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# The co-occurrence of different grassland communities increases the stability of pollination networks

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## ABSTRACT

High heterogeneity of grassland communities supports a high diversity of species and represents a key point for the retention of pollinators in agricultural landscapes. In the present study, we explored whether the co-occurrence of different grassland communities has any effect on the stability of the network of pollination interactions. We monitored pollination interactions in two co-occurring grassland communities, differing in disturbance history and water and nutrient supply. The monitoring was carried out during the summer season (7 surveys). For each survey we compared the role in the pollination networks (i.e., keystone vs. peripheral species) of habitat-specialist and habitat-generalist plant and pollinator species. We found that plant and pollinator species of the two different grassland communities were highly interconnected, revealing that pollination interactions occur at a level of organization above that of the single community. The co-occurrence of the two grassland communities increased the type, number and frequency of contacts, thereby contributing to networks stability. The role of habitat-specialist and habitat-generalist plant and pollinator species in pollination networks was asymmetric, with habitat-specialist plants and habitat-generalist pollinators being keystone species, while habitat-generalist plants and habitat-specialist pollinators being peripheral in the pollination networks. Our results showed that the stability of the network does stem from the co-occurrence of different species pools having different but complementary roles in the pollination networks. From a conservation perspective, the maintenance of different grassland communities is important not only because they allow the conservation of habitat-specialist species, but specifically because plant species specialized in either grassland community are also keystone for the maintenance of the stability of the pollination networks.

## 1. Introduction

Pollinator populations are declining all over the world (Winfree et al., 2009) with unavoidable consequences for the pollination service delivery. Around 60% of both wild and cultivated plant species are expected to potentially suffer from pollination limitation (Aizen et al., 2008), thereby undergoing a decrease of fruit or seed set. At the same time, both domesticated and wild pollinator populations are affected by a range of impacts, such as increasing use of agrochemicals, parasites and diseases as well as habitat loss and climate change (Traveset et al., 2017). Local and global environmental degradation, and the loss of natural and semi-natural habitats appear to be of great importance in determining the decline of pollinator populations (Kosior et al., 2007; Fantinato et al., 2018a). Indeed, several studies suggest that the reduction in wildflowers, which determines a drop of floral resources (i.e., nectar and pollen), plays a major role in pollinators decline (Biesmeijer et al., 2006; Fitzpatrick et al., 2007; Potts et al., 2010). The

decline of floral resources can trigger a negative feedback on mutualistic communities, leading to local pollinator extinctions, which can in turn lead to the decline in pollination services for wild plants, thereby further reducing floral resources for the pollinators (Potts et al., 2010). In the end, the integrity of natural and semi-natural habitats will be affected (Lázaro et al., 2016; Traveset et al., 2017).

Given the economic implications of reduced pollination service, the decline of pollinator populations in agricultural landscapes has received substantial attention. Human disturbance, in the form of large-scale farming and urbanization, typically results in the loss of native vegetation, changes in species composition and reduction of floral resources (Fahrig, 2003; Fischer and Lindenmayer, 2007 Buffa et al., 2018). However, the long history of low-intensity agricultural land use in Europe has also created unique and species-rich plant assemblages, including semi-natural grassland communities. Semi-natural grasslands shaped by traditional farming practices such as grazing or haymaking and with little impact of artificial fertilizers and ploughing, are among

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the most species-rich habitats in Europe (Dengler et al., 2014; Török et al., 2016). Beside the high diversity of plant species (Wilson et al., 2012), they also provide habitat for rare species from different taxonomic groups (Slaviero et al., 2016; Fantinato et al., 2017), including thousands of pollinator species, such as bees, flies, beetles, butterflies (Bastian, 2013; Zulka et al., 2014) and other invertebrates.

The presence of semi-natural grasslands may thus represent a key point for the retention of pollinators in agricultural landscapes. Indeed, although some pollinator-dependent crops can provide local temporal concentration of floral resources, their relatively short flowering period cannot assure the continuity in forage provision needed for long-lived pollinators (Corbet, 1991). Importance of grasslands for survival of plants and pollinators in agricultural landscapes has led several studies to attempt to find which ecological conditions and management practices mostly influence the maintenance of a diverse community of plants and pollinators (Fantinato et al., 2016a, 2019). Findings proved that different grassland communities support different local pools of plant and pollinator species (Öckinger et al., 2012; Valkó et al., 2012), and that only the co-occurrence of grasslands differing in disturbance history as well as in water and nutrient supply, can meet the requirements of a high species diversity (van Klink et al., 2015; Török et al., 2016).

