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Network analysis of phenological units to detect important species in plant-pollinator communities: can it inform conservation strategies?
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Network analysis of phenological units to detect important species in plant-pollinator communities: can it inform conservation strategies?

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Abstract:	Conservation of species is often focused either only on those that are endangered, or on maximising the number recorded on species lists. However, species share space and time with others, thus interacting and building frameworks of relationships that can be unravelled by community-level network analysis. It is these relationships that ultimately drive ecosystem function via the transfer of energy and nutrients. However interactions are rarely considered in conservation planning. Network analysis can be used to detect key species ("hubs") that play an important role in cohesiveness of networks. We applied this approach to plant-pollinator communities on two montane Northern Apennine grasslands, paying special attention to the modules and the identity of hubs. We performed season-wide sampling and then focused the network analyses on time units consistent with plant phenology. After testing for significance of modules, only some modules were found to be significantly segregated from others. Thus, networks were organized around a structured core of modules with a set of companion species that were not organized into compartments. Using a network approach we obtained a list of important plant and pollinator species, including three Network Hubs of utmost importance, and other hubs of particular biogeographical interest. By having a lot of links and high partner diversity, hubs should convey stability to networks. Due to their role in the networks, taking into account such key species when considering the management of sites could help to preserve the greatest number of interactions and thus support many other species.

Network analysis of phenological units to detect important species in plant-pollinator communities: can it inform conservation strategies?

Running title: Conservation of hubs in interaction networks

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ABSTRACT

Conservation of species is often focused either only on those that are endangered, or on maximising the number recorded on species lists. However, species share space and time with others, thus interacting and building frameworks of relationships that can be unravelled by community-level network analysis. It is these relationships that ultimately drive ecosystem function via the transfer of energy and nutrients. However interactions are rarely considered in conservation planning. Network analysis can be used to detect key species ("hubs") that play an important role in cohesiveness of networks. We applied this approach to plant-pollinator communities on two montane Northern Apennine grasslands, paying special attention to the modules and the identity of hubs. We performed season-wide sampling and then focused the network analyses on time units consistent with plant phenology. After testing for significance of modules, only some modules were found to be significantly segregated from others. Thus, networks were organized around a structured core of modules with a set of companion species that were not organized into compartments. Using a network approach we obtained a list of important plant and pollinator species, including three Network Hubs of utmost importance, and other hubs of particular biogeographical interest. By having a lot of links and high partner diversity, hubs should convey stability to networks. Due to their role in the networks, taking into account such key species when considering the management of sites could help to preserve the greatest number of interactions and thus support many other species.

INTRODUCTION

Plant–pollinator interactions play a key functional role in ecosystems because they both facilitate the reproduction of plant species across generations (Ollerton et al. 2011) and also provide direct and indirect opportunities for animal feeding. However, these mainly mutualistic interactions could be disrupted by a range of factors including climate change (e.g. Hegland et al. 2009), land use alteration and changes in agriculture practices (e.g. Ollerton et al. 2014), lack of flower diversity, and increasing pathogens and pesticides (e.g. Goulson et al. 2015). It is likely that such factors are also threatening the pollination services provided (Tylianakis et al. 2010).

Baseline conservation assessments that include listing species diversity and/or the presence of endangered taxa in a given locality is a good first approximation. Nevertheless species exist within a network of interactions with other species, and these interactions themselves are also in need of conservation (Janzen 1974; Tylianakis et al. 2010). Focusing on complex networks where nodes (i.e. species) are connected by functional links such as herbivory, predation, seed dispersal and pollination, allows ecologists to understand the super-structure of these communities (e.g. modules of interacting species Olesen et al. 2007; Watts et al. 2016).

The idea of conserving of interactions is rather old (Janzen 1974), but in practice it has not yet been clarified how it should take place. Ecologists have suggested a number of network features that could be helpful to conservation biologists (Corbet 2000; Tylianakis et al. 2010; Kaiser-Bunbury and Blüthgen 2015). Their arguments mainly rely on (a) the ease of performing network analyses (Tylianakis et al. 2010; Kaiser-Bunbury and Blüthgen 2015), (b) a supposed relation between network indexes and stability/robustness against perturbations (Bascompte et al. 2006; Tylianakis et al. 2010; Santamaría et al. 2016), (c) the possibility of investigating species functional roles (niche) through interactions (Kaiser-Bunbury and Blüthgen 2015), (d) the relationship between a network's species diversity, link distributions among species, and the classical relationship of diversity with stability and with functionality (Kaiser-Bunbury and Blüthgen 2015). Therefore, network analyses have been suggested to be useful, but mainly for monitoring purposes (Tylianakis et al. 2010), such as checking an ecosystem's functioning after the restoration of a degraded habitat (Kaiser-Bunbury and Blüthgen 2015). However, conservation goes beyond just monitoring, but the ways in which network analyses could be further helpful for conservation are not presently clear.

The value of using a network approach to understand and conserve plant-pollinator interactions is hampered by both a limited geographic perspective (there are still large parts of the world that have never been studied) and the temporal resolution of most studies. Network ecologists have traditionally studied cumulative networks over long-periods of sampling, treating all interactions as simultaneous in their analysis. Alternatively, a single short period of sampling has been chosen as representative of the peak activity of the community, or because a target species is active. Either approach results into an over-simplified view because species in a community are dynamic both as to when they come into activity and how long they are active. More recent studies have divided the season into a-priori blocks of time of the same length, e.g. monthly (Basilio et al. 2006), every two-weeks (Kaiser-Bunbury et al. 2010), or even daily (Rasmussen et al. 2013). Nevertheless such seasonal units are chosen arbitrarily and again there is a risk of obscuring the effects of species' phenology.

In this study we aimed to assess how conservation practitioners could (1) define reliable seasonal units compatible with phenology; (2) interpret the structure of ecological networks and thus obtain insights on ecosystem functioning; (3) identify key species (hubs) and their features, that could possibly be the target of specific conservation actions, due to the role played by them in supporting others species by both direct and indirect interactions (Guimerà et al. 2007). We investigated the feasibility of these aims using season-wide sampling of flower visitors performed on two montane semi-dry grasslands differing in species composition in the Northern Apennine (Italian Peninsula). This work is the first of its type on such a southern European mountain chain.

METHODS

Study area

Sampling took place at 1650 m altitude on two semi-dry grasslands in the Montane altitudinal belt of Mt. Lesima (1724 m a.s.l., 44°41'6" N 9°15'26" E, Northern Apennine, Fig. 1) which subjected to different anthropogenic pressure and characterized by different plant composition despite being spatially adjacent (Barcella 2013). In the current study, *Sesleria pichiana - Laserpitium siler* community occurs on steep slopes with N-E exposure and not grazed; and the other, *Brachypodium rupestre - Festuca laevigata* community occurs on S-W slopes and is cattle grazed during the second half of the summer. According to Barcella (2013), both plant communities are important habitats for biodiversity as they belong to the Habitat 6210* of Natura 2000 Network ("semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*) (*important orchid sites)"). Neighbouring areas at lower altitudes are dominated by forests of the beech series *Trochiscantho nodiflori – Fago sylvaticae sigmetum* (Verde et al. 2010). The area surrounding the mountain has 1250–1500 mm average rainfall, 5 °C mean annual temperature and Temperate Oceanic Submediterranean bioclimate (Barcella 2013).

