

# Determinants of the microstructure of plant–pollinator networks

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**Abstract.** Identifying the determinants of biological interactions in mutualistic networks is key to understanding the rules that govern the organization of biodiversity. We used structural equation modeling and dissimilarities in nine ecological variables to investigate community processes underlying the turnover of species and their interaction frequencies (interaction pattern) among highly resolved plant–pollinator networks. Floral and pollinator community composition, i.e., species identities and their abundances, were strong determinants of the microstructure of pairwise interactions among the networks, explaining almost 69% of their variation. Flower and pollinator traits were directly related to interaction patterns, but were partly masked in the model by shared variance with community composition. Time of year and geographic location, floral and pollinator abundances independent of species identity, and relative abundance of exotic flowers had indirect and relatively weak effects on interaction patterns. Our analyses lead to precise predictions about the processes behind the interaction patterns in mutualistic networks. Future understanding of these processes will be aided by studies that evaluate these predictions experimentally at the network level.

**Key words:** forbidden links; indirect interactions; inselbergs; interaction neutrality; mutualistic networks; pollination webs; relative abundance; Seychelles islands; structural equation modeling; Western Indian Ocean.

## INTRODUCTION

Biologists have been studying mutualistic interactions between plants and animals, such as pollination and seed dispersal, to gain insight into ecological and evolutionary processes (Herrera 2002, Waser 2006). Considered in a community context, the study of mutualistic interactions illuminates the processes that drive biodiversity organization and persistence (Fontaine et al. 2006, Kaiser-Bunbury et al. 2010a). Past research on mutualistic networks has identified several network properties that appear to be invariant across different ecosystems, such as the cumulative frequency distribution of the number of species to which a species is linked (degree distribution; Jordano et al. 2003) and the tendency of specialized species to interact with a subset of the mutualists of more generalized species (nestedness; Bascompte et al. 2003). Despite recent progress, understanding the underlying ecological and evolutionary processes that determine the observed architecture and dynamics of mutualistic networks remains a major challenge (Bascompte 2009, Vázquez et al. 2009a).

Several mechanisms have been proposed to explain structural patterns in mutualistic networks, including interaction neutrality, trait matching among interacting species, phylogenetic constraints, and sampling artifacts (reviewed in Vázquez et al. 2009a). Interaction neutrality implies unconstrained and random interactions between plants and pollinators; thus abundant species interact more frequently and with more species than rare species, generating some of the observed network properties (Dupont et al. 2003, Vázquez et al. 2007). In contrast, trait matching among species gives rise to the so-called “forbidden links” (Jordano et al. 2003), interactions that cannot arise because of mismatches in the spatiotemporal distribution and phenotypic traits of species occurring within an interaction network (Stang et al. 2006, Santamaría and Rodríguez-Gironés 2007, Stang et al. 2007, Olesen et al. 2011). Moreover, phylogenetic relationships among species constrain the evolution of phenotypes, imprinting a phylogenetic signal on network structure (Ives and Godfray 2006, Rezende et al. 2007a, b). The observed network structure also can be influenced by sampling artifacts, notably the detection probability of interactions, which is a function of the relative abundance of the species in the network (Vázquez and Aizen 2006, Blüthgen et al. 2008). Evidence indicates that all of these mechanisms contrib-

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TABLE 1. Ecological variables and dissimilarities ( $D$ ) used in the model and their definitions

Ecological variable	Definition of ecological variable	Dissimilarity
Interaction pattern	identity and frequency of pairwise species interactions	$D$ -interaction pattern
Time	month during which the network was collected	temporal distance
Location	site at which the network was collected	spatial distance
Exotic dominance	proportion of exotic flowers in a flowering community	$D$ -exotics
Floral abundance	distribution of the relative abundance of flowers in a community regardless of species' identities	$D$ -floral abundance
Pollinator abundance	distribution of the relative abundance of pollinators in a community regardless of species' identities	$D$ -pollinator abundance
Floral composition	flower community composition reflecting flowering plant species' identities and their abundances	$D$ -floral composition
Pollinator composition	pollinator community composition reflecting pollinator species' identities and their abundances	$D$ -pollinator composition
Floral traits	relative frequency of morphological floral traits (floral complexity) in a community.	$D$ -floral complexity
Pollinator traits	relative frequency of pollinator traits (pollinator size) in a community.	$D$ -pollinator size

*Note:* For detailed descriptions of the calculation of dissimilarities, see Appendix A.4.

ute their share to generating observed network properties (Vázquez et al. 2009a).

When evaluating the mechanisms behind mutualistic network patterns, several studies have focused on aggregate network properties such as connectance, nestedness, and modularity (Olesen et al. 2007, Santamaría and Rodríguez-Gironés 2007, Stang et al. 2007, Vázquez et al. 2007). These properties have the advantage of depicting with a single number some complex network structures that may have relevance for the ecological and evolutionary dynamics of the interacting species. Aggregate statistics, however, constitute a pitfall because the identities of the interacting species and their frequencies of interaction are not considered in these network properties, and many different network configurations can have similar index values. This clearly becomes problematic when trying to understand the processes that determine interactions. As an alternative, some studies have begun to delve into the details of pairwise interactions in mutualistic networks (Vázquez et al. 2009b, Olesen et al. 2011, Verdú and Valiente-Banuet 2011), which we call here the network “microstructure” (Junker et al. 2010).

