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Core–periphery dynamics in a plant–pollinator network

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Abstract

1. Mutualistic networks are highly dynamic, characterized by high temporal turnover of species and interactions. Yet, we have a limited understanding of how the internal structure of these networks and the roles species play in them vary through time.
2. We used 6 years of observation data and a novel statistical method (dynamic stochastic block models) to assess how network structure and species' structural position within the network change throughout subseasons of the flowering season and across years in a quantitative plant–pollinator network from a dryland ecosystem in Argentina.
3. Our analyses revealed a core–periphery structure persistent through subseasons and years. Yet, species structural position as core or peripheral was highly dynamic: virtually all species that were at the core in some subseasons were also peripheral in other subseasons, while many other species always remained peripheral.
4. Our results illuminate our understanding of the dynamics of mutualistic networks and have important implications for ecosystem management and conservation.

KEYWORDS

core–periphery structure, mutualistic networks, plant–pollinator interactions, species role, stochastic block model, temporal dynamics

1 | INTRODUCTION

Studies of plant–animal mutualisms have historically focused on the interactions between one or a few plant species and their animal mutualists (Boucher, James, & Keeler, 1982; Faegri & van der Pjil, 1979). This approach guided decades of research, illuminating our understanding of the natural history, ecology and evolution of plant–animal mutualisms, but at the same time limiting our understanding of how interactions operate in their broader community context (Waser, Chittka, Price, Williams, & Ollerton, 1996). More recently, the use of a network approach to the study of plant–animal mutualistic interactions in their community context has offered new insights into the relative specialization and reciprocal dependence of these interactions and, ultimately, the ecological and evolutionary processes that depend on them (Bascompte & Jordano, 2014; Jordano, 1987; Memmott, 1999; Waser et al., 1996). These studies have revealed that mutualistic networks are usually characterized by a widespread of asymmetric specialization and a nested structure (recently conceived as a type of core–periphery structure; Lee, 2016; A.M. Martín González, unpubl.

data), in which many specialized species interact with a core of highly generalized species (Bascompte, Jordano, Melian, & Olesen, 2003; Vázquez & Aizen, 2004), as well as some degree of modularity (Olesen, Bascompte, Dupont, & Jordano, 2007), all of which are believed to have important ecological and evolutionary implications (Bascompte & Jordano, 2014; Guimarães, Pires, Jordano, Bascompte, & Thompson, 2017; Lomáscolo, Giannini, Chacoff, Castro-Urgal, & Vázquez, 2019; Rohr, Saavedra, & Bascompte, 2014; Thébault & Fontaine, 2010).

Mutualistic networks are also characterized by high temporal variability, with species and interactions switching on and off through time. In other words, these networks exhibit high temporal turnover of species and interactions (CaraDonna et al., 2017; Chacoff, Resasco, & Vázquez, 2018; Petanidou, Kallimanis, Tzanopoulos, Sgardelis, & Pantis, 2008), in spite of an apparent stability in some aggregate network attributes such as connectance and nestedness (Nielsen & Bascompte, 2007; Petanidou et al., 2008). Past studies have shown that the most persistent interactions are those located at the network core (the most densely connected region of the network), which usually involves abundant, frequently interacting species and many occasional peripheral species (Chacoff et al., 2018; Fang & Huang, 2016). What we still do not know is the extent to which the structural properties of the network and the structural position of individual species as core or peripheral vary through time. In other words, is there a persistent set of core species that form the backbone of the network throughout the flowering season and across years? Or is the core itself also highly dynamic, with species switching between core and peripheral positions?

Answering the above questions is essential to understand and predict how different species contribute to community stability and to guide management and conservation efforts. For example, the existence of a stable set of species at the network core could represent a reasonable target for biodiversity conservation—a small, manageable set of keystone species on which to focus conservation efforts (Chacoff et al., 2012; Fleishman, Betrus, Blair, Mac Nally, & Murphy, 2002; Fleishman, Donnelly, Fay, & Reeves, 2007; García-Algarra, Pastor, Iriondo, & Galeano, 2017; Hegland, Dunne, Nielsen, & Memmott, 2010). Conversely, a highly dynamic network core would make that target more elusive, with a larger, variable set of potentially keystone species.

