Temporal switching of species roles in a plant–pollinator network

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Data accessibility statement: This study was performed with the R package `dynsbm` Miele & Matias (2017) available on CRAN at `https://cran.r-project.org/web/packages/dynsbm/`. The authors confirm that, should the manuscript be accepted, the data and code supporting the results will be archived in an appropriate public repository and the data DOI will be included at the end of the article.

Abstract

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. We used six years of observation data and a novel statistical method (dynamic stochastic block models) to assess how network structure and species roles change across time in a quantitative plant–pollinator network from a dryland ecosystem in Argentina. Our analyses revealed a core–periphery structure persistent through seasons and years. Yet, species roles as core or peripheral were highly dynamic: virtually all species that played a core role in some seasons were also peripheral in other seasons, while many other species remained always peripheral. Our results illuminate our understanding of the dynamics of ecological networks and have important implications for ecosystem management and conservation.

Introduction

Plant–animal mutualistic interactions are organized in complex networks characterized by several pervasive structural features, including nestedness (Bascompte *et al.*, 2003), modularity (Olesen *et al.*, 2007), and asymmetry in both specialization (Vázquez & Aizen, 2004) and interaction strength (Bascompte *et al.*, 2006). These properties have important implications for ecological and evolutionary dynamics (Thébault & Fontaine, 2010; Rohr *et al.*, 2014; Bascompte & Jordano, 2014). Mutualistic networks are also highly dynamic, with species and interactions switching on and off through time. In other words, these networks are characterized by a high temporal turnover of species and interactions (Petanidou *et al.*, 2008; CaraDonna *et al.*, 2017; Chacoff *et al.*, 2018), in spite of an apparent invariance in aggregate network attributes such as connectance and nestedness (Petanidou *et al.*, 2008; Nielsen & Bascompte, 2007). What we still don't understand is how much the internal structure of ecological interaction networks varies through time. In addition, little is known about the temporal variation of species "roles"—the structural position of a species in terms of its connections to other species in the network (Guimera & Amaral, 2005). Studying the temporal dynamics of species roles is essential to understand how different species contribute to community stability and to guide management and conservation efforts.

In many previous studies, plant–animal mutualistic networks were analyzed in light of two structural properties, modularity (Olesen *et al.*, 2007) and nestedness (Pawar, 2014), with the appropriate detection methods (e.g., Dormann & Strauss, 2014; Almeida-Neto *et al.*, 2008, respectively). Species roles were defined accordingly in terms of their pattern of intra- and inter-module connections or their position in the nested network (e.g., highly versus little connected species). However, focusing only on these two properties is arguably too restrictive, as networks can show other relevant structural properties (see Figure 1 in Michalska-Smith *et al.*, 2018; Betzel *et al.*, 2018). To circumvent this problem, some authors have suggested the use of "agnostic" methods, which jointly infer structural properties and species roles without any *a priori* assumption. These methods represent a paradigm shift in the study of networks: instead of searching for a particular pattern, we infer one from the data. Thus, assortative (modules) or disassortative, core–periphery, hierarchical or other types of structures (including random) can be identified in the data. Originally developed in the field of social sciences (Holland *et al.*, 1983), *Stochastic Block Models* (SBM; Newman & Leicht, 2007; Daudin *et al.*, 2008) (also called *Group Models*; Allesina & Pascual, 2009) have emerged as a general class of agnostic models. Technically speaking, SBM aim at grouping nodes (species in our case) that are statistically equivalent, "acting" similarly in the network ("playing" the same role). This approach has been recently advocated in Ecology (Michalska-Smith *et al.*, 2018; Allesina & Pascual, 2009; Leger *et al.*, 2015; Kéfi *et al.*, 2016; Ohlmann *et al.*, 2019).

In addition to the difficulties of identifying network structures and species roles, studying network dynamics with a similar perspective to understand role dynamics in a time series of network snapshots (i.e., in a *dynamic network*) remains a methodological challenge. The most trivial approach is to perform independent analyses on each time-specific network; under this approach, there is no role mapping between time steps t and $t + 1$, as roles are defined independently at each time step (Greene *et al.*, 2010), which is arguably a limitation, especially when there is node turnover. Other methods circumventing this limitation are currently emerging, most of them relying on module detection (e.g., Pilosof *et al.*, 2017; Rossetti & Cazabet, 2018). In particular, *dynamic stochastic block models* (dynSBM) (Matias & Miele, 2017) have been recently proposed as an alternative, as they have several advantages over other available methods: (1) they were developed in the agnostic framework which, as we pointed out above, does not assume *a priori* any particular type of network structure; (2) they can handle bipartite networks (such as plant–pollinator); (3) they can model interaction weights (i.e., beyond the binary case); and (4) they were designed to explicitly follow role switches in time.

