Received: 15 November 2020 | Accepted: 14 August 2021
DOI: 10.1111/1365-2435.13915

Functional Ecology
BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Patterns of pollination interactions at the community level are related to the type and quantity of floral resources

Edy Fantinato[1] | Judit Sonkoly[2,3] | Péter Török[2,3,4] | Gabriella Buffa[1]

[1]Department of Environmental Sciences, Informatics and Statistics, University Ca' Foscari of Venice, Venice, Italy
[2]Department of Ecology, University of Debrecen, Debrecen, Hungary
[3]MTA-DE Lendület Functional and Restoration Ecology Research Group, Debrecen, Hungary
[4]Polish Academy of Sciences, Botanical Garden - Center for Biological Diversity Conservation in Powsin, Warszawa, Poland

Correspondence
Péter Török
Email: molinia@gmail.com

Funding information
Nemzeti Kutatási Fejlesztési és Innovációs Hivatal, Grant/Award Number: K 119225 and KH 129483

Handling Editor: Ondrej Mudrák

Abstract

1. A fundamental question in community ecology is how the quantity of floral resources affects pollinator activity and how this relates to the structure and robustness of pollination networks. The issue has been mainly addressed at the species level, while at the community level several questions are still open.
2. Using a species-rich semi-natural grassland as model ecosystem, we explored the relationship between community-level quantity of floral resources, the number of flower visits at community level and descriptors of the structure and robustness of pollination networks. To assess whether patterns of pollination interactions were consistent when using different types of floral resources, we measured three types of floral resources, namely the volume of nectar, the number of pollen grains and the number of flowers.
3. Community-level pollinator visitation rate showed a hump-shaped relationship with the quantity of floral resources. Results were consistent among models employing different measures of floral resources as independent variables. The relationship between the quantity of floral resources and the structure and robustness of the network was not consistent among different types of floral resources; only intermediate levels of nectar volume were associated with high levels of network robustness.
4. The pattern we found is in contrast with some former studies which reported positive linear relationships between the community-level visitation rate of pollinators and the quantity of floral resources. Rather, the observed hump-shaped pattern resembles the relationship previously found between the quantity of floral resources of a given plant species and its visitation rate per flower. Our results highlighted that, by using specific types of floral resources (e.g. the volume of nectar and the number of pollen grains), it is possible to reveal ecological processes that would be masked by using the number of flowers as the sole measure of floral resource.

KEYWORDS
floral resources, nectar volume, network robustness, pollen grains, pollination interactions, visitation rate

1 | INTRODUCTION

Plant–pollinator interactions are crucial for maintaining the biodiversity and functionality of terrestrial ecosystems. A fundamental question in community ecology is how the quantity of floral resources affects pollinator activity (Akter et al., 2017; Klumpers et al., 2019) and how this relates to the robustness of pollination interactions (Biella et al., 2020). So far, the issue has been mainly addressed at the species level. Ecological theory and empirical evidence suggest that the relationship between the quantity of floral resources of a single plant species and its visitation rate per flower is hump-shaped or unimodal (Benadi & Pauw, 2018; Essenberg, 2012; Rathcke, 1983). Increasing availability of floral resources is initially coupled with increasing rate of visitation per flower; however, above a certain threshold in the quantity of floral resources, the visitation rate per flower decreases, because of a decreased density of pollinators (Bergamo et al., 2020; Rathcke, 1983). Veddeler et al. (2006) found that bee density increased with increasing number of inflorescences on single shrubs or branches, while the number of bees per shrub was negatively related to the proportion of co-flowering shrubs in the surrounding. Such findings also demonstrate that competition for pollinators may occur at different scales, from that of single flowers to that of population (Veddeler et al., 2006).

At the community level, the total quantity of floral resources has been found to have a positive linear relationship with total pollinator visitation rate, as more floral resources attract more pollinators (Noordijk et al., 2009; Seifan et al., 2014). Although the relationship is mostly considered positive (Dauber et al., 2010; Ebeling et al., 2008; Seifan et al., 2014), some results suggest that a negative relationship is also possible (Reverté et al., 2019; Veddeler et al., 2006). The contradictory findings may be related to the degree of generalisation of the plant community (Bergamo et al., 2020), the range and spatial distribution of floral resource quantity (Essenberg, 2012; Totland & Matthews, 1998) and the pollinator abundance (Ye et al., 2014), which can all influence pollination interactions, possibly leading to different relationships between pollinator visitation rate and the quantity of floral resources. However, despite increasing scientific attention in recent years (see e.g. Benadi & Pauw, 2018; Braun & Lortie, 2019), the nature of this relationship at the community level remains unclear.