Here we evaluate how the structure of a plant–pollinator network and the structural position of species in the network change throughout subseasons of the flowering season and across years. We focus on a previously published bipartite, weighted (non-binary) plant–pollinator network spanning 6 years in a dryland ecosystem in Villavicencio Nature Reserve, Argentina (Chacoff et al., 2018). The previous study by Chacoff et al. (2018) revealed a low across-year persistence of interactions in this system. That finding opened the key question of whether such high interaction turnover prevents the network from building a persistent core of interacting species and, if not, whether that core is maintained by a persistent species set. These are the questions we attempt to answer in this paper. Given that, as discussed above, plant–animal mutualistic networks exhibit widespread asymmetric specialization, harbouring many specialized species that interact with a core of highly generalized species, we hypothesized that a core–periphery structure would also be pervasive over time; thus, we expected seasonally resolved networks in our study system to be characterized by a persistent core–periphery structure. In addition, given that previous studies had found interactions at the network core to be more persistent over time (Chacoff et al., 2018; Fang & Huang, 2016), we hypothesized that the subseasonal networks would be characterized by the consistent presence of certain species at the network core which would form the 'persistent backbone' of the network. This analysis allowed us to provide a comprehensive picture of the temporal dynamics of the internal structure of this mutualistic network.

Our network representation focuses on the relative ecological effects between the pairs of interacting species (usually referred to as *dependences*, Bascompte, Jordano, & Olesen, 2006; Rohe, Qin, & Yu, 2016). Using dependences allows us to represent the plant–pollinator network as a weighted directed network in which each pair of species A and B is linked by two quantitative ecological effects: the effect of A on B and the (usually distinct) effect of B on A (Vázquez, Ramos-Jiliberto, Urbani, & Valdovinos, 2015). This representation of the interaction network contrasts with the usual representation of ecological interaction networks as undirected, which does not allow differentiating between the effect of species A on species B and the effect of B on A. As these two countervailing effects usually have asymmetric strengths, species structural roles could be misestimated by the conventional symmetric representation. Consequently, we argue that a better representation of ecological networks should be one in which each pair of species is connected by two weighted directed links. Because jointly analysing a series of networks is methodologically challenging (Miele, Matias, Robin, & Dray, 2019), we rely on a recent statistical framework dedicated to this kind of data (dynamic stochastic block models, hereafter dynSBM; Matias & Miele, 2017) to quantify the temporal switching of the structural position of plants and pollinators.

2 | MATERIALS AND METHODS

2.1 | Study site and data collection

Data come from a previously published study describing a plant–pollinator network from pollinator visits to flowers in a dryland ecosystem (Chacoff et al., 2018). Data collection was conducted in sites lying at the lowlands of Villavicencio Nature Reserve, Mendoza, Argentina (32°32′0″S, 68°57′0″W, 1,270 m a.s.l.). Mean annual rainfall ranges 150–350 mm, concentrated during spring and summer (Labraga & Villalba, 2009). Biogeographically, the study sites are located at the Monte desert ecoregion (Roig, Roig-Juñent, & Corbalán, 2009).

Data were collected weekly during 3 months during the flowering season (Austral spring and early summer, September–December) between 2006 and 2011. Pollinator visits to flowers were recorded in two 1-ha sites separated by *c.* 5 km, with two additional 1-ha sites sampled in only in 2006. Data from these sites were combined into a single network to improve sampling completeness of species and interactions occurring in the region. Pollinator visits to flowers were recorded between 7.00 and 14.00 hr in 5-min observation periods, a representative portion of the daily activity period of pollinators in our study sites. The data include 59 plant species, 196 flower visiting insect species and 28,015 interaction events (flower visits) involving 1,050 different pairs of interacting species. Plant abundance was estimated based on the density of flowers of each plant species, as flowers are the relevant plant structure for this interaction type (Vázquez, Chacoff, & Cagnolo, 2009). Flower abundance was estimated during the flowering season of all study years using fixed quadrats/transects. Several rare plant species were absent from our fixed quadrats and transects but present elsewhere in our study site; for those species we assigned an abundance of one flower, the minimum we could have detected with our sampling method. A full account of the methodology can be found in Chacoff et al. (2012, 2018).

