented across the seasons, since climate and phylogeny did not restrict the flowering of most plants regardless of the pollination mode. We also demonstrated that although seasonal blooming strategy predominates, the flowering patterns differed among pollination modes, which indicates that the conditions of some seasons favoured blooming of different species and habits. Additionally, just four out of the 10 pollination modes showed aggregated niche temporal pattern and only large to medium bees had significant temporal nestedness. Finally, seasonality and modularity groupings differed, which indicates the importance of independent grouping method and the relevance of the traditional wet (October to March) and dry (April to September) seasons instead of transitional periods to temporal organization of tropical communities (Snow, 1967; Morellato and Leitão-Filho, 1996).

The proportion of pollination modes at the SGR agrees with those found in other tropical forests (e.g. Table 1): large to medium bees 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 *et al.*, 2006). In our study, the dominance of bee-pollinated plants is also associated to the high proportion of climber species, which are mostly bee-pollinated (Morellato, 1991; Morellato and Leitão Filho, 1996). On the other hand, moth-pollinated species are here underrepresented when compared to tropical rainforests (Bawa *et al.*, 1985, Table 2), but are comparable to those of the seasonal Cerrado savannah vegetation (Oliveira *et al.*, 2004). The proportion of the other pollination modes at SGR semi-deciduous forest is similar to that found in other tropical forests (Bawa *et al.*, 1985, 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

1 Annonaceae (Bawa, 1990; Morellato, 1991; Momose *et al.*, 1998) [see also Supplementary
2 Information].

3 The highest diversity of flowering strategies at SGR also occurred in large to medium
4 bees and fly pollination modes, yet at least three types of strategies were present in all
5 pollination modes. In fact, seasonal strategy predominated among all pollination modes but
6 bats. Despite of the seasonal flowering, pollination by large to medium bees was dominant in
7 every season, suggesting a wide temporal niche. Plant species pollinated by large to medium
8 bees embrace a large diversity of pollination strategies, whose flowers include resources such
9 as oil, pollen, resin, and odouriferous substances besides nectar [Supplementary Information].
10 Bee-pollination mode is the most abundant one in the Venezuelan Central Plain, and is also
11 related to the highest diversity of pollination strategies and vectors (Ramirez, 2005). The
12 occurrence of bee-pollinated plants flowering all year round at the SGR is also associated to
13 the variety of flowering strategies displayed by different species and life forms within this
14 pollination mode, as recorded for other communities as well (Ramirez, 2005; Kato *et al.*,
15 2008). For instance, at the SGR lianas bloom mainly during the wet-to-dry season transition
16 and dry season, whereas trees and treelets concentrate flowering in the dry-to-wet season
17 transition (Morellato and Leitão-Filho, 1996).

18 At the SGR forest, we found aggregated temporal patterns for large to medium bees,
19 diverse insects, butterfly, and moth-pollination, which supports the dominant seasonal
20 flowerings. Besides being aggregated, the flowering of the plants within the large to medium
21 bees pollination mode was nested, which indicates a unique optimum time for reproduction.
22 The apparent contradiction between this result and our above statement of broad temporal
23 niche is explained by the continuous flowering strategy of three species within this pollination
24 mode. We demonstrated that a few long-lasting flowering species have a disproportional
25 effect on SGR community blossoming patterns and that nestedness arises as a result of their

1 influence (Genini *et al.*, pers. obs.).

2 On the other hand, lack of temporal nestedness for moth, butterfly and diverse insects
3 pollination modes suggests that, despite their aggregated patterns, they may have different
4 optimums times for reproduction (Genini *et al.*, pers. obs.). At the SGR, similarly to that
5 recorded in other seasonal forests, moth- and butterfly-pollinated plants flowered during the
6 rainy season when these vectors are more abundant (Frankie, 1975; Haber, 1989; Brown and
7 Freitas, 2000, Ramirez, 2006; Kato *et al.*, 2008). Butterfly and moth populations dynamics in
8 the tropics usually face extremely seasonal environments with marked wet and dry seasons,
9 and their abundance and survival is expected to decrease in the dry season due to scarcity of
10 water, nectar, and fresh new leaves (Bonebrake *et al.*, 2010; Brown and Freitas, 2000;
11 Hussain *et al.*, 2011). Flowering of beetle-pollinated plants was also restricted to the rainy
12 season, as already recorded for other seasonal vegetations (Gostberger, 1989; Ramirez,
13 2006). Conversely, the seasonal flowering of diverse insects-pollinated plants was not
14 affected by the environmental variables evaluated in our study, since it includes a variety of
15 pollination agents that may respond in different ways to environmental cues.

16 At the SGR, blooming of fly, small bees, wasp, and vertebrate-pollinated plants was
17 recorded in all the seasons, without an evident peak of activity, resulting on a broad temporal
18 niche that is not segregated nor aggregated. The irregular and uncertain patterns of fly-
19 pollinated plants have been related to the behaviour of these insects, which do not use flower
20 resources to feed their offspring, and to the fact that these plants are visited by a great variety
21 of other insects (Proctor *et al.*, 1996; Pombal and Morellato 1995; 2000). The aseasonal
22 flowering of wasp-pollinated plants may be related to the predominance of *Ficus* species,
23 since the typical phenological pattern of *Ficus* is annual or supra-annual at the individual
24 level, integrated into a continuous pattern at the population level (Sakai *et al.*, 1999).

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

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 predominant flowering strategy of plants along the year, specially if we consider the moths, butterflies, and beetles grouping. The appearance and abundance of certain pollination modes is influenced by flowering phenology since some pollinators may change their behaviour in response to the availability of flowering species, switching to other resources or migrating when resources are scarce (Sazima *et al.*, 1999; Devy and Davidar, 2003; Kato *et al.*, 2008; Ramirez, 2006). In seasonal forests, a higher diversity of pollination modes is expected during peak flowering periods and, consequently, as diversity of resources increases consumer diversity increases as well (Ramirez, 2006). In our study, most pollination modes were evenly represented along the seasons even when their abundances were variable. The constancy of pollination modes along the year may be related to differences in flowering peaks among life forms that promotes the coexistence of various pollination modes (Ramirez, 2006).

In conclusion, our study is the first one to consider temporal organization of pollination modes in a tropical community and its ecological and evolutionary constraints. We demonstrates the importance of climate seasonality, in the temporal organization of pollination modes. We also show that, In seasonal forests, a higher diversity of pollination modes is expected during peak flowering periods and, consequently, as diversity of resources increases consumer diversity increases as well, and may reduce competition for pollinators and facilitate the use of resources by pollinators year round.

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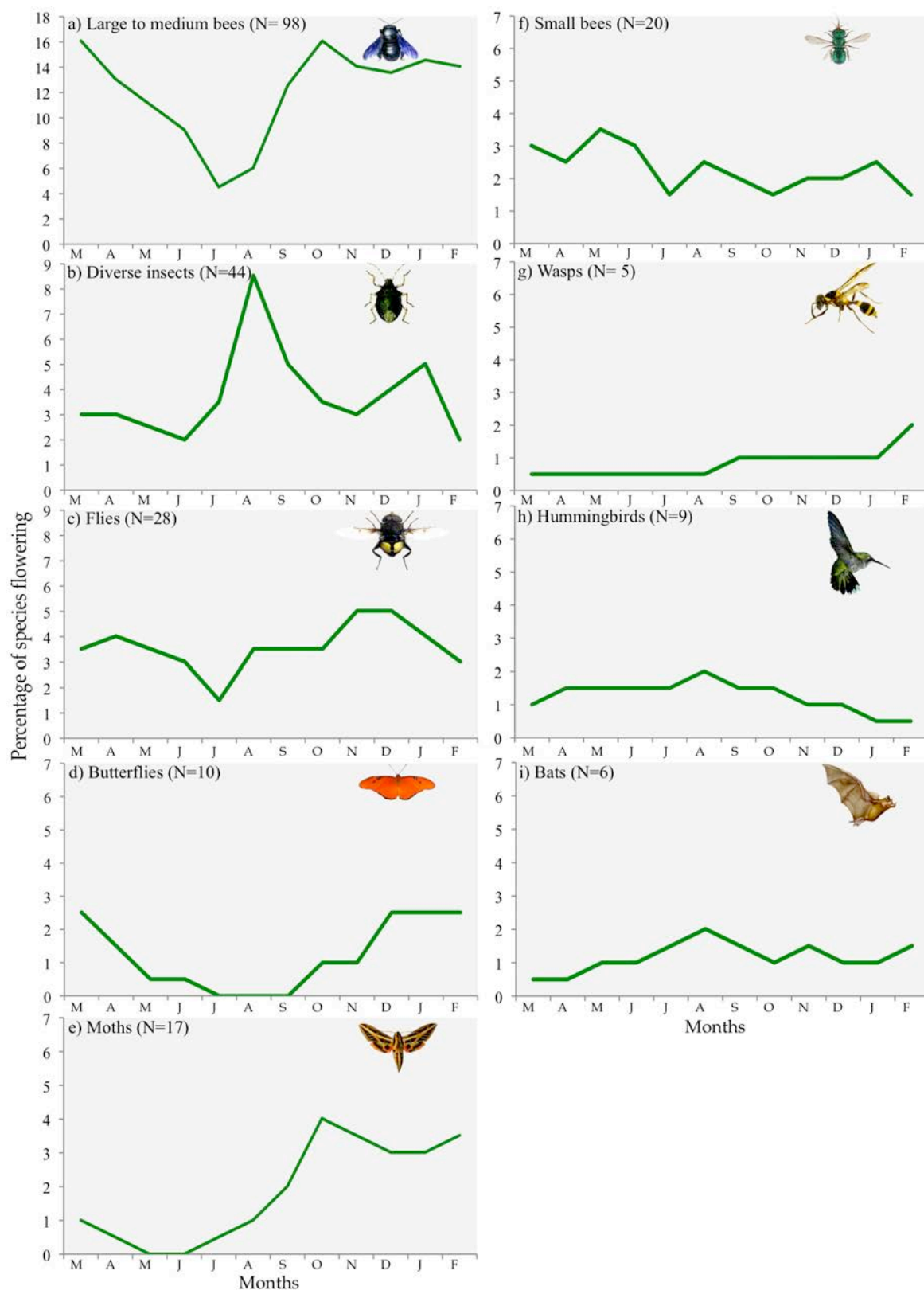


Figure 1. Percentage of plant species flowering in each pollination mode throughout the year at the SGR semi-deciduous forest, south-eastern Brazil. Note the different scale for.

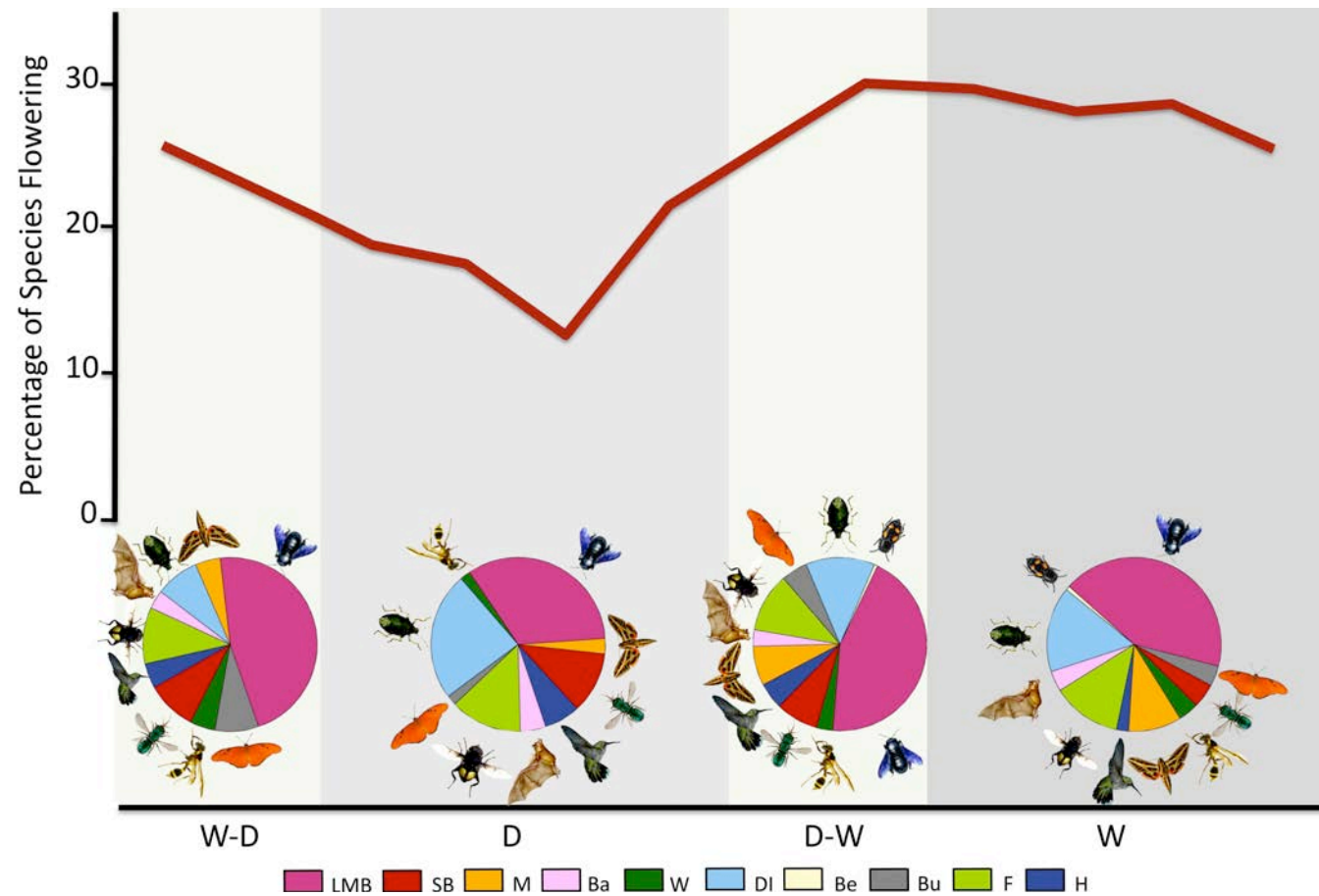


Figure 2. Percentage of plant species flowering in the community (red line) and their proportion by pollination mode according to the seasons (W-D = wet-to-dry transition, D= dry season, D-W= dry-to-wet transition, W= wet season) at the SGR semi-deciduous forest, south-eastern Brazil. LMB= large to medium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

