

Interaction frequency, network position, and the temporal persistence of interactions in a plant–pollinator network

NATACHA P. CHACOFF,^{1,2} JULIAN RESASCO,³ AND DIEGO P. VÁZQUEZ^{4,5,6,7}

¹*Instituto de Ecología Regional, CONICET-Universidad Nacional de Tucumán, Tucumán, Argentina*

²*Facultad de Ciencias Naturales e IML, Universidad Nacional de Tucumán, Tucumán, Argentina*

³*Department of Ecology & Evolutionary Biology, University of Colorado at Boulder, Boulder, Colorado 80309 USA*

⁴*Argentine Institute for Dryland Research, CONICET, Mendoza, Argentina*

⁵*Freiburg Institute for Advanced Studies, University of Freiburg, Freiburg im Breisgau, Germany*

⁶*Faculty of Exact and Natural Sciences, National University of Cuyo, Mendoza, Argentina*

Abstract. Ecological interactions are highly dynamic in time and space. Previous studies of plant–animal mutualistic networks have shown that the occurrence of interactions varies substantially across years. We analyzed interannual variation of a quantitative mutualistic network, in which links are weighted by interaction frequency. The network was sampled over six consecutive years, representing one of the longest time series for a community-wide mutualistic network. We estimated the interannual similarity in interactions and assessed the determinants of their persistence. The occurrence of interactions varied greatly among years, with most interactions seen in only one year (64%) and few (20%) in more than two years. This variation was associated with the frequency and position of interactions relative to the network core, so that the network consisted of a persistent core of frequent interactions and many peripheral, infrequent interactions. Null model analyses suggest that species abundances play a substantial role in generating these patterns. Our study represents an important step in the study of ecological networks, furthering our mechanistic understanding of the ecological processes driving the temporal persistence of interactions.

Key words: *interaction frequency; Monte Desert; nestedness; network core; network dynamics; null model; sampling artifacts; species abundance; temporal variability.*

INTRODUCTION

Ecological communities are highly dynamic, with abundances of component species and their interactions varying greatly over space and time (Poisot et al. 2015). Environmental stressors such as climate change and habitat alteration can destabilize interactions, resulting in disruptions of ecosystem functions and services (Tylianakis et al. 2008, Garibaldi et al. 2011). Thus, understanding the causes and consequences of variation in interactions is key for our basic understanding of the rules that govern ecological communities and to guide science-based management strategies for biodiversity conservation.

Ecological networks are snapshots of who interacts with whom in communities. Previous studies of ecological networks have shown that the occurrence of interactions

varies substantially in time, both within seasons and across years, with potentially profound implications for community stability (Alarcón et al. 2008, Petanidou et al. 2008, Carnicer et al. 2009, Olesen et al. 2011, Fang and Huang 2016, MacLeod et al. 2016). It has been proposed that such high interaction variability could be driven by infrequent interactions, which tend to occur at the periphery of the network, so that frequent interactions at the network core (the most densely connected region of the network) are the most persistent (Olesen et al. 2008, Aizen et al. 2012, Bascompte and Jordano 2014). Recently Fang and Huang (2016) found that interactions with low frequency (i.e., represented by few visits) tended to be more variable across three years than those with high frequency. To our knowledge no studies have evaluated the relationship between temporal variability of interactions and their network position.

We assessed the role of interaction frequency and the position of the interactions in shaping the persistence of interactions in a quantitative plant–pollinator network spanning six years, which represents one of the longest time series published to date for a community-wide

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⁷ Corresponding author: e-mail: dvazquez@mendoza-conicet.gob.ar

quantitative mutualistic network (see also Ponisio et al. 2017). We quantified the magnitude of interannual variation in the structure of this network, and evaluated whether the persistence of interactions is related to their frequency and their position relative to the network core. Furthermore, we assessed the extent to which these patterns could be explained by sampling artifacts rather than real ecological mechanisms using null model analyses.

METHODS

Study site and data collection

We collected the data between 2006 and 2011 from the Monte Desert ecoregion at Villavicencio Nature Reserve, Mendoza, Argentina (32°32' S, 68°57' W, 1270 m above sea level); see Chacoff et al. (2012) for a full account of the study site and data collection methodology. Mean annual rainfall ranges 150–350 mm, concentrated during spring and summer (Labraga and Villalba 2009). Mean annual temperatures between 2006 and 2011 show high interannual similarity, with precipitation in 2008 and 2011 above the average for the study years (Appendix S1: Table S1).

