

# Modularity, pollination systems, and interaction turnover in plant-pollinator networks across space

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**Abstract.** Mutualistic interaction networks have been shown to be structurally conserved over space and time while pairwise interactions show high variability. In such networks, modularity is the division of species into compartments, or modules, where species within modules share more interactions with each other than they do with species from other modules. Such a modular structure is common in mutualistic networks and several evolutionary and ecological mechanisms have been proposed as underlying drivers. One prominent explanation is the existence of pollination syndromes where flowers tend to attract certain pollinators as determined by a set of traits. We investigate the modularity of seven community level plant-pollinator networks sampled in rupestrian grasslands, or *campos rupestres*, in SE Brazil. Defining pollination systems as corresponding groups of flower syndromes and pollinator functional groups, we test the two hypotheses that (1) interacting species from the same pollination system are more often assigned to the same module than interacting species from different pollination systems and; that (2) interactions between species from the same pollination system are more consistent across space than interactions between species from different pollination systems. Specifically we ask (1) whether networks are consistently modular across space; (2) whether interactions among species of the same pollination system occur more often inside modules, compared to interactions among species of different pollination systems, and finally; (3) whether the spatial variation in interaction identity, i.e., spatial interaction rewiring, is affected by trait complementarity among species as indicated by pollination systems. We confirm that networks are consistently modular across space and that interactions within pollination systems principally occur inside modules. Despite a strong tendency, we did not find a significant effect of pollination systems on the spatial consistency of pairwise interactions. These results indicate that the spatial rewiring of interactions could be constrained by pollination systems, resulting in conserved network structures in spite of high variation in pairwise interactions. Our findings suggest a relevant role of pollination systems in structuring plant-pollinator networks and we argue that structural patterns at the sub-network level can help us to fully understand how and why interactions vary across space and time.

**Key words:** Campos rupestres; community; module; pollination syndrome; *QuanBiMo*; rewiring; rupestrian grassland; tropics.

## INTRODUCTION

Pollination syndromes are flower categorizations based on traits such as flower morphology, scent, and reward (Fægri and van der Pijl 1979, Fenster et al. 2004), and the concept provides a hypothesis to explain floral evolution by means of adaptation to pollinators (Ollerton et al. 2009). Whether syndromes are just an outcome of the search of patterns in ecology is still a matter for debate (Waser and Ollerton 2006, Ollerton et al. 2009, Rosas-Guerrero et al. 2014), and attempts to empirically

test the connection between floral syndromes and their supposed pollinators on a community level are rare and have shown mixed results (Hingston and McQuillan 2000, Ollerton et al. 2009, Rosas-Guerrero et al. 2014). In the meta analysis by Ollerton et al. (2009), using data from six communities across three continents, the most common pollinator was only predicted by the closest flower syndrome in approximately 30% of the plant species. The fact that plant-pollinator interactions seem to be more generalized (Waser et al. 1996, Waser and Ollerton 2006) than previously thought, raises further questions regarding the pollination syndrome hypothesis. More recently, however, Rosas-Guerrero et al. (2014) in an extensive review of pollination syndromes and their

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most effective pollinators found support for the syndrome hypothesis and showed that their predictability increases towards the tropics.