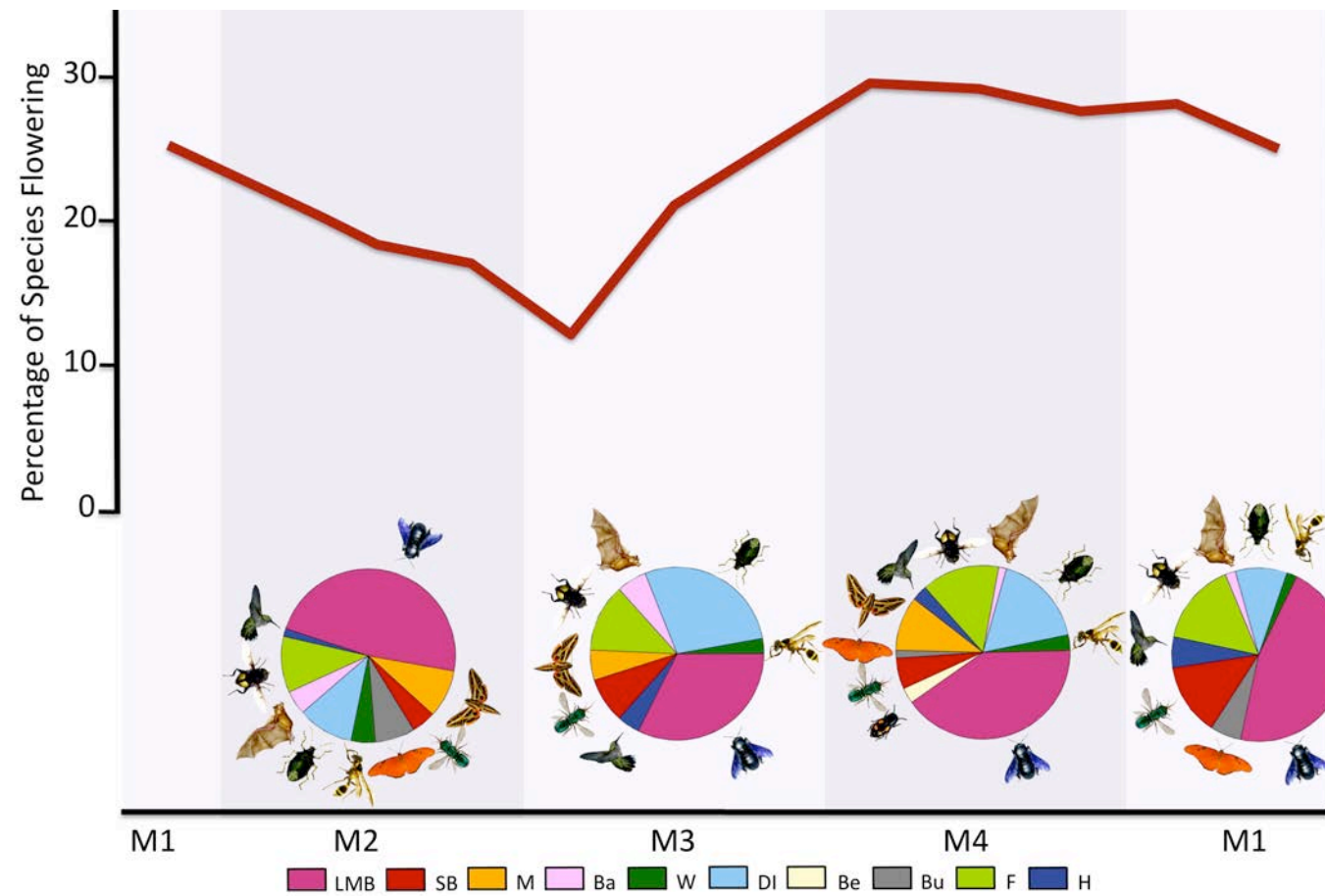


Figure 3. Percentage of plant species flowering in the community (red line) and their proportion by pollination mode according to the independent modules (M1= module1 January to March; M2= module2 April to June; M3= module3 July to September, M4= module4 October-November) at the SGR semi-deciduous forest, 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.

Table 1. Comparison of the proportion of plant species in each pollination mode at four tropical forests.

Percentage of Species	Tropical Lowland Rain Forest (N = 143) Costa Rica (Bawa <i>et al.</i> , 1985)*	Cloud Forest (N = 155) Venezuela (Ramirez, 2004)*	Lowland Dipterocarp Forest (N = 141 ^b) Laos (Kato <i>et al.</i> , 2008)*	Semi-deciduous Forest (N = 199) Brazil (This Study) ^c
Large to medium bees	27.5	73.1 ^a	33.3	49.2
Diverse Insects	15.8	0.0	15.6	22.1
Flies	0.0	2.8	4.3	13.6
Moths	15.9	8.3	5.7	8.0
Hummingbirds	4.3	0.0	0.0	4.5
Small bees	14.0	---	17.7	10.1
Butterflies	4.9	4.2	14.9	5.0
Bats	3.0	2.8	2.2	3.0
Wasps	4.3	0.0	1.4	2.5
Beetles	7.3	2.8	4.9	1.0
Birds	0.0	2.80	---	0.0

* Calculated for 1 pollen vector type, ^a corresponds to all bees, ^b corresponds to zoophilous species, ^c plants with more than one pollination mode were included more than once.

Table 2. Number of plant species (N) by pollination mode and the proportion of distribution according to the flowering strategy at the SGR semi-deciduous forest, south-eastern Brazil.

Pollination mode	N	Flowering Strategy				
		Continuous	Extended	Seasonal	Episodic	Brief
Large to medium bees	98	3.1	11.2	65.3	4.1	16.3
Diverse insects	44	0.0	2.3	70.4	9.1	18.2
Flies	28	7.1	7.1	60.7	3.6	21.5
Moths	17	0.0	23.5	70.6	0.0	5.9
Hummingbirds	9	0.0	33.3	55.6	0.0	11.1
Small bees	20	0.0	10.0	70.0	5.0	15.0
Butterflies	10	0.0	20.0	70.0	0.0	10.0
Bats	6	16.7	50.0	33.3	0.0	0.0
Wasps	5	20.0	20.0	40.0	20.0	0.0
Beetles	2	0.0	0.0	50.0	0.0	50.0

Table 3. Niche temporal flowering pattern for Czechanowski and Pianka Index for each pollination mode at the SGR semi-deciduous forest, south-eastern Brazil.

Pollination modes	Pianka Index	p value	Czechanowski Index	p value
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	0.2	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 (shaded areas) 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 and the percentage of plant species flowering at the SGR semi-deciduous forest, south-eastern Brazil.

Response Variables	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.

SUPPLEMENTARY INFORMATION

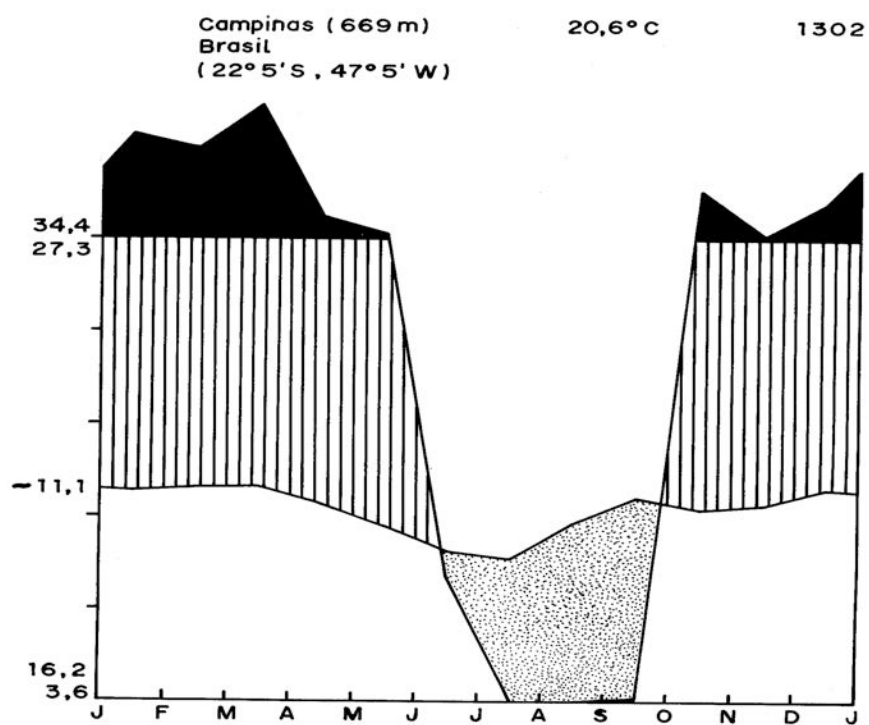


Figure 1. Climatic diagram of the SGR semideciduous forest, south-eastern Brazil, following the convention of Walther and Lieth (1960) for 1965-1987.

Table 1. Phenological data and features associated to pollination of the plant species studied at the SGR semi-deciduous forest, south-eastern Brazil. Pollination mode: B= bats; Be= beetles; Bu= butterflies; DI= diverse insects; F= flies; H= hummingbirds; LMB= large to medium bees; M= moths; SB= small bees; W= wasps. Reward: d= deceit; fp= floral parts; n= nectar; o= oil; os= odoriferous substances; p= pollen; r= resin; sh= shelter; unk= unknown. Pollination mode was determined according to floral morphology, field observations, pollination studies at the SGR, or in the literature for the same species or genus in other areas. Family and species names in alphabetical order.

Family/Species	Flowering	Pollination Mode	Reward	Habit
ACANTHACEAE				
<i>Mendoncia puberula</i>	De - Jun	LMB	n/p	vine
<i>Mendoncia velloziana</i>	Au - De	H	n	vine
AMARANTHACEAE				
<i>Chamissoa altissima</i>	De - May	DI, F	n/p	vine
<i>Pfaffia paniculata</i>	Jul - Au	DI	n/p	vine
ANACARDIACEAE				
<i>Astronium graveolens</i>	Au - Sep	SB, DI	n	tree
<i>Lithrea molleoides</i>	Au - Sep	SB	n	tree
<i>Tapirira guianensis</i>	Sep - No	F, DI	n/p	tree
ANNONACEAE				
<i>Annona cacans</i>	Oc - No	Be	p/fp	tree
APOCYNACEAE				
<i>Aspidosperma cylindrocarpon</i>	Sep - No	M	n	tree
<i>Aspidosperma polyneuron</i>	Oc - Dec	M	n	tree
<i>Aspidosperma ramiflorum</i>	Sep - Oc	M	n	tree
<i>Gonolobus rostratus</i>	No	LMB	n	vine
<i>Metastelma burchellii</i>	Ma	LMB	n	vine
<i>Orthosia</i>	Oc	LMB	n	vine
<i>Oxypetalum appendiculatum</i>	Ja	DI	n	vine
<i>Oxypetalum molle</i>	May	DI	n	vine
<i>Prestonia coalita</i>	No - Ma	LMB, Bu	n	vine
<i>Prestonia riedelii</i>	De - Fe	Bu, LMB	n	liana
<i>Prestonia tomentosa</i>	Ma	Bu, LMB	n	liana
<i>Tassadia propinqua</i>	Ja	LMB	n	vine
ARALIACEAE				
<i>Dendropanax cuneatus</i>	May - Jul	F	n	tree
ARECACEAE				
<i>Euterpe edulis</i>	No - De	DI	n	tree
<i>Syagrus romanzoffiana</i>	No - Ap	SB	n	tree
ARISTOLOCHIACEAE				
<i>Aristolochia arcuata</i>	Jun; No	F	n	vine
<i>Aristolochia labiata</i>	Oc; Fe	F	n	liana
ASTERACEAE				
<i>Bidens brasiliensis</i>	Ma - May	DI	n/p	vine

<i>Calea pinnatifida</i>	Ap; Oc	Bu	n	liana
<i>Dasyphyllum brasiliense</i>	Jun - Jul	DI	n	liana
<i>Dasyphyllum spinescens</i>	Jun - Au	DI	n	liana
<i>Gochnatia polymorpha</i>	Jul - Au, No - Fe, Sep - Oc; De	DI	n	tree
<i>Heterocondylus vitalbae</i>	Au - Sep	DI, F	n/p	vine
<i>Mikania banisteriae</i>	Jul - Au	DI	n	liana
<i>Mikania cynanchifolia</i>	Au	DI	n	vine
<i>Mikania glomerata</i>	Au	DI, F	n/p	liana
<i>Mikania micrantha</i>	Ap - May	DI, F	n/p	vine
<i>Mikania triangularis</i>	Au	DI, F	n/p	liana
<i>Mutisia coccinea</i>	Jun - Au	H	n	liana
<i>Piptocarpha axilaris</i>	Au - Oc	DI	n	tree
<i>Trixis antimenorrhoea</i>	Au	DI, F	n/p	vine
<i>Vernonia erigeroides</i>	Au - Sep	DI	n	tree
BIGNONIACEAE				
<i>Adenocalymma bracteatum</i>	Ap - De	LMB	n	liana
<i>Adenocalymma marginatum</i>	Ja	LMB	n	liana
<i>Amphilophium paniculatum</i>	No - Ja	LMB	n	liana
<i>Amphilophium crucigerum</i>	De - Fe	LMB	n	liana
<i>Anemopaegma chamberlaynii</i>	Mar - May; No	LMB	n	liana
<i>Arrabidaea triplinervia</i>	Fe - Ap	LMB	n	liana
<i>Bignonia campanulata</i>	Oc - De; Ma - Jun	LMB	n	liana
<i>Cuspidaria floribunda</i>	Fe - Ma; Jun	LMB	n	liana
<i>Cuspidaria pterocarpa</i>	Sep	LMB	n	liana
<i>Dolichandra unguis-cati</i>	Sep - No	LMB	n	liana
<i>Fridericia samydoides</i>	No - De	LMB	n	liana
<i>Fridericia speciosa</i>	Oc - Ja	H	n	liana
<i>Handroanthus umbellatus</i>	Sep - Oc	LMB	n	tree
<i>Lundia nitidula</i>	Fe	LMB	n	liana
<i>Lundia obliqua</i>	Fe - Jun	LMB	n	liana
<i>Mansoa difficilis</i>	Sep - De	LMB	n	liana
<i>Paragonia pyramidata</i>	Oc	LMB	n	liana
<i>Pleonotoma tetraquetra</i>	Sep	LMB	n	liana
<i>Pyrostegia venusta</i>	May - Oc	H	n	vine
<i>Stizophyllum perforatum</i>	Sep - Ap	LMB	n	liana
<i>Tanaecium selloi</i>	De	LMB	n	liana
<i>Tynnanthus cognatus</i>	No - De	LMB	n	liana
<i>Tynnanthus fasciculatus</i>	Sep - Oc	LMB	n	liana
<i>Zeyheria tuberculosa</i>	Oc - Ja	LMB	n	tree
BORAGINACEAE				
<i>Cordia ecalyculata</i>	No - De	M, F	n	tree
BURSERACEAE				
<i>Protium heptaphyllum</i>	Sep; Oc	DI	n	tree
CACTACEAE				
<i>Pereskia aculeata</i>	Ja - Ma	LMB	n/p	liana