Data collection

The sampling design was based on three fixed plots of 2.5 x 2.5 m in each plant community during the summer season 2013. Each sampling plot was placed inside the area used to classify the vegetation in a previous study (Barcella 2013). In each plot, the insects visiting flowers and touching plant reproductive structures were captured with a net but without damaging the plants and put in labelled jars. Plots were sampled weekly, twice each sampling day, for 20 minutes each time. During each sampling day the starting plot was chosen at random. During the last three sampling dates, the *Brachypodium rupestre - Festuca laevigata* community was damaged by intense grazing (no plants in flower were present). Therefore, three new plots were defined in less damaged spots inside the same plant community.

Both plants and insects were recorded to species level in most cases. When such detail was impossible to reach due to difficult identification or unavailability of taxonomists, morpho-species were used for plants, such as *Ranunculus* spp. and *Galium* spp., and some specimens of Diptera, Hymenoptera: Ichneumonidae, and Lepidoptera: Micropterigidae.

At each date, the pollination units of each flowering species were counted inside the sampling plots. To do so, we considered both the arrangement of the single flower within an inflorescence and also pollinator behavior (Faegri and van der Pijl 1979). In detail, pollination unit was considered as the whole inflorescence if flowers were organized in a dense cluster with flowers opening sub-simultaneously, so that a medium-size insect pollinator would not need to fly between successive visits; pollination unit was the single flower if flowers were very separated within an inflorescence and had unsynchronized anthesis, so that a pollinator would have to fly between visits.

The two grasslands were different as regards richness of species within plant families, pollination-unit abundance and insect visits (Appendix Table A1, Appendix Figure A1).

Data Analysis

Detection of phenological units

In each community, the flowering phenology was analyzed in order to identify time-units of plants flowering together, here called a “pheno-cluster”. We independently developed an approach similar to Fantinato et al. (2016). For each species, the number of pollination units (defined above) was calculated on each date to give the sequence of pollination units being produced over time. Pairwise Spearman correlations between the number of pollination units per date for each species was then performed. Once two or more species were significantly correlated with each other (but not with other species), a new sequence representative of the correlated species was obtained by computing the mean value of their pollination-units on each date. The newly created variables were included in a Cluster Analysis with Bray-Curtis Similarity Index to detect pheno-clusters. The significance of the obtained pheno-clusters was tested by means of one-way PERMANOVA using the Bray-Curtis index of similarity (Anderson 2001), that is based on the formula $d_{jk} = 1 - \frac{\sum_i |x_{ji} - x_{ki}|}{\sum_i (x_{ji} + x_{ki})}$, where x_{ji} (and x_{ki}) are counts of species x_i in the sample j (and k). The PAST 2.17 statistical software was used (Hammer et al. 2001).

Detection of modules

In each pheno-cluster, quantitative interaction matrices were analysed to detect modules, defined as groups of species that share most of the interactions. Quantitative matrices included count data, i.e. the number of individuals per insect species visiting a given plant species, as suggested by Reitan and Nielsen (2016). The interacting species were re-arranged according to the QuanBiMo algorithm in the R package Bipartite v.2.03 (Dormann et al. 2016). This algorithm develops a hierarchical dendrogram with species more likely to interact being grouped together. It optimises the outcome by random swaps of the branches with a Simulated Annealing Monte Carlo approach and by evaluating whether the newly swapped graph would be more likely than the former one.

There are a number of ways to test the species composition and significance of modules (e.g. Martín González et al. 2012; Pozsgai et al. 2015). In our work, we followed Martín González et al. (2012), using the number of individuals per insect species visiting a given plant species as quantitative variable and modules as groups with a one-way PERMANOVA applying the Bray-Curtis Similarity Index (Anderson 2001). PAST 2.17 statistical software was used (Hammer et al. 2001).

Network analysis

For each pheno-cluster, network analysis was performed on quantitative interaction matrices (see above) to obtain the following network-level indexes: [1] Connectance C is the proportion of realized links, calculated as $C = L/(I \times J)$, where L is the number of interactions, I and J is the number of plant and animal species, respectively, and can vary from 0 to 1 (Blüthgen et al. 2006); Despite its long use in network analysis, Connectance is moderately sensitive to sampling effort (Rivera-Hutinel et al. 2012). Mainly for this reason, Connectance appears to be less efficient in describing networks than other more robust indexes. [2] Interaction Diversity $H_2{}'$ is a measure of generalization of network-level interactions independent to network size (Blüthgen et al. 2006). It is based on the two-dimensional Shannon entropy, which is computed as $H_2 = -\sum_{i=1}^{r}\sum_{j=1}^{c}(p_{ij} \times \ln p_{ij})$, where *r* and *c* refers to rows and columns of a contingency table of interactions between a plant species *i* and pollinator species *j*, and p_{ij} is the proportion of interactions in relation to the respective row total (Blüthgen et al. 2006). Its possible maximum and minimum are obtained from the distribution of interaction totals of the matrix. H_2' ranges between 0 (no specialization) and 1 (perfect specialisation), and it is calculated as follows $H_2' = \frac{H_{2max} - H_2}{H_{2max} - H_{2min}}$ (Blüthgen et al. 2006); [3] Modularity Q for weighted matrices with the QuanBiMo algorithm (Dormann and Strauss 2014), a measure of module-belonging, namely the species strength of being connected within a module. It is computed as follows $Q = \frac{1}{2m} \sum_{ij} \left(A_{ij} - K_{ij}\right) \delta\left(g_i, g_j\right)$, where $m = \sum_{i,j} A_{ij}$, K_{ij} refers to the marginal totals for rows and columns of a weighted interaction matrix A_{ij}, g is a given module to which species *i* (or *j*) is assigned to (Dormann and Strauss 2014). Q ranges from 0 to 1, the higher its value, the more segregated into modules is the network (Dormann and Strauss 2014). Due to its variation with network size, the Modularity index was checked for significance following Dormann and Strauss (2014) by comparing the observed value with standardized z-scores of 100 quantitative null model expectations generated with *r2dtable* algorithm. For the computation of the above-mentioned indexes [1]-[3], the R package *bipartite* v.2.03 was used. Finally, [4] Nestedness based on Overlap and Decreasing Fill (NODF, Almeida-Neto et al. 2008) was computed using the software ANINHADO (Guimarães and Guimarães 2006). This metric is based on two properties: decreasing fill and paired overlap. In brief, in a matrix with n rows and m columns, it detects the degree of nestedness (N_p) between pairs of columns and pairs of rows by comparing the marginal totals ("decreasing fill") and the percentage of filled (≠0) matrix cells which are located at the same position ("paired overlap"), $NODF = {\sum N_p} \Big/ \left[\frac{n(n-1)}{2}\right] + \left[\frac{m(m-1)}{2}\right]$. It ranges from zero (un-nested) to 100 (fully nested). The statistical significance of NODF was tested using 1000 random binary null models built by the *ER* algorithm, in which the presence or absence of interactions are randomly assigned.

Key species

The standardized among-module connectivity (c-values) and within-module degree (z-values) were computed at a species level for each pheno-cluster. [5] The c-values are a measure of the contribution of a species in connecting species of the other modules, calculated as $c = 1 - \sum\left({k_{is}}/{k_i}\right)^2$, where k_{is} is links number of species i to other species in module s, and k_i is its total amount of links (Guimerà and Nunes Amaral 2005); [6] the z-values are a measure of the contribution of a species in connecting species of the same modules, calculated as $z = {k_{it} - \bar{k}_{t_i}}/{\sigma_{k_{t_i}}}$, where k_{it} is links number of species i to species within its own module t, $\bar{k}_{t_i}$ is the links average of all species of module t and $\sigma_{k_{t_i}}$ is its standard deviation (Guimerà and Nunes Amaral 2005). To detect key species, critical thresholds were found as 95% quantiles of null model distributions for c and z values, as shown by Dormann and Strauss (2014), computed from the 100 quantitative null models used to test the significance of Modularity Q [3].