We observed plant–pollinator interactions (Appendix S2: Fig. S1) during the flowering period (September–January) in 2006–2011, at four 1-ha sites in 2006 and the two most distant of those sites in 2007–2011, separated by ca. 5 km. Data from the sites were combined into a single network to improve representation of the plant species present in the region. Pollinator visits to flowers were sampled weekly from 7:00 to 14:00, a representative portion of the daily activity period of pollinators in our

study sites. To sample pollinator visits to flowers we conducted 5-min observations of a flowering branch (for shrubs, trees, and vines) or a whole plant or group of plants (for herbaceous plants). To quantify interactions, we recorded the identity of plant and pollinator species and the frequency of visits (i.e., number of contacts between a pollinator and flower's reproductive part). Unknown specimens were collected and keyed to the highest taxonomic resolution possible by experts (see *Acknowledgments*). Flower abundance was quantified weekly using transects and quadrats within sites, in 2006 using 40 2 × 2 m fixed quadrats per site, in 2007 using five 50 × 2 m fixed transects, and in 2008–2010 using two fixed 50 × 2 m transects plus four fixed 20 × 8 m quadrats. Transects and quadrats were regularly spaced to maximize spatial coverage within each site. Sampling effort differed among years (Table 1). On average we conducted 620 (239 SD) samples (5 min observation to a flowering plant) per year.

Statistical analyses

Interannual similarity in species and interaction composition.—To quantify interannual similarity between species composition and interactions, we calculated Bray-Curtis similarity (1 – Bray-Curtis dissimilarity, which ranges from 0 to 1) between all pairwise combinations of years. We report Bray-Curtis similarity values as percentages for ease of interpretation (i.e., 100 × Bray-Curtis similarity). Plant and pollinator species data used for these analyses were the incidence matrices of year-by-species of plants or pollinators observed in the field during transect

TABLE 1. Sampling effort, sampling completeness, network metrics, and their interannual variation for the plant–pollinator network of Villavicencio.

Statistic	Year						CV (%)
	2006	2007	2008	2009	2010	2011	
Sampling effort and completeness							
Total censuses	532	372	530	836	460	988	38.55
Censuses w/links	294	261	365	394	251	661	41.40
Links observed (%)†	44	49	52	50	47	55	7.68
Network metrics							
No. plant species	23	35	44	37	36	46	22.08
No. insect visitor species	72	70	102	103	65	113	24.01
No. links	181	222	371	325	222	512	40.62
No. interactions	4,370	2,166	3,537	6,807	3,866	7,269	42.41
Connectance	0.11	0.09	0.08	0.08	0.09	0.10	12.75
Links per species	1.9	2.11	2.54	2.32	2.20	3.22	19.42
Linkage density	4.96	4.96	7.12	4.92	4.11	8.05	26.97
Shannon diversity	3.79	4.45	4.93	3.86	3.51	4.99	14.71
H_2'	0.41	0.52	0.49	0.47	0.48	0.42	9.09
Interaction evenness	0.51	0.57	0.58	0.47	0.45	0.58	11.04
NODF	22.14	20.35	25.53	23.1	27.07	29.60	13.86
wNODF	15.45	11.04	15.11	15.2	15.27	22.34	23.20

Note: NODF and wNODF are measures of nestedness.

† Calculated as the percent of observed links relative to the total links estimated by the Chao2 asymptotic estimator.

surveys or interaction censuses. Similarly, to quantify interannual similarity in interactions we calculated Bray-Curtis similarity for plant-by-pollinator interaction matrices using both the binary (incidence) and quantitative (visitation frequency) interactions for all pairwise combinations of years. We used the Bray-Curtis similarity metric because it is appropriate for comparisons using composition and relative abundance (Legendre and Legendre 1998, Anderson et al. 2011). To calculate similarity, we used the `vegdist` function from the `vegan` package (Oksanen et al. 2013) in R (R Core Team 2015).