Moving beyond studies of single species of plants and pollinators and their interactions, ecological network analysis has proven useful over the last couple of decades (Jordano 1987, Memmott 1999, Bascompte et al. 2003, Bascompte and Jordano 2013). The main strength of a network approach in ecology is the possibility of detecting emergent patterns in a community of interacting species, and network studies have indeed revealed community level interaction patterns such as asymmetry (Vázquez and Simberloff 2002, Bascompte et al. 2006), power law degree distributions (Jordano et al. 2003), and modularity (Dicks et al. 2002, Lewinsohn et al. 2006, Olesen et al. 2007). Modularity is the division of a network into compartments, or modules, where species within modules interact more strongly with each other than with species from other modules. Modules thus represent sub-networks within a network. Such an organization is partly caused by convergent trait sets and modules can be considered as co-evolutionary units (Olesen et al. 2007). In a pollination network context, such units could correspond to pollination syndromes (e.g., Danieli-Silva et al. 2012), or rather, plant syndromes and their corresponding functional group of pollinators. As the concept of pollination syndromes is highly plant-centered, we here instead use the term pollination systems to define groups of plants and pollinators from complementing pollination syndromes (plants) and functional groups (pollinators). For instance, bees would be expected to interact more strongly with plants exerting a bee pollination syndrome than with e.g., plants exerting a bird pollination syndrome. Indeed, the detection of modularity in a network presents a pattern useful for testing hypotheses regarding pollination systems, while further posing the challenge to discover what determines the identity of closely interacting groups of species. Few studies so far have explored these questions (Dicks et al. 2002, Olesen et al. 2007, Dupont and Olesen 2009, Danieli-Silva et al. 2012, González et al. 2012, Maruyama et al. 2014) and some empirical support has been found for pollination systems as drivers of modularity (Dicks et al. 2002, Danieli-Silva et al. 2012, González et al. 2012). These studies are either based on a single network or on a meta analysis of networks from different locations, however. How patterns of modularity and pollination systems vary across space within an ecosystem is hitherto unstudied. Exploring this variation can reveal the consistency of patterns and drivers.

Recent studies find that plant-pollinator interactions are highly labile across space and time, supporting the increasing consensus that pairwise specialization is rare, while generalization might be more common than previously thought (Dupont et al. 2009, Burkle and Alarcon 2011, Olesen et al. 2011b, Carstensen et al. 2014). That is, even between species that co-occur repeatedly through time or across space, interactions might change, or

“rewire.” Which factors affect this rewiring of interactions and whether any interactions are more consistent across space and time still need further investigation. Carstensen et al. (2014) demonstrated that local flower abundance is important for the realization of pairwise interactions as expected from earlier work (Vázquez et al. 2005, Canard et al. 2012), but also that interactions with high local frequencies are more consistent across space. If pollination systems truly represent groups of co-adapted plants and pollinators, it could be hypothesized that interactions within such groups should be more consistent across space as well.

Using a set of seven spatially explicit community level plant-pollinator networks, we aim to explore yet unanswered questions regarding the spatial variation of interactions. Specifically we ask: (1) Are networks consistently modular across space? (2) Do interactions among species of the same pollination system occur more often inside modules, compared to interactions among species of different pollination systems? And (3) are interactions within pollination systems more consistent across space than interactions between pollination systems? We hypothesize that interacting species from the same pollination system are more often assigned to the same module than interacting species from different pollination systems and, as interactions between species from different pollination systems likely are more coincidental, they are less consistent across space.

## METHODS

### *Study sites and field observations*

We collected the data in seven areas of rupestrian grasslands, or *campos rupestres*, in the National Park of Serra do Cipó and its buffer zone, Morro da Pedreira, located in the southern end of the Espinhaço mountain chain, in the state of Minas Gerais, SE Brazil. *Campos rupestres* are characterized by a species-rich vegetation of mostly small sclerophyllous evergreen shrubs and herbs associated with rocky outcrops and quartzitic or sandy soils with high aluminium and low nutrient contents (Alves and Kolbek 1994, Benites et al. 2007, Silveira et al. 2016), and represent the dominant vegetation type between 1000–1400 m a.s.l. in Serra do Cipó. The seven sites were located a minimum of 1.4 km and a maximum of 8.5 km apart, all within an altitudinal range of 1073–1260 m a.s.l., and with similar wind exposition, soil substrate, and floral species richness. Plant-pollinator interactions were sampled from early October to mid December 2012 by means of flower-based focal observations. At each site, we sampled ten 1 m<sup>2</sup> plots along a 200 m long curvilinear transect. In each of these plots, we observed flowering plants for 15 min, considering as pollinators all flower visitors touching plant reproductive organs. We sampled one site per day with a fixed weekly rotation among sites. Sampling accumulated to 6 d per site and 252 h of observation over 44 d,

resulting in a total of 2,271 observed interactions. Plants and pollinators were collected and subsequently identified to the highest possible taxonomic resolution (genus or species level in most cases) with the aid of specialists. See Carstensen et al. (2014) for further details.