Relationships between hubs and species diversity

In order to relate both the among-module connectivity ([5] c- values) and the within-module participation ([6] z-values) with species-specific features, a PCA ordination was performed on the c- and z- values of insect species. We focused only on insects because, unlike the plants, they were present in all levels of the hubs hierarchy (see Table 2). This ordination was tested for a *post-hoc* correlation (and its significance tested after 10000 permutations) with the following species-specific features: [7] degree N, that is the (normalized) number of links per species; [8] the Specialization index d', that is the species-specific counterpart of H_2' and recalls the Kullback-Leibler distance $d_i = \sum_{j=1}^{c} (p'_{ij} \ln\frac{p'_{ij}}{q_j})$. For a species i, this index compares p'_{ij}, the proportion of interactions (with a partner j) considered in relation to the respective row total, with q_j, the partner j availability obtained as proportion of all its interactions in relation to the total number of interactions. Then, d' is the standardization between the possible maximum and minimum of d_i (Blüthgen et al. 2006); [8] per-species Shannon diversity, that provides a measure of partner diversity for each species (Kaiser-Bunbury and Blüthgen 2015) calculated as $H = -\sum_{i=1}^{S} p_i \log_b p_i$, where p_i proportion of interactions for a species i and S is the number of species. The PCA and *post-hoc* correlation were performed in the R package *vegan* v. 2.3, and the computation of the above-mentioned indexes [5]-[8] was performed in the R package *bipartite* v.2.03.

RESULTS

Topology of plant-pollinator networks

The *Sesleria pichiana - Laserpitium siler* community had a higher number of interactions and greater species richness (1677 interactions, 34 plant species of 14 families and 145 insect species of 8 orders, 44 families, morpho-species included). In contrast, the *Brachypodium rupestre - Festuca laevigata* community was poorer (323 plant-pollinator interactions, 29 plant species of 16 families and 76 species of insects of 5 orders, 30 families, morpho-species included).

Sesleria pichiana - Laserpitium siler community was organized into three pheno-clusters (PCs): (1) an initial short one of 2 weeks; (2) a longer central phase of 5 weeks; and (3) a final one of 2 weeks ($F_{PC1\text{-}PC2} = 3.64$, $p_{PC1\text{-}PC2} < 0.05$; $F_{PC2\text{-}PC3} = 3.72$, $p_{PC2\text{-}PC3} < 0.05$). In *Brachypodium rupestre - Festuca laevigata* community, 2 significant pheno-clusters of respectively 5 and 4 weeks were identified ($F_{PC1\text{-}PC2} = 5.61$; $p_{PC1\text{-}PC2} < 0.01$).

A network analysis was performed on species interacting within the same pheno-cluster (Fig. 2). Connectance and Nestedness were low in the networks. However, all network indexes varied highly between pheno-cluster (Table 1).

Modules of interacting species

A low number of modules was detected by the QuanBiMo algorithm, with a mean of 4.4 modules per pheno-cluster.

After testing for pair-wise significance of such modules, we found that several ones were not significantly distinct from the others (Appendix Table A2). Within significant modules, we detected recurrent members defined taxonomically, as follows. *Bombus* spp. (Hymenoptera: Apidae) visited mainly Fabaceae and Lamiaceae plants. Such modules could be called "Large-Apidae". A long array of insect species of many groups (Diptera, but also fewer Hymenoptera, Lepidoptera and Coleoptera) interacted with few plant species (e.g. Asteraceae, Apiaceae, Rosaceae, Ranunculaceae). Such latter modules could be called "Wide-core". The remaining species would belong to a "Mixed-composition" interacting group.

Among-module and within-module key species

Species values of among-module connectivity (c-values) and within-module participation (z-values) for pollinators and plants of both communities are shown in Fig. 3. Only a minor fraction of species is detectable. The taxonomic identities of key species are listed in Table 2. Following the categories given in Olesen et al. (2007), only insect species fitted the categories of "Network-Hub" (both high c- and z-values) and "Connectors" (high c-values). Instead, both insects and plants fitted the category of "Module-Hub" (high z-values). The remaining majority of species had both low c- and z-values and they were therefore categorized as "Peripherals". Finally, some species were multiple hubs as their role as key species changed depending on the phenological unit or on the community.

Relationships between hubs and species diversity

The PCA ordination axes explained species c- and z- values (PC1=92%, PC2=2.3%). Such ordination axes were highly correlated with species links number N ($r^2 = 0.57$, $p < 0.001$) and partner diversity ($r^2 = 0.63$, $p < 0.001$), while they were moderately correlated with species-level specialization d' ($r^2 = 0.13$, $p < 0.001$). The ordination biplot (Fig. 4) shows that specialization is mainly related to z values, while partner diversity and links tend to be more related to c values.

DISCUSSION

Ecology of montane plant-pollinator networks

Montane ecosystems have received low attention from network ecologists even though altitude affects many factors that would influence foraging strategies and thus the communities (Miller-Struttmann and Galen 2014; Watts et al. 2016). Despite that, it is possible to list some recurrent features. Variation of networks along altitudinal gradients might be due to the higher rate at which insect richness decreases (Viterbi et al. 2013) compared to that of flowers (Olesen and Jordano 2002). Accordingly, flower visitation has been found to decline along altitudinal gradients (Zhao et al. 2016), e.g. by over 50% between the lower and the upper alpine belts (Arroyo et al. 1985). As a result of these patterns, Connectance also progressively decreases with altitude (Olesen and Jordano 2002).

Our networks were rather variable between pheno-clusters (Fig. 2, Table 1). Generally, Connectance varied from low to medium levels of the typical range of altitudinal networks, the maximum value recorded at altitudes higher than 1500 m a.s.l. being about 0.3 (Olesen and Jordano 2002). Despite that, some links overlap between species, as given by the index H_2'. Therefore, the ecological strategy of these networks swings between low and medium levels of generalization. At least a proportion of species is generalist and high-altitude pollination networks have not shown high specialization so far (Dupont et al. 2003; Fang and Huang 2012; Watts et al. 2016).

At higher elevations, the network nestedness decreases (Ramos-Jiliberto et al. 2010). Our networks also exhibited low levels of nestedness. The ecological interpretation of this is that (a) altitudinal systems may be relatively fragile, assuming that network stability is increased by nestedness (Burgos et al. 2007); and (b) few species cover key roles in the network ("hub") (Jordano et al. 2006). In fact, key species were detected in rather low numbers in our systems (Fig. 3).

Relationships between hubs and species diversity

Network nodes within a given module are made more connected by Module Hubs, which would be those ones sharing most of the interactions with other species of the same module (Martín González et al. 2010). In turn, Connectors share many links among various modules, thus connecting several compartments of the network (Guimerà and Nunes Amaral 2005). Network Hubs maximize both the within-module and the among-module connectivity (Olesen et al. 2007). Therefore, a hierarchy of important species can take place: within-module level, between-modules level or entire-network level. Without a network approach, this is an aspect of community ecology that would be undetected.

Our hubs are a rather diverse set of species from different families (Table 2). However, being-a-Hub is related to some species-level features. Specialization index d' appears to be more related with z- values rather than with c-values (Fig. 4). This highlights that Module Hubs tend to be less generalist than other Hub types, as some interactions occur only within modules. Instead, higher-level Hubs link among various modules, with the result that they are more generalist.