These studies have shown that our ability to predict network microstructure is limited, in spite of the relatively high predictive ability of aggregate network statistics. Furthermore, such studies are limited because the data used for the analyses are themselves aggregates, represented as a single plant  $\times$  animal interaction matrix for all sites and observation periods of a particular study. A different approach would be to construct multiple interaction matrices, one for each time  $\times$  site combination, and then evaluate whether the pairwise dissimilarities among interaction matrices are explained by dissimilarities in predictor variables of interest, such as temporal and spatial overlap among sampled networks, species composition and their relative abundances, and species traits (Poisot et al. 2012).

Here we use network dissimilarities ( $D$ ) and structural equation modeling (SEM; Shipley 2000, Grace 2006, Kline 2011) to evaluate the relative contribution of

ecological variables (Table 1) in determining network microstructure. Throughout the manuscript, “dissimilarity” refers to a function (a dissimilarity or distance coefficient) that takes its maximum value (1) for two objects (matrices or vectors) that are entirely different, and 0 for two objects that are identical (Legendre and Legendre 1998). For example, a dissimilarity index would measure the extent to which two communities differ in terms of the abundances of their species, floral and pollinator traits, or the identity and frequency of interactions. SEM assesses hypothesized causal relationships among a given set of variables in a hierarchical manner, accounting for direct, indirect, and reciprocal effects. Our analytical approach correlates pairwise network dissimilarities in several ecological variables, i.e., we compare dissimilarities among networks involving one variable with dissimilarities involving another variable. This approach allows us to compare among networks a set of distinct ecological variables that define communities. Specifically, we ask how geographic and temporal proximity between plant–pollinator communities and abundance, community composition, plant and pollinator traits, and the degree of invasion by exotic flowering plant species influence pairwise interaction dynamics, here referred to as “interaction pattern,” in 48 highly resolved and fully quantitative pollination networks. The hypothesized causal model (Fig. 1; see path justifications in Appendix A: Table A1) follows largely the hierarchy of mechanisms proposed by Vázquez et al. (2009a) and includes increasingly specific information on species and link properties and identities.

## METHODS

### *Study system*

Data on plant–pollinator interactions were collected between September 2007 and April 2008 at six sites on Mahé, the largest granitic island of the Seychelles, Indian Ocean (4°40' S, 55°26' E). All sites represent mid-altitude (300–580 m), discrete “inselberg” plant com-

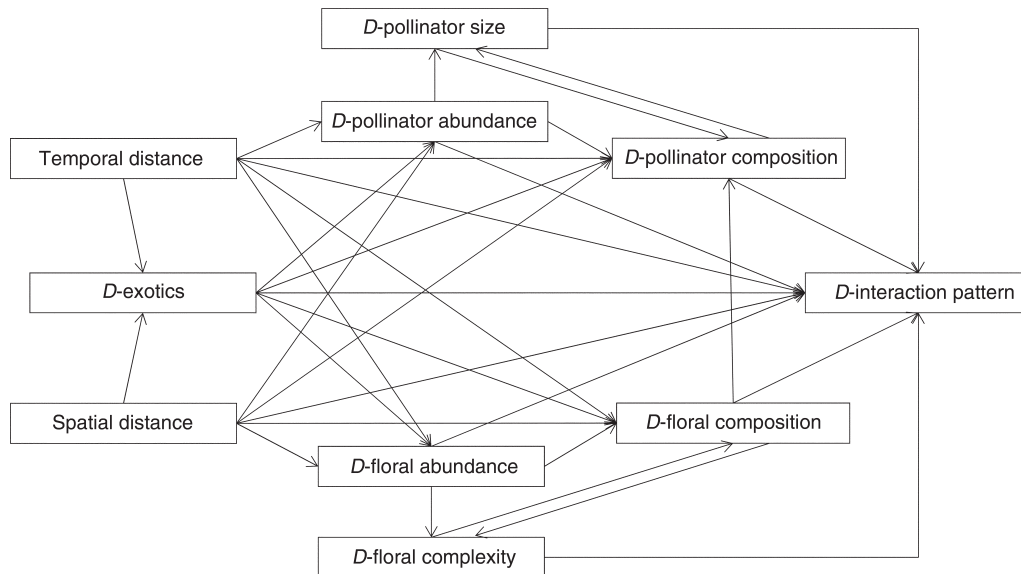


FIG. 1. Path diagram describing the hypothesized causal relationship between dissimilarities ( $D$ ) that express the degree of association between networks in several ecological variables (Table 1). Justifications of the relationships between the ecological variables shown in the complete model (model A) are presented in Appendix A: Table A1. See Fig. A1 for the path diagrams of two reduced (nested) hypothesized models, in which either composition (model B) or trait (model C) dissimilarities were entered separately.

munities consisting of shrubs, small trees, palms, and screw palms (*Pandanus* spp.), with an average canopy height of 2–3 m. Surrounded by exotic-dominated forest, inselbergs are steep-sided monolithic outcrops harboring some of the last remaining endemic plant communities in the Seychelles. Some inselbergs experience encroachment by invasive exotic plant species, resulting in a different degree of plant invasion across inselbergs. The study sites ranged from 0.7 to 1.7 ha in size and were, on average, separated by  $4.47 \pm 3.41$  km (mean  $\pm$  SD; range 0.88–10.30 km) (see Appendix A: Table A2). Although study sites were located within potential flying ranges of some pollinators (e.g., carpenter bees and hawkmoths), we considered the pollinator communities largely independent across sites, especially considering the small number of interactions by these particular pollinators. A detailed description of site characteristics and plant and pollinator communities is given elsewhere (Kaiser-Bunbury et al. 2011).