The co-occurrence of grassland communities hosting different pools of species does certainly increase the regional species pool. However, increased diversity of species showing high habitat specialization does not necessarily correspond to improved stability of the network of pollination interactions, which is a function of the type, number and frequency of interactions (Kaiser-Bunbury and Blüthgen, 2015; Fantinato et al., 2019, 2018b). Arguably, we might expect that species with a narrow ecological niche, i.e. being specialized in one grassland community, will likely interact with species of their own community, resulting in a highly compartmentalized (i.e. selective) network of pollination interactions. Conversely, species characterized by a broader ecological tolerance (i.e., habitat-generalist species) can occur in more than one grassland community, thereby contributing to connect different communities through dispersal events. This, in turn, will contribute to enhance the redundancy of pollination interactions by widening the type, number and frequency of contacts (Blüthgen and Klein, 2011).

We can thus hypothesize that within the regional species pool, species specialized in a particular grassland community would occupy a much more peripheral position in the network of pollination interactions and play a marginal role in sustaining the network structure. Conversely, species occurring in more than one grassland community should exhibit a high degree of connection with the other species, playing an important role in sustaining the structure of the overall pollination network (i.e., keystone species; *sensu* Koski et al., 2015;

Traveset et al., 2018), ultimately increasing its stability. We addressed the hypothesis by answering the following questions: (i) are different co-occurring grassland communities interconnected through pollination networks? (ii) do habitat-specialist and habitat-generalist plant and pollinator species show different roles in pollination networks?

## 2. Materials and methods

### 2.1. Study area

The study took place in the Euganean Hills (NE Italy), a group of 81 volcanic hills ranging from 27 to 601 m a.s.l. Average annual rainfall is 720 mm (Kaltenrieder et al., 2010), distributed according to an equinoctial pattern; two peaks, in correspondence to the months of April and September, are intermingled with two minima, in the months of December and July. Annual mean temperature is 13.0 °C; the highest average temperature values can be found in July, while the lowest in December. Bioclimatic classification (Rivas-Martínez, 2008) shows a Temperate-Oceanic type, with the exception of the southern part of the study area where a Temperate-Continental bioclimate can be observed.

The history of human influence on the land use of the Euganean Hills dates back to the Neolithic; from 4300 to 4400 cal. BP sedimentary pollen analysis proved pasture and grassland species, together with *Castanea*, *Juglans* and *Olea*, to constantly occur in the study area (Kaltenrieder et al., 2010). The presence of humans since ancient times resulted in a fine-scale landscape structure with arable fields, orchards, groves, and semi-natural grasslands intermingled with natural habitats, such as forests and rocky outcrops, in a complex agricultural landscape. The study area hosts two semi-natural grassland communities. Open pioneer grasslands are characterized by sparse vegetation cover and are dominated by low-growing dwarf shrubs (chamaephytes; e.g., *Artemisia alba* Turra). They establish on poorly developed calcareous soils characterized by low water retention capacity and high leaching rates (Fantinato et al., 2016b). Dense late-successional grasslands are dominated by perennial herbaceous plants (hemicryptophytes; e.g., *Bromus erectus* Huds.), and establish on more developed calcareous soils, with higher water retention capacity (Fantinato et al., 2016b). Historically, the two grassland communities have been maintained through different management practices. The low productivity of open pioneer grasslands made them suited for grazing, while late-successional grasslands are mowed for hay making (Fig. 1). Nowadays, management practices slowed down, and grasslands are mowed or grazed every three years (Fantinato et al., 2016a)

### 2.2. Data collection

Altogether 26 plots of 2 m × 2 m were selected using a stratified



Fig. 1. Physiognomy of the pioneer grasslands (left) and the late-successional grasslands (right).

random sampling design on two co-occurring grassland communities. Overall, 13 plots were placed on open pioneer grasslands, and 13 plots on dense late-successional grasslands.

The monitoring season started on 15th of April and ended on 14th of July 2016, the time of the year in which both grassland communities showed flowering species and active pollinators. We surveyed the 26 plots every 15 days, for a total of seven surveys. At each survey we censused and identified pollinators. Since previous investigations (Fantinato et al., 2018a) in the study area proved that recorded animal-pollinated plants are predominantly pollinated by diurnal flying insects, pollinator surveys were performed under warm and sunny weather conditions. Pollination interactions were monitored for 14 min per plot, split into two 7-min sets distributed during two daily intervals (from 10 a.m. to 1 p.m. and from 1 p.m. to 4 p.m.) to ensure the observation of pollinators showing different daily periods of activity (Fantinato et al., 2018a). We considered and counted as pollinators only those insects visiting flowers for more than 1 s, and getting in direct contact with the floral reproductive organs (Hegland and Totland, 2005).