As z- and c- values were highly correlated with partner diversity and degree, hubs have a high number of partners and links. This matches other pollination networks, in which hubs interact with about half of the visiting species (Martín González et al. 2010). Moreover, higher partner diversity of a Hub has been related to wider resource/partner usage (Kaiser-Bunbury and Blüthgen 2015). This relates hubs to the classical stability view on species diversity, as wider resource usage decreases the need for specific resources to survive (Kaiser-Bunbury and Blüthgen 2015). Such diversity also relates to the functionality of the system and in fact when hubs are selectively removed, networks break down faster than removing random nodes (Albert et al. 2000; Jeong et al. 2001). So, empirical evidence clearly shows that Network Hubs provide stability to the entire system, with also moderate contribution of Connectors (Reis et al. 2014), while the loss of Module Hubs is likely to result in module fragmentation. Therefore, it is clear that the cohesiveness of the system is provided by such a hierarchy (Olesen et al. 2007).

Modules of interacting species

Instead of species tightly enclosed into modules, as commonly found (Olesen et al. 2007; Martín González et al. 2012; Larson et al. 2014) we obtained a more variable structure. The networks of our study showed an unorganized plethora of companion nodes, such as the species in non-significant modules, interacting with a well-structured core, the significant "Large-Apidae" and "Wide-Core" modules. Such a core would be consistent in time despite the year-to-year turnover of species in the networks and its taxonomic composition also matches other temperate altitudinal systems (Fang and Huang 2012).

Why phenological units are useful

Within each plant community, we obtained independent networks that resulted from the detection of phenological units. Previously, network ecologists have typically overlooked the time component (but see Valverde et al. 2016), though more recent studies have divided the season into a-priori time periods of the same length (Basilio et al. 2006; Kaiser-Bunbury et al. 2010; Rasmussen et al. 2013). On one hand, the latter is a useful approach in order to shed light on the dynamics of systems across time. On the other hand, the risk of obscuring species' phenologies might take place and it might also affect the independency of each unit. Therefore, phenological units are useful to network analyses at least for three reasons. Firstly, such an approach is consistent with the phenology of species, as they have strong effects on interaction networks (Martín González et al. 2012; Valverde et al. 2016). Secondly, it might be useful to replicate networks in time instead of in space in order to obtain independent plant-pollinator networks from a low number of sites. Thirdly, applied to conservation, it allows one to monitor the entire season, and thus identify key species consistently with seasonal dynamics.

CONCLUSIONS

In this study three insect species were shown to be important for the entire network by being Network Hubs: *Bombus rupestris* (Hymenoptera: Apidae), *Micrinus heteromorphus* (Coleptera: Malachiidae) and *Eristalis tenax* (Diptera: Syrphidae). Moreover, four important taxa were also distinctive from a biogeographical perspective, being Alps endemics occurring out of the known range (the above mentioned Malachiidae) or South-European orophytes occurring only in specific sectors of the Alps and Apennines where they are not present together (*Phyteuma ovatum*, *Phyteuma scorzonerifolium* and *Hypericum richeri*). They might be considered for conservation for their double role under both network and biogeographical perspectives, as also suggested by Paraskevopoulou et al. (2015) in benthic networks. Thus, some species, either common or regionally rare, might turn out to be important for the conservation of other species. Some of the identified hubs could need specific protection, perhaps according to their life histories or known threats (Corbet 2000; Kaiser-Bunbury and Blüthgen 2015).

As suggested by Corbet (2000), conserving networks would necessarily imply that we (a) indentify the modules; (b) indentify the hubs that sustain them; (c) assess their vulnerability. In these terms, previous work has successfully identified those invasive species that should be management priorities by sharing the interaction module with a rare native species of conservationist interest (Larson et al. 2014). Therefore, practitioners should consider species not only as mere lists but also view them within the framework of their interactions, and the work of Larson et al. (2014) provides a good example of its application and feasibility.

As we found that some modules are not reliable units, we also suggest that conservation of networks should not only focus on modules but should consider identifying the whole hierarchy of hubs (not only those of the modules).

Network analyses are useful for monitoring robustness and ecosystem functioning. Given the role played by phenology in the interactions, the entire season should be studied in order to cover the seasonal dynamics; in this work we showed how to deal with such a task, namely identifying reliable seasonal units. Moreover, it could also inform the conservation of habitats by helping the planning and scheduling of specific management actions. This may be particularly important when key plant or insect species are subjected to disturbance through inappropriate habitat management such as grazing and mowing at the wrong time (Tarrant et al. 2013).

ACKNOWLEDGEMENTS

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REFERENCES

Albert, R., H. Jeong, and A. L. Barabasi. 2000. Error and attack tolerance of complex networks. *Nature*. 406: 378–382.

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. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* 26: 32–46.

Arroyo, M. T. K., J. J. Armesto, and R. B. Primack. 1985. Community studies in pollination ecology in the high temperate Andes of central Chile II. effect of temperature on visitation rates and pollination possibilities. *Plant Syst. Evol.* 149: 187–203.

Barcella, M. 2013. *Montane grasslands of the Northern Apennine: syntaxonomy, synchorology, sinecology, pasture analysis and pasture modeling - Unpublished PhD thesis*. Università di Pavia.

Bascompte, J., P. Jordano, and J. M. Olesen. 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*. 312: 431–433.

Basilio, A. M., D. Medan, J. P. Torretta, and N. J. Bartoloni. 2006. A year-long plant-pollinator network. *Austral Ecol.* 31: 975–983.

Blüthgen, N., F. Menzel, and N. Blüthgen. 2006. Measuring specialization in species interaction networks. *BMC Ecol.* 6: 9.

Burgos, E., H. Ceva, R. P. J. Perazzo, M. Devoto, D. Medan, M. Zimmermann, and A. María Delbue. 2007. Why nestedness in mutualistic networks? *J. Theor. Biol.* 249: 307–313.

Corbet, S. A. 2000. Conserving compartments in pollination webs. *Conserv. Biol.* 14: 1229–1231.

Dormann, C. F., J. F. and B. Gruber, with additional code from M. Devoto, J. Iriondo, R. S. and D. Vazquez, N. Blüthgen, and A. C. S. and M. Rodriguez-Girones. 2016. *bipartite: Visualising Bipartite Networks and Calculating Some (Ecological) Indices*.

Dormann, C. F., and R. Strauss. 2014. A method for detecting modules in quantitative bipartite networks. *Methods Ecol. Evol.* 5: 90–98.

Dupont, Y. L., D. M. Hansen, and J. M. Olesen. 2003. Structure of a plant–flower-visitor network in the high-altitude sub-alpine desert of Tenerife, Canary Islands. *Ecography*. 26: 301–310.

Faegri, K., and L. van der Pijl. 1979. *The principles of pollination ecology*. Pergamon Press.

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.

Fantinato, E., S. Del Vecchio, A. Slaviero, L. Conti, A. T. R. Acosta, and G. Buffa. 2016. Does flowering synchrony contribute to the sustainment of dry grassland biodiversity? *Flora - Morphol. Distrib. Funct. Ecol. Plants*. 222: 96–103.

Goulson, D., E. Nicholls, C. Botías, and E. L. Rotheray. 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*. 347: 1255957.

Guimarães, P. R., and P. Guimarães. 2006. Improving the analyses of nestedness for large sets of matrices. *Environ. Model. Softw.* 21: 1512–1513.

Guimerà, R., and L. A. Nunes Amaral. 2005. Functional cartography of complex metabolic networks. *Nature*. 433: 895–900.

Guimerà, R., M. Sales-Pardo, and L. A. N. Amaral. 2007. Classes of complex networks defined by role-to-role connectivity profiles. *Nat. Phys.* 3: 63–69.

Hammer, Ø., D. A. T. Harper, and P. D. Ryan. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Paleontol. Electrónica*. 4: 1–9.