#### Plant–pollinator interaction networks

In total, 48 quantitative interaction networks (8 months  $\times$  6 sites) were collected following protocols designed for heterogeneous vegetation dominated by shrubs and small trees (Kaiser-Bunbury et al. 2009, 2011). Nonindependence between network samples was accounted for by including temporal and spatial distances in the model. Data collection on networks consisted of plant–pollinator observations and independent counts of flowers across each inselberg community. The detection of plant–pollinator interactions is inherently problematic; completeness of all interactions in a

network is unlikely (Chacoff et al. 2012), and the sampling design should be adjusted according to the research question (Gibson et al. 2011). Here, we aimed at comparing the species-based microstructure of networks, thereby ensuring that each flowering plant species was observed for a similar amount of time (see Appendix A.1) to allow for comparisons among individual species (Ollerton and Cranmer 2002). We also evaluated the sensitivity of our interaction data to sample size effects. Rarefaction analysis found interaction data to be robust under a range of subsample sizes (Appendix A: A.1; Appendix B: Fig. B4), indicating that networks of different sizes were comparable.

We recorded visitation frequency of individual pollinator species by counting individuals on flowers during several 30-min observation periods. Each woody flowering plant species was observed for a total of  $\sim 3$  h at each site and month (Kaiser-Bunbury et al. 2011), accumulating an average observation time per network of  $24.2 \pm 7.6$  h (mean  $\pm$  SD; see Appendix A: A.1). We used the total number of visits of each pollinator taxon as a measure of pollinator abundance at each relevant flowering plant species. The networks included interactions between 37 flowering plant species (Appendix A: Table A3) and 83 pollinator species (Appendix A: A.1, Table A4).

With the interaction data, we constructed 48 plant–pollinator interaction matrices (for each of six sites and eight sampling months). In each matrix, interaction frequency between an animal species  $i$  and a plant species  $j$  was quantified as mean visitation frequency per

hour of animal species  $i$  multiplied by the floral abundance of plant species  $j$  visited by  $i$  (Kaiser-Bunbury et al. 2009, 2010a). Floral abundance, defined as the mean number of floral units per cubic meter, was recorded in cubes placed randomly along transects at the beginning of each month. One floral unit (referred to as “flower” hereafter) was defined as one individual flower, or a cluster of flowers in the case of palm inflorescences (Kaiser-Bunbury et al. 2011). By using interaction frequency as a function of floral abundance sampled per area (i.e., mean floral density) and collecting interaction data during peak flowering of each plant species, the influence of sampling bias was strongly reduced.

#### *Definition of predictor variables and dissimilarities*

We used nine predictor variables to explore the turnover over time and space in species and the frequency of their pairwise interactions among interaction matrices (Table 1; for more detailed explanations, see Appendix A.2–4): time of year and geographic location of networks; the distribution of the relative abundance of flowers and pollinator individuals available in each network regardless of species’ identities (called floral and pollinator abundance); species composition, i.e., species’ identities and their abundances, of flowers and pollinators in a community; the proportion of exotic flowers in a community (see Appendix A.2 for an inclusion justification). This variable was calculated as  $(F - F_{\text{nat}})/F$ , where  $F$  is floral abundance of all species and  $F_{\text{nat}}$  is floral abundance of native species in a network; and the relative frequency of morphological floral and pollinator trait classes.

To calculate the relative frequency of floral traits, we used a scoring system assessing the width and depth of nectar tubes, floral symmetry and presentation pattern of pollen, the dimensionality of flowers, and the orientation of the corolla (Appendix A.2; hereafter referred to as floral complexity). Morphological floral traits were scored individually on a scale with six levels (Appendix A: Table A5) and added up to a species-specific floral complexity score. Lower scores reflect lower complexity and thus easier access to nectar and pollen by potential pollinators. We grouped species according to total scores across the four traits in five equal-sized categories of floral complexity (Appendix A.2). The frequency of each complexity category was weighted by the sum of the floral abundance of all species assigned to a given complexity category in a network. Similarly, pollinator size based on thorax width and body length was used to define functional groups of pollinators. Body size is highly correlated with proboscis length of flower-visiting insects (Stang et al. 2006). We classified thorax width and body length into eight equal-sized categories and weighted the frequency of each size category by the sum of the mean pollinator interaction frequency of all species in each size category (Appendix A.3).

To allow a direct comparison between variables, we used dissimilarities of the respective variables between networks in our models. We computed  $48 \times 48$  lower triangular dissimilarity matrices (hereafter prefixed by “ $D$ ” and shortened; Table 1) and used these matrices to assess the relationships between predictor variables and interaction patterns among networks. Dissimilarities between each pair of networks (1128 possible combinations) were calculated with the semi-metric Bray-Curtis dissimilarity index (Bray and Curtis 1957) in the *vegdist* function of the *vegan* package (Oksanen et al. 2010) in R 2.15 (R Development Core Team 2012; see Appendix A.4 for a detailed description of the dissimilarity matrices and the Supplement for R code). To assess the relationship between a pair of variables in our SEM models, we calculated the Mantel matrix correlation index (mantel function, *vegan*) between their dissimilarity matrices. Because the data were not normally distributed and some pairs of variables showed nonlinear but monotonic relationships (Fig. A2, Appendix A.5), we used the nonparametric Spearman correlation coefficient (Shibley 2000).