#### *Pollination systems and modularity*

Pollination systems indicate an expected preference, or increased affinity, in interactions between plants and pollinators. Independently of visitation data, we categorized plants into one of four pollination syndromes based on basic floral traits (size, shape, color, scent, and reward): bee pollination, butterfly pollination, bird pollination, and diverse insect pollination (Appendix S1, Fægri and van der Pijl 1979). Pollinators were grouped into four corresponding functional groups: bees, butterflies, birds, and diverse insects. Diverse insects include wasps, beetles, and flies (see Appendix S2). Each observed unique interaction was then defined either as conforming to pollination system, e.g., a bee interacting with a bee pollination syndrome plant, or as not conforming to pollination system, e.g., a bee interacting with a bird pollination syndrome plant. Respectively, we term these interactions as being *within pollination system* and being *between pollination systems* (Fig. 1).

For each site, we constructed a weighted interaction matrix with plant species in rows and pollinator species in columns, each representing a bipartite plant-pollinator network. We analyzed each network for modularity using the QuanBiMo algorithm (Dormann and Strauss 2014) to maximize the modularity metric  $Q$ . This algorithm creates a random division of the network as a starting point, upon which it performs random swaps of species; each swap followed by a new evaluation of  $Q$ . After  $10^6$  swaps without any improvement in  $Q$  the algorithm stops.  $Q$  indicates the modularity level of the network and ranges from 0 to 1. Optimizing it is a matter of finding the configuration of modules with the least number of links between modules and the maximum number of links within modules. As the algorithm is a stochastic process results may vary among computations. For each network, we therefore used the modular configuration with the highest  $Q$  from 50 independent computations. To test the significance of the modularity values ( $Q$ ) of the empirical networks, we computed null expectations based on 100 random networks with the same marginal totals as the empirical one. The modularity of each random network was also computed 50 times from which the highest  $Q$  was used to calculate the average  $Q$  across the 100 random networks. We standardized  $Q$  values into  $z$ -scores using the formula