Hegland, S. J., A. Nielsen, A. Lázaro, A.-L. Bjerknes, and Ø. Totland. 2009. How does climate warming affect plant-pollinator interactions? *Ecol. Lett.* 12: 184–195.

Janzen, D. H. 1974. The deflowering of Central America. La deforestación de Centroamérica. *Nat. Hist.* 83.

Jeong, H., S. P. Mason, A.-L. Barabási, and Z. N. Oltvai. 2001. Lethality and centrality in protein networks. *Nature*. 411: 41–42.

Jordano, P., J. Bascompte, and J. M. Olesen. 2006. The ecological consequences of complex topology and nested structure in pollination webs. In N.M. Waser and J. Ollerton (eds.), *Plant-pollinator interactions: from specialization to generalization*. University of Chicago Press, Chicago. pp. 173–199.

Kaiser-Bunbury, C. N., and N. Blüthgen. 2015. Integrating network ecology with applied conservation: a synthesis and guide to implementation. *AoB Plants*. 7: plv076.

Kaiser-Bunbury, C. N., S. Muff, J. Memmott, C. B. Müller, and A. Caflisch. 2010. The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. *Ecol. Lett.* 13: 442–452.

Larson, D. L., S. Droege, P. A. Rabie, J. L. Larson, J. Devalez, M. Haar, and M. McDermott-Kubeczko. 2014. Using a network modularity analysis to inform management of a rare endemic plant in the northern Great Plains, USA. *J. Appl. Ecol.* 51: 1024–1032.

Martín González, A. M., S. Allesina, A. Rodrigo, and J. Bosch. 2012. Drivers of compartmentalization in a Mediterranean pollination network. *Oikos*. 121: 2001–2013.

Martín González, A. M., B. Dalsgaard, and J. M. Olesen. 2010. Centrality measures and the importance of generalist species in pollination networks. *Ecol. Complex.* 7: 36–43.

Miller-Struttmann, N. E., and C. Galen. 2014. High-altitude multi-taskers: bumble bee food plant use broadens along an altitudinal productivity gradient. *Oecologia*. 176: 1033–1045.

Olesen, J. M., J. Bascompte, Y. L. Dupont, and P. Jordano. 2007. The modularity of pollination networks. *Proc. Natl. Acad. Sci.* 104: 19891–19896.

Olesen, J. M., and P. Jordano. 2002. Geographic patterns in plant–pollinator mutualistic networks. *Ecology*. 83: 2416–2424.

Ollerton, J., H. Erenler, M. Edwards, and R. Crockett. 2014. Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. *Science*. 346: 1360–1362.

Ollerton, J., R. Winfree, and S. Tarrant. 2011. How many flowering plants are pollinated by animals? *Oikos*. 120: 321–326.

Paraskevopoulou, S., N. Monokrousos, I. Kappas, and T. J. Abatzopoulos. 2015. Spatio-temporal variability of benthic macrofauna in a coastal lagoon assessed by ecological interaction networks. *Community Ecol.* 16: 10–22.

Pozsgai, G., J. Baird, N. A. Littlewood, R. J. Pakeman, and M. Young. 2015. Interspecific networks in ground beetle (Coleoptera: Carabidae) assemblages. *Ecol. Indic.* 68: 134–141.

Ramos-Jiliberto, R., D. Domínguez, C. Espinoza, G. López, F. S. Valdovinos, R. O. Bustamante, and R. Medel. 2010. Topological change of Andean plant–pollinator networks along an altitudinal gradient. *Ecol. Complex.* 7: 86–90.

Rasmussen, C., Y. L. Dupont, J. B. Mosbacher, K. Trøjelsgaard, and J. M. Olesen. 2013. Strong impact of temporal resolution on the structure of an ecological network. *PLoS ONE*. 8: e81694.

Reis, S. D. S., Y. Hu, A. Babino, J. S. Andrade Jr, S. Canals, M. Sigman, and H. A. Makse. 2014. Avoiding catastrophic failure in correlated networks of networks. *Nat. Phys.* 10: 762–767.

Reitan, T., and A. Nielsen. 2016. Do Not Divide Count Data with Count Data; A Story from Pollination Ecology with Implications Beyond. *PLOS ONE*. 11: e0149129.

Rivera-Hutinel, A., R. O. Bustamante, V. H. Marín, and R. Medel. 2012. Effects of sampling completeness on the structure of plant–pollinator networks. *Ecology*. 93: 1593–1603.

Santamaría, S., J. Galeano, J. M. Pastor, and M. Méndez. 2016. Removing interactions, rather than species, casts doubt on the high robustness of pollination networks. *Oikos*. 125: 526–534.

Tarrant, S., J. Ollerton, M. L. Rahman, J. Tarrant, and D. McCollin. 2013. Grassland restoration on landfill sites in the East Midlands, United Kingdom: an evaluation of floral resources and pollinating insects. *Restor. Ecol.* 21: 560–568.

Tylianakis, J. M., E. Laliberté, A. Nielsen, and J. Bascompte. 2010. Conservation of species interaction networks. *Biol. Conserv.* 143: 2270–2279.

Valverde, J., J. M. Gómez, and F. Perfectti. 2016. The temporal dimension in individual-based plant pollination networks. *Oikos*. 125: 468–479.

Verde, S., S. Assini, and C. Andreis. 2010. Le serie di Vegetazione della regione Lombardia. In C. Blasi (ed.), *La Vegetazione d'Italia*. Palombi & Partner, Roma. pp. 53–82.

Viterbi, R., C. Cerrato, B. Bassano, R. Bionda, A. Hardenberg, A. Provenzale, and G. Bogliani. 2013. Patterns of biodiversity in the northwestern Italian Alps: a multi-taxa approach. *Community Ecol.* 14: 18–30.

Watts, S., C. F. Dormann, A. A. M. González, and J. Ollerton. 2016. The influence of floral traits on specialisation and modularity of plant-pollinator networks in a biodiversity hotspot in the Peruvian Andes Watts S, Dormann CF, González AMM, Ollerton J. *Ann. Bot.* in press.

Zhao, Y.-H., Z.-X. Ren, A. Lázaro, H. Wang, P. Bernhardt, H.-D. Li, and D.-Z. Li. 2016. Floral traits influence pollen vectors' choices in higher elevation communities in the Himalaya-Hengduan Mountains. *BMC Ecol.* 16: 26.

Appendix

Table A1 - Main plant families of the two plant communities (*Sesleria pichiana - Laserpitium siler* community = *SPLScom*, *Brachypodium rupestre - Festuca laevigata* community = *BRFLcom*), specifying the proportional diversity as percentage of species in each family with respect to the total species and the pollination units per family. Only the most representative plant families are shown.

SPLScom	Proportional diversity (% sp.)	Pollination units (% sp.)	BRFLcom	Proportional diversity (% sp.)	Pollination units (% sp.)
Fabaceae	15.09	40.48	Fabaceae	21.95	19.05
Asteraceae	13.21	23.96	Asteraceae	12.20	4.76
Liliaceae	11.32	7.23	Caryophyllaceae	12.20	4.76
Caryophyllaceae	9.43	9.73	Orchidaceae	7.32	4.76
Orchidaceae	9.43	1.98	Campanulaceae	7.32	7.14
Campanulaceae	5.66	5.43	Dipsacaceae	7.32	2.38
Apiaceae	5.66	4.92	Lamiaceae	4.88	2.38
Dipsacaceae	5.66	6.28	Rosaceae	4.88	4.76

Table A2 - Pairwise statistics between modules each phenological unit (pheno-cluster = PC) for both grasslands (*Sesleria pichiana - Laserpitium siler* community = SPLScom, *Brachypodium rupestre - Festuca laevigata* community = BRFLcom), one-way non-parametric Manova (Anderson 2001) with Bray-Curtis index of similarity. Significance (bold) is calculated after 9999 permutations.