### 2.3. Data analysis

To evaluate the role of species in pollination networks, as well as the organization of pollination interactions when different grassland communities spatially co-occur, we adopted the network approach, in which plant and pollinator species represent the network nodes, while interactions between plants and pollinators are the links between nodes. The network approach allows to calculate several metrics at both the species and the whole network level and to describe the network structure and the role of species in the functioning of the whole network.

We created 7 quantitative pollination interaction matrices (one per survey), in which rows represented pollinator species, columns plant species and entries the number of contacts between each pair of plant and pollinator species. We chose to organize pollination interactions in one matrix per survey to avoid the formation of impossible interactions through pollinator sharing between plant species flowering during different surveys (i.e., forbidden links; Olesen et al., 2010).

For each pollination interaction matrix, we calculated three quantitative descriptors of the structure of pollination networks (i.e., network selectiveness, weighted nestedness and quantitative modularity; in the R-based package *bipartite*; Dormann et al., 2008). Besides being a necessary step in the analysis of species role in pollination networks, these attributes are relevant for the comprehension of the network structure and functioning. Network selectiveness (Blüthgen et al., 2006) is linked to the redundancy of interaction, which influences the resistance and resilience of pollination networks by acting as a buffer against species loss. Weighted nestedness (WNODF; Galeano et al., 2009) is a measure of the asymmetry of interactions. In a nested network, specialist species interact with generalist partners, while generalist species interact with both specialist and generalist partners. This means that as specialists are lost from the network, the core of interacting generalists remains unaltered (Tylianakis et al., 2010). A nested structure is supposed to minimize inter-specific competition, thereby enhancing the coexistence of a higher number of species and to increase network stability (Vázquez and Aizen, 2004; Thébault and Fontaine, 2010). Beside the nestedness organization of interactions, network modularity (Q; Dormann and Strauss, 2013) has been highlighted to hugely influence the capability of pollination networks to withstand perturbations (i.e., species loss). Modularity describes the degree to which species interactions are organized in modules, or compartments, in which species belonging to the same module interact more between each other than with species belonging to other modules (Olesen et al., 2007). A modular organization of interactions makes the overall pollination network more resistant and resilient against the spread of secondary extinctions through modules (Tylianakis et al., 2010). The significance of network selectiveness, weighted nestedness and

quantitative modularity was assessed against a null model obtained by constructing 1000 randomized networks with identical margin totals as the empirical network and comparing the index values between observed and random networks using the null model 'r2d' (Guimerà and Amaral, 2005).

At the species level, we chose indices revealing the role of each plant and pollinator species in the network of pollination interactions. Specifically, we calculated species selectiveness (Blüthgen et al., 2006), which measures the exclusiveness of a species partner spectrum compared with other species in the network; species strength (S; Bascompte et al., 2006), which measures the degree of dependence of a given species partners on the selected species; nested contribution (n; Saavedra et al., 2011), which measures how individual species' interactions contribute to the degree of nestedness, calculated at the community level and compared to a random null model; weighted closeness centrality (wCC; Ballantyne et al., 2017), as a measure of the centrality of individual species within the topography of the network; standardized connection (c; Olesen et al., 2007) and participation values (z; Olesen et al., 2007), which measure the degree of connection of a species between modules and within its own module, respectively.

To identify differences between pioneer and late-successional grasslands in the composition of plant and pollinator species we reported all temporal observations into two presence/absence matrices: a plant species  $\times$  plot matrix and a pollinator species  $\times$  plot matrix. Differences in the composition of plants and pollinators between pioneer and late successional grasslands were tested by conducting two one-way PERMANOVAs (one for plants and one for pollinators; Anderson and ter Braak, 2003) with 9999 permutations using the R-based package *vegan* (version 2.4; Oksanen et al., 2016). Plant and pollinator species were used as dependent variables and grassland communities as fixed factor.