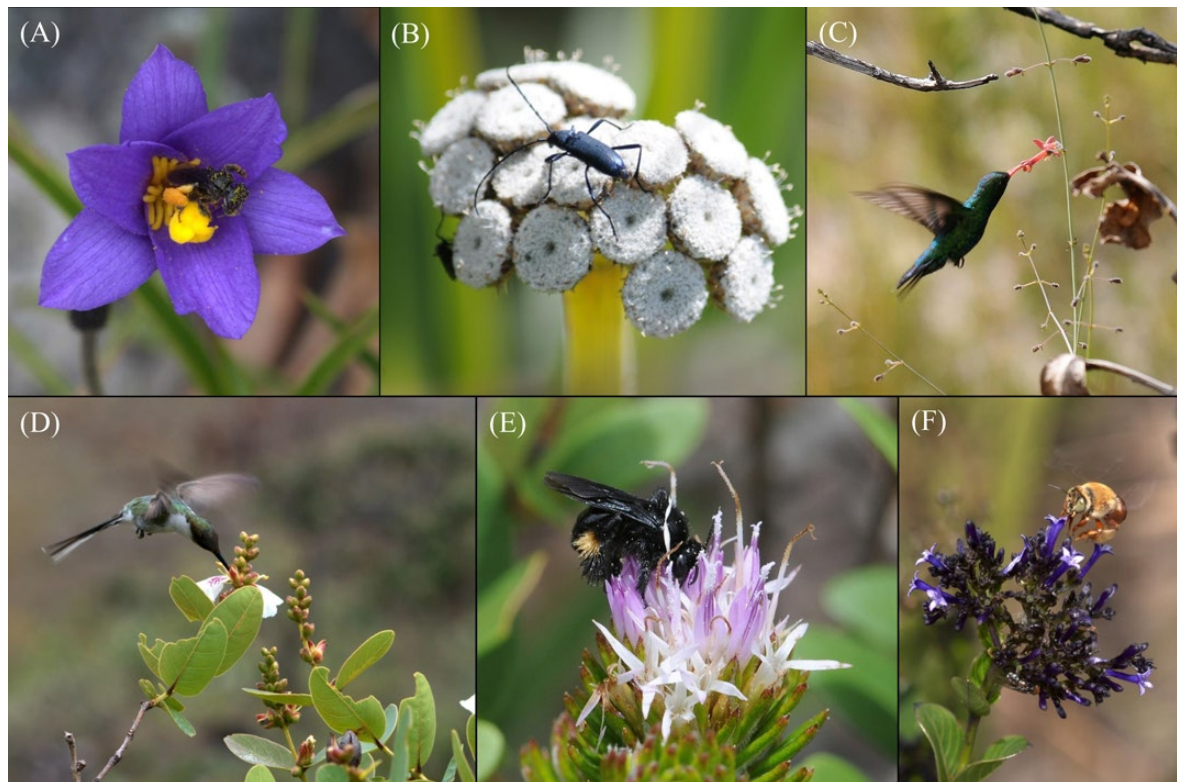


FIG. 1. Examples of plant-pollinator interactions within pollination systems (A–C) and between pollination systems (D–F). (A) *Vellozia* sp. and *Tetrapedia* sp. (B) *Paepalanthus bromelioides* and a Cerambycidae beetle. (C) *Hylenia macrantha* and *Chlorostilbon lucidus*. (D) *Qualea dichotoma* and *Heliactin bilophus*. (E) *Lychnofores* sp. and *Tetrapedia* sp. (F) *Declieuxia fruticosa* and *Centris* sp. All photos by Daniel W. Carstensen.



$z_Q = (Q_{\text{observed}} - \bar{Q}_{\text{null}}) / \text{SD}_{Q_{\text{null}}}$  in order to assess the significance of the empirical networks. The  $z$ -score measures the number of standard deviations the  $Q$  of the empirical network deviates from the average  $Q$  of the random networks. When  $z$ -scores are above 1.96 the empirical network is considered significantly modular. For comparison, we also analyzed the binary transformed networks using the algorithm of Guimerà and Amaral (2005) in the software MODULAR (Marquitti et al. 2014). The modularity obtained here was similarly compared to 100 random networks with the same marginal totals as the empirical one by standardizing  $Q$  values into  $z$ -scores.

To test whether interactions among species from the same pollination system (i.e., within pollination system interactions) would significantly more often be inside modules than interactions among species from different pollination systems (i.e., between pollination system interactions), we calculated, for each site, the percentages of within and between pollination system interactions that were also inside the same module. Percentages from all sites were pooled together to calculate the mean, and the test for significant difference was performed using a Welch's  $t$ -test. We did these analyses both using the results from the weighted and the binary modularity, as well as using both the frequency of interactions (weighted interactions) and presence/absence interaction data (binary interactions) to define the percentages of within and between pollination system interactions that were inside modules.

#### Interaction turnover

To test the spatial consistency of interactions within pollination system vs. interactions between pollination systems we examined each unique pairwise interaction for turnover between all 21 site-pair combinations. For each site-pair comparison, in order to account for species turnover between sites, we excluded species unique to one site and only looked at the interactions among the set of species found at both sites. We then defined the remaining pairwise interactions as “consistent” if occurring in both

sites or “turning over” if occurring in only one site (see Carstensen et al. 2014 for a detailed explanation). Then, using the two categories on whether interactions are within or between pollination systems, we tested whether the two groups differed significantly in the amount of interaction turnover among sites. We used a contingency table and Fisher's exact test to assess whether interactions within pollination systems showed a significantly different proportion of turnover events than interactions between pollination systems.

## RESULTS

The weighted modularity was consistently high across all seven sites, with all sites being significantly more modular than expected by random. Networks were divided into 6–9 modules, defining a compartmentalized structure within each of the seven plant-pollinator networks (Table 1, Fig. 2). Binary modularity also showed high modularity across sites, dividing networks into 7–9 modules. No site, however, showed modularity significantly different from random (Table 1, Appendix S2: Table S1).