SPLScom

P C 1

F \ p	Large Apidae	Mixed composition	Large-core
Large Apidae		0.18	**0.048**
Mixed composition	16.00		0.33
Large-core	**19.73**	4.63	

P C 2

F \ p	Mixed composition 1	Mixed composition 2	Mixed composition 3	Large Apidae	Large-core
Mixed composition 1		1.00	0.21	0.11	0.08
Mixed composition 2	2.03		0.20	0.12	0.22
Mixed composition 3	2.18	2.73		**0.001**	**0.001**
Large Apidae	1.39	1.39	**3.16**		**0.0001**
Large-core	1.40	1.18	**2.65**	**2.55**	

P C 3

F \ p	Large-core	Mixed composition 1	Large Apidae 1	Large Apidae 2	Mixed composition 2
Large-core		0.51	0.10	0.41	0.30
Mixed composition 1	0.80		0.33	0.34	0.33
Large Apidae 1	2.04	2.67		0.33	0.34
Large Apidae 2	1.09	1.15	1.49		0.34
Mixed composition 2	1.69	1.66	2.89	1.70	

BRFLcom

P C 1

F \ p	Large-core	Large Apidae 1	Mixed composition 1	Large Apidae 2	Mixed composition 2
Large-core		**0.009**	0.097	**0.008**	0.165
Large Apidae 1	**4.264**		0.067	**0.008**	0.198
Mixed composition 1	1.548	8.127		**0.044**	0.333
Large Apidae 2	**2.065**	**4.590**	**2.405**		0.162
Mixed composition 2	1.117	7.137	2.667	1.531	

P C 2

F \ p	Mixed composition 1	Mixed composition 2	Large-core	Large Apidae
Mixed composition 1		0.101	0.056	0.091
Mixed composition 2	3.096		0.089	**0.019**
Large-core	1.486	2.080		**0.007**
Large Apidae	2.056	**3.714**	**2.632**	

Appendix's figure captions

Figure A1 - Functional groups expressed as absolute percentage, plants referring to location of nectar in the corolla (A) and insects referring to pseudo-taxonomic groups (B) of *Sesleria pichiana - Laserpitium siler* community and *Brachypodium rupestre - Festuca laevigata* grasslands (=SPLScom and BRFLcom, respectively).

TABLES

Table 1. Features of each phenological unit (pheno-cluster = PC) of each grassland (*Sesleria pichiana - Laserpitium siler* community = SPLScom, *Brachypodium rupestre - Festuca laevigata* community = BRFLcom) . ‡is significance of Modularity computed with 100 quantitative null models with r2dtable algorithm of Bipartite package for R. * is for significance as p<0.05 with 1000 binary null-model with ER algorithm in AHINDADO.

	SPLScom			BRFLcom	
	PC 1	P C 2	P C 3	PC 1	P C 2
General features					
Length in weeks	2	5	2	5	4
Visited plants no. sp.	8	26	10	18	15
Visiting insect no. sp.	13	114	57	53	42
Network features					
Connectance	0.18	0.07	0.16	0.07	0.13
M (modularity)	0.51 ‡	0.09 ‡	0.34 ‡	0.59 ‡	0.40 ‡
NODF (nestedness)	18.6	19.3 *	22.3 *	9.7	25.6 *
H_2'	0.71	0.64	0.53	0.72	0.46

Table 2. Taxonomic identity of Hub species of Figure 3, Hub type and belonging community are provided (*Sesleria pichiana - Laserpitium siler* community = SPLScom, *Brachypodium rupestre - Festuca laevigata* community = BRFLcom).

Plants	Family	Hub type	Community	Label in fig. 3
Lathyrus montanus	Fabaceae	Module Hub	SPLScom	Pl.1
Laserpitium siler	Apiaceae	Module Hub	SPLScom	Pl.2
Lotus corniculatus	Fabaceae	Module Hub	BRFLcom	Pl.3
Alchemilla glaucescens	Rosaceae	Module Hub	BRFLcom	Pl.4
Phyteuma ovatum	Campanulaceae	Module Hub	BRFLcom	Pl.5
Phyteuma scorzonerifolium	Campanulaceae	Module Hub	BRFLcom	Pl.6
Hypericum richeri	Hypericaceae	Module Hub	BRFLcom	Pl.7
Insects	Order: Family	Hub type	Community	Label in fig. 3
Formica picea	Hymenoptera: Formicidae	Module Hub	SPLScom; BRFLcom	In.1
Chrysotoxum cautum	Diptera: Syrphidae	Module Hub	SPLScom	In.2
Chiastocheta lophota	Diptera: Anthomyiidae	Module Hub	SPLScom; BRFLcom	In.3
Botanophila sp.	Diptera: Anthomyiidae	Module Hub	SPLScom	In.4
Bombus soroeensis	Hymenoptera: Apidae	Connector; Module Hub	SPLScom	In.5
Bombus lapidarius	Hymenoptera: Apidae	Module Hub	SPLScom	In.6
Bombus rupestris	Hymenoptera: Apidae	Network Hub; Connector; Module Hub	SPLScom; BRFLcom	In.7
Micrinus heteromorphus	Coleptera: Malachiidae	Network Hub; Module Hub	SPLScom; BRFLcom	In.8
Sepsis sp.	Diptera: Sepsidae	Module Hub	SPLScom; BRFLcom	In.9
Eristalis tenax	Diptera: Syrphidae	Network Hub	SPLScom	In.10

Episyrphus balteatus	Diptera: Syrphidae	Connector	SPLScom	In.11
Pieris brassicae	Lepidoptera: Pieridae	Connector; Module Hub	SPLScom; BRFLcom	In.12
Vanessa cardui	Lepidoptera: Nymphalidae	Module Hub	SPLScom	In.13
Bombus lucorum	Hymenoptera: Apidae	Module Hub	BRFLcom	In.14

Figure captions

Figure 1. Sampling area in the Northern Apennine. From the left: Italy; sub-horizontal view on Oltrepò Pavese; vertical view of Mt. Lesima. The orange polygon refers to *Brachypodium rupestre - Festuca laevigata* community; the blue refers to *Sesleria pichiana - Laserpitium siler* community. Black diamonds are the sampling plots.

Figure 2. Plant-pollinator networks of each phenological unit (PC) of each grassland (*Sesleria pichiana - Laserpitium siler* community = SPLScom, *Brachypodium rupestre - Festuca laevigata* community = BRFLcom). Each block represents a species, its size is proportional to the total number of interactions, line-width shows the abundance of interactions between the two linked partners.

Figure 3. Among-module connectivity (c-) and within-module participation (z-) for species of each phenological unit (PC) of both grasslands (*Sesleria pichiana - Laserpitium siler* community = SPLScom, *Brachypodium rupestre - Festuca laevigata* community = BRFLcom). Thresholds are 95% quantiles from 100 null models (mean in black ± sd in grey). Plot areas refers to important roles as [A]: Module-hub, [B]: Network-hub, [C]: Connector. Species labels are listed in Table 2.

Figure 4. Ordination PCA biplot of insects' among-module connectivity (c-) and the within-module participation (z-) values. A *post-hoc* correlation was performed with Links (= number of links per species), d (= Specialization index d') and Diversity (= Shannon diversity). Variable arrows point to the direction of increasing gradient (most rapid change of the variable), their size is proportional to the r^2 of the correlation with the ordination for the *post-hoc* variables (with the ordination-axes for c- and z- values).