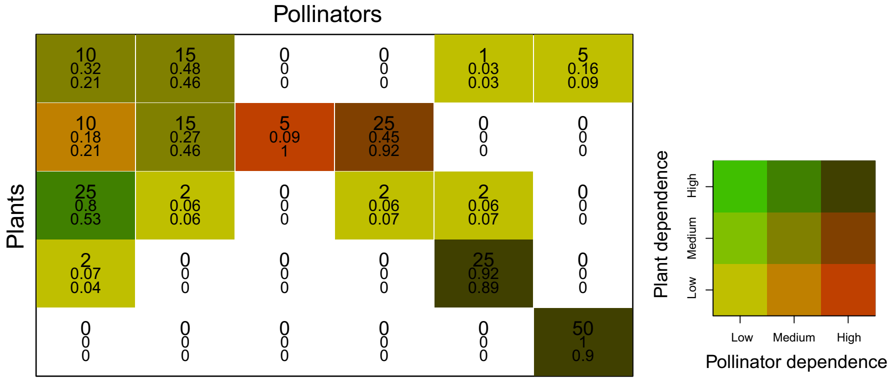
2.2 | Building plant–pollinator dependence networks

We aggregated the data by pooling the number of visits of any pollinator to any plant into three subseasons of approximately equal length throughout the flowering season of each year (before 1 November, after 30 November and in between). Such level of aggregation allowed us to consider seasonal dynamics at a temporal grain that was not too fine nor too coarse to allow a reasonable seasonal representation of network structure.

For any subseason, we built a plant–pollinator *dependence network D*, a directed weighted network representing the relative dependences among plant and pollinator species (Bascompte et al., 2006; Rohe et al., 2016). From the number of visits in a time interval X_{ij} between any pair of species of plant and pollinator (i, j), we considered two directed and weighted edges (i.e. links) in *D*: the dependence of plant i on pollinator j, $D_{ij}=X_{ij}/\sum_{j} X_{ij}$, representing the number of visits of pollinator j to plant i divided by the total number of visits received by plant i; and the reciprocal dependence of pollinator j on plant i, $D_{ji}=X_{ij}/\sum_{i} X_{ij}$, representing the number of visits of pollinator j to plant i divided by the total number of visits done by j. Applying this approach to our raw data, we obtained a time series of 18 dependence networks. To represent these networks graphically, we showed the successive bipartite matrices (plants in rows, pollinators in columns) using a colour code accounting for the two values D_{ij} and D_{ji} for any species pair (i, j; see an example in Figure 1).

2.3 | Inferring topology and species' structural position in the dynamic network

Some authors have recently suggested the use of statistical methods which jointly infer structural properties and species positions (Allesina & Pascual, 2009; Kéfi, Miele, Wieters, Navarrete, & Berlow, 2016; Leger, Daudin, & Vacher, 2015; Michalska-Smith, Sander, Pascual, & Allesina, 2018; Ohlmann et al., 2019). Originally developed in the field of social sciences (Holland, Laskey, & Leinhardt, 1983), *Stochastic Block Models* (SBM; Daudin, Picard, & Robin, 2008; Newman & Leicht, 2007)—also called *Group Models* by Allesina and Pascual (2009)—aim at grouping nodes (species in our case) that are statistically equivalent, 'acting' similarly in the network, that is, having an equivalent 'structural position'. These methods follow a



10 0.32 0.21	15 0.48 0.46	0 0 0	0 0 0	1 0.03 0.03	5 0.16 0.09
10 0.18 0.21	15 0.27 0.46	5 0.09 1	25 0.45 0.92	0 0 0	0 0 0
25 0.8 0.53	2 0.06 0.06	0 0 0	2 0.06 0.07	2 0.06 0.07	0 0 0
2 0.07 0.04	0 0 0	0 0 0	0 0 0	25 0.92 0.89	0 0 0
0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	50 1 0.9

FIGURE 1 Hypothetical representation of a dependence network between five plant species (rows) and six pollinator species (columns) to illustrate the concept of a dependence network and how it is represented graphically in this paper. Each cell is coloured according to the legend and filled with the number of visits (top value in larger font), the plant and pollinator dependence values D_{ij} (middle) and D_{ji} (bottom). The legend shows the colour code accounting for the two dependence values for any species pair (i, j; darker green represents higher the plant dependence; stronger red represents higher the pollinator dependence). This example shows the advantage of studying dependence values instead of raw interaction frequency data. The number of visits in cells (3,1), (2,4) and (4,5) are all equal to 25. Meanwhile, these number of visits do not characterize the same kind of interaction, as shown by the dependence values. Indeed, plant 3 is highly dependent on pollinator 1 (the reverse is not true), pollinator 4 is highly dependent on plant 2 (the reverse is not true) whereas plant 4 and pollinator 5 are mutually dependent and have a quasi-exclusive relationship. Lastly, the number of visits in cell (5,6) is twice the number in cell (4,5) but the dependence values are comparable (dependence is scale invariant)

particular paradigm: instead of searching for a particular pattern, we infer one from the data. SBM can handle weighted networks with appropriate statistical distributions; we chose them for their ability to decipher core–periphery structure in network data (as mentioned in fig. 1 in Betzel, Medaglia, & Bassett, 2018), as they can infer groups of core species and peripheral species.