CARICACEAE

<i>Jacaratia spinosa</i>	Oc - No	M	n	tree
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CELASTRACEAE

<i>Maytenus ilicifolia</i>	De	DI	n	treelet
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CONVOLVULACEAE

<i>Ipomoea cairica</i>	Ap - May	LMB	n	vine
<i>Ipomoea hederifolia</i>	Ap - Jun	H, Bu	n	vine
<i>Ipomoea indica</i>	Feb - Ap	LMB	n	vine
<i>Ipomoea quamoclit</i>	Ma - Ap	Bu, H	n	vine
<i>Merremia macrocalyx</i>	Ap - Jun	LMB	n	vine

CUCURBITACEAE

<i>Melothria pendula</i>	Ma, Au - Sep	SB	unk	vine
<i>Momordica charantia</i>	No - Ap	SB	n	vine
<i>Wilbrandia hibiscoides</i>	De - Jun	SB	unk	vine

DIOSCOREACEAE

<i>Dioscorea multiflora</i>	Ap	F	n	vine
<i>Dioscorea pseudomacrocapsa</i>	Ma; No	F	n	vine

EUPHORBIACEAE

<i>Croton floribundus</i>	Oc - De	F	n/p	tree
<i>Croton salutaris</i>	Oc - Ja	F, SB	n/p	tree
<i>Dalechampia olfersiana</i>	Jul	LMB	r	liana
<i>Dalechampia pentaphylla</i>	Sep - Jun	LMB	r	liana
<i>Dalechampia stipulacea</i>	Jun - Oc	LMB	r	liana
<i>Dalechampia triphylla</i>	Jun	LMB	r	liana
<i>Pachystroma longifolium</i>	De - Ja	DI	n/p	tree

LECYTHIDACEAE

<i>Cariniana estrellensis</i>	No	LMB	n	tree
<i>Cariniana legalis</i>	Ja - Fe	LMB	n	tree

FABACEAE

<i>Bauhinia rufa</i>	Oc - May	Ba	n/p	shrub/treelet
<i>Cassia ferruginea</i>	Oc - Ja	LMB	p	tree
<i>Copaifera langsdorffii</i>	De - Ja	LMB	n	tree
<i>Hymenaea courbaril</i>	Oc - No	LMB	n/p	tree
<i>Schizolobium parahyba</i>	Se - No	LMB	n	tree
<i>Canavalia parviflora</i>	Ma - Ap	LMB	n	liana
<i>Canavalia picta</i>	Ap - May	LMB	n	liana
<i>Centrolobium tomentosum</i>	Ja - Ma	LMB	n	tree
<i>Dalbergia frutescens</i>	Oc - No	LMB	n/p	liana
<i>Dioclea rufescens</i>	Oc - No	LMB	n	liana
<i>Dioclea violacea</i>	Fe - Ma	LMB	n	liana
<i>Erythrina falcata</i>	Jul - Sep	H	n	tree
<i>Lonchocarpus guillemineanus</i>	No - De	LMB	n	tree
<i>Luetzelburgia guaissara</i>	De - Ma	LMB	n	tree
<i>Machaerium nyctitans</i>	Ma	LMB	n	tree
<i>Myroxylon peruiferum</i>	Jul - Au	LMB	n	tree
<i>Platypodium elegans</i>	Oc - De	LMB	n	tree

<i>Vigna candida</i>	De - Ap	LMB	n	vine
<i>Acacia polyphylla</i>	Ja	M, Bu	n	tree
<i>Inga luschnathiana</i>	Sep - Ma	M	n	tree
<i>Inga marginata</i>	Au	M	n	tree
<i>Inga uruguensis</i>	Jul - No; Fe	Ba, M	n	tree
<i>Piptadenia gonoacantha</i>	No - Ma	M	n/p	tree
MAGNOLIACEAE				
<i>Magnolia ovata</i>	No - Dec.	Be	p/fp	tree
MALPIGHIACEAE				
<i>Alicia anisopetala</i>	Ma - Jun	LMB	o/p	liana
<i>Banisteriopsis adenopoda</i>	Ja - Ap	LMB	o/p	liana
<i>Banisteriopsis anisandra</i>	Sep	LMB	o/p	liana
<i>Banisteriopsis argyrophylla</i>	Ma - May	LMB	o/p	liana
<i>Banisteriopsis muricata</i>	Fe - Ap	LMB	o/p	liana
<i>Dicella bracteosa</i>	Au - Fe	LMB	o/p	liana
<i>Diplopterys lutea</i>	Au - Oc	LMB	o/p	liana
<i>Diplopterys pubipetala</i>	Oc	LMB	o/p	liana
<i>Heteropterys bicolor</i>	Oc - No	LMB	o/p	liana
<i>Heteropterys intermedia</i>	Ma; De	LMB	o/p	liana
<i>Heteropterys orinocensis</i>	Au - Oc	LMB	o/p	liana
<i>Mascagnia cordifolia</i>	Sep - Oc	LMB	o/p	liana
<i>Mascagnia sepium</i>	Sep - Oc	LMB	o/p	liana
<i>Stigmaphyllon lalandianum</i>	Ja - Ap	LMB	o/p	liana
<i>Tetrapteris cotoneaster</i>	Ja; May; No	LMB	o/p	liana
<i>Tetrapteris xylosteifolia</i>	Sep	LMB	o/p	liana
MALVACEAE				
<i>Ceiba speciosa</i>	Fe - Ap	H, Ba, Bu	n	tree
<i>Pseudobombax grandiflorum</i>	Jun - Se	Ba	n	tree
MELIACEAE				
<i>Cabralea canjerana</i>	Se - Oc	M	n	tree
<i>Cedrela fissilis</i>	Oc	M	n	tree
<i>Guarea macrophylla</i>	Oc - Fe	M	n	tree
<i>Trichilia catigua</i>	Ma - Jun	F	n	tree
<i>Trichilia claussenii</i>	Sep	F	n/p	tree
<i>Trichilia hirta</i>	No	DI, F	n	tree
<i>Trichilia pallida</i>	De - Jun, Au - Sep	F, DI	n/p	tree
MORACEAE				
<i>Ficus enormis</i>	Ja - Ap	W	sh	tree
<i>Ficus eximia</i>	Fe - Ap	W	sh	tree
<i>Ficus luschnathiana</i>	Ap; Jul - No	W	sh	tree
MYRTACEAE				
<i>Campomanesia guaviroba</i>	Sep	LMB	p	shrub/treelet
<i>Eugenia moraviana</i>	Sep - Oc	LMB	p	shrub/treelet
PASSIFLORACEAE				
<i>Passiflora amethystina</i>	Au	LMB	n	vine
<i>Passiflora miersii</i>	Ja - Ma	LMB	n	vine
<i>Passiflora suberosa</i>	Ja - De	W	n	vine

<i>Passiflora vespertilio</i>	Ja - Ap	M	n	vine
POLYGALACEAE				
<i>Diclidanthera laurifolia</i>	Oc	LMB	n	liana
RHAMNACEAE				
<i>Colubrina glandulosa</i>	Ma - Ap	DI	n	tree
<i>Gouania latifolia</i>	Ma - Ap	DI, F	n/p	liana
<i>Gouania virgata</i>	Ja - Ap	DI, F	n	liana
<i>Rhamnidium elaeocarpum</i>	Oc - No	DI	n	tree
RUBIACEAE				
<i>Chiococca alba</i>	Ja	DI	n?	liana
<i>Coutarea hexandra</i>	Fe	M	n	tree
<i>Manettia cordifolia</i>	Ap - May	H	n	vine
RUTACEAE				
<i>Esenbeckia leiocarpa</i>	No - Ja	F, DI	n	tree
<i>Galipea jasminiflora</i>	De - Ap	Bu, F	n	shrub/treelet
<i>Metrodorea nigra</i>	Oc - No	F	n	tree
<i>Metrodorea stipularis</i>	No - Ja	F, DI	n	tree
<i>Zanthoxylum caribaeum</i>	Sep - Oc	DI	n	tree
<i>Zanthoxylum fagara</i>	Jul - Oc	DI	n	tree
<i>Zanthoxylum juniperinum</i>	No	DI	n	tree
<i>Zanthoxylum rhoifolium</i>	Au	DI	n	tree
<i>Zanthoxylum riedelianum</i>	Au - Oc	DI	n	tree
SALICACEAE				
<i>Casearia decandra</i>	Au	DI	n	tree
<i>Casearia gossypiosperma</i>	Oc - No	DI	n	tree
<i>Casearia sylvestris</i>	Au - Se	DI	n	treelet
SAPINDACEAE				
<i>Cardiospermum grandiflorum</i>	Ap - May	LMB, SB	n/p	liana
<i>Diatenopteryx sorbifolia</i>	Sep - Oc	LMB, SB	n	tree
<i>Paullinia pinnata</i>	Oc - No	LMB, SB	n/p	liana
<i>Paullinia rhomboidea</i>	Ja - Ma	LMB, SB	n/p	liana
<i>Serjania caracasana</i>	Ma - Jun	LMB, SB	n/p	liana
<i>Serjania communis</i>	May - Jul	LMB, SB	n/p	liana
<i>Serjania grandiflora</i>	Jun - Jul	LMB, SB	n/p	liana
<i>Serjania hebecarpa</i>	Sep	LMB, SB	n/p	liana
<i>Serjania multiflora</i>	May - Au	LMB, SB	n/p	liana
<i>Serjania reticulata</i>	May - Jun	LMB, SB	n/p	liana
<i>Thinouia mucronata</i>	Ja	LMB, SB	n/p	liana
<i>Urvillea laevis</i>	Ma - May	LMB, SB	n/p	liana
SAPOTACEAE				
<i>Chrysophyllum gonocarpum</i>	Ap, Oc - No	DI	n	tree
<i>Chrysophyllum marginatum</i>	Ja	DI	n	treelet
SOLANACEAE				
<i>Cyphomandra sciadostylis</i>	Sep - Ma	LMB	os/p	shrub/treelet
<i>Solanum concinnum</i>	Au	LMB, SB	p	liana
<i>Solanum hazenii</i>	Ja - Dec	LMB	p	tree

<i>Solanum pabstii</i>	No - Jun	LMB	p	vine
<i>Solanum pseudoquina</i>	Au - Oc	LMB	p	tree
<i>Solanum swartzianum</i>	Ja - Dec	LMB	p	tree
<i>Solanum wendlandii</i>	De - Fe	LMB	p	liana
STERCULIACEAE				
<i>Helicteres ovata</i>	Ap - Ja	Ba	n/p	shrub/treelet
TILIACEAE				
<i>Heliocarpus americanus</i>	Jul - Au	DI	n/p	tree
<i>Luehea divaricata</i>	De - Ap	LMB	n	tree
<i>Luehea speciosa</i>	May - No	Ba	n/p	tree
TRIGONIACEAE				
<i>Trigonia nivea</i>	Ma - May	LMB	n/p	liana
URTICACEAE				
<i>Cecropia glaziovii</i>	Ja - De	F	p	tree
<i>Cecropia hololeuca</i>	Ja - De	F	p	tree
<i>Cecropia pachystachya</i>	Ja - De	F	p	tree
VERBENACEAE				
<i>Aloysia virgata</i>	Jun - Sep	DI	n/p	treelet
<i>Citharexylum myrianthum</i>	No - De	M	n	tree
<i>Petreaea volubilis</i>	Oc - De	Bu	n	liana
VITACEAE				
<i>Cissus verticillata</i>	Fe, Sep - No	W	N	vine

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Table 2. Number of plant species (N) by pollination mode and their distribution according to the seasons at the SGR semi-deciduous forest, south-eastern Brazil. W-

D= wet-to-dry transitional season, D= dry season, D-W= dry-to-wet transitional season, W= wet season

Pollination modes	N	W-D	N	D	N	D-W	N	W
		Mar - Apt		May - Aug		Sept - Oct		Nov - Feb
Large to medium bees	40	46.51	35	33.33	72	44.17	56	42.42
Diverse insects	7	8.14	25	23.81	21	12.88	21	15.91
Flies	9	10.47	14	13.33	18	11.04	17	12.88
Moths	4	4.65	3	2.86	12	7.36	13	9.85
Hummingbirds	4	4.65	7	6.67	8	4.91	3	2.27
Small bees	8	9.30	12	11.43	13	7.98	6	4.55
Butterflies	7	8.14	2	1.90	8	4.91	5	3.79
Bats	3	3.49	5	4.76	5	3.07	5	3.79
Wasps	4	4.65	2	1.90	5	3.07	5	3.79
Beetles	0	0.00	0	0.00	1	0.61	1	0.76
TOTAL	86	100	105	100	163	100	132	100

Table 3. Number of species (N) by pollination mode and their distribution in the four modules (M1 to M4) at the SGR semi-deciduous forest, south-eastern Brazil.

Pollination modes	N	M1	N	M2	N	M3	N	M4
		Apr - Jun		Jan - Mar		Jul - Set		Oct- Dec
Large to medium bees	24	46.15	32	47.06	23	32.39	28	40.58
Diverse insects	5	9.62	8	11.76	20	28.17	12	17.39
Flies	8	15.38	7	10.29	9	12.68	10	14.49
Moths	0	0.00	6	8.82	4	5.63	7	10.14
Hummingbirds	3	5.77	1	1.47	3	4.23	2	2.90
Small bees	7	13.46	3	4.41	6	8.45	4	5.80
Butterflies	3	5.77	5	7.35	0	0.00	1	1.45
Bats	1	1.92	3	4.41	4	5.63	1	1.45
Wasps	1	1.92	3	4.41	2	2.82	2	2.90
Beetles	0	0.00	0	0.00	0	0	2	2.90
TOTAL	52	100	68	100	71	100	69	100

Capítulo 3

Temporal dynamic in a plant-hawmoth network
and the spatial coupling links

Temporal dynamic in a plant-hawkmoth network and the spatial coupling links

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1 **Summary**

2 **1.** Ecological networks provide insights on the organization, stability and
3 persistence of biodiversity. However, they are often statically depicted and
4 lack temporal resolution thus, temporal dynamics in pollination networks need
5 further examination. Besides, flower-visitation networks are usually treated as
6 isolated, as if they were uncoupled from their surroundings, however networks
7 are coupled by species with large home ranges.