Figure 1

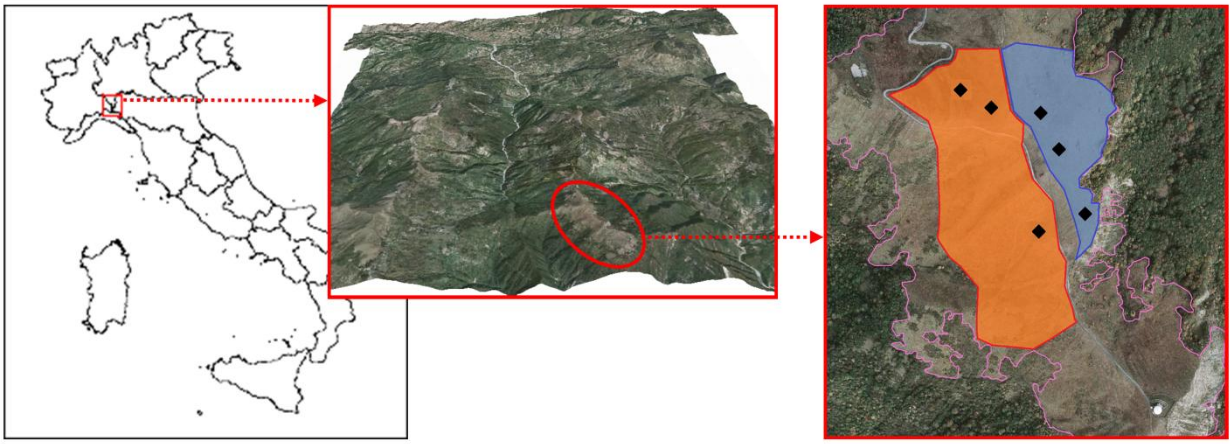


Figure 2

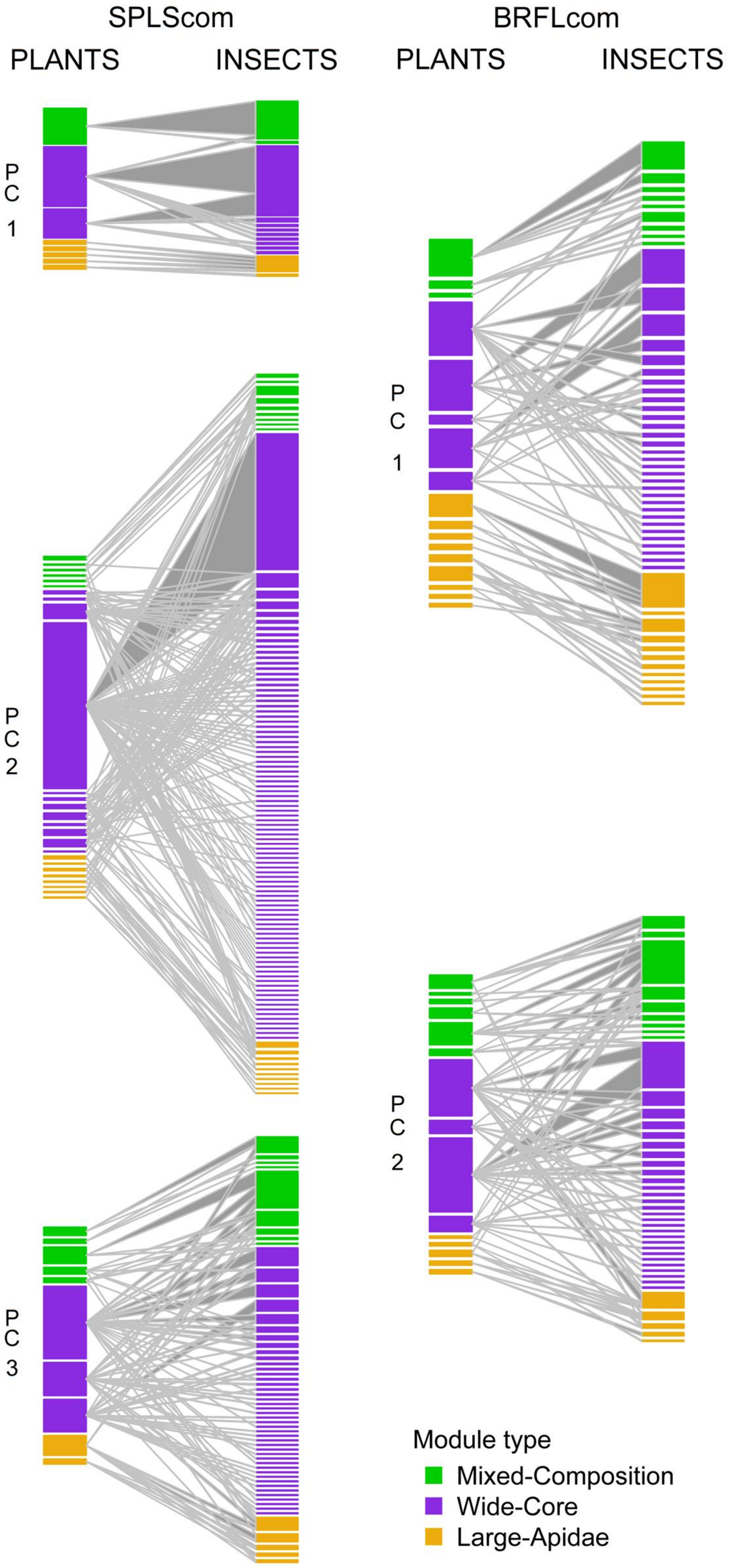

SPLScom
BRFLcom
PLANTS
INSECTS
PLANTS
INSECTS
PC 1
PC 2
PC 3
PC 1
PC 2
Module type
Mixed-Composition
Wide-Core
Large-Apidae