Furthermore, studying network dynamics requires a method that can handle and model the whole time series of network snapshots (i.e. in a *dynamic network*). Recently, Matias and Miele (2017) proposed an extension of SBM for dynamic networks called dynSBM. Under this approach, the structural position of any species can vary over time. In other words, each structural group (for instance a core group) is inferred using the complete series, but the group membership can vary from any time step to another. Here we rely on a modified version of this approach dedicated to bipartite networks (see Supporting Information) implemented in the R package DYNSBM (Matias & Miele, 2019). Importantly, the number of groups is constant and selected with the elbow method (Supporting Information and Figure S1).

3 | RESULTS

3.1 | A persistent core–periphery structure

By applying the dynSBM algorithm, we found that the Villavicencio plant–pollinator network is organized as a core–periphery structure (Figure 2). This network structure comprises two components, each one composed of a group of plants and a group of pollinators. The first

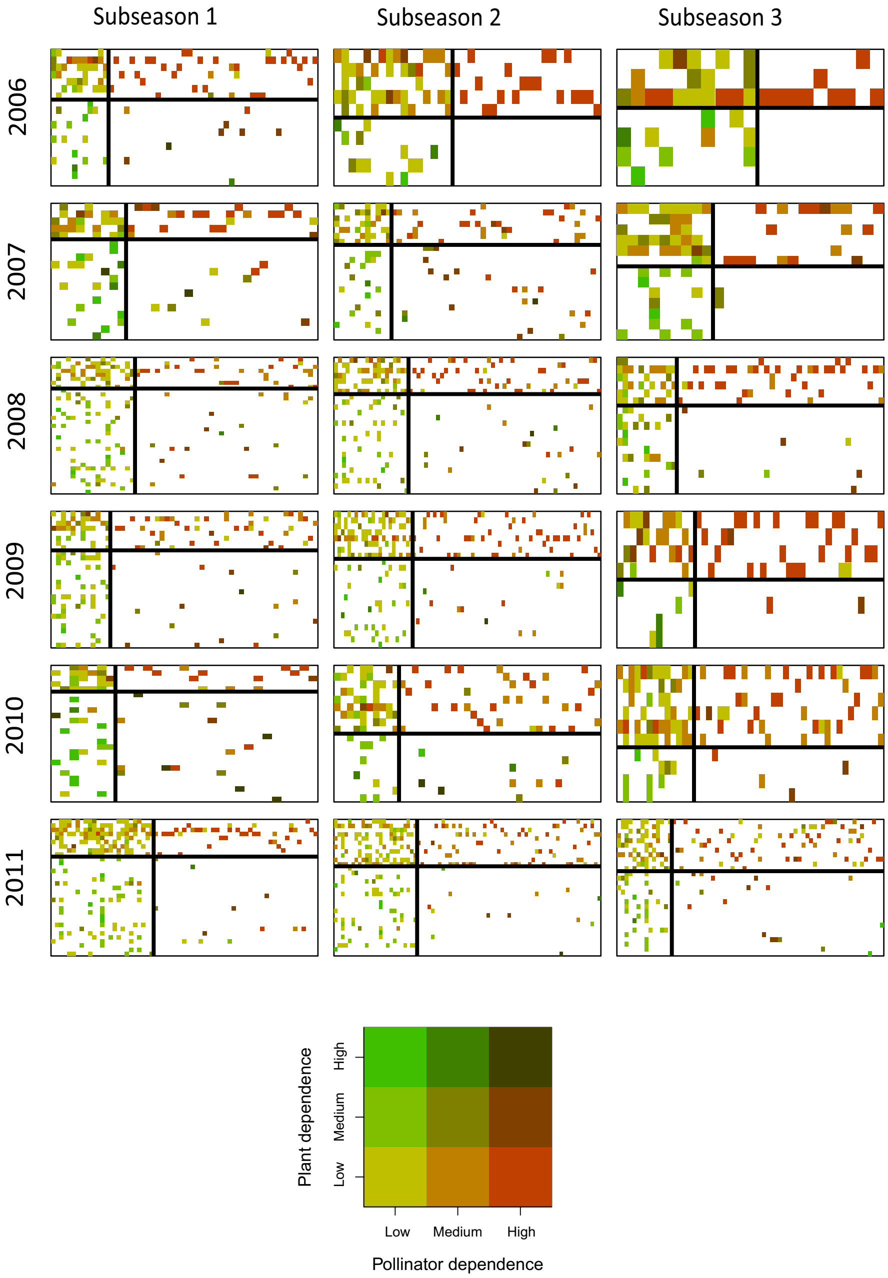


FIGURE 2 Temporal dynamics of Villavicencio plant–pollinator network for three subseasons of the flowering season for six study years (2006–2011). For each matrix, cells represent the plant and pollinator dependence values between a plant (rows) and pollinator (columns) species, with a colour computed as a mixture of the two dependence values according to the legend. Rows and columns were reorganized according to the dynSBM group membership: dark lines separating each matrix delineate the group boundaries (core/peripheral group of plants above/below the horizontal line; core/peripheral group of pollinators on the left/right of the vertical line)

component consists of one group of plant species and one group of pollinator species forming a persistent cohesive module (the network *core*), while the second component was composed of a group of plants and a group of pollinators in the network *periphery* (Figure S1). The proportions of species in these groups varied only modestly through time (chi-squared test: $\chi^2 = 64.92$, $df = 51$, $p = 0.09$) in spite of being unconstrained in dynSBM (Figure 2); in contrast, these proportions varied widely in randomized networks (Figure S3).