Besides the relationship between floral resource quantity and pollinator visitation rate, two other main points remain unexplored at the community level. First, the influence of the quantity of floral resources on the structure and robustness of pollination interactions. In the last decades, pollination interactions have been increasingly studied using an ecological network approach (Jordano, 2016; Vanbergen et al., 2017). Ecological networks represent ecological community structure and depict interactions among species, providing the opportunity for a holistic assessment of ecosystem structure and functioning (Fantinato, 2019; Kaiser-Bunbury & Blüthgen, 2015; Vázquez et al., 2009). In particular, the pollination network approach has been extensively applied to the study of a variety of ecological questions, as a way of assessing the relationship between observed patterns and drivers of plant–pollinator interactions (Stock et al., 2020). Although understanding which factors influence the structure and robustness of pollination networks is increasingly urgent in the ongoing pollinator decline (Biesmeijer et al., 2006; Potts et al., 2010), the influence of the quantity of floral resources is still a poorly studied issue, which indeed received so far little attention (Brosi et al., 2017; Goldstein & Zych, 2016; Wang et al., 2020). The second issue regards the effects of different types of floral resources on the community-level patterns of pollination interactions. Plants can offer several types of floral rewards to pollinators, such as nectar, pollen, oil and resin (Fenster et al., 2004). Studies at the single-species level highlighted that the available quantity of nectar and pollen deeply influences plant interactions with pollinators (e.g. Fowler et al., 2016; Justino et al., 2012), but the community-level availability of nectar and pollen has been largely neglected (Szigeti et al., 2016; but see Biella et al., 2019 and Hicks et al., 2016). Frequently, the number of flowers is used as a proxy of the quantity of floral resources (e.g. Bergamo et al., 2020; Hoyle et al., 2018; Szigeti et al., 2016). Nevertheless, its capacity to reveal ecological processes has not been verified.

In this study, we explored pollination interactions in a species-rich grassland ecosystem to determine how the quantity of different types of floral resources (i.e. the total volume of nectar, the total number of pollen grains and the total number of flowers) relates to pollinator visitation rate, descriptors of network structure (i.e. connectance, complementary specialisation, weighted nestedness and quantitative modularity) and network robustness (based on the topological coextinction model; TCM; Memmott et al., 2004). Specifically, we addressed three questions: (a) How does the community-level quantity of floral resources influence the visitation rate of pollinators? (b) How does the community-level quantity of floral resources influence network structure and robustness? and (c) Do different measures of floral resources show consistent relationships with pollinator visitation rate and network structure and robustness?

2 | MATERIALS AND METHODS

2.1 | Study system

Field sampling was carried out in a species-rich grassland ecosystem of the Euganean Hills, North-East Italy (45.265706N, 11.698977E). The Euganean Hills experience a warm-rainy climate (Kaltenrieder et al., 2010). The mean annual temperature is 13.0°C with a mean high temperature of 23.8°C in July and a low of 3.2°C in January. The average annual rainfall is 720 mm, peaking in April and September and lowering in July and December.

In this study, we selected four independent grasslands. The minimum distance between grasslands was 1.2 km and the average grassland surface was of 6.89 ± 1.11 ha (*M* ± *SD*). Selected grasslands were surrounded by a similar landscape matrix consisting of deciduous forests, olive groves and vineyards (Fantinato et al., 2019a). In the past, grasslands were commonly managed by low intensity mowing practices, but since the 1980s, many grasslands have experienced increasing abandonment (Slaviero et al., 2016). The grasslands in our study have been mowed every 3 years since the year 2003 (Fantinato et al., 2018).