Here we evaluate how group structure and species roles change across time in a bipartite, weighted (non-binary) plant–pollinator network spanning six years in a dryland ecosystem in Villavicencio Nature Reserve, Argentina (Chacoff *et al.*, 2018). Our network representation focuses on the relative ecological effects between pairs of interacting species (usually referred to as *dependences* Bascompte *et al.*, 2006; Rohe *et al.*, 2016). Working under the dynSBM framework, we quantify the temporal switching of structural roles of plants and pollinators. This analysis allows us to provide a comprehensive picture of the temporal dynamics of the internal structure of a mutualistic network.

Material and methods

Study site and data collection

We used a dataset describing a plant–pollinator network from pollinator visits to flowers in a dryland ecosystem. Data were collected weekly during three months during the flowering season (Austral spring and early summer, September–December) 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). The data include 59 plant species, 196 flower visitor species, and 28015 interaction events (flower visits) involving 1050 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. Flower abundance was estimated during the flowering season of all study years using fixed quadradts/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.* (2018, 2012).

Building plant–pollinator dependence networks

We aggregated the data by pooling the number of visits of any pollinator to any plant in 3 sub-seasons by year (before November 1st, after November 30th 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 representation of network structure.

For any sub-season, we built a plant-pollinator *dependence network* D, a directed weighted network representing the relative dependences among plant and pollinator species. 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 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 graphically these networks, we showed the successive bi-adjacency matrices (plants in rows, pollinators in columns) using a color code accounting for the two values D_{ij} and D_{ji} for any species pair (i, j) (see an example in Figure 1).

Inferring roles in the dynamic network

Recently, Matias and Miele proposed an extension of SBM for dynamic networks called dynSBM (Matias & Miele, 2017). Under this approach, role assignment is defined not only by a SBM (one per time step) but also by a Markov chain that models the role switches at each time interval. Here we rely on a modified version of this approach dedicated to bipartite networks, where each SBM has the same parameters values at each time step. Importantly, the number of groups/roles is constant and selected with an appropriate heuristics (Supplementary Figure S1). Role assignment (i.e., SBM group membership) can change over time, but there is no constraint for the roles to be present at each time step (see Supplementary Figure S3). Indeed, if species play, say, roles “red” and “blue” at time t but roles “red” and “yellow” at time $t + 1$, there will be three groups in dynSBM (red, blue and yellow). Relying on various statistical distributions to model edge presence and strength, dynSBM can model directed or undirected, binary or weighted edges. Here we categorize the edge weights (dependence values) into three levels corresponding to *low*, *medium* and *high* dependence (lower than 0.2, in between and larger than 0.8, respectively). Thus, we used dynSBM with multinomial distributions.

Results

A persistent core-periphery structure The dynSBM algorithm selected four roles/groups of nodes (Supplementary Figure S1), two for plants and two for pollinators. The proportions of species in these groups persisted through time, in spite of being unconstrained in dynSBM (Figure 2); in contrast, these proportions varied widely in randomly perturbed networks (Supplementary Figure S3). The first group of plants (top rows of the matrices in Figure 2) consisted of species visited by many pollinator species, especially by the first group of pollinators (left columns of the matrices in Figure 2), which visited many plant species. Species in the first groups of plants and pollinators are weakly dependent on their interaction partners (Supplementary Figure S2). Statistically speaking, these two groups form a "module" of generalized plant and pollinator species with low mutual dependence among them. The second group of plants (bottom rows of the matrices in Figure 2) includes species visited mostly by pollinators of the first group; 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 (Supplementary Figure S2). Likewise, the second group of pollinators (right columns of the matrices in Figure 2) includes species interacting mostly with plants of the first group, also asymmetrically dependent on plants that are not reciprocally dependent on them. In addition, there are only a few interactions between species of the second groups of plants and pollinators (with no particular trend regarding the reciprocal dependence; Figure Supplementary S2).

The observed network organization as one persistent cohesive module plus a number of species gravitating around this module can be termed a "core–periphery" structure, with the first group of plants and pollinators forming the *core* of the network and the second group representing *peripheral* species. Thus, for any time step, we observed a substantial fraction of interactions between species in the core characterized by weak reciprocal dependences (because they have many partners), plus another fraction of interactions between (plants or pollinator) species in the core and peripheral species, characterized by highly asymmetric dependences, with peripheral species depending strongly on core species, and core species depending only weakly on peripheral species (see Figure 3).