Core and peripheral species differ markedly in terms of their linkage patterns. The core group of plants (top rows of matrices in Figure 2) consisted of species visited by many pollinator species, especially species in the core group of pollinators (left columns of matrices in Figure 2), which visited many plant species. Species in these core groups of plants and pollinators are weakly dependent on their interaction partners (Figure S2). Thus, the network core can be envisioned as a densely connected 'module' of generalized plant and pollinator species with low mutual dependence among them (Figure 3). In contrast, the peripheral group of plants (bottom rows of matrices in Figure 2) includes species visited mostly by core pollinator species; dependence is highly asymmetric for these plants, in the sense that they are highly dependent on pollinators who are not reciprocally dependent on their host plants (Figure S2). Likewise, the peripheral group of pollinators (right columns of matrices in Figure 2) includes species interacting mostly with core plants, also asymmetrically dependent on plants that are not reciprocally dependent on them (Figure 3). In addition, there are only a few interactions between peripheral plant and pollinator species, with no particular trend regarding their reciprocal dependence (Figure S2).

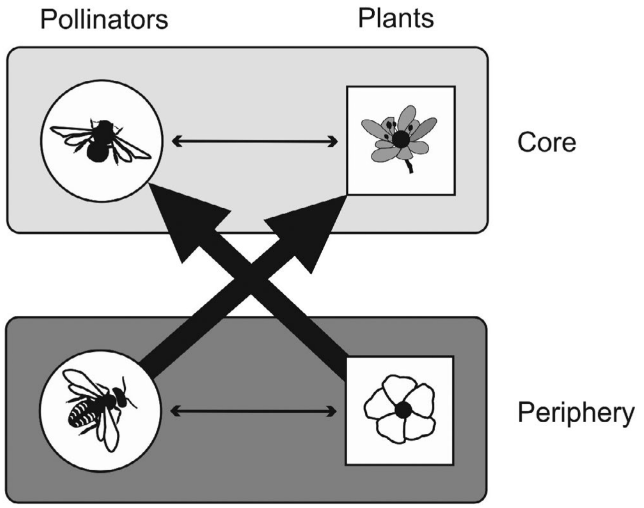


FIGURE 3 Graphical representation of the core–periphery structure found in our dynamic plant–pollinator network. Arrows depict dependences of one species (arrow origin) on another (arrow tip). Arrow widths are proportional to typical dependence values between groups. Pollinators/plants of the network periphery are strongly dependent on plants/pollinators that belong to the network core

3.2 | The core–periphery structure is robust to changes in species diversity and composition

The core–periphery structure persisted despite two sources of variation: the diversity of species and their identities. First, the diversity of plant and pollinator species varied over time, so that each year the number of plant species in bloom tended to decrease from the first to the third subseason, whereas the number of pollinator species tended to peak in the second subseason (Figure S4); yet, the proportion of core plant species increased from the first to the third subseason each year (Figure 2; plant core group in the upper part of each matrix). Thus, the size of the plant core group was independent of plant diversity. Second, the identity of interacting species and their activity (as measured by the total number of floral visits received by a plant or performed by a pollinator) changed greatly from one time step to another, resulting in substantial temporal variation in the species assembly (Figure S5). Yet, despite these variations in the interactions at the species level, the core–periphery structure persisted over time.