Network statistics.—We calculated several descriptive metrics for each yearly network: plant species richness, pollinator species richness, connectance (the proportion of all possible interactions realized); links per species (a binary measure of interaction richness: the mean number of unique binary links per species, where a link is the connection of two species in the network through interaction events), linkage density (a quantitative measure of interaction diversity, weighted by the total number of interactions of each species; see details and formulas in Bersier et al. 2002, Dormann et al. 2009), interaction diversity (Shannon diversity index calculated for interactions), interaction evenness (Shannon evenness of interaction matrix), network specialization H_2' (ranging from 0, indicating no specialization, to 1, indicating maximum specialization; Blüthgen et al. 2006), and nestedness (NODF and wNODF; Almeida-Neto et al. 2008). Connectance, links per species, and NODF were calculated on the binary interaction matrix, whereas linkage density, interaction diversity, interaction evenness, network specialization, and wNODF were calculated on the quantitative (weighted) interaction matrix. We calculated all network metrics using the `bipartite` package in R (Dormann et al. 2008). We used the coefficient of variation expressed as a percentage ($\%CV = 100 \times \text{standard deviation}/\text{mean}$) as a measure of variability of the network metrics across the years (see Lehman and Tilman 2000, Garibaldi et al. 2011); thus, a large $\%CV$ represents low temporal persistence of a given network metric.

Quantification of interaction persistence, frequency and distance to the network core.—We quantified interaction persistence in two ways: (1) as the number of years in which it was observed (range 1–6); and (2) as the inverse of the coefficient of variation of interaction frequency across years ($1/CV = \text{mean}/\text{standard deviation}$). Interaction frequency is the number of flower visits observed in a given year between each pair of species. The total frequency of each pairwise interaction was the number of times each interaction occurred across the six years. Proximity to the core of the nested network (henceforth “proximity to core”) was calculated for each interaction as one minus the standardized Euclidean distance to the upper-left cell in the nested matrix (NODF) for the six years combined. Specifically, for a given cell ij , the unstandardized distance to the network core was

$D_{ij} = \sqrt{R_i^2 + R_j^2}$, where R_i and R_j are the distances of row i and column j to the first row and column, respectively, standardized so that they vary between zero (first row or column) and one (last row or column). Thus, if I is the total number rows in the matrix, then the relative distance for row i is $R_i = 1 - (i - 1)/(I - 1)$; similarly, if J is the total number of columns in the matrix, the relative distance for column j is $R_j = 1 - (j - 1)/(J - 1)$. All D_{ij} values were then standardized by dividing them by the maximum D_{ij} value for the network, so that maximum distance was 1 (corresponding to the lower right cell of the nested matrix). Proximity to the network core was then calculated as $1 - D_{ij}$. When calculating the relationship between measures of interaction persistence and interaction frequency of proximity to the network core, zeros (interactions not observed) were not included in the analysis.

Relationship between interaction frequency, distance to network core, and interaction persistence.—We calculated the Spearman rank correlation between the persistence measures and proximity to core and interaction frequency. In addition, because abundant species that interact frequently may be over-represented in the network core, we used linear models to disentangle the effects of proximity to the network core and interaction frequency on interaction persistence. We used interaction frequency, proximity to core, and their statistical interaction as predictors, and persistence calculated as either number of years or $1/CV$. When persistence was number of years, we used a generalized linear model with a beta-binomial error distribution and log link function with function `mle2` in the `bbmle` package of R; when persistence was $1/CV$, the model evaluated was a general linear model with a normal error distribution (function `lm` in R).

Null model analyses.—We conducted null model analyses to further assess the ecological significance of our results. We created two null models. The most basic model assumed homogeneous interaction probabilities among species, thus representing the absence of any ecological structure. The algorithm thus distributes the observed number of interactions among all pairs of species (the sum of all visitation observations recorded during each study year). This model is constrained to have the same number of plant and pollinator species, total number of interactions (flower visits), and connectance as the observed matrix to be randomized, and the additional constraint that all species have at least one interaction. Thus, the model generated 1,000 randomized interaction matrices for each of the six study years, for which the correlations between interaction frequency or distance to the network core and interaction persistence were calculated, and then compared with the observed correlations (see R code in Data S1).