8 **2.** In that form, we present here data from a temporal flower-visitation
9 network of a forest fragment in the Northeast Brazilian steppe (“caatinga”).

10 **3.** The network consists on flower visiting hawkmoths and their nectar plants.
11 Data were collect along a 27m. period. We evaluated changes in species and
12 interactions using additive diversity partitioning for 22 monthly transitions and
13 for the seasonal transitions. We also estimated the coupling links (i.e. links
14 coming from nearby areas) in the total network and in the seasonal networks.

15 **4.** We found a strong temporal dynamic with hawkmoths species disappearing
16 during the dryer months and a relative constant presence (but variable in
17 number) of coupling links in the local network throughout the study period.
18 The high turnover of interaction was partly driven by species turnover and by
19 re-wiring of links. Thus, the network showed a strong temporal component
20 tied to a spatial component represented by the coupling links.

21 **5.** To conclude, strong flyers like hawkmoths are important as spatial
22 couplers, gluing local networks together, and thus blurring network borders
23 and adding stability to the local network. However the spatial coupling is
24 linked to a strong temporal dynamic.

- 1 Key words: flower-visitation networks, temporal dynamic, beta diversity,
- 2 coupling links

1 INTRODUCTION

2 Ecological network studies provide insights on the structure of species-
3 rich communities since allowed us to go from very specific interactions
4 involving a few species to the study of whole systems, improving our
5 understanding of the organization, stability and persistence of biodiversity
6 (Bascompte *et al.*, 2003; Jordano *et al.*, 2003). Ecological networks are most
7 often statically depicted based on data cumulated over a plot size and study
8 period defined by the researcher (Bascompte *et al.*, 2003; Elberling & Olesen,
9 1999). This pooling of data may obstruct deeper insights into the processes
10 behind biodiversity (Olesen *et al.*, 2011). Thus, in order to understand the
11 dynamics of biodiversity we need temporally data of ecological networks
12 (Olesen *et al.*, 2010). However, a few datasets are further partitioned into a
13 sequence of successive time slices making it possible to study the seasonal
14 or annual dynamics in detail (Lundgren & Olesen, 2005; Basilio *et al.*, 2006;
15 Olesen *et al.*, 2008; Petanidou *et al.*, 2008, Alarcon *et al.*, 2008).

16 In the same way, most network studies focus on a local spatial scale,
17 but the spatial boundaries of these networks are often arbitrarily defined (i.e.,
18 the study site). Nevertheless, ecological networks are seldom isolated and to
19 study them in isolation is to assume the ecological dynamics at local level is
20 uncoupled from what happens in the neighborhood areas. Local networks are
21 coupled to each other by species with large home ranges, such as large
22 herbivores and top predators in food webs (Dobson, 2009), mammals and
23 large birds in seed dispersal systems (Jordano *et al.*, 2007), and pollinators
24 such as bats (Horner *et al.*, 1998) or altitudinal migratory hummingbirds
25 (Levey & Stiles, 1992). Thus these vagile species blur network borders adding

1 stability to ecological interactions (Hassell *et al.*, 1994; Moore & Hunt 1988,
2 McCann *et al.*, 1998, Holt *et al.*, 2002, Buldyrev *et al.*, 2010).

3 Owing to temporal and spatial variability of ecological interactions the
4 next step in the study of ecological networks will be to explore how relevant is
5 this spatiotemporal variation to the organization of ecological networks. In this
6 sense, some systems, such as pollination of flowering plants by insects are
7 particularly prone to show temporal and spatial variation. For instance, even
8 in tropics, where seasonality is less pronounced than in temperate regions,
9 seasonality influences temporal dynamics of plants and their pollinating
10 animals. The more seasonal the climate is, with the presence of a restrictive
11 growing season, the lower the diversity in plant phenological patterns within a
12 site (Morellato *et al.*, 2000). In the same way, the dynamics of key pollinators,
13 such as butterflies and their allies (Lepidoptera) are influenced by extremely
14 seasonal environments (i.e. wet and dry season) (Bonebrake *et al.*, 2010;
15 Brown & Freitas, 2002). For instance, butterfly and moth abundance and
16 survival decrease during the dry season due to the scarcity of water, poor
17 nectar and dry vegetation (Hussain *et al.*, 2011; Haber & Frankie, 1989).

18 Pollination networks have been studied extensively in recent years
19 (Olesen *et al.*, 2010). However, all studies are single-network studies, or if
20 several networks are included the coupling links are not explored. Many
21 flower-visiting animals can be expected to act as spatial couplers, e.g.
22 euglossine bees (Janzen 1971), flying foxes (e.g. Cox *et al.*, 1991), trap-lining
23 hummingbirds (e.g. Lindberg & Olesen 2001) and hawkmoths (e.g. Nilsson *et al.*, 1985). Their role as spatial couplers and consequently stabilizers of local
24 network dynamics need to be explored.
25

Here we describe and analyse the seasonal and spatial dynamics of a simple flower–visitation network. Networks consisted of two interacting communities, viz. a community of nectar–producing flowering plants and a community of nectar–drinking hawkmoths (Lepidoptera: Sphingidae). These animals are often extreme flyers locating nectar sources over huge distances (Haber & Frankie, 1989). Thus they may act as important spatial couplers, linking spatially separated local networks together. Hawkmoths carried pollen on their body either from the local, the regional network or both. Pollen on the body surface doubtlessly reveals which plants the animals have visited. Thus if a hawkmoth was foraging in the local network but carried pollen from a plant species that was not flowering in this network, we inferred that it was a spatial coupler between the local and the regional network.

Therefore, we focused upon (i) a description of the topology of the pooled network; (ii) the monthly and seasonal turnover of species and links in the network; and (iii) the coupling links in the network.

MATERIALS AND METHODS

STUDY SITE

The study was undertaken from October 2004 until February 2007, in a forest remnant at the Ecological Reserve of Tapacurá (Estação Ecológica de Tapacurá-UFPE) at 08°01' S; 35°11' W, in the district of São Lourenço da Mata, Pernambuco, Northeastern Brazil (Andrade-Lima, 1960; Veloso *et al.*, 1990). The study site has distinct dry and rainy seasons. The rainy season is from March to August and the dry season from September to February (Sudene, 1990, Primo, 2008). The vegetation corresponds to a semideciduous Atlantic Rain Forest remnant of 400 ha. surrounded by sugar

1 cane and agricultural pastures (Andrade & Rodal, 2004).

2 Hawkmoths were sampled during 27mo. (Primo, 2008). A 250W
3 mercury-vapor light source, positioned against a white wall of an old
4 construction in the Reserve Station facing the forest, was used to attract
5 moths. Specimens were collected on two consecutive new moon nights per
6 month from 17.30h to 2.30h of the following day. Moths were killed by an
7 injection of ethyl acetate in the posterior part of the thorax. Each specimen
8 was then placed in an entomological envelope and prepared in the laboratory.
9 Moths were identified using d'Abrera (1986) and Kitching and Cadiou (2000)
10 and the reference collection at UFPE (Universidade Federal de Pernambuco).
11 The pollen preparations of each species were mounted in pure glycerin
12 gelatin and in glycerin gelatin stained with basic fuchsin solution, covered with
13 a cover glass and sealed with paraffin (Louveaux *et al.*, 1978, Wittmann &
14 Schlindwein, 1995).

15 DATA ANALYZES

16 We use the pollen loads data to create a visitation matrix of all
17 hawkmoth–flowering plant species in the site over a period of 27 months
18 (Primo, 2008). We calculated the level of nestedness of the pooled matrix with
19 the program *ANINHADO* (Guimarães & Guimarães, 2006). We compared the
20 observed degree of nestedness of the network with 1000 replicates using null
21 model CE, in which the probability of a given cell to be occupied is the
22 average of the probabilities of occupancy of its row and column (Bascompte
23 *et al.*, 2003). We estimated the modularity index M using the simulated
24 annealing algorithm provided by Guimerà (Guimerà & Amaral, 2005). We ran
25 100 randomizations of the empirical network and calculated the significance

1 level of the observed M by comparing it with the average randomized M
 2 (Guimerà & Amaral, 2005).

3 SAMPLING ROBUSTNESS

4 To assess if we had recorded enough interactions to describe this network,
 5 we generated an accumulation curve with the number of interactions as a
 6 function of the number of pollen loads events sampled (Guimarães *et al.*,
 7 2007; Jordano *et al.*, 2009). We estimated average and standard deviation of
 8 the number of interactions for any given fraction of the number of events
 9 recorded in 1000 iterations. After generating this curve, we used the drc
 10 package in R (<http://www.r-project.org/>) and the dose–response model to
 11 extrapolate the curve. We then used the Michaelis–Menten equation to
 12 assess the asymptotic value of the curve (Donatti *et al.*, 2011).

13 TEMPORAL TURNOVER

14 We divided the pooled matrix into 22 monthly time slices (in four
 15 months no interactions were recorded) to assess temporal dynamic of species
 16 and interactions from one month to the other.

17 Individual species and links may enter or disappear from the network
 18 when passing from one month to the next. To evaluate the temporal dynamic
 19 of plants and sphingids species and links we used the additive diversity
 20 partitioning (Veech, 2002, Loureau, 2000). Beta diversity, β , was originally
 21 introduced by Whittaker to describe changes in species composition and
 22 abundance across environmental continua such as gradients of elevation and
 23 moisture (Veech, 2002). In that way, we calculated β and α diversity of links
 24 and species among successive networks, thus α diversity = (number o links
 25 observed in a given month + number of links/species in the previous month)/2

1 and γ diversity = number of links/species observed in a given month + number
 2 of links/species in the previous month - number of shared links/species. Since
 3 $\gamma = \beta + \alpha$, we calculated β for all the network transitions (i.e. 21 transitions).

4 COUPLING LINKS

5 We used data of the flowering phenophase of hawkmoth-visited plant
 6 species in the local site to identify coupling links (Primo, 2008; Souza, 2005).
 7 We defined an interaction as a coupling link whenever a hawkmoth species
 8 was found carrying pollen of a plant species that was not in flower in the study
 9 site at that time. The coupling links estimation is conservative since we do not
 10 have the phenology of all the plant species in the area and we restrict the
 11 foreign links to plant species with known phenology during the study period.
 12 Links involving *Cleome spinosa*, which belongs to the surrounding matrix of
 13 the study fragment, were always classified as foreign.

14 RESULTS

15 The pooled matrix exhibited a total of 53 species from which 28 and 25
 16 were plant and hawkmoths species respectively (Fig. 1). We observed a total
 17 of 126 interactions (*I*) from 259 events of pollen loads. Using the Michaelis–
 18 Menten equation we estimated to have sampled 79.2% of the interactions
 19 occurring in this community (Fig. 2). The pooled hawkmoth-plant visitation
 20 matrix was nested ($NODF=25.4$, $p=0.001$), but not modular ($M= 0.32$, $p= n.s.$).

21 Most plant and hawkmoths species were found during the rainy
 22 season. Thus, 6.9 ± 2.9 plant species were found in the rainy season and 2.3
 23 ± 2.1 during the dry season, while 5.7 ± 2.9 and 1.5 ± 1.6 species of
 24 hawkmoths were found during the rainy and dry season respectively (Fig. 1).
 25 The monthly transitions showed a strong temporal dynamic of γ diversity both

1 for links and species (Fig. 3). A higher γ diversity of species and links was
 2 found during the rainy seasons (Fig. 3). The β diversity of species ranged
 3 from 19.2 to 42.5% and for links ranged from 37.5 to 96.5% (Fig. 3), indicating
 4 re-wiring of links could be an important component of the monthly variation in
 5 links (Fig. 3).

6 The seasonal variation in β and α diversity of links was rather constant
 7 ranging from 42.6 to 49.4 % (Fig. 4) but likewise the monthly β and α diversity
 8 indicated a high seasonal turnover. The turnover of species from one season
 9 to the other was higher than the links turnover ranging from 70.7% to 57.5%.
 10 Thus, the seasonal turnover of links was partly driven by the seasonal species
 11 turnover (Fig. 4).

12 From the total number of interactions sampled 61.1 % were entirely
 13 from the local site, 11.1 % included between 50 and 33 % coupling links, and
 14 27.8 % of the links were entirely coupling links (Fig. 5). Thus, 37.9 % of the
 15 links are partly or entirely from outside the local area. Coupling links were
 16 present in 65% of the monthly slices and since more links were found during
 17 the rainy season, more coupling links occurred within this period (Fig. 6).

18 **DISCUSSION**

19 Ecological networks are based on matrices built upon observations
 20 cumulated during a given time period, which in published studies of pollination
 21 networks varies from one week (Mosquin & Martin, 1967), two seasons
 22 (Olesen *et al.*, 2008) four years (Petanidou *et al.*, 2008) or more than a
 23 decade (Olesen *et al.*, 2011). The time slices of these studies varied from
 24 days, months to years. However, independently of the temporal scale, they all

1 proved the strong seasonal dynamic inherent to ecological systems (Basilio *et*
2 *al.*, 2006; Olesen, *et al.*, 2008, Petanidou *et al.*, 2008).

3 Accordingly, we found a high temporal turnover of species and
4 interactions in our plant-sphingid visitation network as shown by our high beta
5 diversity. High beta diversity is expected when species are restricted to a low
6 number of months, causing the species and link composition of different
7 months to differ strongly (Fleming *et al.*, 2006). Sphingids fauna is
8 characterized by a highly seasonal population dynamics with sphingids
9 abundance decreasing in response to rainfall in tropical seasonal forests
10 (Gómez-Nucamendi *et al.*, 2000, Gusmão & Duarte, 2004). Seasonality in this
11 group is mainly related to their life cycle, since larvae forage on the leaves of
12 some selected host plants and need humidity to pupate (Haber & Frankie,
13 1989). In addition, plants species may also be severely affected by
14 seasonality and concentrate flowering in the most propitious times (Wright,
15 1996). Thus, the high turnover of interactions in our network was partly driven
16 by species turnover and by re-wiring of links (i.e. switching partners) likewise
17 in other plant-butterfly visitation network (Olesen *et al.*, 2011). In addition, high
18 species turnover may be associated to the foraging patterns of hawkmoths
19 that do not forage within a single area and consequently increase local
20 species turnover (Haber and Frankie, 1989).