Across the seven networks, the proportion of interactions classified as being within pollination system was 52–73% (Table 1). Interactions within pollination system (Mean = 60.9, SD = 6.6) were thus overall more common than interactions between pollination systems (Mean = 39.1, SD = 6.6,  $t(12) = 6.2$ ,  $P < 0.0001$ ). Using the modular configuration from the weighted or binary modularity analyses we obtained similar results; the mean percentage (across all sites) of interactions inside modules was significantly higher for within pollination system interactions than for between pollination system interactions, both when using weighted and binary interactions (Table 2). Apart from one case (site “Elefante” when using binary modularity and binary interaction data), all sites showed a higher proportion of interactions inside modules for within pollination system interactions (Appendix S2: Tables S2–S3).

After excluding species unique to one site, we used the remaining 1,019 pairwise interactions to test for turnover of within pollination system and between pollination

TABLE 1. Network size and results of the modularity analyses for each of the seven study sites.

| Network (site) | Plants | Pollinators | $Q_{\text{weighted}}$ | Weighted no. modules | $Q_{\text{binary}}$ | Binary no. modules | Percentage of int. within PS |
|----------------|--------|-------------|-----------------------|----------------------|---------------------|--------------------|------------------------------|
| Cedro          | 25     | 67          | 0.50*                 | 6                    | 0.58                | 7                  | 64                           |
| Midway         | 25     | 51          | 0.52*                 | 7                    | 0.49                | 9                  | 62                           |
| Gigante        | 28     | 67          | 0.43*                 | 7                    | 0.50                | 8                  | 60                           |
| Paulino        | 25     | 84          | 0.57*                 | 9                    | 0.53                | 8                  | 57                           |
| Soizig         | 23     | 65          | 0.52*                 | 9                    | 0.61                | 9                  | 58                           |
| Tinkerbell     | 22     | 55          | 0.52*                 | 8                    | 0.63                | 8                  | 52                           |
| Elefante       | 33     | 72          | 0.55*                 | 9                    | 0.55                | 8                  | 73                           |

Notes: The seven columns show, for each network, the number of plant and pollinator species, the observed modularity level ( $Q_{\text{weighted}}$ ) and number of modules from the weighted modularity, the observed modularity level ( $Q_{\text{binary}}$ ) and number of modules from the binary modularity, and the proportion of interactions that are within pollination systems (PS). Asterisks indicate significantly different modularity from random. Full table including  $z$ -scores is reported in Table S1 (Appendix S2).