The second null model, originally proposed by Vázquez et al. (2007), distributed interactions observed

in each study year according to interaction probabilities among species determined by relative abundances of the plant and pollinator species in that year (calculated as flower abundance recorded in that year for plants, and as number of individuals recorded at flowers of any plant species for pollinators), again with the additional constraints that the number of species, the number of interactions, and connectance are the same as in the observed matrix and that each species has at least one interaction. The algorithm again generated 1,000 randomized interaction matrices for each year, for which the above four correlations were calculated (see Data S1). This model thus represents neutrality of interactions, in the sense that it assumes that individuals (not species) interact randomly, and the probability of interaction among a pair of species is determined by the number of individuals that belong to each of the species (Vázquez et al. 2007). By doing so, we exclude other ecological processes likely to influence interactions, for instance the matching of traits among interacting species, which has been shown to be an important process shaping the structure of plant–animal mutualistic networks. This null model does not mean, however, that there are no ecological processes whatsoever; rather, it assumes that it is species abundance alone that drives the interactions.

In both models, the justification for the decision of requiring that each species has at least one interaction is that only species with interactions were part of the data collected in the field; plants with no visits (e.g., wind-pollinated plants) or pollinator species never recorded in the study were not included. The justification for maintaining the number species, the number of interactions and connectance was that these were not response variables of interest, but basic characteristics of the interaction matrix to study, so we reasoned that it was better to keep them constant. An additional justification for constraining connectance to be the same as in the original interaction matrix comes from the observation that null models with unconstrained connectance usually generate randomized matrices with unrealistically high connectances (Morales and Vázquez 2008).

RESULTS

Across the six study years, we observed 59 species of plants interacting with 196 species of pollinators in 28,015 interaction events involving 1,050 links (pairs of interacting species; Appendix S1: Fig. S1; Table 1). Of the 1,050 links, 673 (64%) were observed in only one year, 166 (15.8%) in two years, 89 (8.57%) in three years, 69 (6.57%) in four years, 33 (3.14%) in five years, and only 20 (1.9%) in all six years (Fig. 1; Appendix S1: Fig. S1). The frequencies of interactions were also highly uneven: few interactions were highly frequent and most were infrequent (Fig. 1; Appendix S1: Fig. S1). The percentage of interactions observed each year ranged 44–55% (Chao2 estimator) in spite of a high percentage of detection of the pollinator fauna (Chacoff et al. 2012), and was unrelated to sampling effort (Spearman correlation: $r = 0.5$, $n = 6$, $P = 0.35$).

Plant species richness ranged 23–46 species across years, with a %CV of 22%. Pollinator species richness ranged 65–113 species, with a %CV of 24%. The number of links was substantially more variable, ranging 181–512, with a %CV of 40% (Table 1). Network metrics were less variable than the numbers of species and interactions, in all cases with %CV < 20% except linkage density and wNODF (26.9% and 23.20%, respectively; Table 1).

Across the six study years, mean Bray-Curtis similarity between years calculated on the binary (presence–absence) data was 73% (SD = 9%) for plant species composition, 59% (SD = 6%) for pollinator composition, and 32% (SD = 5%) for binary interactions. When we considered the quantitative data to calculate Bray-Curtis similarity for interactions (i.e., using interaction frequency, how many times a pair of species was observed interacting), mean interannual similarity for interactions was lower (23%, SD = 4%). Surprisingly, there was no correlation between the similarities from the binary and quantitative matrices (Spearman's $r = 0.03$, $P = 0.93$). The latter result is likely a consequence of the different weights given to frequent and rare interactions in the quantitative and qualitative similarity indices: more weight is given to

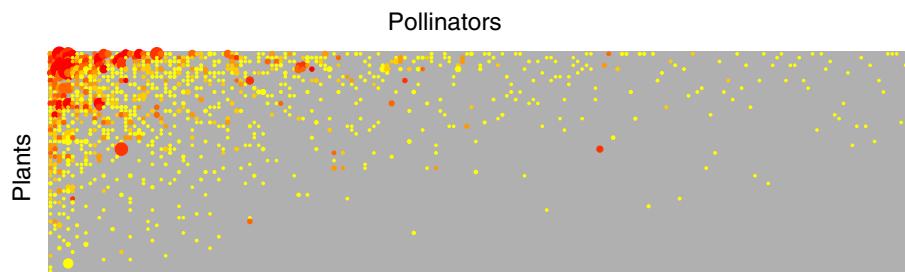


FIG. 1. Matrix depicting combined plant-pollinator network of 1,050 unique interactions among 59 plant species (columns) and 196 pollinators (rows) across the six years of the study in Villavicencio Monte Desert, Argentina. Interactions are arranged to show nestedness. Heat ramp colors indicate the number of years that an interaction occurred from 1 to 6 yr, with hotter colors representing more years. Circle size represents interaction frequency. Interactions that occurred in many years (red) are mostly restricted to the upper left corner in the matrix core and also tend to have high interaction frequency (large circles).

frequent interactions in the quantitative case than in the binary case, in which more weight is comparatively given to rare interactions.