#### *Structural equation models: specification and analysis*

Correlation coefficients were used to specify three hypothesized models (Fig. 1; Appendix A: Fig. A1, Table A1) for evaluating the interdependences among the dissimilarity matrices using structural equation modelling (SEM; Shibley 2000). Although our analytical approach allows us to compare among networks a set of distinct ecological variables, it also imposes constraints on our ability to distinguish between the confounding effects of species identities. This is problematic when analyzing the effect of species abundance on interactions, which is critical in assessing the role of neutrality as a determinant of network structure. The key issue here is to distinguish between the effect of the statistical distribution of abundances in the community and the effect of species-specific abundances. In other words, we distinguish between, first, the distribution of abundances in floral and pollinator communities to describe abundance without information on species identity (i.e., a comparison of frequency distributions similar to a chi-square comparison) and, second, floral and pollinator community composition, which describe species’ identities and their abundances in the networks. To further tease apart the influence of interaction neutrality and trait matching on network microstructure in addition to the full causal model (model A), we constructed two nested versions, in which either community compositions (model B) or traits (model C) were entered separately (Appendix A: Fig. A1). Processes such as environmental filtering can structure communities (Webb et al. 2002, Sargent and Ackerly 2008), resulting in communities that are composed of species with similar traits. Equally, communities that are similar in species composition may also be similar in the distribution of traits (Appendix A: Table A1). This two-

Model A)  $\chi^2 = 40.0$ ,  $P = 0.07$ ; RMSEA = 0.0195 (90% CI: 0, 0.0322); CFI = 0.9969; BIC = -156.8

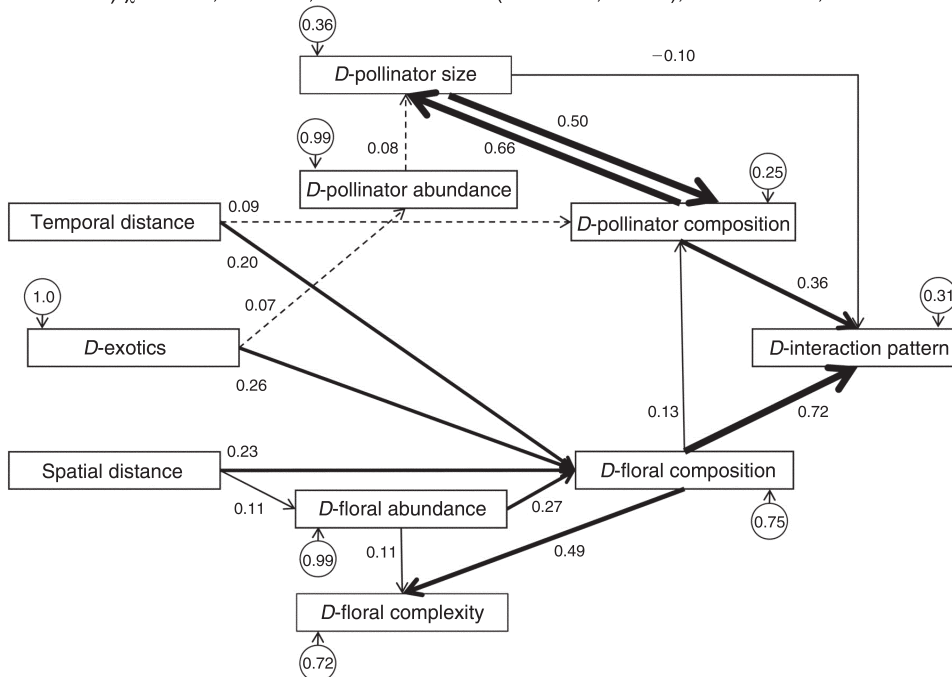


FIG. 2. Best-fitting structural equation models examining direct and indirect relationships between dissimilarities in ecological variables and network dissimilarities ( $D$ ) in interaction patterns. Shown are (A) a complete model and two reduced models without traits (B) and without composition variables (C). The width of the arrows reflects the strength of dependency between two variables. Normalized estimates are shown on the paths. Numbers enclosed in the circles represent the standardized values of the errors. Only significant paths ( $P < 0.001$ ) are presented. RMSEA is the root mean square error of approximation; CFI is the comparative fit index; BIC is the Bayesian information criterion.

way biological feedback is indicated by the reciprocal relationship between composition and trait variables in the hypothesized model A (Fig. 1). Fitting models B and C with only one of the two variables allowed us to quantify the amount of variation in network microstructure that is determined by community composition and traits separately.