Habitat specialization of plant species was defined by performing an Indicator Species Analysis (ISA; Dufrière and Legendre, 1997). We performed ISA using the *multpat* function in R package *indicspecies* (De Cáceres and Legendre, 2009; De Cáceres et al., 2010) and choosing 'r.g' as the statistical value to identify species fidelity to a grassland community. Only species with  $P$ -values  $< 0.1$  were considered specialized for a grassland community (Hart and Chen, 2008; Kumar et al., 2017). Therefore, we defined as habitat-specialist pollinators all those species visiting exclusively habitat-specialist plants or visiting habitat-generalist plants exclusively in one of the two grassland communities. To detect differences in the role of habitat-specialist and habitat-generalist plant species in pollination networks we performed one-way PERMANOVA with 9999 randomizations and Tukey Test (Anderson and Ter Braak, 2003). We used metrics describing plant species role in pollination networks (i.e.,  $d'$ ,  $S$ ,  $n_i$ , wCC,  $c$  and  $z$ ) as dependent variables, and habitat specialization of species (i.e., habitat-specialist vs. habitat-generalist species) as fixed factor. We followed the same procedure to compare the role in pollination networks of habitat-specialist and habitat-generalist pollinators. We used the values of metrics describing plant and pollinator species role in pollination networks calculated in each survey as replicates. All calculations were done within the R statistical framework (R Development Core Team, 2012).

### 3. Results

Overall, we recorded 411 contacts between 27 plant and 63 pollinator species. Composition of both plant and pollinator species differed widely between pioneer and late-successional grassland communities (plants; pseudo- $F_{1,25} = 5.230$ ;  $P < 0.0001$ ; pollinators; pseudo- $F_{1,65} = 1.901$ ;  $P = 0.001$ ) showing narrow groups of shared species. Specifically, 7 plant species were specialized in pioneer grasslands and 5 in late-successional grasslands, while 15 species were in common between grassland communities (i.e., habitat-generalist species; Table 2). Among plant families (13 families), Fabaceae, Gentianaceae, Lamiaceae, Liliaceae, Orchidaceae, Rubiaceae and Scrophulariaceae

**Table 1**Network parameters for each survey.  $H'_2$ : complementary specialization; WNODF: weighted nestedness; Q: quantitative modularity. (\*\*\*)  $P < 0.001$ .

Survey	1st	2nd	3rd	4th	5th	6th	7th
$H'_2$	0.364***	0.503***	0.638***	0.424***	0.593***	0.538***	0.619***
WNODF	17.342***	10.655***	2.391***	5.857***	7.842***	5.952***	7.692***
Q	0.421***	0.534***	0.705***	0.562***	0.585***	0.667***	0.494***

were in common between grassland communities, while Cistaceae, Convolvulaceae, and Plantaginaceae occurred only in pioneer grasslands, and Dipsacaceae, Geraniaceae, and Linaceae in late-successional grasslands. As for pollinator species, 24 were specialized in pioneer grasslands, 24 in late-successional grasslands, while 21 species were in common between grassland communities (i.e., habitat-generalist species). All recorded pollinators were insects, and belonged to six orders: Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera and Orthoptera. Although orders of pollinating insects were not clearly associated with different grassland communities, Hymenoptera were the most representative order among shared pollinators (52% of species).

Values of network selectiveness, nestedness and modularity were nonrandom during all the monitoring surveys ( $H'_2$ , WNODF and Q;  $P < 0.001$ ; Table 1), revealing a high network stability and capability to withstand possible perturbations (i.e., resistance and resilience).

Significant differences in the role in pollination networks of plant species specialized in pioneer and late-successional grasslands (habitat-specialists), and those in common between grassland communities (habitat-generalists) were revealed by PERMANOVA (pseudo- $F_{1,57} = 4.534$ ;  $P = 0.006$ ). Tukey tests indicated that pollinator species depended more on habitat-specialist plant species than on habitat-generalist species (S;  $P_{pion. vs. comm.} = 0.042$ ;  $P_{late-succ. vs. comm.} = 0.009$ ; Fig. 2). Furthermore, habitat-specialist plant species had both higher standardized connection (c) and participation values (z) than habitat-generalist plant species (c;  $P_{pion. vs. comm.} = 0.040$ ;  $P_{late-succ. vs. comm.} = 0.038$ ; z;  $P_{pion. vs. comm.} = 0.004$ ;  $P_{late-succ. vs. comm.} = 0.018$ ; Fig. 2), indicating that plant species specialized in either grassland community were more connected with both species of their module, and of the other modules than habitat-generalist species (Fig. 2). Plant species with high values of strength coupled with high values of standardized connection and participation value were *Convolvulus cantabrica* L., *Globularia bisnagarica* L. and *Helianthemum nummularium* ssp. *obscurum* (Čelak.) Holub. in pioneer grasslands, while *Crepis vesicaria* ssp. *taraxacifolia* (Thuill.) Thell., *Dorycnium herbaceum* Vill., *Geranium sanguineum* L. and *Linum tenuifolium* L. in late-successional grasslands.