2.2 | Field sampling

In each grassland, we placed 10 permanent sampling plots of 2 m × 2 m using a stratified random sampling design (Random points inside polygons; Quantum GIS Development Team, 2020). The minimum distance between plots was set at 25 m. In each plot, we recorded the presence of entomophilous plants and the number of flowers per plant species once every 15 days, from 1st April to 30th September in 2016 (12 survey dates in total). For plant species whose flowers appear together in a recognisable floral unit (e.g. *Thymus pulegioides* L.), we calculated the total number of flowers by multiplying the number of floral units by the mean number of flowers per floral unit, based on counts from five specimens of each species. Flower heads of Asteraceae, Dipsacaceae and Plantaginaceae were treated as single flowers. To assess the structure and robustness of pollination interactions during each survey, we recorded visiting animals in each plot by observing the number of interactions between each plant and flower visitor. We counted only those visitors that made direct contact with the floral reproductive organs and visited the flower for more than 1 s, so could be considered as potential pollinators (Hegland & Totland, 2005). During each survey (for a total of 12 surveys; once every 15 days), each plot was monitored for 14 min, split up into two 7-min subsets (one between 10 a.m. and 1 p.m., and one between 1 p.m. and 4 p.m.) to ensure the observation of pollinators with differing daily periods of activity (Fantinato et al., 2019b; Lázaro et al., 2016). Overall, we monitored plant–pollinator interactions for 4,368 min and identified plants ($S = 42$) and flower visitors ($S = 106$) to species or morphospecies (see Appendix S1 for sampling completeness estimation).

2.3 | Nectar and pollen

For each entomophilous plant species occurring in sampling plots ($S = 42$), we determined the quantity of nectar and pollen of 5–10 randomly chosen flowers of different individuals (depending on availability; Cornelissen et al., 2003) growing within a radius of 10 m from the plots. Samples of nectar and pollen were collected as standing crop (i.e. true quantities available to pollinators; Kearns & Inouye, 1993) from freshly opened flowers on rainless days, between 8 a.m. and 10 a.m. We chose to quantify floral resources as standing crop to incorporate environmental influences, such as climate conditions, on floral resource provision. Floral resource measurements were made at the level of single flowers for all taxa. For plant species showing flower heads (i.e. Asteraceae, Dipsacaceae and Plantaginaceae), the number of open flowers was counted in five floral units in order to scale-up estimates of nectar volume and pollen grain number from single flower to floral unit. Specifically, we multiplied the volume of nectar and the number of pollen grains measured in one flower for the mean number of flowers per flower head (for details on floral resource quantification, see Appendix S2).

2.4 | Network parameters

Overall, we created 48 visitation matrices; in each matrix, we gathered pollination interactions recorded in the 10 permanent plots belonging to a grassland during one survey (4 grasslands × 12 surveys). We chose to organise plant–pollinator interactions in different matrices for each survey to avoid the formation of impossible interactions through pollinator sharing between plant species that flower in different periods (i.e. forbidden links; Olesen et al., 2010). Thus, for each pollination matrix, we calculated the richness of entomophilous plant and pollinator species, the visitation rate of pollinators (i.e. the number of flower visits observed in a grassland during one survey) and four descriptors of network structure. Descriptors of network structure were quantified by using the networklevel and computeModules functions in the R-based package bipartite (bipartite package version 2.08; Dormann et al., 2008); specifically, we calculated network connectance (C; Dunne et al., 2002), complementary specialisation (H_2'; Blüthgen & Klein, 2011), weighted nestedness (wNODF; Galeano et al., 2009) and quantitative modularity (Qobs; Dormann & Strauss, 2014). Standardised z-scores (z = [observed − null mean]/null σ) were calculated for network connectance (C), complementary specialisation (H_2'), weighted nestedness (wNODF) and modularity (Q) to test for significant differences from the null model distribution. Moreover, we quantified the robustness of each pollination matrix by applying the topological co-extinction model (TCM; Burgos et al., 2007; Memmott et al., 2004). Details on descriptors of network structure and robustness are reported in Appendix S3.

2.5 | Statistical analysis

As a first step, we quantified the total quantity of floral resources produced per grassland during each survey, that is, total volume of nectar, total number of pollen grains and total number of flowers. We quantified the total volume of nectar and the total number of pollen grains per grassland by multiplying the average nectar volume and the average number of pollen grains by the number of flowers per species recorded in the 10 permanent plots and summing results. The total number of flowers was quantified by summing the number of flowers counted in the 10 permanent plots per grassland.

We used the volume of nectar, the number of pollen grains and the total number of flowers per grassland from each survey as explanatory variables in the models. The three explanatory variables were used separately in different models to compare their influence on dependent variables.