3.3 | Species in the core are also sometimes peripheral

Species structural positions were highly dynamic. Almost all species that were in the core in some subseasons were also peripheral in other subseasons (except one plant and one pollinator species); however, a large proportion of peripheral species never became part

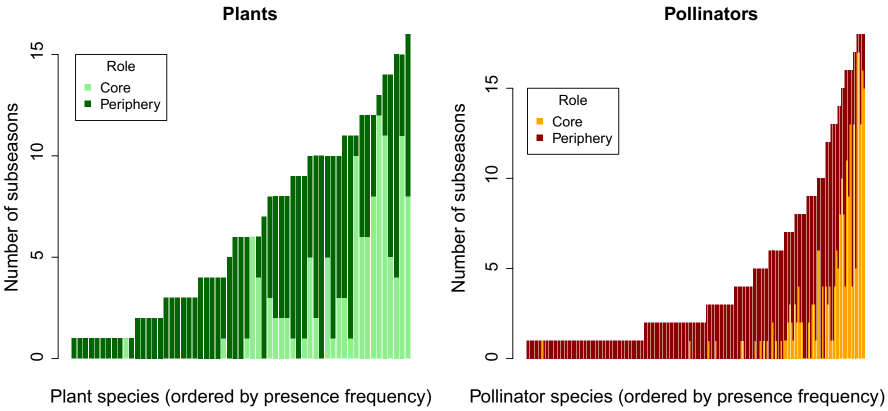


FIGURE 4 Temporal shifts in species structural positions. Each stacked bar (one by species) represents the number of subseasons any species was found in the core (light colour) or in the periphery (dark colour). Bars were ranked according to the number of subseasons any species was observed and present in the network. For plants (left) and pollinators (right)

of the core (52% for plants, 72% for pollinators; see Figure 4). Thus, only a subset of species was ever part of the core, and virtually no species occupied that position persistently through time.

There was a positive correlation between overall species presence (i.e. the number of subseasons a species was recorded interacting) and their presence in the core: the more frequently a plant or a pollinator species was present in the community, the more frequently it was found in the core (see Figure 4; Figure S6). Furthermore, for plant species for which we have independent abundance data, we observed that their abundance tended to be higher when they are in the core than when they are peripheral (Figure S7).

4 | DISCUSSION

Our analysis using dynamic stochastic block models allowed us to delve into the topological dynamics of a plant–pollinator network. In a nutshell, we found that this network is characterized by a core–periphery structure persistent throughout the flowering season and across years, while exhibiting high temporal switching of species structural positions. These results offer a unique temporal perspective into the dynamics of mutualistic networks.

The core–periphery structure was maintained in spite of high temporal variation in species richness and composition. The distribution of dependences also persisted over time, with highly asymmetric dependences for most peripheral species, which tended to interact with core species; thus, core species influence strongly peripheral species, with weak reciprocal effects from peripheral to core species. In turn, interactions among core species tended to be more symmetric, albeit with weaker dependences. This dependence structure has important implications for the evolutionary dynamics of interacting species (Bascompte et al., 2006), as in this system symmetric ecological effects among plants and pollinators have been associated with a greater opportunity for coevolution (Lomáscolo et al., 2019).