21 In our local plant–hawkmoth network, all these flower–visiting insects
22 also vary in their foraging range and thus in their importance as spatial
23 couplers. The most extreme non–couplers may not even forage over our
24 entire local network. Thus within the small space occupied by the local
25 network some links become forbidden because of spatial constraints (Olesen

1 *et al.*, 2010). Spatial couplers like hawkmoths counteract these constraints. If
2 a network is expanded in space, non-couplers (i.e. only local links) make it
3 more heterogeneous or modular because of spatial linkage constraints, i.e.
4 the non-coupling animals make network more likely to fragment. The spatial
5 couplers, however, act as connectors keeping the network coherent, i.e. they
6 are the network glue. Thus the variation in foraging range of animals causes
7 the network between plants and flower-visiting animals to become
8 heterogeneous, and even hierarchical in its structure.

9 Moreover, within species individual hawkmoths vary in their body size
10 (i.e. surface for pollen load) (Primo, et al 2008), and in the ability to fly long
11 distances. Thus, strongest couplers are larger and stronger flyers. The same
12 must be the case for birds-of-prey in which individuals differ in their home
13 range size, i.e. one gender may be more sedentary than the other, or maybe
14 juveniles are more sedentary than adults.

15 In that form, our results suggest that differences in flowering
16 phenophase among local and regional populations sustain a metacommunity
17 of hawkmoths. Somewhere in the fragmented regional network there might
18 always be flowering individuals of a species sustaining hawkmoths and
19 functioning as a hawkmoth species source for the local network. Thus these
20 long-flying hawkmoths become important to local network stability and crucial
21 for the maintenance of fragmented environments like the Caatinga.

22 To conclude, strong flyers like hawkmoths are important as spatial
23 couplers, gluing local networks together, and thus blurring network borders.
24 However, this coupling has a strong temporal dynamics. Next steps are to
25 break down the dichotomy between couplers and non-couplers and analyse

the differential coupling effect of different animals on the heterogeneous structure of ecological networks as well as the temporal dynamic of systems involving mutualist partners that are affected differently by seasonality.

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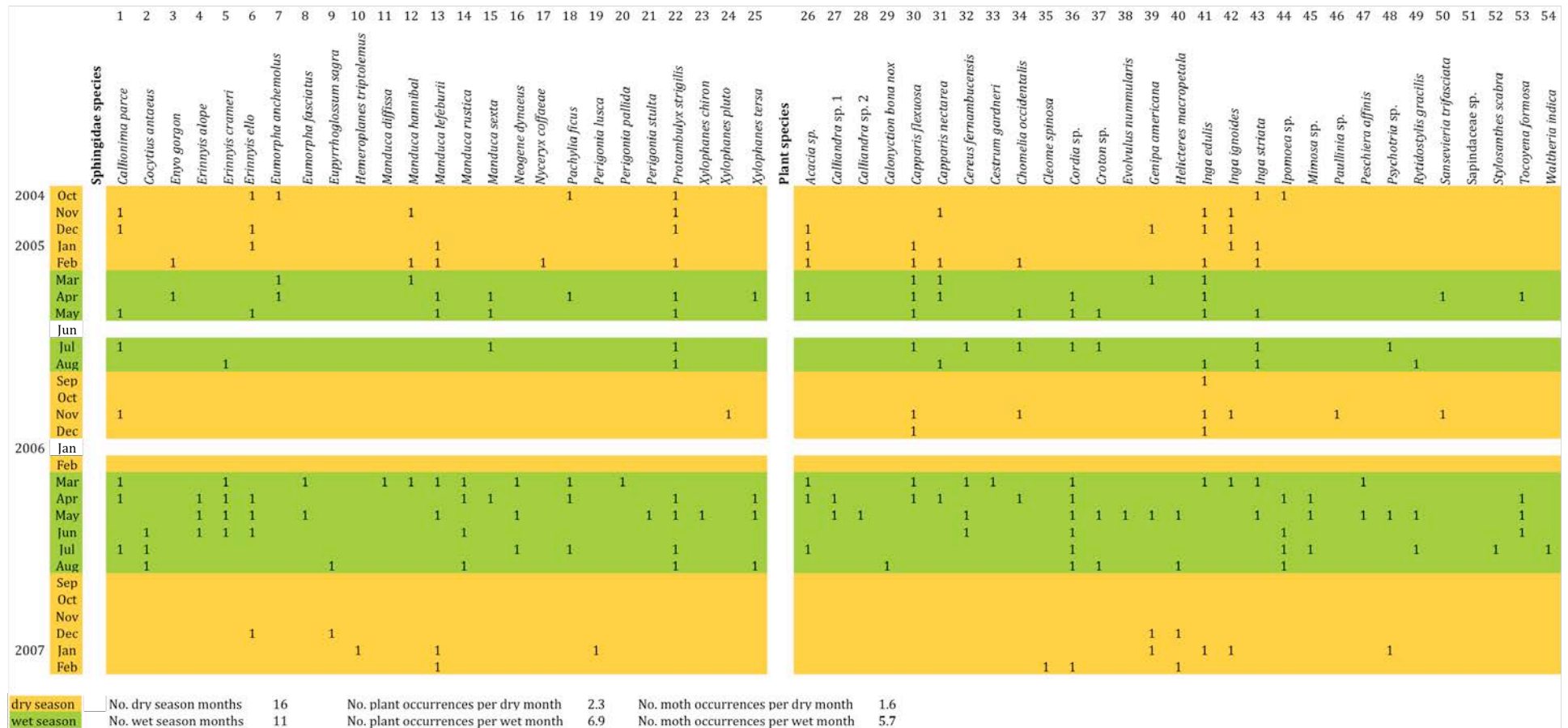


Figure 1. Temporal species occurrence. No sampling was made in June 2005 and January 2006.

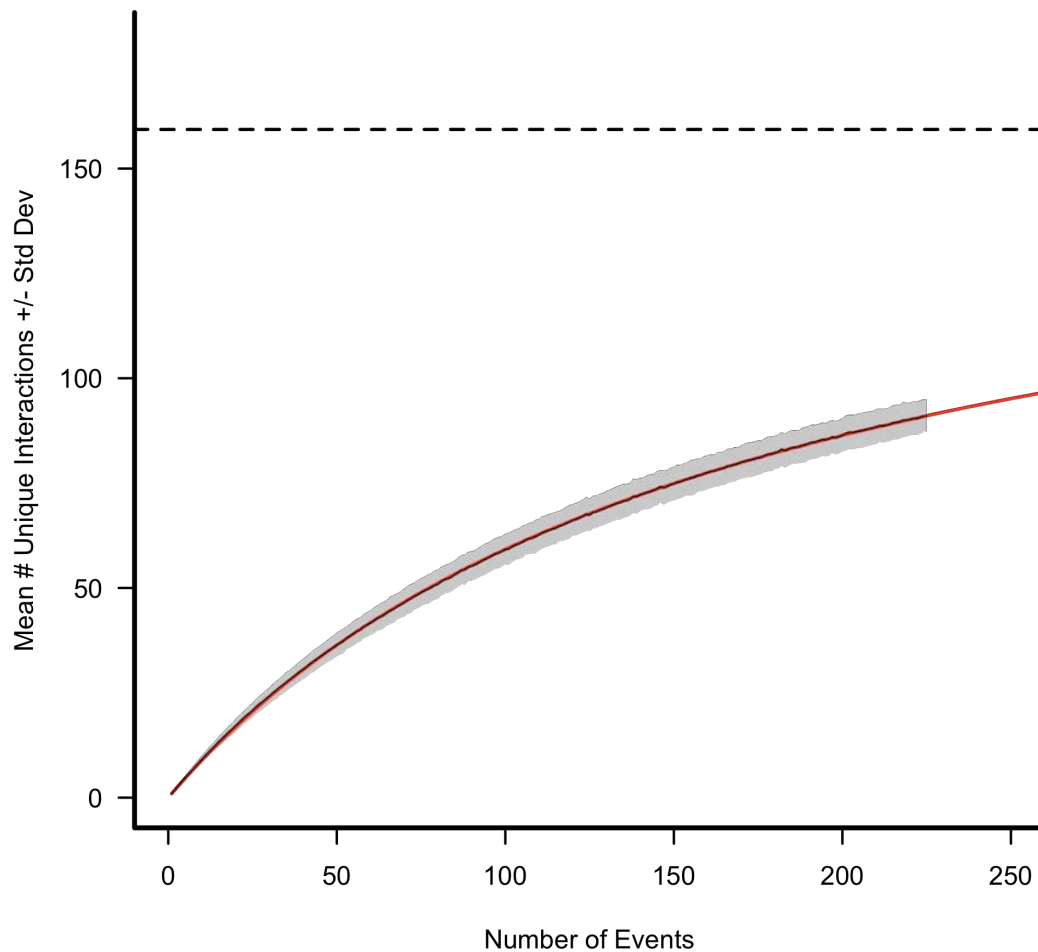


Figure 2. Accumulation curve with the average (in black) and the standard deviation (in grey) of the number of pollen loads interactions in 1000 iterations, as a function of the number of pollen load events. The red line shows the extrapolation of the curve and the dashed line represents the asymptotic value for the number of pollen load interactions. We sampled 259 events of pollen loads, 126 pollen loads interactions and estimated the asymptote for the number of seed dispersal interactions to be approximate

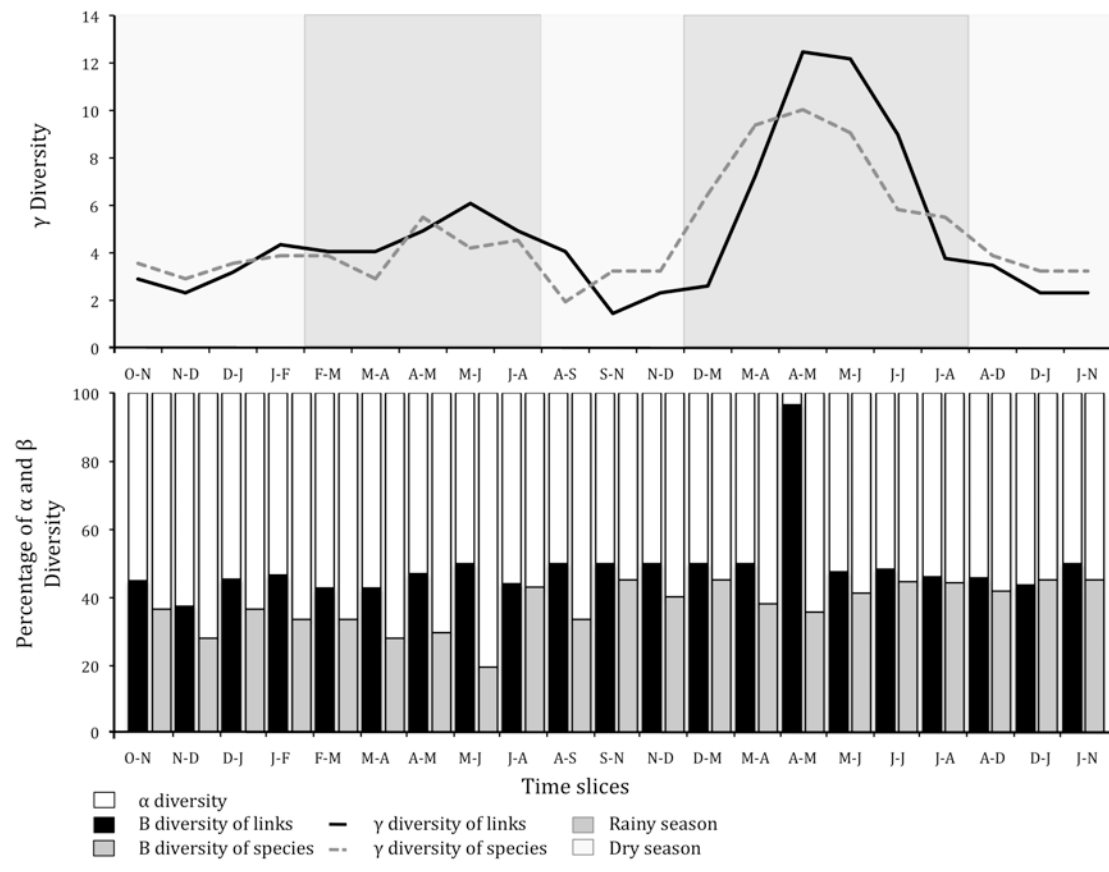


Figure 3. γ , α and β diversity of species and links across the monthly transitions. O-N= transition October- November

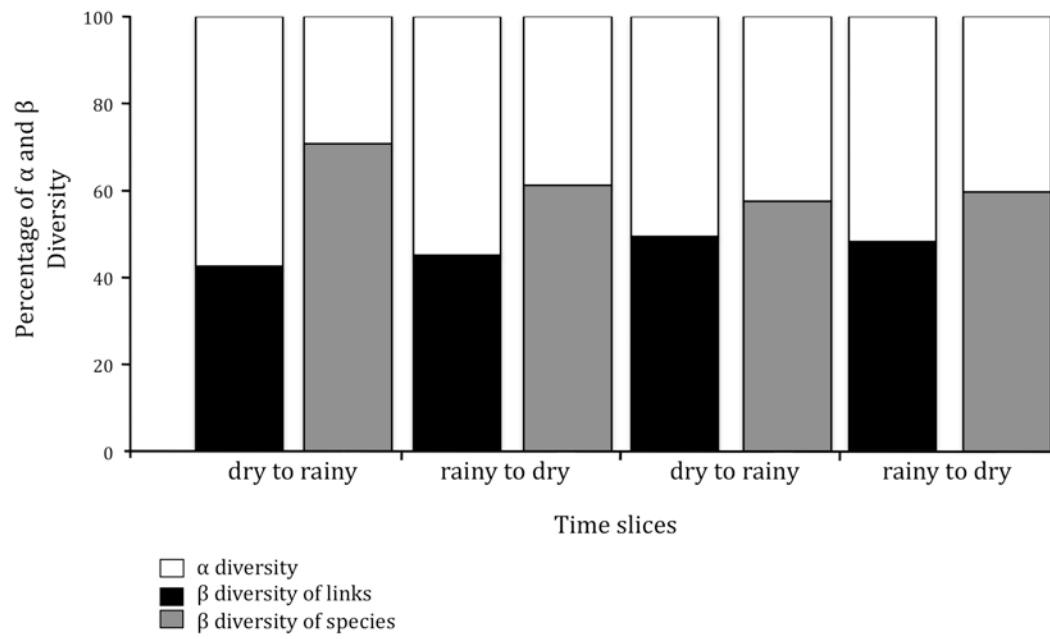


Figure 4. α and β diversity of species and links across the seasonal transitions.