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 pollinators varied over time. Each year the number of plant species in bloom tended to decrease from the first to the third sub-season, whereas the number of pollinators species tended to peak in the second sub-season (Supplementary Figure S4); yet, the proportion of core plant species increased from the first to the third sub-season (Figure 2; plant core group in the upper part of each matrix). Therefore, plant core size was not proportional to 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 (Supplementary Figure S5). Yet, despite these variations at the species level, the core–periphery structure persisted over time.

Species in the core can switch their role Species roles were highly dynamic. Almost all species that were in the core at some point eventually became peripheral (except one plant and one pollinator species); however, most peripheral species never became part of the core (52% for plants, 72% for pollinators; see Figure 4). Thus, only a subset of species were ever part of the core, but virtually no species played that role persistently through time.

There was a positive correlation between overall species presence (i.e. the number of sub-seasons a species 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 and Supplementary Figure S6). Furthermore, for plant species for which we have abundance data, we observed that their abundance tended to be higher when they are in the core than when they are peripheral (Supplementary Figure S7). Finally, contrary to our expectation, species role switching was unrelated with changes in assembly structure (Supplementary Figure S8).

Discussion

Our analysis of the temporal dynamics of a plant–pollinator network using dynamic stochastic block models revealed a core–periphery structure persistent through seasons and years. This structure was maintained despite 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; in turn, interactions among core species tended to be more symmetric, albeit with weaker dependences. These findings are in line with those of previous studies showing that plant–animal mutualistic networks exhibit a nested structure (Bascompte *et al.*, 2003) persistent over the years (Petanidou *et al.*, 2008; Chacoff *et al.*, 2018). Nestedness has been shown to be related to core–periphery structure (Lee, 2016), and is characterized by a core of highly connected generalist species and many peripheral species connected asymmetrically to the generalist species in the core (Bascompte *et al.*, 2003; Vázquez & Aizen, 2004; Bascompte *et al.*, 2006). The observed core–periphery structure is also related to modularity (another structural feature frequent in plant–pollinator networks; Olesen *et al.*, 2007), in that we detected the persistent presence of a cohesive module (the core). Thus, our results suggest that the studied network exhibits a temporally persistent structure that is both nested and modular.

The novelty of our methodological approach allowed us to examine species role switching

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with unprecedented accuracy. In contrast to the observed persistence of the core-periphery structure, we found that species roles are highly dynamic: virtually all species that played a core role in some seasons were also peripheral in other seasons, while many other species remained always peripheral. In other words, although the core–periphery structure persists over time, the taxonomic identity of the core changes drastically through seasons and years, and no species can be identified as playing permanently a core role. Thus, the plant–pollinator network studied here exhibited an enormous temporal variation not only in the occurrence of interactions, as documented by previous studies (Petanidou *et al.*, 2008; CaraDonna *et al.*, 2017; Chacoff *et al.*, 2018), but also in the network roles played by interacting species.

The latter finding has far-reaching practical implications, as the idea of focusing management and conservation efforts on a small subset of species at the network core (Fleishman *et al.*, 2002, 2007; Hegland *et al.*, 2010; Chacoff *et al.*, 2012; García-Algarra *et al.*, 2017) may be difficult to achieve, given that no species play that role consistently over time in the long run. 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. In fact, as we have shown, only a small fraction of species found in the core of the network at a given time are actually found consistently at the network core through seasons and years. Therefore, it is unlikely that a single static characterization of an ecological network could reveal its true core species. In contrast, our results suggest that the identification of core species as candidates for management actions requires allocating a greater sampling effort into capturing the temporal dynamics of ecosystems, although this practice could imply relaxing efforts into capturing detailed community structure and detection of very rare species, which which are unlikely to be part of the network core. That said, our findings do indicate that certain species are likely to be found playing a key role as part of the network core in most seasons and years, which would make them adequate targets for conservation efforts. Plant species in this group include *Condalia microphilla*, *Larrea divaricata*, *Prosopis flexuosa* and *Zuccagnia punctata*, all of which had been identified in a previous study as part of the network core of the nested network constructed based on four years of data (Chacoff *et al.*, 2012). Likewise, flower visitors in this group included *Apis mellifera*, *Augchloropsis* sp., *Bombus opiphex*, *Centris brethesi*, *Copestylum aricia*, and *Xylocopa atamisquensis*, which had again been identified in the same study (Chacoff *et al.*, 2012) as part of the core of the nested network.