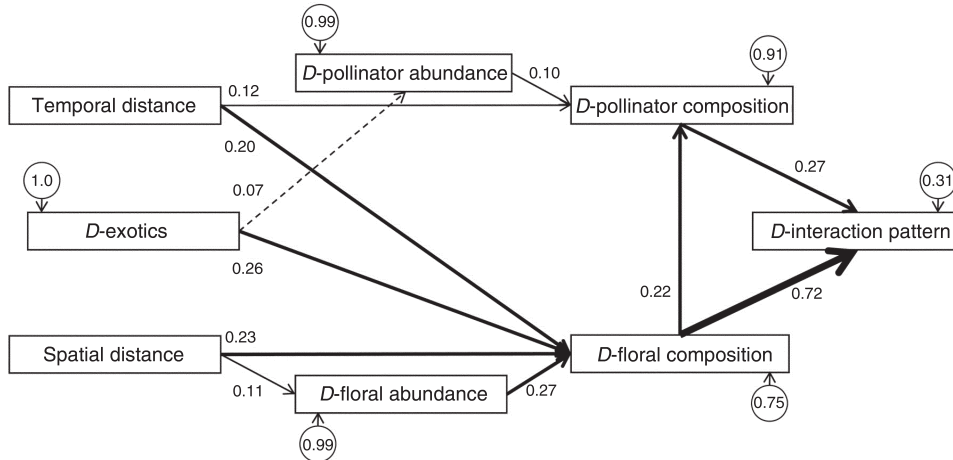
Model specification, evaluation, and adaptation was based on the SEM workflow process proposed by Grace et al. (2010; see also Grace and Keeley 2006). Structural equation modeling was conducted with the sem function of the sem library in R using maximum-likelihood estimation (Fox et al. 2012). We started with the full model and generated more parsimonious, nested models by removing paths with coefficients  $< 0.1$  (Maestre et al. 2010) and a simultaneous improvement of the model fit. Model selection was based on the Bayesian information criterion (BIC). We evaluated model fit by comparing several goodness-of-fit indices belonging to three index classes to overcome the limitations of individual indices and classes (Appendix A: A.5 and Table A6). In addition, the chi-square goodness of fit was used to evaluate the adequacy of model fit (Grace and Keeley 2006; but see Bentler and Bonett 1980 for limitations at large sample sizes).

## RESULTS

Network size, number of visits, and interaction frequency varied substantially across the eight months and six locations studied, indicating large fluctuations in pollinator and floral diversity between temporally and geographically proximate networks (Appendix B: Fig. B1). Interaction frequency of pollinators varied up to 14-fold within a site (Casse Dent; interaction frequency varied by a mean of  $8.1\text{-fold} \pm 1.4$  SE) and 12-fold within a month (March;  $5.6 \pm 1.0$ ; Appendix B: Table B1). These variations exclude outliers in interaction frequency at La Réserve (December) and Tea Plantation (April), which were a consequence of localized mass flowering of two abundant plant species (*Pyrostria bibracteatum* at La Réserve; *Chrysobalanus icaco* at Tea Plantation) that attracted large numbers of introduced honey bees (*Apis mellifera adansonii*) and endemic solitary bees (*Lasioglossum mahense*). Total floral abundance, reflecting the amount of floral resource available in a given community, varied similarly, albeit on a slightly reduced level (12-fold at Copolia,  $7.1 \pm 1.4$ , mean  $\pm$  SE; 11-fold in March,  $4.8 \pm 1.2$ ).

Bray-Curtis dissimilarities in the Seychelles networks ranged from 0 to 1 across all variables. Networks showed relatively moderate dissimilarities in five

Model B)  $\chi^2 = 25.7, P = 0.06; RMSEA = 0.0231$  (90% CI: 0, 0.0391); CFI = 0.9945; BIC = -86.8



Model C)  $\chi^2 = 10.8, P = 0.55; RMSEA = 0.0001$  (90% CI: 0, 0.0278); CFI = 1; BIC = -73.6

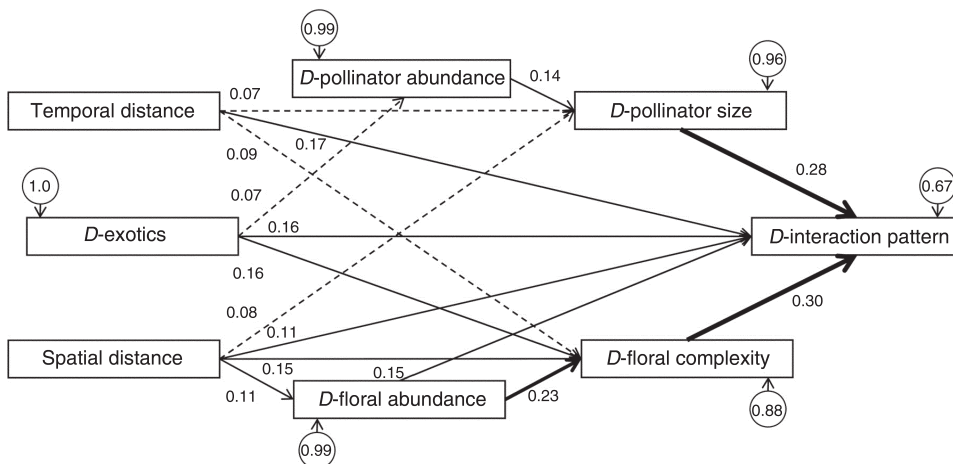


FIG. 2. Continued.

predictor variables (see Table 1 for variable names; all values are mean  $\pm$  SD): *D*-floral abundance,  $0.35 \pm 0.22$ ; *D*-pollinator abundance,  $0.25 \pm 0.18$ ; *D*-pollinator composition,  $0.44 \pm 0.14$ ; *D*-floral complexity,  $0.44 \pm 0.21$ ; *D*-pollinator size,  $0.31 \pm 0.14$ . Networks were highly dissimilar in *D*-floral composition ( $0.77 \pm 0.16$ , range 0.09–1) and *D*-interaction pattern ( $0.84 \pm 0.13$ , range 0.35–1), and relatively similar in the dominance of exotic plant species (*D*-exotics:  $0.08 \pm 0.06$ , range 0–0.20).