In spite of the above persistence of the core–periphery structure over time, the network position occupied by plant and pollinator species was highly dynamic: virtually all species that played a core role in some subseasons were also peripheral in other subseasons, while many other species always remained peripheral. Furthermore, presence in the network core was related to overall species presence: species present in many subseasons tended to be more consistently at the core than species present only in few subseasons. Previous studies had documented that nestedness (which, as pointed out above, can be viewed as a particular type of core–periphery structure, Lee, 2016) characterizes many plant–animal mutualistic networks (Bascompte et al., 2003) and that such structure is persistent over the years (Chacoff et al., 2018; Díaz-Castelazo et al., 2010; Díaz-Castelazo, Sánchez-Galván, Guimarães, Raimundo, & Rico-Gray, 2013; Petanidou et al., 2008) in spite of an enormous temporal variation in the occurrence of interactions (CaraDonna et al., 2017; Chacoff et al., 2018; Petanidou et al., 2008). Our findings extend those results, indicating that species structural position in the network is also highly dynamic. Thus, while the core–periphery structure persists over time, the taxonomic identity of the core changes drastically throughout the flowering season and across years, and no species can be identified as playing permanently a core role.

The latter finding has important implications for our understanding of the dynamics of ecological communities, as it implies that no species will play a central role in the community all the time; in contrast, species seem to alternate in their positions as core or peripheral, resulting in a highly dynamic community organization. The above finding also has far-reaching practical implications, as the idea of focusing management and conservation efforts on a small subset of species at the network core (Cagua, Wootton, & Stouffer, 2019; Chacoff et al., 2012; Fleishman et al., 2002, 2007; García-Algarra et al., 2017; Hegland et al., 2010; Maia, Vaughan, & Memmott, 2019) may be difficult to achieve, given that virtually no species plays that role consistently over time in the long run. Our findings do indicate that a small subset of species is likely to be found playing a key role as part of the network core in many subseasons and years, which brings them close to the notion of 'core' species and would make them adequate targets for conservation efforts. Plant species in this group include *Condalia microphylla*, *Larrea divaricata*, *Prosopis flexuosa* and *Zuccagnia punctata* whereas flower visitors in this group include *Augochloropsis* sp., *Bombus opiphex*, *Centris brethesi*, *Copestylum aricia* and *Xylocopa atamisquensis*. However, the latter group also includes a non-native, the honeybee *Apis mellifera*, which indicates that this invasive species has become dominant in this system not only in terms of abundance but also of interactions, and is now fully integrated into the plant–pollinator network as part of the densely connected network core, as has been observed in natural habitats around the world (Hung, Kingston, Albrecht, Holway, & Kohn, 2018). All these species are abundant generalists with extremely high interaction frequencies, which suggest that the consistent presence of these species in the core is mostly driven by their high abundances and interaction frequencies (Chacoff et al., 2018, 2012). In addition, the fact that these species belong to different families, and in the case of insects, even different orders, suggests that their presence in the core is not explained by their phylogenetic relatedness.

However, most other core species were core in a substantially smaller fraction of subseasons (see Figure 4). These species could be viewed as *quasi-core* species, in the sense that they are present in the core only intermittently. Thus, the identification of core species based on one or a few years of sampling—as done in most studies published so far—could be misleading, and a single static characterization of an ecological network will fail to reveal its true core–periphery structure. In this sense, the idea of species 'coreness' (Borgatti & Everett, 2000; Lee, 2016) is not just a black-or-white property determined only by the position of a species in a static or aggregated network, but a relative concept determined by the temporal consistency of the position occupied by a species. Therefore, identifying core species as candidates for management actions requires allocating a greater sampling effort into capturing the temporal dynamics of ecosystems, even if this practice implies relaxing efforts to capture some details of community structure and the detection of very rare species, which are unlikely to be part of the network core or to contribute significantly to community robustness to environmental perturbations. Of course, many peripheral species may be unique in terms of their conservation value because of their phylogenetic history or their functional roles. But to achieve community stability in terms of their resilience and robustness to environmental change we need to identify species whose roles will be key to maintain such stability. Species that are consistently present at the core of the interaction network are likely to have that role (see Kaiser-Bunbury, Muff, Memmott, Müller, & Caflisch, 2010), as they may be important interaction partners for many other species in the community, thus representing a temporal backbone of the community around which many other species will gravitate.

To conclude, we believe these results illuminate our understanding of the dynamics of ecological networks, indicating the persistence of a core–periphery structure in spite of substantial changes in species richness, composition, interactions and structural position in the network. Yet, we believe we have only scratched the surface of the temporal dynamics of ecological networks. One possible avenue for future research would be to apply the methods used here to analyse other datasets, to assess the generality of our findings.

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AUTHORS' CONTRIBUTIONS

All the authors conceived the study and wrote the manuscript. V.M. conducted the analyses.

DATA AVAILABILITY STATEMENT

Data are publicly available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.j6q573n9j (Vázquez & Chacoff, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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