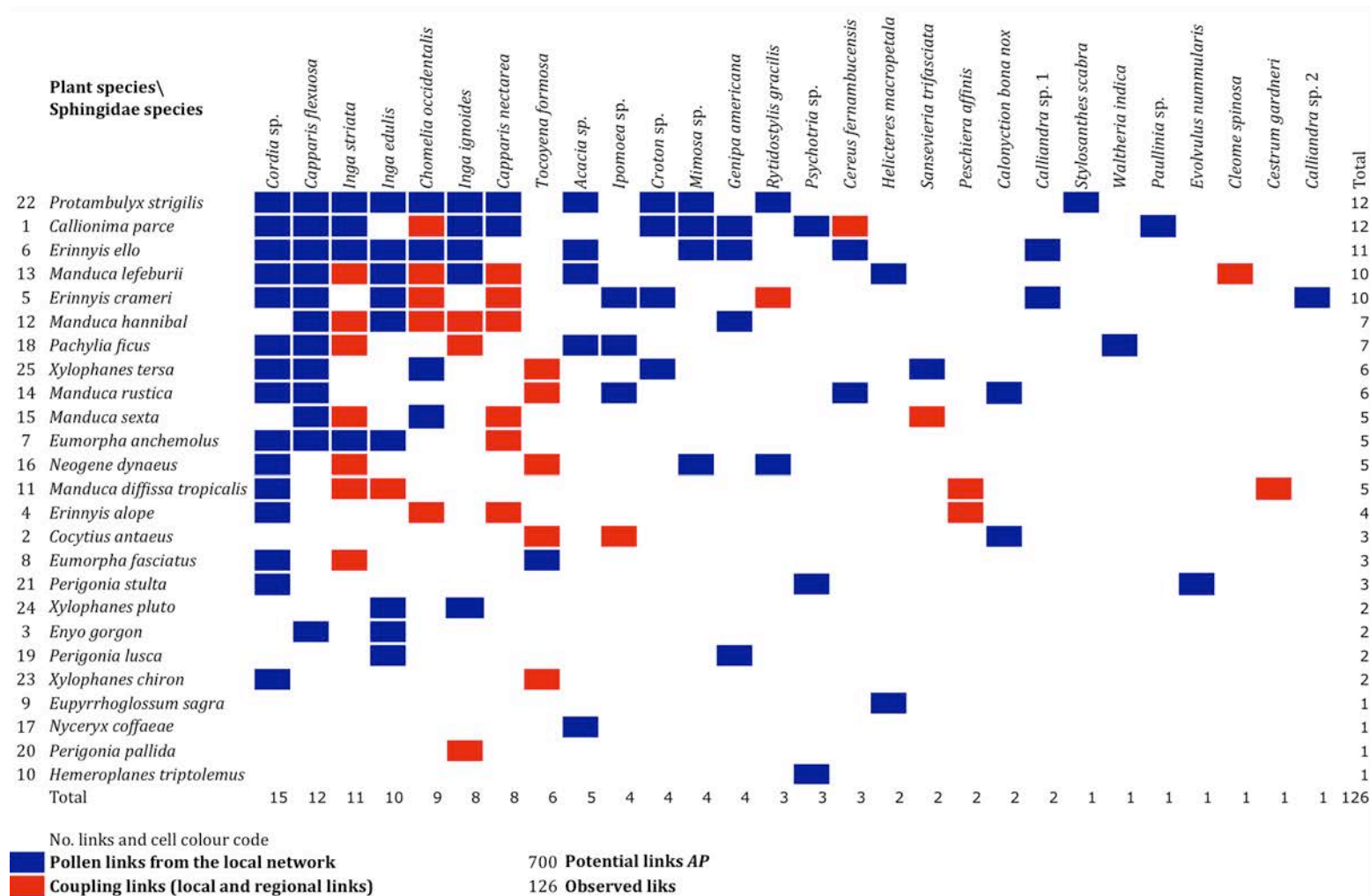


Figure 5. Plant-Sphingids interaction network showing coupling and local links.

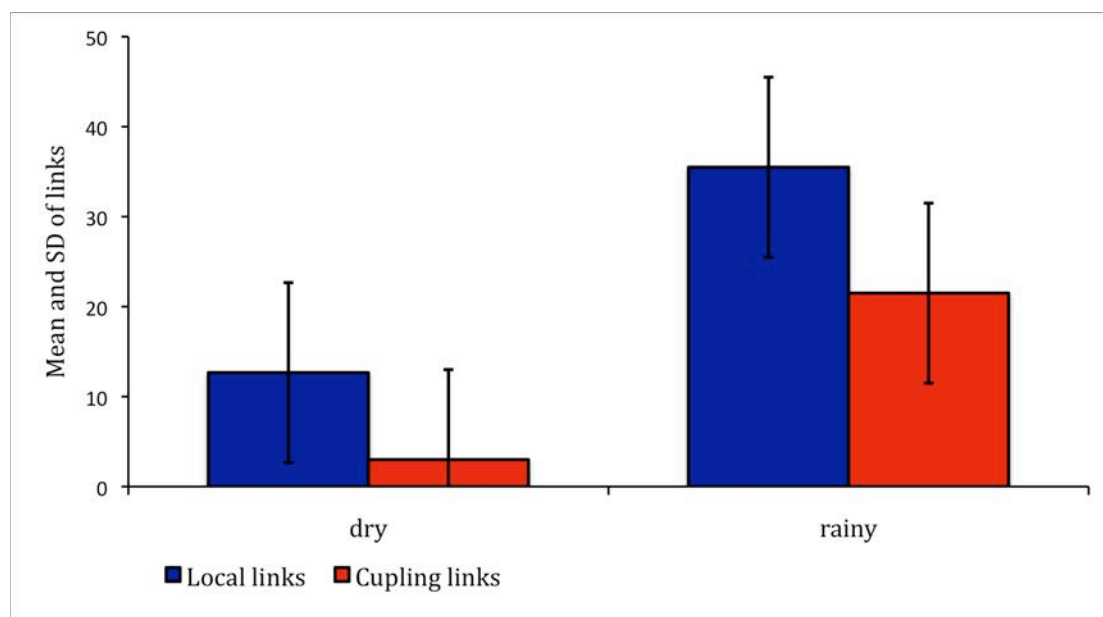


Figure 6. Mean and std. of coupling and local links in the dry and rainy season.

Capítulo 4

Cheaters in mutualisms networks

Cheaters in mutualism networks

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Mutualism-network studies assume that all interacting species are mutualistic partners and consider that all links are of one kind. However, the influence of different types of links, such as cheating links, on network organization remains unexplored. We studied two flower-visitation networks (Malpighiaceae and Bignoniaceae and their flower visitors), and divide the types of link into cheaters (i.e. robbers and thieves of flower rewards) and effective pollinators. We investigated if there were topological differences among networks with and without cheaters, especially with respect to nestedness and modularity. The Malpighiaceae network was nested, but not modular, and it was dominated by pollinators and had much fewer cheater species than Bignoniaceae network (28% versus 75%). The Bignoniaceae network was mainly a plant-cheater network, being modular because of the presence of pollen robbers and showing no nestedness. In the Malpighiaceae network, removal of cheaters had no major consequences for topology. In contrast, removal of cheaters broke down the modularity of the Bignoniaceae network. As cheaters are ubiquitous in all mutualisms, the results presented here show that they have a strong impact upon network topology.

Keywords: cheaters; modularity; nestedness; network topology; pollination

1. INTRODUCTION

Species are organized into complex networks through their interactions or links (e.g. Bascompte 2009). In almost all studies, links are only of one kind, e.g. predatory or parasitic (but see Melián *et al.* 2009). In mutualism networks, we assume that all interactions are beneficial, e.g. the exchange of pollination service for floral rewards (e.g. Elberling & Olesen 1999). In plant-animal mutualisms, rewards and services are also exploited by non-mutualistic species. In pollination networks, 'pollinator' is used as a generic term for all kinds of flower visitor (Elberling & Olesen 1999). This is a common simplification. However, animals visit flowers for many reasons, e.g. florivory, ovule/seed predation and nectar and pollen harvesting

with or without pollen transfer (e.g. Inouye 1983; Strauss & Whittall 2006).

The implications of this link diversity to the structure, stability and dynamics of networks are unknown. Melián *et al.* (2009), for example, found that strong links and a high ratio of mutualistic : consumer/resource links were important for the diversity of networks. In food webs, parasites are major determinants of stability (Lafferty *et al.* 2006), strongly affecting network features. Among network features recorded in mutualistic networks are nestedness, in which the links of specialists are subsets of the links of more generalized species (Bascompte *et al.* 2003), and modularity, in which species are organized into small, strongly linked groups or modules, which are loosely interlinked (Olesen *et al.* 2007).

We investigated two flower-visitation networks: a set of Malpighiaceae and Bignoniaceae species and their flower visitors. For both, visitors were categorized as pollinators, cheaters or both. A flower visitor was a pollinator, if it contacted anthers and stigma, or a cheater, if it obtained its reward without any contact (Inouye 1983). In the Bignoniaceae network, cheaters were further categorized as either nectar or pollen robbers. First, the topology of networks was described and then cheaters were removed to analyse their influence. If cheaters interact with generalist plants, their removal may reduce nestedness and increase modularity by reducing the number of across-module interactions (Olesen *et al.* 2007). If cheaters interact with different sets of related species, their elimination may decrease modularity. We addressed the questions: what are the differences and similarities in topology of the visitation, pollination and plant-cheater networks, especially with respect to modularity and nestedness? And how are cheater species distributed within networks?

2. MATERIAL AND METHODS

(a) Study site and dataset

We used data from literature to identify the types of interaction between flower visitors and (i) Malpighiaceae (Sigrist 2001; Sigrist & Sazima 2004) and (ii) Bignoniaceae (Amaral 1992) in a 250 ha fragment of semi-deciduous, seasonal forest (Santa Genebra Municipal Reserve, SGR), Campinas, SE Brazil (22°49' S, 47°7' W).

The networks are presented as adjacency matrices depicting plant-animal interactions, in which matrix element $r_{ij} = 1$, if plant species i interacts with animal species j and zero otherwise (e.g. Bascompte *et al.* 2003). Each visitation network was split into two submatrices, *viz.* a pollination matrix of plants and pollinators and a plant-cheater matrix (electronic supplementary material). Additionally, we operated with two kinds of cheater for Bignoniaceae, *viz.* nectar and pollen robbers, and split the plant-cheater matrix into a pollen robbery matrix of plants and pollen robbers, and a nectar robbery matrix of plants and nectar robbers.

(b) Network statistics

The linkage level L of a species denotes its number of links (Olesen *et al.* 2007). The level of nestedness n was estimated using the NODF metric (Almeida-Neto *et al.* 2008) and the software ANINHADO (Guimarães & Guimarães 2006). Significance of NODF was tested using a null model described in Bascompte *et al.* (2003).

To estimate the level of modularity, module number and species network role, we used an algorithm by Guimerà & Amaral (2005; see the electronic supplementary material, Olesen *et al.* 2007). Among-module distribution of cheater species was assessed by a co-occurrence analysis (electronic supplementary material).

3. RESULTS

The topology of the visitation networks clearly looks different in the two families (figure 1). The

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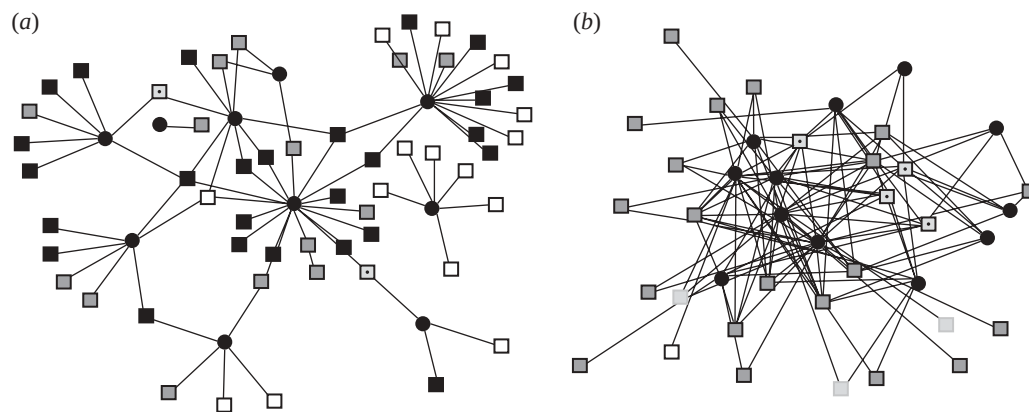


Figure 1. Network indicating different roles of animal species and links to plant species in (a) Bignoniaceae and (b) Malpighiaceae. Dark grey filled square, pollinator; unfilled square, pollen robber; black filled square, nectar robber; light grey filled square, oil robber; black square with centre dot, mix role (pollinator/robber); black filled circle, plants.

Table 1. Descriptive statistics for the matrices of Malpighiaceae and Bignoniaceae and their visitors. Number of visitors $\leq$ (number of pollinators + number of cheaters) because some visitors were both pollinator and cheater. The cheating matrix is the combined nectar and pollen robbery matrices. A and P , number of animal and plant species, resp.; I , number of interactions; C , connectance (I/AP); $\langle L_m \rangle$ and $\langle L_n \rangle$, average animal and plant linkage level, resp.; s.d., standard deviation; M and N , observed modularity and nestedness, resp.

matrix	Malpighiaceae			Bignoniaceae				
	visitation	pollination	cheating	visitation	pollination	cheating	nectar robbery	pollen robbery
A	29	25	8	57	16	43	29	14
P	12	12	10	10	9	8	7	5
I	116	91	25	75	20	55	41	14
C	0.33	0.30	0.31	0.13	0.14	0.16	0.20	0.20
range of A	1–11	1–11	1–7	1–4	1–2	1–4	1–4	1
range of P	3–18	1–15	1–6	1–19	1–5	2–14	1–13	1–5
$\langle L_m \rangle \pm$ s.d.	4.0 ± 3.01	3.6 ± 2.8	3.1 ± 2.2	1.3 ± 0.69	1.3 ± 0.45	1.3 ± 0.73	1.4 ± 0.87	1.0 ± 0
$\langle L_n \rangle \pm$ s.d.	9.7 ± 5.3	7.6 ± 4.1	2.5 ± 1.8	7.5 ± 5.7	2.2 ± 1.4	6.9 ± 4.4	5.9 ± 4.3	2.8 ± 2.0
M	n.s.	n.s.	n.s.	0.65**	n.s.	0.63*	n.s.	0.70*
N	0.59**	0.57**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

$p > 0.05$ n.s.