Both measures of interaction persistence were positively correlated with total interaction frequency, so that the most frequent interactions were the most persistent, both when taking interaction occurrence across years as a measure of interaction persistence (Spearman's $r = 0.70$) and $1/\text{CV}$ ($r = 0.67$; Figs. 1, 2A, C). Similarly, interaction persistence was positively correlated with the proximity to the network core, so that as the proximity to the core of the nested matrix increased, interactions became more persistent, for both measures of persistence (interaction occurrence across years, $r = 0.40$, 95% CI = $[-0.06, 0.06]$; $1/\text{CV}$ of interaction frequency, $r = 0.40$, 95% CI = $[-0.06, 0.06]$; Figs. 1, 2B, D). When considered simultaneously in a linear model, both interaction frequency and proximity to the network core were significant predictors of interaction persistence for both measures of interaction persistence (Appendix S1: Table S2). In addition, when interaction persistence was measured as $1/\text{CV}$ of interaction frequency there was a significant, negative, statistical interaction between the two predictors, so that far from the network core the

relationship between persistence and interaction frequency is more strongly positive than close to the core (Appendix S1: Table S2).

The null model with homogeneous interaction probabilities produced correlations significantly weaker than those observed in our data (Fig. 3). The second null model with interaction probabilities determined by abundance produced stronger correlations between persistence and the frequency and position of interactions, matching closely the observed correlations for interaction frequency and exceeding observed correlations for proximity to core (Fig. 3). The better predictive ability of the null model for interaction frequency makes sense, considering that the product of plant and pollinator relative abundances is more correlated with the interaction frequency between those species (Spearman's correlations by year [mean \pm SD]: $r = 0.30 \pm 0.02$) than with the corresponding cell's proximity to the network core ($r = 0.01 \pm 0.03$).

DISCUSSION

The high interannual variability in the occurrence and frequency of pairwise interactions observed in our