Figure 3

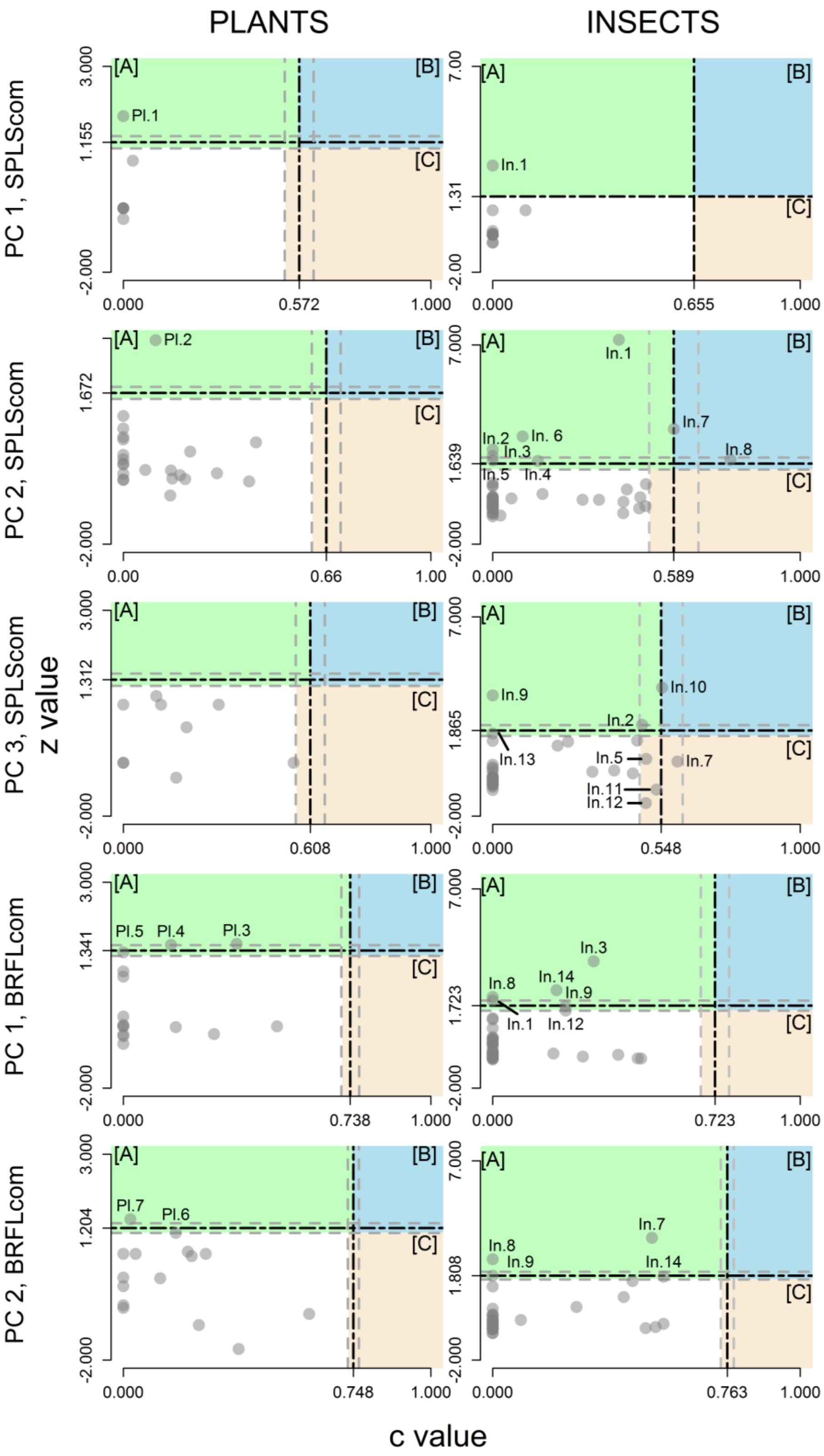

PLANTS
INSECTS
PC 1, SPLScom
PC 2, SPLScom
PC 3, SPLScom
PC 1, BRFLcom
PC 2, BRFLcom
z value
c value
[A]
[B]
[C]
3.000
1.155
-2.000
0.000
0.572
1.000
Pl.1
7.00
1.31
-2.00
0.655
In.1
1.672
0.00
0.66
1.00
Pl.2
7.000
1.639
0.589
In.2
In. 6
In.3
In.5
In.4
In.7
In.8
1.312
0.608
1.865
0.548
In.9
In.10
In.13
In.11
In.12
1.341
0.738
Pl.5
Pl.4
Pl.3
1.723
0.723
In.14
1.204
0.748
Pl.7
Pl.6
1.808
0.763

Figure 4

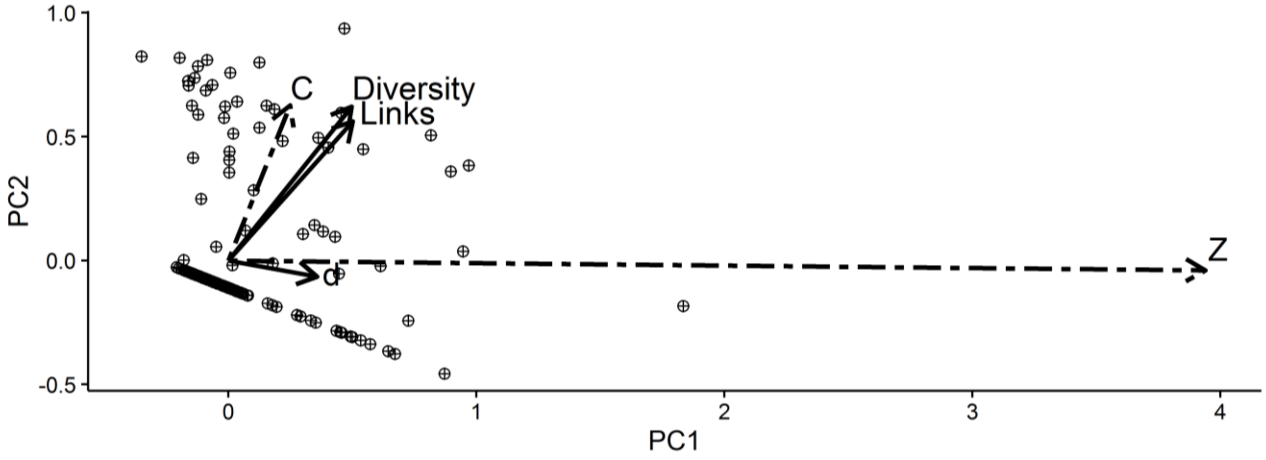
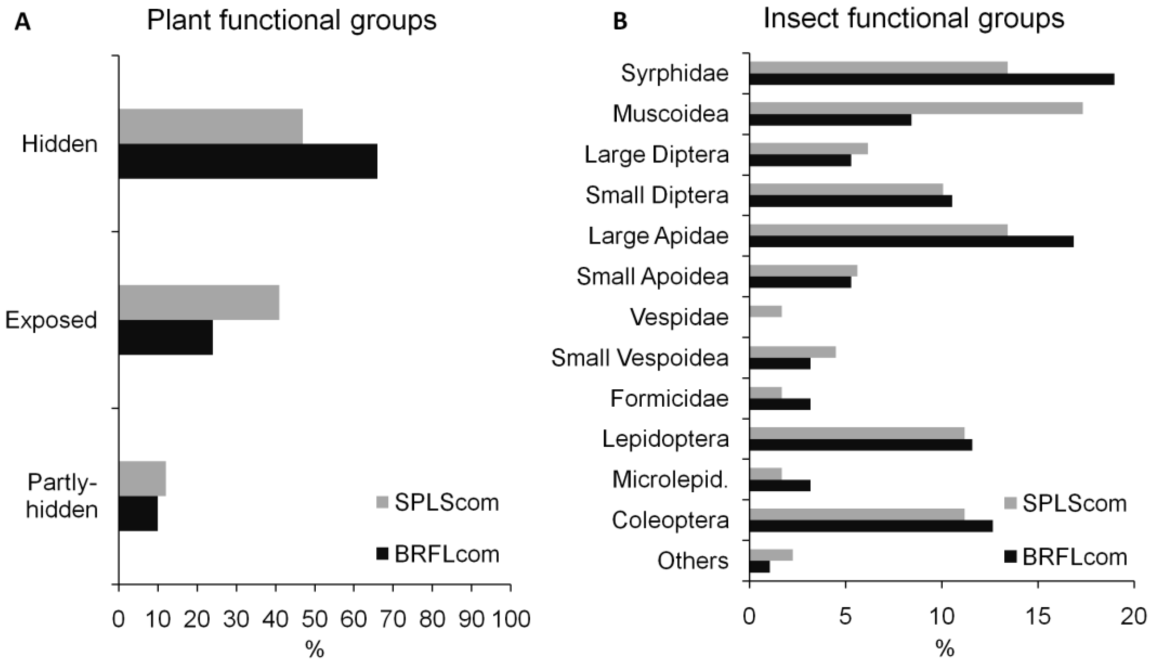


Figure A1


A
Plant functional groups
Hidden
Exposed
Partly-hidden
SPLScom
BRFLcom
0 10 20 30 40 50 60 70 80 90 100
%
B
Insect functional groups
Syrphidae
Muscoidea
Large Diptera
Small Diptera
Large Apidae
Small Apoidea
Vespidae
Small Vespoidea
Formicidae
Lepidoptera
Microlepid.
Coleoptera
Others
SPLScom
BRFLcom
0 5 10 15 20
%