* $p < 0.05$.

** $p < 0.01$.

Malpighiaceae network had fewer species but more links and thus a higher connectance than the Bignoniaceae network (table 1). The Malpighiaceae network was nested, but not modular, whereas the Bignoniaceae network was modular, but not nested (table 1). Removing cheaters from the visitation networks had completely different outcomes in the two networks: it did not affect nestedness in the Malpighiaceae network, but destroyed modularity in the Bignoniaceae network (table 1). Thus, pollinators caused nestedness in the Malpighiaceae network, and cheaters caused modularity in the Bignoniaceae network. These differences may be due to a smaller proportion of cheaters in the Malpighiaceae network (28% versus 75%, table 1) and/or a higher food–plant specificity among Bignoniaceae cheaters (1.3 versus 3.1, table 1).

The visitation matrix of Bignoniaceae had nine modules, each with 2–14 species. Most species were peripherals ($N = 62\%$, figure 2), i.e. with only one to two links to other species, but three species were connectors between modules, viz. the nectar-robbing bees *Xylocopa suspecta*, *Oxaea flavescens* and *Euglossa*

annectans. The plants *Adenocalyma bracteatum* and *Anemopaegma chamberlaynii* were module hubs, whereas *Arrabidaea triplinervia* was a network hub (figure 2). Cheaters show much less co-occurrence among modules in the Bignoniaceae visitation matrix than expected by chance (C score = 0.86, $P = 0.0002$), indicating that cheaters were overdispersed among modules. However, one module was composed exclusively of cheaters and *Lundia obliqua*. The plant–cheater matrix of Bignoniaceae had seven non-connected modules with 3–12 peripheral species. Here, the same bee species as in the visitation matrix were classified as connectors, whereas *A. bracteatum* and *A. triplinervia* were module hubs. The pollen robbery matrix had five modules with two to six species, and all animals were peripherals ($L_m = 1.0$, table 1).

4. DISCUSSION

The Bignoniaceae and Malpighiaceae visitation networks have similar number of plants, whereas flower-visiting animal species are twice as frequent in

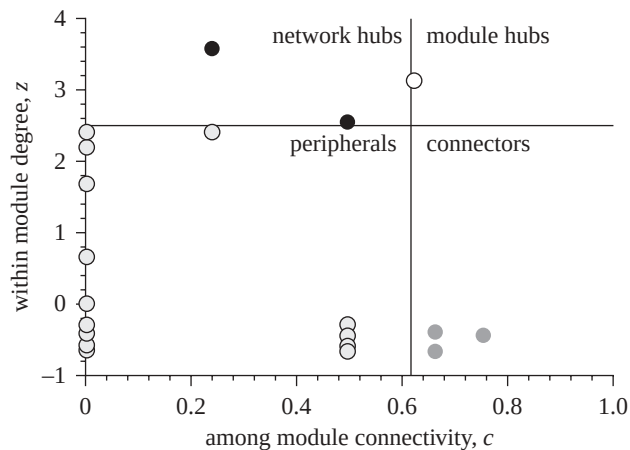


Figure 2. Species roles according to a zc -plot for Bignoniaceae visitation matrix.

the Bignoniaceae network. This is due to the cheaters, which are three times as common in the Bignoniaceae network. Thus, the Malpighiaceae network is essentially a pollination network, whereas the Bignoniaceae network is a plant–cheater network. As in other pollination networks (Bascompte *et al.* 2003), the Malpighiaceae network is nested, but also non-modular, which may reflect its small size (Olesen *et al.* 2007). Another Malpighiaceae–bee network was strongly nested, but, in contrast to ours, showed a low degree of modularity (Bezerra *et al.* 2009).

The Bignoniaceae networks had a completely different topology from our Malpighiaceae networks. In the Bignoniaceae networks, connectance is only half of that in the Malpighiaceae networks, indicating that the Bignoniaceae networks are more specialized. In addition, the Bignoniaceae visitation network was non-nested, but modular. The reason for this was the many specialized links (i.e. one or two animals visiting one plant species only) between pollen robbers and their plants. Pollen robbery is similar to herbivory, and herbivory networks are strongly modular (Lewinsohn *et al.* 2006). An increase in cheating in visitation networks may decrease nestedness, but increase modularity. Large pollination networks are modular (Olesen *et al.* 2007). However, this assumes that all links are pollinatory. We show that, besides phylogenetic clustering and trait convergence (Olesen *et al.* 2007), consumer/resource links, such as cheating links, also contribute to modularity.

Malpighiaceae is pan(sub)tropical with *ca* 1250 species, with oil flower species restricted to the neotropics. Female bees collect pollen and oil, which is used as larval provision and for nest cell walls (Sigris & Sazima 2004). In this study, 26 of the 29 bee visitor species were known oil collectors (Vogel 1974). The oil-collecting species made 93–96% of all links in the matrices. Thus, the Malpighiaceae visitation and pollination networks are bee pollination–floral-oil systems, and the small cheating networks are a floral-oil harvesting system. However, floral resources in Malpighiaceae species seem difficult to exploit by visiting animals without pollinating. As Bezerra *et al.* (2009) indicated, the phylogenetic and ecological similarity among partners results in a high nested pattern in this flower-oil system.

Bignoniaceae is a predominantly neotropical family with *ca* 800 species pollinated by insects, birds and bats (Gentry 1980). Bignoniaceae flowers are much more diverse than Malpighiaceae, allowing a much larger array of flower visitors the access to their flower rewards. In the network, 54 per cent, 23 per cent and 23 per cent of the animals were bees, butterflies and others (Diptera, Coleoptera and hummingbirds), respectively. Bees were mainly pollinators or nectar robbers; butterflies and hummingbirds were mainly nectar robbers, and most of the ‘others’ were pollen robbers. Nectar robbers act as the glue of the Bignoniaceae network, connecting the modules and increasing the cohesiveness of the network, while pollen robbers show more specialized links. The distribution of cheaters among modules might imply that robbers are overdispersed in niche space leading to the observed modular pattern, and/or may be a result of flower features such as calyx thickness and pubescence and corolla shape, which constrains the foraging of bees. Finally, the proportion of cheaters was three times higher in Bignoniaceae networks than in Malpighiaceae networks. The reasons might be that (i) the adaptations of the morphology and behaviour of visitors to flowers of the Malpighiaceae are much tighter, making it more difficult to harvest rewards without pollinating, and (ii) the oil resource is more costly than nectar to produce, resulting in a more specialized, conservative flower-pollination system, and the adapted visitors morphology and behaviour on Malpighiaceae flowers.

Nestedness adds robustness to a network and shortens the distance between species (Bascompte *et al.* 2003). Thus, cheaters, such as Bignoniaceae pollen robbers, may have a strong impact upon network stability by destroying nestedness and enforcing modularity. The importance of modularity for networks is less known, although a modular structure may slow down the spread of disturbances (Olesen *et al.* 2007). Cheaters are a ubiquitous part of maybe all mutualisms, and they seem to be important to the overall stability and integration of natural systems.

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Appendix.

Bignoniaceae visitation network	<i>Arrabidea triplinervia</i>	<i>Adenocalyma bracteatum</i>	<i>Anemopaegma chamberlainii</i>	<i>Arrabidea samydoidea</i>	<i>Stizophyllum perforatum</i>	<i>Lundia obliqua</i>	<i>Arrabidea selloi</i>	<i>Adenocalyma marginatum</i>	<i>Pithecoctenium crucigerum</i>	<i>Amphilophium vauthieri</i>	L_m
<i>Oxaea flavescens</i> (Andrenidae)	1		1	1	1						4
<i>Xylocopa suspecta</i> (Apidae)	1		1	1	1						4
<i>Euglossa annectans</i> (Apidae)	1	1	1								3
<i>Centris bicolor</i> (Apidae)			1	1							2
<i>Centris discolor</i> (Apidae)			1						1		2
<i>Centris mocsaryi</i> (Apidae)			1						1		2
<i>Cymaenes tripunctata</i> (Hesperiidae)	1	1									2
<i>Epicharis flava</i> (Apidae)	1								1		2
<i>Euglossa pleosticta</i> (Apidae)	1	1									2
<i>Eulaema nigrita</i> (Apidae)	1		1								2
<i>Temenis laothoe</i> (Nymphalidae)					1		1				2
<i>Xylocopa brasiliatorum</i> (Apidae)	1		1								2
<i>Xylocopa</i> sp. 1 (Apidae)	1							1			2
<i>Agroceridae</i> sp. 1 (Diptera)		1									1
<i>Aphididae</i> sp. 1						1					1
<i>Ascia monuste</i> (Pieridae)				1							1
<i>Augochlora</i> sp. 1 (Halictidae)		1									1
<i>Battus polydamas</i> (Papilionidae)					1						1
<i>Bombus brasiliensis</i> (Apidae)							1				1
<i>Cecidomyiidae</i> sp. 1 (Diptera)						1					1
<i>Centris collaris</i> (Apidae)										1	1
<i>Centris similis</i> (Apidae)				1							1
<i>Chamaemyiidae</i> sp. 1 (Diptera)						1					1
<i>Chloropidae</i> sp. 1 (Diptera)						1					1
<i>Cobalopsis catocala</i> (Hesperiidae)		1									1
<i>Curculionidae</i> sp. 1						1					1
<i>Cymaenes gisca</i> (Hesperiidae)				1							1
<i>Diptera</i> sp. 1		1									1
<i>Epicharis cf. grandior</i> (Apidae)	1										1
<i>Epicharis analis</i> (Apidae)	1										1
<i>Epicharis rustica</i> (Apidae)		1									1
<i>Euglossa cordata</i> (Apidae)	1										1
<i>Eulaema</i> sp. 1 (Apidae)		1									1
<i>Euplusia auriceps</i> (Apidae)	1										1
<i>Exaerete smaragdina</i> (Apidae)	1										1
Indetermined sp.					1						1
<i>Lauxaniidae</i> sp. 1 (Diptera)						1					1
<i>Melanotrochilus fuscus</i> (Trochilidae)			1								1
<i>Nannotrigona testaceicornis</i> (Apidae)							1				1
<i>Papilio astyalus</i> (Papilionidae)					1						1
<i>Paratetrapedia</i> sp. 1 (Apidae)				1							1

[illegible]

Malpighiaceae visitation network	<i>Dicella bracteosa</i>	<i>Banisteriopsis adenopoda</i>	<i>Stigmaphyllon lalandianum</i>	<i>Banisteriopsis muricata</i>	<i>Mascagnia anisopetala</i>	<i>Tetrapteryx guilleminiana</i>	<i>Heteropteryx aceroides</i>	<i>Mascagnia cordifolia</i>	<i>Banisteriopsis lutea</i>	<i>Tetrapteryx phlomoides</i>	<i>Mascagnia sepium</i>	<i>Banisteriopsis pubipetala</i>	L_m
<i>Epicharis flava</i> (Apidae)	1	1	1	1	1	1	1		1	1	1	1	11
(<i>Para</i>) <i>Tetrapedia</i> sp. 1 (Apidae)	1	1	1	1	1	1	1		1	1	1	1	11
<i>Centris</i> spp. (Apidae)	1	1	1	1	1		1	1	1	1			9
<i>Epicharis affinis</i> (Apidae)	1	1	1	1	1	1	1			1			8
<i>Centris mocsaryi</i> (Apidae)	1	1	1	1	1	1		1					7
<i>Paratetrapedia</i> sp. 2 (Apidae)	1	1	1	1			1	1				1	7
<i>Centris collaris</i> (Apidae)	1	1	1	1	1	1							6
<i>Plebeia droryana</i> (Apidae)	1		1	1			1	1			1		6
<i>Epicharis schrottkyi</i> (Apidae)	1	1	1	1	1			1					6
<i>Tetrapedia diversipes</i> (Apidae)		1	1			1	1	1					5
<i>Centris bicolor</i> (Apidae)	1		1		1				1	1			5
<i>Monoeca</i> sp. 1 (Apidae)	1	1	1	1									4
<i>Centris discolor</i> (Apidae)	1	1			1								3
<i>Epicharis obscura</i> (Apidae)		1	1	1									3
<i>Paratetrapedia</i> sp. 1 (Apidae)	1	1	1										3
<i>Monoeca</i> sp. 2 (Apidae)		1	1		1								3
<i>Centris tarsata</i> (Apidae)									1		1		2
<i>Centris nitens</i> (Apidae)	1							1					2
<i>Epicharis analis</i> (Apidae)	1			1									2
<i>Centris fuscata</i> (Apidae)		1				1							2
<i>Paratetrapedia velutina</i> (Apidae)			1			1							2
<i>Centris trigonoides</i> (Apidae)	1		1										2
<i>Trigona spinipes</i> (Apidae)								1					1
<i>Monoeca</i> sp. 3 (Apidae)							1						1
<i>Apis mellifera</i> (Apidae)					1								1
<i>Paratetrapedia</i> sp. 3 (Apidae)		1											1
<i>Nannotrigona testaceicornis</i> (Apidae)		1											1
<i>Centris aenea</i> (Apidae)	1												1
<i>Centris labrosa</i> (Apidae)	1												1
L_n	18	17	17	12	11	8	8	8	5	5	4	3	116

Bignoniaceae pollination network	<i>Pithecoctenium crucigerum</i>	<i>Stizophyllum perforatum</i>	<i>Anemopaegma chamberlaynii</i>	<i>Arrabidaea samydoides</i>	<i>Amphilophium vauthieri</i>	<i>Adenocalyma bracteatum</i>	<i>Arrabidaea selloi</i>	<i>Arrabidaea triplinervia</i>	<i>Adenocalyma marginatum</i>	L_m
<i>Epicharis flava</i> (Apidae)	1		1							2
<i>Eulaema nigrata</i> (Apidae)	1	1								2
<i>Centris mocsaryi</i> (Apidae)		1	1							2
<i>Centris discolor</i> (Apidae)		1	1							2
<i>Epicharis analis</i> (Apidae)	1									1
<i>Rathymus cf. unicolor</i> (Carabidae)	1									1
<i>Euplusia auriceps</i> (Apidae)	1									1
<i>Epicharis rustica</i> (Apidae)					1					1
<i>Eulaema</i> sp. 1 (Apidae)					1					1
<i>Centris bicolor</i> (Apidae)				1						1
<i>Centris similis</i> (Apidae)						1				1
<i>Papilio astyalus</i> (Papilionidae)				1						1
<i>Battus polydamas</i> (Papilionidae)				1						1
<i>Bombus brasiliensis</i> (Apidae)							1			1
<i>Centris collaris</i> (Apidae)								1		1
<i>Xylocopa</i> sp. 1 (Apidae)									1	1
L_n	5	3	3	3	2	1	1	1	1	20