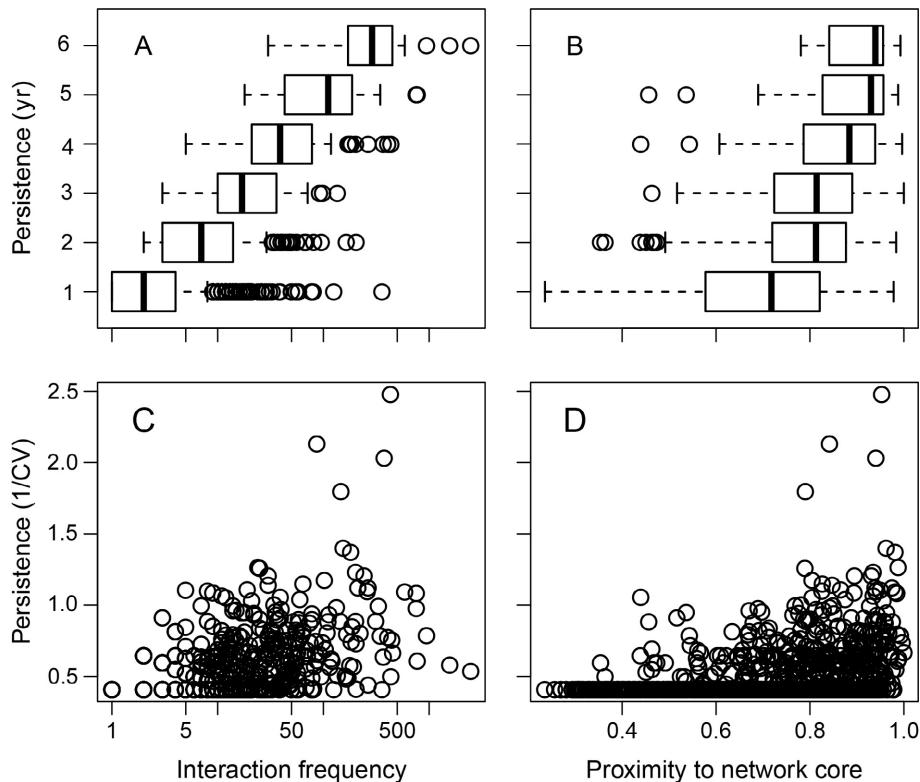


FIG. 2. Relationship between measures of interaction persistence, (A, C) interaction frequency, and (B, DP) proximity to the network core (the most densely connected region of the network). Persistence was measured as the number of years an interaction was observed (A, B) and $1/\text{CV}$ of the interaction frequencies across years (B, C). Interaction frequency, shown in log-scale, represents the number of years each interaction was observed across all study years. Proximity to the network core is one minus the standardized Euclidean distance to the upper-left cell in the nested matrix (see *Methods: statistical analyses* for details).

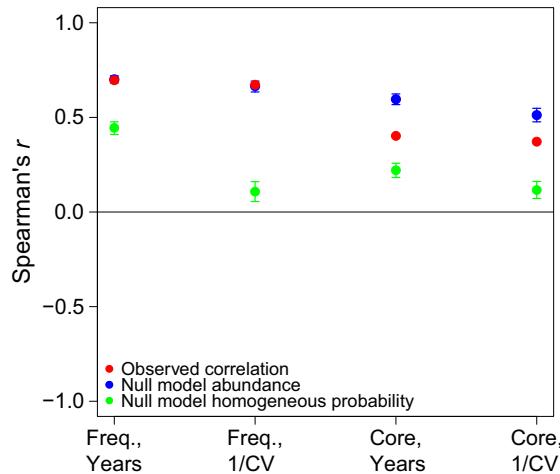


FIG. 3. Results of null model analyses to assess the ecological significance of the correlation between interaction frequency (Freq.) or proximity to the network core (Core) and the stability measures: number of years (Years) or the inverse of the coefficient of variation of interaction frequency (1/CV). Red symbols represent the observed correlations, green symbols represent the mean \pm the confidence intervals for the null model assuming homogeneous probability, and blue symbols represent the mean \pm the confidence intervals for the null model assuming that interaction probabilities are determined by species abundances. Both models were constrained to preserve the original connectance and to require that each species had at least one interaction.

system was correlated with the frequency of interactions and their position in the network: highly frequent interactions at the network core tended to be the most persistent. However, before drawing any conclusions about these relationships, we must address the crucial question of whether these patterns result from real ecological processes or from sampling artifacts.

Our null model analyses indicated that the distribution of abundances among species explains, at least partially, the above correlations. In our simplest null model, which assumed homogeneous interaction probabilities among species and thus lacked any ecological structure, predicted correlations between interaction frequency, distance to the network core and interaction persistence substantially lower than observed. Thus, clearly, some ecological structure is needed to produce the observed correlations. In contrast, our second null model, which assumed that interaction probabilities were determined by species abundances, came closer to predicting the observed correlations, although the prediction was closer for interaction frequency than for distance to the network core, for which the observed correlations were lower than the null model expectation. The latter result is not surprising, as abundance is more strongly correlated with interaction frequency than with distance to the network core. Thus, the null model analyses indicate that species abundance is a sufficient explanation of the correlation between interaction frequency and persistence, but an insufficient

explanation for the correlation between distance to the network core and interaction persistence. However, what these null model analyses do not tell us is *how* abundance influences the observed patterns. In other words, these models do not allow us to distinguish between a real neutral ecological process, whereby individuals tend to interact randomly, leading to abundant species interacting more frequently and with more species, and a sampling artifact, whereby species abundance determines the detection probability of interactions, producing a spurious correlation between interaction frequency and interaction persistence. Likewise, given that frequent interactions tend to be at or closer to the network core, the same sampling artifact could also produce a spurious correlation between distance to the network core and interaction persistence. Future studies should attempt to distinguish between these two possibilities.