To conclude, we have attempted to assess the temporal dynamics of the structure of a plant–pollinator network using a novel agnostic method that allows detecting multiple classes of structures in systems with high species and interaction turnover through time. These results are intriguing, and 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 roles. Yet, we believe we have only scratched the surface of the temporal dynamics of ecological networks. Future studies should apply the methods used here to analyze other datasets, to assess the generality of our findings.

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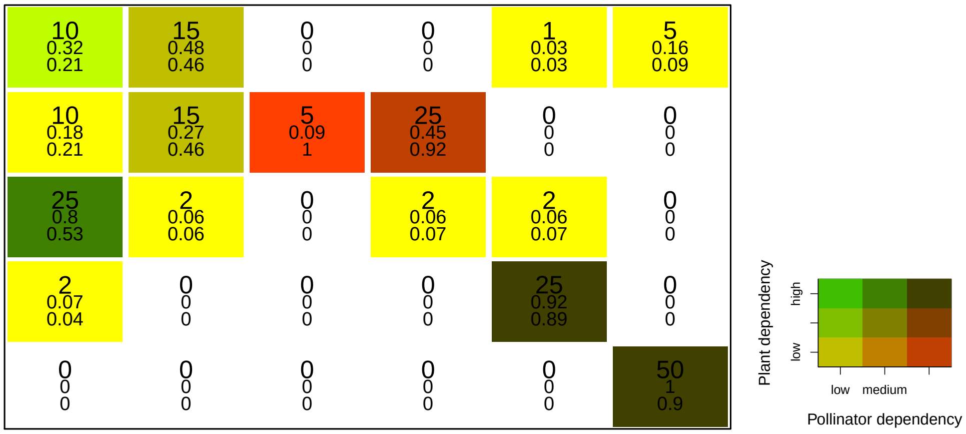

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25 0.8 0.53	2 0.06 0.06	0 0 0	2 0.06 0.07	2 0.06 0.07	0 0 0
2 0.07 0.04	0 0 0	0 0 0	0 0 0	25 0.92 0.89	0 0 0
0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	50 1 0.9

Figure 1: Representation of a dependence network between 5 plants (rows) and 6 pollinators (columns). Each cell is colored according to the legend and filled with the number of visits, the plant and pollinator dependence values D_{ij} and D_{ji} successively. The legend shows the color code accounting for the two dependence values for any species pair (i, j) (the greener, the higher the plant dependence; the more red, the higher the pollinator dependence). This example shows the advantage of studying dependence values instead of raw 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).