*D*-interaction pattern showed significant bivariate correlations (Bonferroni-corrected  $\alpha = 0.001$ ) with all variables except spatial distance and *D*-floral abundance (Appendix A: Fig. A2; Appendix B: Table B2). When analyzed using SEM, *D*-interaction patterns were directly related to differences in *D*-floral and *D*-pollinator composition, and only indirectly related to spatial and temporal distance, *D*-exotics, and *D*-floral

and *D*-pollinator abundance (Fig. 2, model A). All dissimilarity variables combined explained 69% of the observed variance in the dissimilarity of interactions matrices, and model fit indices indicated a good fit of the accepted model to the data (Appendix A: Table A6). *D*-interaction pattern, i.e., the change of network microstructure over time and space, can be best determined by *D*-floral and *D*-pollinator compositions, which include information on species' identity and their abundances. *D*-floral composition exerted a 2.5 times stronger total effect (the sum of direct and indirect effects) on *D*-interaction pattern than *D*-pollinator composition, and an almost 4.0 times stronger effect than spatial and temporal distance and *D*-exotics (Table 2). *D*-floral and *D*-pollinator abundance, *D*-floral complexity, and *D*-pollinator size showed no direct influence on *D*-interaction pattern and weak total effects, except for *D*-floral abundance (Table 2,

TABLE 2. Total effects of explanatory variables on the response variable in all three models.

Dissimilarity	Interaction pattern		
	Model A	Model B	Model C
Temporal distance	0.18	0.19	0.22
Spatial distance	0.20	0.20	0.18
<i>D</i> -exotics	0.20	0.20	0.21
<i>D</i> -floral abundance	0.20	0.21	0.22
<i>D</i> -pollinator abundance	0.01	0.03	0.04
<i>D</i> -floral composition	0.76	0.78	...
<i>D</i> -pollinator composition	0.29	0.27	...
<i>D</i> -floral complexity	0	...	0.30
<i>D</i> -pollinator size	0.08	...	0.28

Notes: The total effect one variable has on another is the sum of its direct and indirect effects (Grace 2006). In model A, *D*-floral complexity has no direct or indirect effect (on *D*-interaction pattern, due to the suppression effect caused by the strong intercorrelations between *D*-floral complexity and *D*-floral composition (for bivariate correlations, see Appendix B: Table B2) in combination with the strong effect of *D*-floral composition on *D*-interaction pattern. In the absence of *D*-floral composition from the model (model C), the total effect of *D*-floral complexity is the highest of all explanatory variables. Ellipses indicate variables that were not included in the model.

model A). Differences in *D*-floral composition were best explained by spatial and temporal distance among networks, and changes in *D*-exotics and *D*-floral abundance. On the contrary, *D*-pollinator composition remained unexplained by most of the dissimilarity variables. An exception was the strong reciprocal relationship between *D*-pollinator composition and *D*-pollinator size; similarly, *D*-floral complexity showed a robust, but only unidirectional, dependency on *D*-floral composition (Fig. 2, model A).

To investigate the individual contribution of composition and trait variables in determining interaction patterns, we developed two nested versions of model A. These models assume that most of the dynamics in *D*-interaction pattern are explained either by differences in dissimilarities in community compositions (model B) or traits (model C). Model statistics indicated a lower fit of models B and C to the data compared to model A (Fig. 2; Appendix A: Table A6), but the overall structure of models A and B and total effects of the variables on *D*-interaction pattern were very similar. Changes in *D*-floral and *D*-pollinator composition explained a similar degree of species and interaction turnover in model B, and all other dissimilarity metrics showed only indirect relationships with *D*-interaction pattern (Fig. 2, Table 2). This pattern changed, however, when composition metrics were replaced by trait metrics. Six of seven dissimilarities established direct, but relatively weak links to *D*-interaction pattern (Fig. 2, model C), explaining 36% of the variance in dissimilarities in interaction matrices, and about half of the variance in interaction patterns explained by species composition in model B. Noticeable were the total effects of *D*-

floral complexity and *D*-pollinator size (0.30 and 0.28, respectively), which were absent or weakly negative in the presence of *D*-composition variables (model A). The direct path between *D*-floral complexity and *D*-interaction pattern in model C, the large discrepancy between the bivariate correlation of *D*-floral complexity and *D*-floral composition ( $r_s = 0.52$ ; Appendix B: Table B2), and the insignificant total effect between the two variables in model A suggest a strong suppression effect. Here, suppression refers to the fact that the intercorrelation between *D*-floral composition and *D*-interaction pattern and between *D*-floral composition and *D*-floral complexity causes the effect of *D*-floral complexity on *D*-interaction pattern to be unconnected to their net intercorrelations. A similar, yet slightly weaker, effect was observed between *D*-pollinator size and *D*-interaction pattern. Model C has shown that changes in *D*-floral complexity and *D*-pollinator size across sites and dates indeed corresponded with changes in *D*-interaction pattern, yet only when composition dissimilarities were not included in the same model.