Similarly, the role of pollinator species in pollination networks significantly differed between habitat-specialists and habitat-generalists (pseudo- $F_{1,117} = 17.353$ ;  $P < 0.0001$ ). Tukey tests revealed that habitat-generalist pollinator species had a significantly higher strength (S), standardized connection (c) and participation value (z) than habitat-specialist pollinator species (S;  $P_{pion. vs. comm.} = 0.0003$ ;  $P_{late-succ. vs. comm.} = 0.004$ ; c;  $P_{pion. vs. comm.} = 0.0003$ ;  $P_{late-succ. vs. comm.} = 0.042$ ; z;  $P_{pion. vs. comm.} = 0.041$ ;  $P_{late-succ. vs. comm.} = 0.012$ ; Fig. 2). Therefore, in contrast to plant species, habitat-generalist pollinator species connected species within and between modules significantly better than those specialized in either grassland community.

Pollinator species with high values of strength coupled with high values of standardized connection and participation value were *Apis mellifera* (L., 1758), *Anthidium manicatum* (L., 1758), *Bombus hortorum* (L., 1761), *B. terrestris* (L., 1758), *Episyrphus balteatus* (De Geer, 1776) and *Osmia rufohirta* (Latreille, 1811), which were in common between grassland communities (i.e., habitat-generalist species).

#### 4. Discussion

Semi-natural grasslands support a high diversity of strict habitat-specialist species, representing important habitats for biodiversity

conservation (Ekroos and Kuussaari, 2012). Moreover, by considering the pollination interactions our study allowed us to demonstrate that the different grassland communities are interconnected through pollination networks, and that processes like pollination occur at a level of organization above that of the single community. Besides their role in enhancing the regional species pool and hosting species of conservation concern, our findings suggest that mosaics of different grasslands contribute to the long-lasting provision of ecosystem services by enhancing the stability of the pollination network.

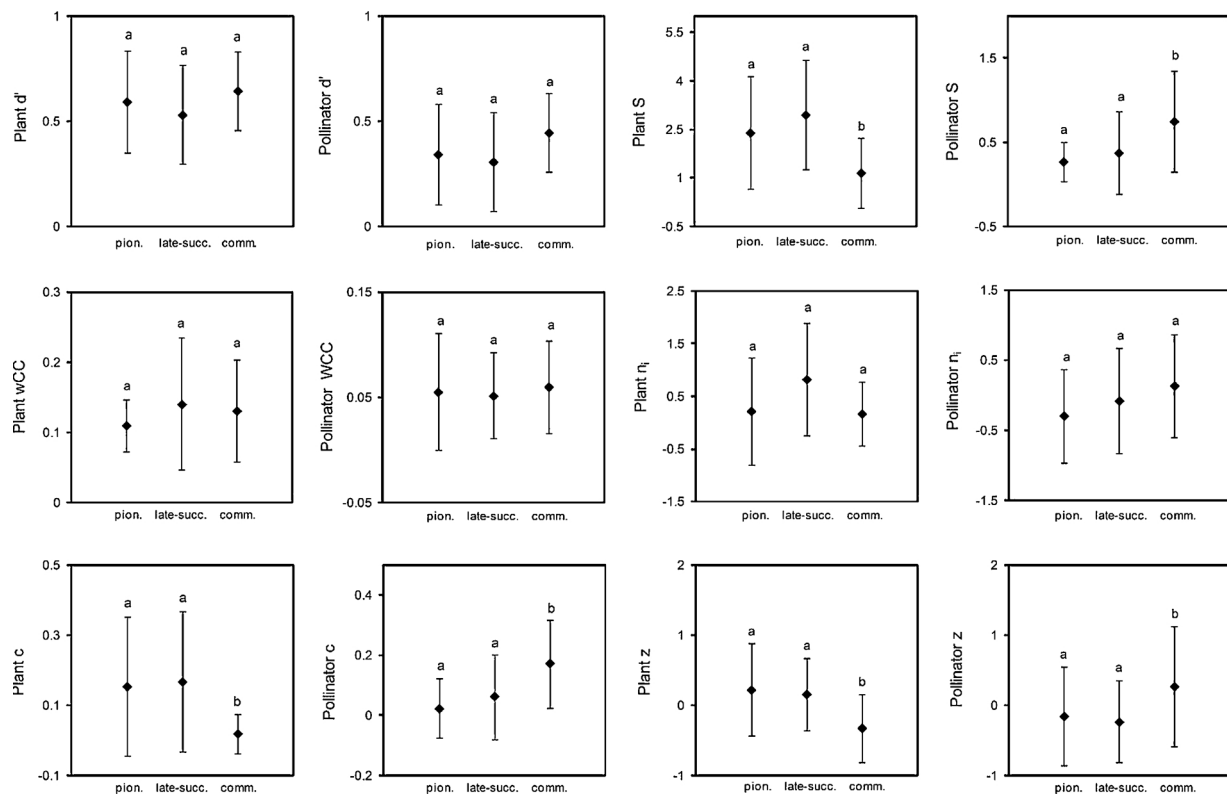
Indeed, plant and pollinator species of the two different grassland communities were highly interconnected and did not form two distinct sets of interactions, increasing the type, number and frequency of contacts. As a result, the pollination networks showed a moderate to low degree of selectiveness (i.e., of compartmentalization;  $H'_2$ ), coupled with a significantly nested organization of interactions (WNODF) and a significant modular structure (Q). This result is particularly important, since a nested organization of interactions is assumed to increase system stability by decreasing the probability of local extinction of peripheral species, which are considered the most vulnerable network members (Fortuna and Bascompte, 2006; Joppa et al., 2010). Concurrently, a modular structure slows the spread of secondary extinctions, further increasing the stability of pollination networks (e.g., Krause et al., 2003).