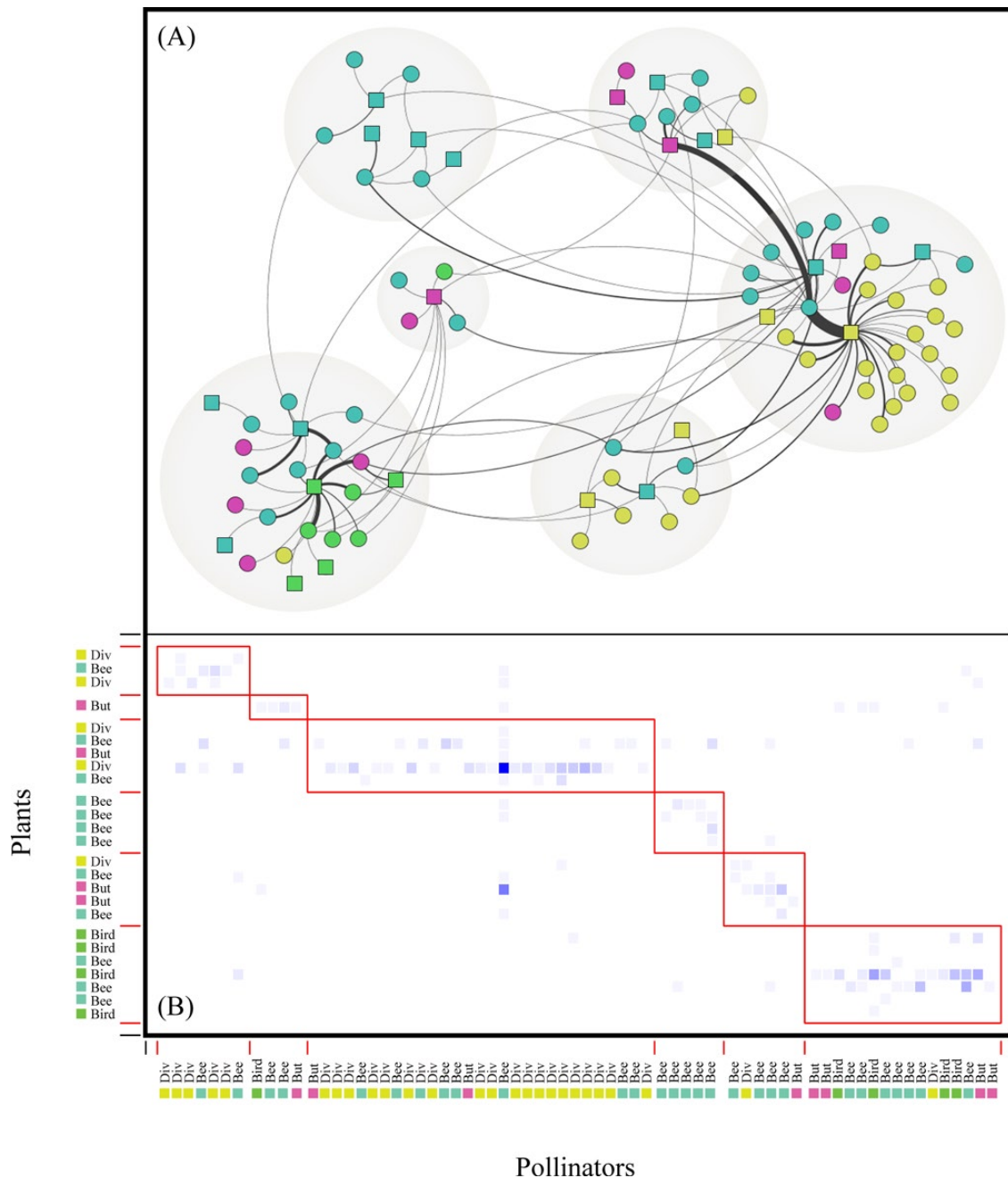


FIG. 2. The modular division and pollination system classifications of the Cedro network. (A) shows the network divided into the six modules. The nodes of the network are represented by squares (plants,  $n = 25$ ) and circles (pollinators,  $n = 67$ ) and are color-coded according to pollination systems. The thickness of the lines scale with the frequency of the interactions. (B) shows the interaction matrix organized in the modular pattern with plant species in the rows and pollinator species in the columns. As in (A), species are colored according to pollination systems: Cyan: bee pollination system, purple: butterfly pollination system, green: bird pollination system, and yellow: diverse insect pollination system. Interactions between species are marked by a blue square inside the matrix, the more frequent the interaction, the stronger the color.

system interactions. 667 site-pair comparisons of pairwise interactions were classified as being within pollination system, with the remaining 352 classified as being between systems. 485 (73%) of the 667 interactions within pollination system showed turnover between sites, while 273

(78%) of the 352 interactions between pollination systems showed turnover. Despite this higher turnover for interactions between pollination systems, Fisher's exact test did not show a significant difference in the turnover of interactions between the two groups ( $P = 0.09$ , power = 0.40).