#### DISCUSSION

By using structural equation models and studying dissimilarities of interaction networks over time and space, we could show that network microstructure is, for our data, directly determined by species composition (i.e., species identities and their abundances). The influence of other predictor variables on interaction patterns, such as the relative abundance of flowers, pollinators, and exotic plants in the community independent of their species identities, time of year, and geographic location, was predominantly indirect, relayed through pollinator and, more so, floral composition. Floral and pollinator traits explained variations in interaction pattern either indirectly through reciprocal feedback with community compositions or directly in the absence of composition variables from the model (model C). This suggests that the dynamics of pairwise interactions in our networks were primarily determined by ecological processes that regulate community composition. Time of year, geographic location, relative abundance, and exotic flowers contributed to explaining community composition, although their overall effect size was relatively small, explaining only 13% and 8% of the variation of floral and pollinator composition, respectively.

Our analysis of network microstructure has thus enabled us to tease apart the relative importance of different variables affecting variation in pairwise interactions over time and space. In the following, we will discuss the relative contribution of the predictor variables in determining dynamics of pairwise interactions and will speculate on the possible underlying mechanisms that drive the observed patterns in network microstructure.

*Determinants of interaction patterns*

Our modeling approach reveals insights on the complex interplay between floral and pollinator traits, abundance, and community composition and their role in determining temporal and spatial dynamics in mutualist interactions. Previous work suggested that mechanisms determining interaction patterns are primarily based on two types of ecological and evolutionary processes: interaction neutrality, and links that are constrained by morphological matching or temporal and spatial distance (Vázquez et al. 2009a). In scenarios where neutrality is the driving force behind interaction patterns, interaction frequencies are largely explained by relative abundances (Vázquez et al. 2007). Alternatively, if links are constrained, we expect strong direct relationships between traits and interaction patterns, and temporal and spatial distance and interaction patterns. Our models suggest that neither of the two processes is the dominant driver of network microstructure, because most of the interactions are determined by species-specific characteristics and consistently strong links between the other variables and interaction pattern are absent. Nevertheless, morphological traits used in our analysis explain about half of the variance of interaction patterns related to species identity and their abundance (composition variables). Model C, the model without composition variables and without the statistical interference of collinearity between traits and composition (suppression effect), clearly indicates that flower and pollinator morphology is an underlying driver of pairwise interactions. This effect is masked by the dominance of species identity in models A and B. It is thus reasonable to assume that some of the remaining variance in the dissimilarity of interaction pattern explained by species identity and their abundance will be species-specific traits that were not individually identified and tested in our analysis. Such traits may include reward abundance (nectar and pollen), flower color, scent, size and display height, and visitation speed (e.g., Harder 1985, Hegland and Totland 2005, Sletvold et al. 2010, Junker et al. 2013).

In search of possible ecological explanations underlying our modeling results, we consider ecological selection of species that have different sets of traits as one of the general processes that form ecological communities (Vellend 2010). That means that floral composition can be at least partly explained by selection of species with certain floral traits, making changes in traits a somewhat deterministic process linked to community composition. Equally, floral and pollinator composition are the result of selection processes driven by plant–pollinator interactions. Thus, in the model that included both compositions and traits, the direct links between dissimilarities in traits and interaction patterns were masked by dissimilarities in composition, which contain the most parsimonious combination of traits inherent to species identities. A second explanation for the lower influence of traits on pairwise interactions is

that the traits tested here determine a threshold above which species can potentially interact (Stang et al. 2007, 2009). Flowers with a low complexity show weak constraints in floral resource accessibility and can interact with most pollinator species. Conversely, plants with restrictive flowers have fewer potential visitors, permitting higher explanatory power in determining pairwise interactions based on traits. We have shown that the Seychelles networks are dominated by simple flowers (Appendix B: Fig. B2) and many small pollinators (Appendix B: Fig. B3), with few morphological restrictions on pairwise interactions. We expect that in a morphologically more restrictive floral community (e.g., in some parts of the Mediterranean biome; Petanidou and Potts 2006, Stang et al. 2007, 2009), floral and pollinator traits may express a stronger direct influence on interaction patterns if tested independently of floral and pollinator composition. Finally, our networks contained many pollen feeders, such as flies and beetles, which are typically abundant in island, high-altitude, and low-latitude pollinator communities (Kaiser-Bunbury et al. 2010b). The foraging behavior of these pollinators is less strongly influenced by floral restrictiveness compared to obligate nectar feeders, but they instead rely on other floral traits, such as copious pollen and sweet scent, common in beetle-pollinated plants (Faegri and van der Pijl 1979). Although our floral complexity index accounted for access of pollen-feeding insects to flowers, future studies should also consider pollen quality and quantity as a potentially important floral trait (Stang et al. 2006).