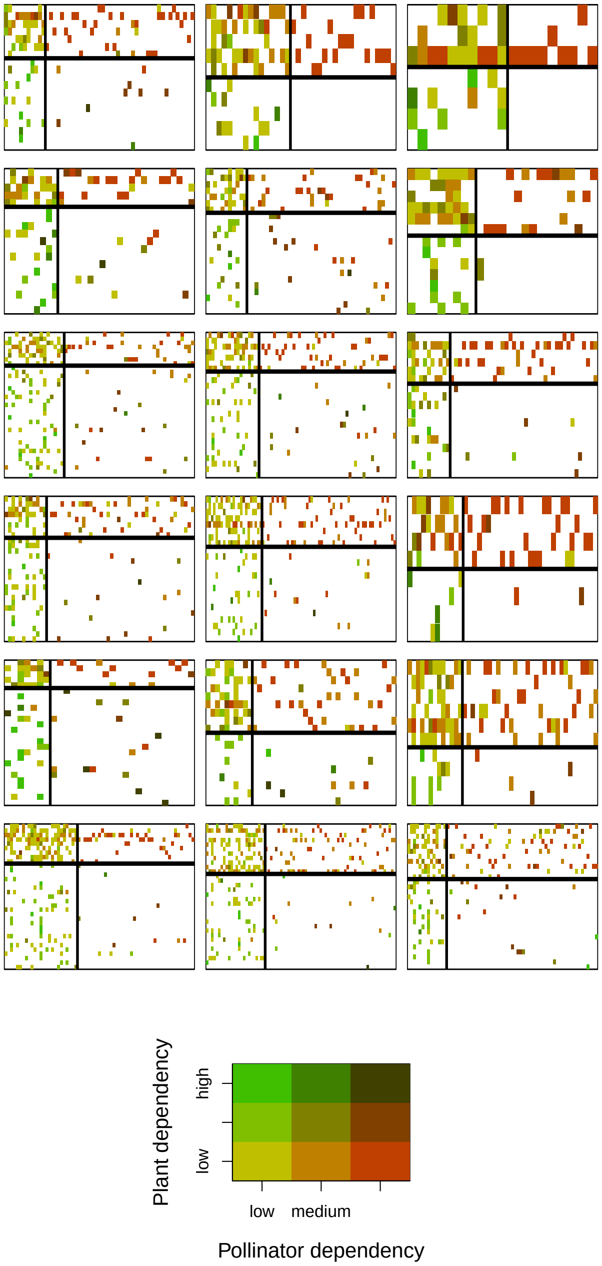

Figure 2: Representation of the 18 dependence networks into colored matrices. For any matrix, each cell represents the plant and pollinator dependence values between any species of plants (rows) and pollinators (columns), with a color computed as a mixture of the two dependence values according to the legend. Rows and columns were reorganized according to the dynSBM group membership: dark lines separating each matrix delineate the group boundaries (first/second group of plants above/below the horizontal line; first/second group of pollinators on the left/right of the vertical line).

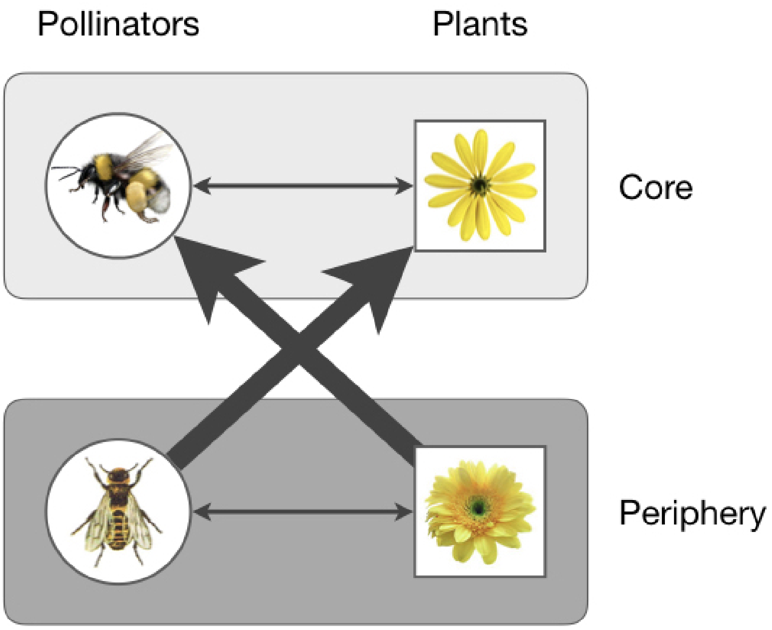

Figure 3: Graphical representation of the core-periphery structure found in our dynamic plant-pollinator network. Arrows depict dependences of one species (arrow origin) on another (arrow tip). Arrow widths are proportional to typical dependence values between groups. Pollinators/plants of the network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

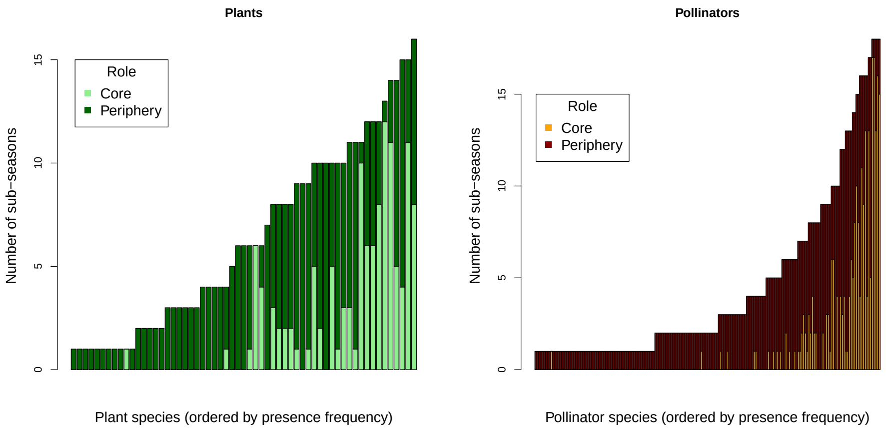

Figure 4: Species'role shifts and temporal occurrence. Each stacked bar (one by species) represents the number of sub-seasons any species was found in the core (light color) or in the periphery (dark color). Bars were ranked according to the number of sub-seasons any species was observed and present in the network. For plants (left) and pollinators (right).