When the role of plant and pollinator species in pollination networks was assessed, significant differences emerged between habitat-specialist and habitat-generalist species. Specifically, habitat-specialist plants were more important than habitat-generalists in the maintenance of pollinator species, with plant species growing either in pioneer or in late-successional grassland showing significantly higher values of strength (S) than those growing indistinctly in both grassland communities. Furthermore, habitat-specialist plants had significantly higher values of standardized connection (c) and participation value (z) and were, therefore, more connected with other species in other modules and within their modules than habitat-generalist plants. Being at the core of pollination networks, habitat-specialist plants can thus be considered keystone species, and their loss caused by grassland abandonment or destruction would eventually lead to the collapse of networks' structure (Fortuna et al., 2013; Fantinato et al., 2019) and to the loss of pollination service.

On the other hand, pollinator species showed an opposite pattern, with habitat-generalists being more important than habitat-specialists in the sustainment of grasslands' pollination networks. Indeed, habitat-generalist pollinators exhibited a significantly higher strength (S) than those specialized in either grassland community, revealing that plant species depended more on habitat-generalists than on habitat-specialist pollinators. Furthermore, habitat-generalist pollinators connected species within and between network modules more than habitat-specialists (i.e., they showed higher values of standardized connection – c, and of participation value – z). In heterogeneous landscapes, pollinator species that visit a wide range of plant communities may exert a stabilizing effect by widening the range of interactions (i.e., the redundancy of pollination interactions), ultimately conferring stability to the pollination networks (Blütghen et al., 2011; Kaiser-Bunbury et al., 2015; Fantinato et al., 2019). In this regard, it is worth to consider that little variation could be observed between the identity of keystone pollinator species recorded in grassland communities and those found in a huge variety of ecosystems (Olesen et al., 2007). Indeed, according to the

**Table 2**  
 Plant species subdivision according to the Indicator Species Analysis ( $P < 0.1$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ). For each plant species, we reported their frequency of occurrence in the pioneer and late-successional grasslands as well as pollinator species involved for more than 50% of the interactions. Abbreviations: pion., pioneer grasslands; late-succ., late-successional grasslands.