We believe that floral complexity and pollinator size, as a proxy of proboscis length (Stang et al. 2006), are the most appropriate variables to represent the conceptual idea of interaction constraints imposed by morphological traits (see also Eklöf et al. 2013). However, the use of floral and pollinator complexity and size classes, respectively, could be one of the reasons why traits did not explain much of the variance of the interaction patterns in the presence of community composition variables. Ideally, one would use continuous data on flower morphology, e.g., corolla depth, proboscis length, or body mass for all individuals within species and between populations, and independent data on pollinator abundance to investigate trait constraints, but such data were not available for our networks due to sampling restrictions in the National Park. To reduce a potential bias of our methodology and the category sizes on the model fit, we conducted the same analysis with more and fewer categories (Appendix A.2–3), all of which generated similar qualitative effects. By further comparing the relationships between pollinator size and continuous and categorical variables of flower traits both of the Seychelles networks and of more specialized networks from the Mediterranean biome (M. Stang, data not shown), we are confident that our approach adequately meets our assumptions about the influence of



morphological constraints on plant–pollinator interactions.

*Deviation from the hypothesized model and model limitations*

The best-fitting model (model A) deviated from our hypothesized full model in several ways. One marked difference was the minor explanatory significance of spatial and temporal variation on plant–pollinator interactions. This implies that, although the co-occurrence of species in time and space is a necessary condition for species to interact, spatiotemporal overlap of mutualists per se is not sufficient for explaining dynamics in pairwise interactions. Further, the small distance and time effects suggest that networks are relatively predictable across time and space, given the relevant ecological information. Should this result be replicated for other regions, then the methods that we have presented here should have broad application. However, we recognize that this has yet to be validated using independent data sets. Our findings deviate from those of other plant–pollinator/seed disperser networks that suggest that 20–30% of unobserved links are due to temporal (Olesen et al. 2011) and geographic uncoupling (Jordano et al. 2006). One possible explanation is that networks that span a full flowering season include many species with phenophases that do not overlap, and thereby inflate the importance of spatiotemporal uncoupling on network structure (Medan et al. 2006, Vázquez et al. 2009a, Kaiser-Bunbury et al. 2010a). This can occur in networks that extend across long flowering seasons (several months; Basilio et al. 2006), that cover very short flowering seasons, which show high species turnover, e.g., in the Mediterranean (Jordano et al. 2006), and at high latitudes (Olesen et al. 2011), or those that contain species with extended flowering and pollinator flight periods. The latter may have been the case in the Seychelles communities, as the mean flowering time across all species ( $4.97 \pm 0.36$  months) and the mean flight period ( $5.31 \pm 0.23$  months; calculated for 62% of all pollinator species accounting for 99.2% of all interactions) was relatively extensive compared to the total flowering season of eight months. Floral and pollinator composition were also largely independent of time and space, contradicting previous studies, which found marked intra-annual seasonality (Medan et al. 2006, Petanidou and Potts 2006) and daily variation (Olesen et al. 2008) in flowering plant and pollinator communities.

The absence of direct paths between dissimilarities in exotic flowers and most other variables suggests that exotic flowers did not significantly change pollinator behavior and community composition. It is perhaps surprising that in such a heavily invaded community as the Seychelles, variation in the availability of flowers of exotic species among sites and in time had only a minor effect on network structure, while elsewhere highly attractive and abundant exotic flowering plants directly

affect pollinator abundance and species richness (e.g., in the UK; Lopezaraiza-Mikel et al. 2007). Changes in pollinator visitation rates caused by exotic flowering plants independent of abundance are also reported (Ghazoul 2006, Kandori et al. 2009). In these cases, exotics seemed to alter floral composition instead, thus indirectly affecting interaction patterns (see also Ghazoul 2004, Morales and Traveset 2009). Williams et al. (2011) recently described that in North America the use of, and preference for, exotic plants by bees were correlated with plant abundance instead of with a group characteristic of exotic plants. Our data confirm that exotic plants in the Seychelles do not display group characteristics in flower morphology. Exotic plants that are abundant in our networks, however, have relatively complex flowers, which may explain their overall reduced influence on interaction patterns because they attract a lower diversity of pollinators. A similar pattern was observed for plant–pollinator communities on other islands where generalized pollinators visit mostly open and easily accessible flowers (e.g., in Mauritius; Kaiser-Bunbury et al. 2009).

#### CONCLUSION

Our data are consistent with the proposition that species' identities and their abundances across communities were the main drivers of pairwise interactions in pollination networks, thereby strongly influencing interaction turnover and contributing significantly to the formation of network architecture. Changes in the floral composition alone explained ~45% of corresponding changes in interaction patterns. Although abundance and morphological traits played only a minor role in determining network microstructure when information on species' identity was available, the strong reciprocal relationship between trait and composition variables indicated that traits are part of the mechanisms that influence community composition.

Our findings underline the importance of community composition and thereby contribute to understanding the link between species interaction and community data. To refine the predictions, however, mechanisms behind community structure need to be experimentally unraveled and quantified, which will eventually establish the degree to which deterministic and stochastic processes in communities affect network structure. Moreover, to generalize our findings, further theoretical and experimental exploration on more diverse communities is required. Such communities may display dynamics more strongly associated with morphological or phenological constraints compared to our island networks.

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#### SUPPLEMENTAL MATERIAL

##### Ecological Archives

Appendices A and B and a Supplement are available online: <http://dx.doi.org/10.1890/14-0024.1.sm>