If the patterns observed and the results of the null model analysis can be taken as an indication of a true ecological effect of abundance (as opposed to a sampling artifact), we can conclude that there seems to be positive correlations between interaction frequency or distance to the network core and interaction persistence, and that such correlations seem to be driven by the distribution of abundance among species in our study system. Together with the recent study of Fang and Huang (2016), our results point to the importance of the frequency and network position of interactions as an explanation of the temporal dynamics of mutualistic interactions reported in previous studies (Petanidou et al. 2008, Fang and Huang 2012, but see Alarcón et al. 2008). Furthermore, given the key role of interaction frequency in determining interaction strength (Vázquez et al. 2005, 2012), and of interaction strength for the persistence of mutualistic networks (Okuyama and Holland 2008), our findings emphasize the importance of frequent interactions at the network core for the functioning and persistence of plant–pollinator interactions.

Our work highlights the need for future studies on interaction persistence to continue working to disentangle frequency and network position from interaction detectability. Provided that the patterns reported here can be indeed interpreted as the result of real ecological processes and not purely the result of sampling artifacts, our findings have important implications for the ecological and evolutionary dynamics of interacting plants and pollinators. Past studies have shown that mutualistic networks are highly nested, which implies that generalist species tend to interact cohesively, forming a network core of high connectivity and strong reciprocal influences, while specialists interact asymmetrically with generalists (Bascompte et al. 2003, Vázquez and Aizen 2004). Such structure implies that the most generalized species at the network core have the greatest potential for reciprocal ecological effects; in contrast, specialists should track their generalist, abundant, interaction partners, with little opportunity for the ecological and evolutionary coupling of their dynamics (Bascompte et al.

2003, Vázquez and Aizen 2004, Vázquez et al. 2007, Bascompte and Jordano 2014). Given that frequent interactions also tend to be the most generalized in terms of number of interaction partners (Vázquez and Aizen 2003), our findings reinforce the above view of the dynamics of mutualistic networks.

Given the key role of species interactions for ecosystem functioning and the services they provide (Kremen 2005), conservation efforts should target not only species but also interactions (Tylianakis et al. 2010, Valiente-Banuet et al. 2015). Plant–pollinator interactions play a fundamental role in many ecosystems (Ollerton et al. 2011) and offer a valuable service for agriculture (Klein et al. 2007). Together with previous studies of the temporal and spatial dynamics of plant–pollinator networks (Alarcón et al. 2008, Petanidou et al. 2008, Olesen et al. 2011, Aizen et al. 2012, Fang and Huang 2012), our results underscore the dynamic nature of these networks and reveal the importance of interaction frequency and network position as meaningful determinants of the spatiotemporal persistence of plant–pollinator interactions.