Plant species	ISA value		Number of samples		Most interacting pollinator species	
	Pion.	Late-succ.	Pion.	Late-succ.		
Plant species specialized in pioneer grasslands	<i>Bupleurum veronense</i> Turra	0.462*	9	3	<i>Euclitidae</i> sp. (Lacordaire, 1857), <i>Polistes gallicus</i> (L., 1767)	
	<i>Convolvulus cantabrica</i> L.	0.500*	7	1	<i>Andrena aglissima</i> (Scopoli, 1770), <i>Episyrphus balteatus</i> (De Geer, 1776), <i>Hoplitis claviventris</i> (Thomson, 1872), <i>Scavea selenitica</i> (Meigen, 1822)	
	<i>Fumana procumbens</i> (Dunal.) Gren. & Godr.	0.544*	11	4	<i>Apis mellifera</i> (L., 1758), <i>Oedemera flavipes</i> (Fabricius, 1792)	
	<i>Globularia bisnagarica</i> L.	0.727***	9	0	<i>Osmia rufohirta</i> (Latreille, 1811), <i>Tropinota hirta</i> (Poda, 1761), Tettigoniidae sp. (Krauss, 1902)	
	<i>Helianthemum nummularium</i> subsp. <i>obscurum</i> (Čelak.) Holub	0.632**	12	4	<i>Andrena subopaca</i> (Nylander, 1848), <i>Apis mellifera</i> (L., 1758), <i>Bombus hortorum</i> (L., 1761), <i>Bombus terrestris</i> (L., 1758), <i>Episyrphus balteatus</i> (De Geer, 1776), <i>Eristalis arbustorum</i> (L., 1758), <i>Eristalis tenax</i> (L., 1758)	
	<i>Hippocrepis comosa</i> L.	0.426	4	0	<i>Anthidium manicatum</i> (L., 1758), <i>Osmia rufohirta</i> (Latreille, 1811), <i>Polyommatus icarus</i> (Rottemburg, 1775)	
	<i>Teucrium chamaedrys</i> L.	0.426	4	0	<i>Bombus hortorum</i> (L., 1761), <i>Bombus terrestris</i> (L., 1758)	
	<i>Dorycnium herbaceum</i> Vill.	0.433	1	5	<i>Apis mellifera</i> (L., 1758), <i>Andrena haemorrhoa</i> (Fabricius, 1781), <i>Scolia hirta</i> (Schrank, 1781)	
	<i>Geranium sanguineum</i> L.	0.365	1	4	<i>Apis mellifera</i> (L., 1758), <i>Episyrphus balteatus</i> (De Geer, 1776), <i>Oedemera flavipes</i> (Fabricius 1792), <i>Polyommatus icarus</i> (Rottemburg, 1775), <i>Sphaerophoria scripta</i> (L., 1758)	
	<i>Linum tenuifolium</i> L.	0.500*	1	7	<i>Apis mellifera</i> (L., 1758), <i>Lygaeus saxatilis</i> (Scopoli, 1763), <i>Vanessa cardui</i> (L., 1758)	
Plant species specialized in late-successional grasslands	<i>Scabiosa triandra</i> L.	0.617**	2	9	<i>Bombus hortorum</i> (L., 1761), <i>Geron halteralis</i> (Wiedemann in Meigen, 1820), <i>Polyommatus icarus</i> (Rottemburg, 1775)	
	<i>Thymus pulegioides</i> L.	0.617**	2	10	<i>Apis mellifera</i> (L., 1758), <i>Megachile leachella</i> (Curtis, 1828), <i>Polyommatus icarus</i> (Rottemburg, 1775)	
	<i>Anacamptis pyramidalis</i> (L.) Rich.	0.120	2	1	<i>Tropinota squalida</i> (Scopoli, 1783), <i>Vanessa cardui</i> (L., 1758), <i>Zygaena carniolica</i> (Scopoli, 1763)	
	<i>Centaurium erythraea</i> Rafn.	0.120	1	2	<i>Polyommatus icarus</i> (Rottemburg, 1775)	
	<i>Crepis vesicaria</i> subsp. <i>taraxacifolia</i> (Thuill.) Thell.	0.200	0	1	<i>LasioGLOSSUM brevicorne</i> (Schenck, 1870), <i>Melitta haemorrhoidalis</i> (Fabricius, 1775)	
	<i>Erygium amethystinum</i> L.	0.182	2	4	<i>LasioGLOSSUM morio</i> (Fabricius, 1793), <i>Oedemera flavipes</i> (Fabricius 1792), <i>Scolia hirta</i> (Schrank, 1781)	
	<i>Galium lucidum</i> All.	0.288	2	0	<i>Cryptophagidae</i> sp. (Kirby, 1826), <i>Episyrphus balteatus</i> (De Geer, 1776)	
	<i>Galium verum</i> L.	0.077	5	6	<i>Lygaeus saxatilis</i> (Scopoli, 1763)	
	<i>Himantoglossum adriaticum</i> H. Baumann	0.288	2	0	<i>Apis mellifera</i> (L., 1758), <i>Anthidium manicatum</i> (L., 1758), <i>Colletes daviesianus</i> (Smith, 1846)	
	<i>Melampyrum barbatum</i> Waldst. & Kit.	0.097	3	2	<i>Bombus hortorum</i> (L., 1761), <i>Bombus pascuorum</i> (Scopoli, 1763), <i>Bombus terrestris</i> (L., 1758)	
<i>Muscari comosum</i> L. Mill.	0.000	1	1	<i>Bombus hortorum</i> (L., 1761), <i>Dasygaster hirtipes</i> (Fabricius, 1793)		
<i>Onobrychis arenaria</i> (Kit.) DC.	0.000	1	1	<i>Bombus hortorum</i> (L., 1761), <i>Bombus pascuorum</i> (Scopoli, 1763), <i>Bombus terrestris</i> (L., 1758)		
<i>Ononis natrix</i> L.	0.120	2	1	<i>Bombus hortorum</i> (L., 1761), <i>Bombus pascuorum</i> (Scopoli, 1763), <i>Bombus terrestris</i> (L., 1758)		
<i>Stachys recta</i> L.	0.233	4	2	<i>Bombus hortorum</i> (L., 1761), <i>Osmia aurulenta</i> (Panzer, 1799)		
<i>Spartium junceum</i> L.	0.182	4	7	<i>Bombus hortorum</i> (L., 1761), <i>Xylocopa violacea</i> (L., 1758)		
<i>Thymus glabrescens</i> subsp. <i>deciptens</i> (Heinr. Braun) Domin	0.288	2	0	<i>Apis mellifera</i> (L., 1758), <i>Episyrphus balteatus</i> (De Geer, 1776), <i>Melitta didyma</i> (Esper, 1779)		
<i>Trifolium campestre</i> Schreb.	0.361	0	3	<i>Andrena dorsata</i> (Kirby, 1802)		