Malpighiaceae pollination network	<i>Dicella bracteosa</i>	<i>Banisteriopsis adenopoda</i>	<i>Stigmaphyllon lalandianum</i>	<i>Banisteriopsis muricata</i>	<i>Mascagnia anisopetala</i>	<i>Mascagnia cordifolia</i>	<i>Tetrapteryx guilleminiana</i>	<i>Banisteriopsis lutea</i>	<i>Heteropteryx aceroides</i>	<i>Tetrapteryx phlomoides</i>	<i>Mascagnia sepium</i>	<i>Banisteriopsis pubipetala</i>	L_m
<i>Epicharis flava</i> (Apidae)	1	1	1	1	1		1	1	1	1	1	1	11
<i>Centris</i> spp. (Apidae)	1	1	1	1	1	1		1	1	1			9
<i>Epicharis affinis</i> (Apidae)	1	1	1	1	1		1		1	1			8
<i>Centris mocsaryi</i> (Apidae)	1	1	1	1	1	1	1						7
<i>Centris collaris</i> (Apidae)	1	1	1	1	1		1						6
<i>Epicharis schrottkyi</i> (Apidae)	1	1	1	1	1	1							6
<i>Centris bicolor</i> (Apidae)	1		1		1			1		1			5
<i>Plebeia droryana</i> (Apidae)	1			1		1					1		4
<i>Monoeca</i> sp. 1 (Apidae)	1	1	1	1									4
(<i>Para</i>) <i>Tetrapedia</i> sp. 1 (Apidae)		1					1	1	1				4
<i>Centris discolor</i> (Apidae)	1	1			1								3
<i>Epicharis obscura</i> (Apidae)		1	1	1									3
<i>Monoeca</i> sp. 2 (Apidae)		1	1		1								3
<i>Centris tarsata</i> (Apidae)								1			1		2
<i>Centris nitens</i> (Apidae)	1					1							2
<i>Epicharis analis</i> (Apidae)	1			1									2
<i>Centris fuscata</i> (Apidae)		1					1						2
<i>Tetrapedia diversipes</i> (Apidae)						1	1						2
<i>Centris trigonoides</i> (Apidae)	1		1										2
<i>Monoeca</i> sp. 3 (Apidae)									1				1
<i>Trigona spinipes</i> (Apidae)						1							1
<i>Paratetrapedia</i> sp. 2 (Apidae)						1							1
<i>Apis mellifera</i> (Apidae)					1								1
<i>Centris aenea</i> (Apidae)	1												1
<i>Centris labrosa</i> (Apidae)	1												1
L_n	15	12	11	10	10	8	7	5	5	4	3	1	91

Bignoniaceae cheating network	<i>Arrabidea triplinervia</i>	<i>Adenocalyma bracteatum</i>	<i>Anempagema chamberlaynii</i>	<i>Arrabidea samyoides</i>	<i>Lundia obliqua</i>	<i>Stizophyllum perforatum</i>	<i>Arrabidea selloi</i>	<i>Adenocalyma marginatum</i>	L_m
<i>Oxaea flavescens</i> (Andrenidae)	1		1	1		1			4
<i>Xylocopa suspecta</i> (Apidae)	1		1	1		1			4
<i>Euglossa annectans</i> (Apidae)	1	1	1						3
<i>Temenis laothoe</i> (Nymphalidae)						1	1		2
<i>Cymaenes tripunctata</i> (Hesperiidae)	1	1							2
<i>Euglossa pleosticta</i> (Apidae)	1	1							2
<i>Xylocopa brasiliatorum</i> (Apidae)	1		1						2
<i>Pseudagochloropsis</i> cf. <i>pandora</i> (Halictidae)								1	1
Trochilidae sp. 2 (Trochilidae)								1	1
<i>Nannotrigona testaceicornis</i> (Apidae)							1		1
<i>Paratrigona lineata</i> (Apidae)							1		1
Indetermined sp.						1			1
<i>Urbanus procne</i> (Hesperiidae)						1			1
Aphididae sp. 1					1				1
Cecidomyiidae sp. 1 (Diptera)					1				1
Chamaemyiidae sp. 1 (Diptera)					1				1
Chloropidae sp. 1 (Diptera)					1				1
Curculionidae sp. 1					1				1
Lauxaniidae sp. 1 (Diptera)					1				1
<i>Ascia monuste</i> (Pieridae)				1					1
<i>Cymaenes gisca</i> (Hesperiidae)				1					1
<i>Paratetrapedia</i> sp. 1 (Apidae)				1					1
<i>Paratetrapedia</i> sp. 2 (Apidae)				1					1
<i>Centris bicolor</i> (Apidae)			1						1
<i>Melanotrochilus fuscus</i> (Trochilidae)			1						1
Agroceridae sp. 1 (Diptera)		1							1
<i>Augochlora</i> sp. 1 (Halictidae)		1							1
<i>Cobalopsis catocala</i> (Hesperiidae)		1							1
Diptera sp. 1		1							1
<i>Perichares lotus</i> (Hesperiidae)		1							1
<i>Perichares philetes</i> (Hesperiidae)		1							1
Sarcophagidae sp. 1 (Diptera)		1							1
<i>Trigona spinipes</i> (Apidae)		1							1
Trochilidae sp. 1 (Trochilidae)		1							1

Bignoniaceae nectar robbery network	<i>Arrabidaea triplinervia</i>	<i>Adenocalyma bracteatum</i>	<i>Anemopaegma chamberlaynii</i>	<i>Arrabidaea samydoidea</i>	<i>Stizophyllum perforatum</i>	<i>Adenocalyma marginatum</i>	<i>Arrabidaea selloi</i>	L_m
<i>Oxaea flavescens</i> (Andrenidae)	1		1	1	1			4
<i>Xylocopa suspecta</i> (Apidae)	1		1	1	1			4
<i>Euglossa annectans</i> (Apidae)	1	1	1					3
<i>Euglossa pleosticta</i> (Apidae)	1	1						2
<i>Cybaeus tripunctata</i> (Hesperiidae)	1	1						2
<i>Xylocopa brasilianorum</i> (Apidae)	1		1					2
<i>Temenis laothoe</i> (Nymphalidae)					1		1	2
Trochilidae sp. 2 (Trochilidae)						1		1
Indetermined sp.					1			1
<i>Urbanus procyon</i> (Hesperiidae)					1			1
<i>Paratetrapedia</i> sp. 1 (Apidae)				1				1
<i>Paratetrapedia</i> sp. 2 (Apidae)				1				1
<i>Cybaeus gisca</i> (Hesperiidae)				1				1
<i>Ascia monuste</i> (Pieridae)				1				1
<i>Centris bicolor</i> (Apidae)			1					1
<i>Melanotrochilus fuscus</i> (Trochilidae)			1					1
<i>Euglossa cordata</i> (Apidae)	1							1
<i>Exaerete smaragdina</i> (Apidae)	1							1
<i>Urbanus viterboana</i> (Hesperiidae)	1							1
<i>Strymon</i> sp. 1 (Lycaenidae)	1							1
<i>Epicharis</i> cf. <i>grandior</i> (Apidae)	1							1
<i>Xylocopa frontalis</i> (Apidae)	1							1
<i>Xylocopa</i> sp. 1 (Apidae)	1							1
<i>Perichares lotus</i> (Hesperiidae)		1						1
<i>Perichares philetes</i> (Hesperiidae)		1						1
<i>Cobalopsis catocala</i> (Hesperiidae)		1						1
<i>Vettius diversus</i> (Hesperiidae)		1						1
Trochilidae sp. 1 (Trochilidae)		1						1
Aphididae sp. 1		1						1
L_n	13	9	6	6	5	1	1	41

Bignoniaceae pollen robbery network	<i>Adenocalyma bracteatum</i>	<i>Lundia obliqua</i>	<i>Arrabidaea selloi</i>	<i>Adenocalyma marginatum</i>	<i>Arrabidaea triplinervia</i>	<i>L_m</i>
<i>Paratrigona</i> sp. 1 (Apidae)				1	1	
<i>Pseudagochloropsis</i> cf. <i>pandora</i> (Halictidae)				1	1	
<i>Paratrigona lineata</i> (Apidae)			1		1	
<i>Nannotrigona testaceicornis</i> (Apidae)			1		1	
Chloropidae sp. 1 (Diptera)		1			1	
Chamaemyiidae sp. 1 (Diptera)		1			1	
Lauxaniidae sp. 1 (Diptera)		1			1	
Cecidomyiidae sp. 1 (Diptera)		1			1	
Curculionidae sp. 1		1			1	
<i>Trigona spinipes</i> (Apidae)	1				1	
<i>Augochlora</i> sp. 1 (Halictidae)	1				1	
Agroceridae sp. 1 (Diptera)	1				1	
Diptera sp. 1	1				1	
Sarcophagidae sp. 1 (Diptera)	1				1	
<i>L_n</i>	5	5	2	1	1	14

Pollinator and cheater

Nectar robber

Pollen robber

SUPPLEMENTARY ELECTRONIC MATERIAL

ADDITIONAL MATERIALS & METHODS

Each network (visitation matrix) was split into two matrices describing interactions between plants and pollinators only (pollination matrix) and robbers only (robbery matrix). Information on the matrices is detailed in the Appendix.

Modularity Analysis

The Guimerà's algorithm is based on simulated annealing to identify the modules and to compute modularity M , ranging from 0 to $(1-1/\text{number of modules})$, according to increasing modularity (for further details, see Guimerà & Amaral 2005a; Olesen *et al.* 2007). We ran 100 randomizations of the empirical network and calculated significance level of the observed M .

We characterized the role of a species using its within-module degree z and among-module connectivity c (Guimerà & Amaral 2005a). High z -values imply in well connected species to other species within the same module (Guimerà & Amaral 2005a). c of a species is close to one if its links are randomly distributed among all modules and zero if all its links are within its own module (for further details, see Olesen *et al.* 2007). In this study, we follow Olesen *et al.* (2007) classification of species roles in relation to their zc scores into peripherals ($z \leq 2.5$ and $c \leq 0.62$), connectors ($z \leq 2.5$ and $c > 0.62$), module hubs ($z > 2.5$ and $c \leq 0.62$) and network hubs ($z > 2.5$ and $c > 0.62$).

Co-occurrence Analysis

Using *Ecosim* (Gotelli & Entsminger 2009), a co-occurrence analysis was made to assess among-module distribution of cheater species. The C -score Index of *Ecosim* gives the tendency for ecologically related species to occur in different modules. Thus a C -score larger than expected if community assembly was random, indicates that cheaters are over-dispersed across modules.

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Conclusões Gerais

Neste trabalho demonstramos que os padrões de floração em nível de comunidade de uma floresta tropical semidecídua são agregados e aninhados temporalmente. O aninhamento implica numa sobreposição assimétrica do nicho temporal onde espécies que possuem períodos de floração curtos estão compreendidas dentro do período de floração das espécies de floração longa. A assimetria no nicho temporal pode gerar padrões de competição assimétricos entre as espécies quando os polinizadores são um recurso limitante. Por outro lado, o aninhamento temporal pode reduzir a competição e aumentar o número coexistentes. Por exemplo o aninhamento pode facilitar a manutenção dos polinizadores no tempo por que? Explicar. Independentemente das consequências do aninhamento temporal, o fato das espécies de floração longa gerarem esse padrão aninhado embora a ocorrência dessas espécies chegue no máximo a 10 % das espécies nas florestas tropicais indica um efeito desproporcional dessas espécies na organização temporal das comunidades.

Nós também demonstramos que florestas semidecíduas do sudeste do Brasil apresentam uma alta diversidade de modos de polinização, comparáveis a outras florestas tropicais e que essa diversidade está representada ao longo de todas as estações. Adicionalmente, o clima e a filogenia não restringiram a floração da maior parte das espécies independentemente do modo de polinização. Apesar disso, as estratégias de floração sazonais predominaram em

todos os modos de polinização menos por morcegos, indicando que cada modo apresentou um padrão particular de floração que leva a uma grande diversidade de estratégias reprodutivas entre as espécies. Portanto, mesmo em ambiente sazonal onde existe um período mais favorável para a reprodução, todos os modos de polinização estiveram representados ao longo do ano, mesmo que em diferentes proporções. Isso poderia reduzir a competição por polinizadores e facilitar a sua manutenção ao longo do ano.

As redes de interações usualmente são representadas como representações estáticas da natureza. No entanto, alguns estudos têm avaliado a dinâmica temporal dessas redes e demonstrado a grande variação em vários atributos como número de enlaces, tamanho do sistema dentre outros (Olesen *et al.*, 2008; 2011; Petanidou *et al.*, 2008; Basílio *et al.*, 2006). No nosso estudo nós confirmamos a grande dinâmica temporal em uma rede de polinizadores devido a variação mensal e sazonal na diversidade beta nas espécies e interações. Além do mais, no caso do estudo 1, da rede esfingófila, nos evidenciamos a importância das diferenças fenológicas na floração das espécies de nossa rede local e nas redes adjacentes na manutenção das populações de esfingídeos.

Finalmente, nós demonstramos que as redes de visitantes florais podem variar no seu nível de antagonismo, sendo que existem redes com uma maior frequência de pilhadores que outras. As redes onde os pilhadores são mais frequentes são mais especializadas e, portanto, mais antagonistas. Nós observamos que a estrutura da rede

de visitantes florais está relacionado ao nível de especialização dos enlaces, enquanto que dentro de uma rede os visitantes exploram todos os recursos presentes contribuindo com um padrão aninhado, a rede com mais enlaces antagonistas (i.e. com mais pilhadores) apresenta um padrão modular. As redes antagonistas apresentam padrões modulares de interações e a remoção dos pilhadores mostrou que eles contribuem na geração desse padrão modular e reforça a importância do tipo de enlace na estrutura de redes de interações.

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