TABLE 2. The mean percentage of interactions inside modules for between and within pollination system (PS) interactions for weighted and binary modularity.

| Interaction type | Weighted modularity |      |           |     |          |    |          | Binary modularity |      |           |      |          |    |          |
|------------------|---------------------|------|-----------|-----|----------|----|----------|-------------------|------|-----------|------|----------|----|----------|
|                  | Between PS          |      | Within PS |     | <i>t</i> | df | <i>P</i> | Between PS        |      | Within PS |      | <i>t</i> | df | <i>P</i> |
|                  | Mean                | SD   | Mean      | SD  |          |    |          | Mean              | SD   | Mean      | SD   |          |    |          |
| Weighted         | 74.0                | 7.3  | 84.9      | 7.4 | −2.8     | 12 | 0.017    | 53.3              | 14.6 | 73.1      | 11.7 | −2.8     | 11 | 0.017    |
| Binary           | 66.3                | 10.3 | 77.4      | 7.3 | −2.3     | 11 | 0.040    | 66.6              | 7.6  | 76.4      | 8.2  | −2.3     | 12 | 0.041    |

Notes: Interaction type indicates whether the frequency (weighted) or simply the presence (binary) of interactions was used to calculate the means. Difference between means was tested using a Welch's *t*-test. Also included are standard deviations (SD), *t*-statistics, degrees of freedom (df), and the *P*-value. The mean percentage of interactions inside modules were significantly higher for within PS interactions than for between PS interactions in all cases ( $P < 0.05$ ).

## DISCUSSION

We found a spatial consistency in network modularity level and in the grouping of species from the same pollination systems. At the level of pairwise interactions, we found a trend, but no significant effect, of pollination systems on spatial interaction consistency. That is, when looking at each pairwise interaction, those within the same pollination system and those between pollination systems did not differ significantly in their probability of turnover among sites. However, the consistent high modularity and predominance of within pollination system interactions inside modules, indicate that trait matching, as represented by pollination systems, drives a spatially conserved interaction structure.

Modularity is a commonly observed pattern in plant–pollinator networks; however modularity levels and number of modules vary widely depending on the size and type of the community in question (Olesen et al. 2007). Our seven networks, equally sampled during the same season and within the same region, all showed high levels of modularity for both weighted and binary networks. While all weighted networks were significantly modular, none of the binary networks were so. A large difference in significance levels between weighted and binary modularity has been reported previously (e.g., Schleuning et al. 2014) and is likely caused by the fact that weighted networks contain more information than binary ones (Dormann and Strauss 2014). Specific to our networks, some pairwise interactions were highly frequent compared to the mean (e.g., *Bombus pauloensis* and *Aspilota jolyana*), and the strength of such interactions are not considered in the binary networks. Our findings indicate that the modularity level is conserved across space if networks are of similar sizes and sampled in ecologically similar areas. To our knowledge, no previous study has investigated the spatial variation of modularity across a set of sites within a region, but we can compare our results with the conserved levels of modularity over time (Dupont et al. 2009, Burkle and Alarcon 2011).

Plant and pollinator distribution over time and space can be important drivers of network structure by constraining species interactions (Vazquez et al. 2009, Olesen

et al. 2011a, Vizentin-Bugoni et al. 2014). Maruyama et al. (2014) found that even though phenological overlap was important to determine interaction frequency between species of hummingbirds and plants, it did not lead to the formation of distinct modules in plant–hummingbird networks. Meanwhile, González et al. (2012) showed a strong effect of phenology in structuring an insect–plant pollination network into modules. Along the year, spatiotemporal variation in phenology could thus affect network structure locally, for instance by local mass flowering events or the presence of species with prolonged flowering. As our study focused on the effect of space, we restricted our data collection to an intense ~2 month period representing the flowering peak of the early rainy season (Carstensen et al. 2014) in order to minimize phenological turnover during sampling.

Our results show that interacting species of the same pollination system are consistently more often grouped with each other than they are with species from other pollination systems. Instead of defining modules strictly conforming to specific pollination systems (e.g., bee pollination modules or bird pollination modules) we argue that our more general approach is appropriate in the case of pollination systems, as modules rarely comprise species from only one pollination system (Fig. 2). Indeed, plants are often pollinated by pollinators not conforming to their syndrome and visited by pollinators from more than one functional group (Dicks et al. 2002, Ollerton et al. 2009). We demonstrate, however, that pollination systems do correspond to a higher tendency of interactions being formed between certain subsets of plants and pollinators. Furthermore, the fact that interactions conforming to pollination systems more often are also within modules, indicate a modular structure partly driven by pollination systems.