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LITERATURE CITED

- Aizen, M. A., M. Sabatino, and J. M. Tylianakis. 2012. Specialization and rarity predict nonrandom loss of interactions from mutualist networks. *Science* 335:1486–1489.
- Alarcón, R., N. M. Waser, and J. Ollerton. 2008. Year-to-year variation in the topology of a plant–pollinator interaction network. *Oikos* 117:1796–1807.
- Almeida-Neto, M., P. Guimarães, P. R. Guimarães, R. D. Loyola, and W. Ulrich. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117:1227–1239.
- Anderson, M. J., et al. 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters* 14:19–28.
- Bascompte, J., and P. Jordano. 2014. *Mutualistic networks*. Princeton University Press, Princeton, New Jersey, USA.
- Bascompte, J., P. Jordano, C. J. Melián, and J. M. Olesen. 2003. The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences USA* 100:9383–9387.
- Bersier, L.-F., C. Banašek-Richter, and M.-F. Cattin. 2002. Quantitative descriptors of food web matrices. *Ecology* 83:2394–2407.
- Blüthgen, N., F. Menzel, and N. Blüthgen. 2006. Measuring specialization in species interaction networks. *BMC Ecology* 6:9.
- Carnicer, J., P. Jordano, and C. J. Melián. 2009. The temporal dynamics of resource use by frugivorous birds: a network approach. *Ecology* 90:1958–1970.
- Chacoff, N. P., D. P. Vázquez, S. B. Lomáscolo, E. L. Stevani, J. Dorado, and B. Padrón. 2012. Evaluating sampling completeness in a desert plant–pollinator network. *Journal of Animal Ecology* 81:190–200.
- Dormann, C. F., B. Gruber, and J. Fründ. 2008. Introducing the bipartite package: analysing ecological networks. *R News* 8/2:8–11.
- Dormann, C. F., J. Fründ, N. Blüthgen, and B. Gruber. 2009. Indices, graphs and null models: analyzing bipartite ecological networks. *Open Ecology Journal* 2:7–24.
- Fang, Q., and S.-Q. Huang. 2012. Relative stability of core groups in pollination networks in a biodiversity hotspot over four years. *PLoS ONE* 7:e32663.
- Fang, Q., and S. Huang. 2016. Plant–pollinator interactions in a biodiverse meadow are rather stable and tight for 3 consecutive years. *Integrative Zoology* 11:199–206.
- Garibaldi, L. A., et al. 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecology Letters* 14:1062–1072.
- Klein, A.-M., B. E. Vaissière, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tschamtkke. 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B* 274:303–313.
- Kremen, C. 2005. Managing ecosystem services: what do we need to know about their ecology? *Ecology Letters* 8:468–479.
- Labraga, J. C., and R. Villalba. 2009. Climate in the Monte Desert: past trends, present conditions, and future projections. *Journal of Arid Environments* 73:154–163.
- Legendre, P., and L. Legendre. 1998. *Numerical Ecology*. Elsevier, Amsterdam, The Netherlands.
- Lehman, C. L., and D. Tilman. 2000. Biodiversity, stability, and productivity in competitive communities. *American Naturalist* 156:534–552.
- MacLeod, M., M. A. Genung, J. S. Ascher, and R. Winfree. 2016. Measuring partner choice in plant–pollinator networks: using null models to separate rewiring and fidelity from chance. *Ecology* 97:2925–2931.
- Morales, J. M., and D. P. Vázquez. 2008. The effect of space in plant–animal mutualistic networks: insights from a simulation study. *Oikos* 117:1362–1370.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2013. *vegan: community ecology package*. <https://cran.r-project.org/web/packages/vegan/>
- Okuyama, T., and J. N. Holland. 2008. Network structural properties mediate the stability of mutualistic communities. *Ecology Letters* 11:208–216.
- Olesen, J. M., J. Bascompte, H. Elberling, and P. Jordano. 2008. Temporal dynamics in a pollination network. *Ecology* 89:1573–1582.
- Olesen, J. M., C. Stefanescu, and A. Traveset. 2011. Strong, long-term temporal dynamics of an ecological network. *PLoS ONE* 6:e26455.
- Ollerton, J., R. Winfree, and S. Tarrant. 2011. How many flowering plants are pollinated by animals? *Oikos* 120:321–326.

- Petanidou, T., A. S. Kallimanis, J. Tzanopoulos, S. P. Sgardelis, and J. D. Pantis. 2008. Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. *Ecology Letters* 11:564–575.
- Poisot, T., D. B. Stouffer, and D. Gravel. 2015. Beyond species: why ecological interaction networks vary through space and time. *Oikos* 124:243–251.
- Poniso, L. C., M. P. Gaiarsa, and C. Kremen. 2017. Opportunistic attachment assembles plant–pollinator networks. *Ecology Letters* 20:1261–1272.
- R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org
- Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11:1351–1363.
- Tylianakis, J. M., E. Laliberté, A. Nielsen, and J. Bascompte. 2010. Conservation of species interaction networks. *Biological Conservation* 143:2270–2279.
- Valiente-Banuet, A., et al. 2015. Beyond species loss: the extinction of ecological interactions in a changing world. *Functional Ecology* 29:299–307.
- Vázquez, D. P., and M. A. Aizen. 2003. Null model analyses of specialization in plant–pollinator interactions. *Ecology* 84:2493–2501.
- Vázquez, D. P., and M. A. Aizen. 2004. Asymmetric specialization: a pervasive feature of plant–pollinator interactions. *Ecology* 85:1251–1257.
- Vázquez, D. P., W. F. Morris, and P. Jordano. 2005. Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecology Letters* 8:1088–1094.
- Vázquez, D. P., C. J. Melián, N. M. Williams, N. Blüthgen, B. R. Krasnov, and R. Poulin. 2007. Species abundance and asymmetric interaction strength in ecological networks. *Oikos* 116:1120–1127.
- Vázquez, D. P., S. B. Lomáscolo, M. B. Maldonado, N. P. Chacoff, J. Dorado, E. L. Stevani, and N. L. Vitale. 2012. The strength of plant–pollinator interactions. *Ecology* 93:719–725.

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