**Fig. 2.** Mean ( $\pm$  SD) values of selectiveness ( $d'$ ), strength (S), weighted closeness centrality (wCC), nestedness contribution ( $\eta_1$ ), standardized connection (c) and participation values (z), of plant and pollinator species specialized in pioneer and late-successional grasslands, as well as in common between grassland communities. Different letters indicate significant differences among species groups. Abbreviations: pion., pioneer grasslands; late-succ., late-successional grasslands; comm., in common.

literature, the functional role of pollinator species is less variable than that of plant species (e.g., [Burkle and Irwin, 2009](#); [Nielsen and Totland, 2014](#); [Koski et al., 2015](#)), with Hymenoptera playing a crucial role in sustaining pollination networks in many ecosystems of the world (e.g., [Fang and Huang, 2012](#); [Forup and Memmott, 2005](#)).

Summarizing, the role of habitat-specialist and habitat-generalist plant and pollinator species in pollination networks was asymmetric, with habitat-specialist plants and habitat-generalist pollinators being keystone species, while habitat-generalist plants and habitat-specialist pollinators being peripheral in the topography of pollination networks. Interestingly, plant species pollination and ecological niche (e.g., with regard to the variety of grassland communities in which they can occur) did not show comparable breadths. In other words, plant species with broad ecological tolerance do not necessarily interact with a wide spectrum of pollinator species, and not necessarily occupy a central role in the network of pollination interactions. Certainly, our findings deserve further investigation, but results might originally contribute with new insights on the understanding of trade-offs in different aspects of plant species life history.

Semi-natural grasslands are among the most important habitats in Europe ([Gigante et al., 2018](#); [Janssen et al., 2018](#)). However, they are severely threatened by changes in land use, both through intensification of agriculture as well as abandonment followed by decreased habitat quality and the consequent decline of the biodiversity they host ([Valkó et al., 2014](#)). Being characteristic of agricultural landscapes grassland communities can crucially contribute to the pollination service retention by providing a stable habitat available for foraging and life cycle completion of pollinators. By focusing on pollination interactions, we found that the maintenance of different grassland communities is important because they improve the redundancy, namely the resistance and resilience, of the pollination networks. Indeed, our findings show that the stability of the network stems from the co-occurrence of

different species pools having different, but complementary roles in pollination networks. From a conservation perspective, the maintenance of different grassland communities is important not only because they allow the conservation of habitat-specialist species, but specifically because plant species specialized in either grassland community are also keystone for the maintenance of the stability of pollination networks.

## Declarations of interest

None.

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