We hypothesized that interactions formed among species from the same pollination system should be less labile across space than interactions formed among species from different pollination systems. We could not confirm such a direct difference in the turnover of interactions within and between pollination systems; however, our test did yield a low *P*-value showing a rather strong tendency, and our low test power (0.40)

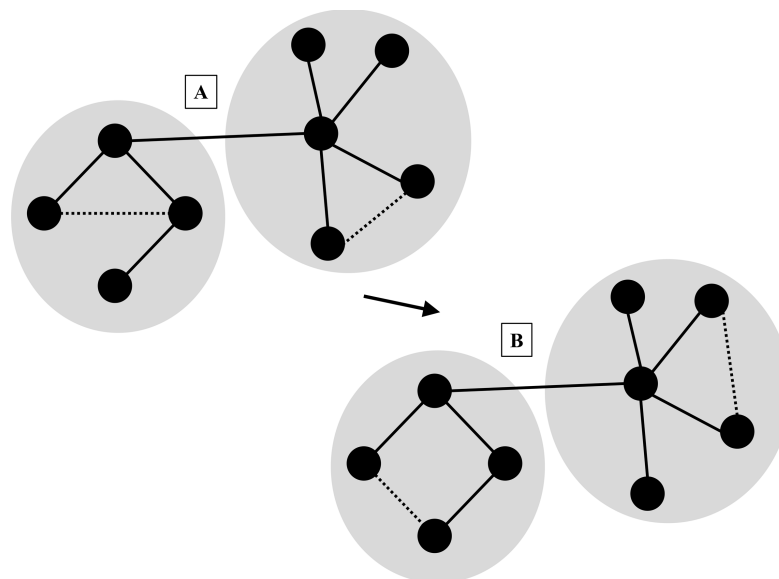


FIG. 3. Schematic representation of spatial interaction rewiring in a modular network, where within-module interactions change identity but remain inside their module. In this way the structural configuration at the modular level is conserved across space in spite of high pairwise interaction turnover. Black circles represent species and large grey circles represent modules. Dotted lines represent interactions that rewire from network A to network B.

entails a high probability of a type II error. A larger sample size would decrease this probability, and we encourage this type of analysis to be repeated on other suitable data sets. Local flower abundance has been shown to be important for the realization of pairwise interactions (Carstensen et al. 2014), and perhaps such forces interfere with the detection of any effect that pollination systems might have on interaction consistency. Based on our results, we argue that when interactions are lost or gained across space, new interactions are likely formed within pollination systems rather than between. Despite high temporal and spatial turnover in the identity of pairwise interactions, communities could thus maintain the structure of interactions at the level of modules, rewiring their links within these groups, but rarely across (Fig. 3).

The difficulty of confirming interaction patterns as expected on the basis of floral syndromes or pollination systems is likely related to the high lability in interactions over time and space (Olesen et al. 2008, Petanidou et al. 2008, Dupont et al. 2009, Carstensen et al. 2014, Simanonok and Burkle 2014); however, within these highly variable patterns, some pairwise interactions are more consistent across space (Carstensen et al. 2014). It seems then, that it is possible to identify more consistent elements within the detailed structures of networks. As we show here, even interactions that are readily rewired across space might be so in a non-random fashion, so that species change their interactions among a certain subset of the potentially available interaction partners in the network. This subset is then partly governed by

pollination systems, in turn maintaining modular structures across space. With an increasing effort to understand the spatial variability of interactions (Poisot et al. 2012, 2015, Carstensen et al. 2014, Kissling and Schleuning 2015, Trøjelsgaard et al. 2015), more studies are needed on the spatial variation of modularity, its connection to pollination systems, and other possible determinants. Future studies could explore further whether interactions are rewired across space and time in a predictable manner. We argue that structural patterns at the sub-network level can help us to fully understand why interactions vary across space and time.

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