To explore the relationship between the quantity of floral resources, the visitation rate of pollinators per grassland, the

TABLE 1 Summary table of the mean quantity of floral resources for each plant species (number of flowers per floral unit, nectar volume and number of pollen grains) derived from 5 to 10 randomly chosen flowers of different individual plants. Asterisks indicate values of nectar volume derived from the literature (Petanidou & Smets, 1995). Cases of missing nectar or of uncollectible pollen were indicated with a dot

	Mean number of flowers per floral unit	Mean nectar volume (μl) per flower ± *SD* (μl)	Mean pollen grain number per flower ± *SD*
Anacamptis morio	7.40 ± 3.05	.	.
Anacamptis pyramidalis	67.80 ± 19.66	.	.
Bupleurum baldense	186.40 ± 144.07	0.06 ± 0.00	1,890.00 ± 186.27
Centaurium erythraea	1.00 ± 0.00	.	2,522.00 ± 367.07
Colchicum autumnale	1.00 ± 0.00	0.99 ± 0.62	2,394.00 ± 727.53
Convolvulus cantabrica	1.00 ± 0.00	0.22 ± 0.00	10,980.00 ± 1,897.89
Crepis vesicaria subsp. *taraxacifolia*	1.00 ± 0.00	0.83 ± 0.03	17,776.00 ± 14,086.20
Cytisus hirsutus	1.00 ± 0.00	1.68 ± 0.31	7,512.00 ± 919.19
Eryngium amethystinum	1.00 ± 0.00	0.16 ± 0.04	7,283.33 ± 77,459.2
Euphorbia cyparissias	17.00 ± 3.08	.	5,424.00 ± 1,230.80
Euphorbia helioscopia	10.40 ± 0.89	.	2,000.00 ± 254.95
Fumana procumbens	1.00 ± 0.00	.	1,800.00 ± 728.07
Galium lucidum	682.00 ± 84.97	.	2,164.00 ± 942.16
Galium verum	990.00 ± 171.03	.	2,418.00 ± 1,319.70
Geranium sanguineum	1.00 ± 0.00	0.10 ± 0.01	2,600.00 ± 804.98
Globularia bisnagarica	1.00 ± 0.00	0.69 ± 0.95	37,862.40 ± 5,688.40
Helianthemum nummularium subsp. *obscurum*	1.00 ± 0.00	.	582.00 ± 31.14
Himantoglossum adriaticum	52.00 ± 22.21	.	.
Hippocrepis comosa	8.00 ± 0.00	1.10 ± 0.51	5,152.00 ± 616.70
Linum tenuifolium	1.00 ± 0.00	.	1,212.00 ± 159.74
Lotus herbaceus	21.00 ± 3.08	0.01*	1,052.00 ± 691.17
Melampyrum barbatum subsp. *carstiense*	6.67 ± 2.36	0.20 ± 0.00	13,214.00 ± 4,257.43
Microthlaspi perfoliatum	13.20 ± 2.77	.	728.00 ± 46.04
Muscari comosum	84.40 ± 18.72	1.21 ± 0.35	3,924.00 ± 406.05
Muscari neglectum	25.20 ± 3.03	1.40 ± 0.00	5,964.00 ± 593.36
Odontites luteus	19.20 ± 4.81	.	1,467.20 ± 239.35
Onobrychis arenaria	34.60 ± 7.99	1.27 ± 0.40	5,666.12 ± 4,544.16
Ononis natrix	25.80 ± 8.70	.	50,328.00 ± 4,104.50
Ophrys bertolonii subsp. *benacensis*	1.00 ± 0.00	.	.
Ophrys sphegodes	1.00 ± 0.00	.	.
Orchis purpurea	37.00 ± 11.14	.	.
Orchis simia	23.40 ± 5.03	.	.
Pilosella officinarum	1.00 ± 0.00	0.90 ± 0.07	56,520.00 ± 4,527.88
Potentilla pusilla	1.00 ± 0.00	.	23,040.00 ± 11,263.55
Salvia pratensis	31.20 ± 10.23	0.21 ± 0.10	4,636.00 ± 1,168.62
Scabiosa triandra	1.00 ± 0.00	0.29 ± 0.08	75,776.00 ± 21,427.20
Spartium junceum	8.80 ± 4.09	.	104,300.00 ± 20,099.00
Stachys recta	40.00 ± 10.69	0.33 ± 0.19	6,528.00 ± 470.44
Teucrium chamaedrys	33.00 ± 7.18	0.86 ± 0.14	7,474.00 ± 297.28
Thymus oenipontanus	32.40 ± 3.85	1.06 ± 0.48	496.00 ± 174.15
Thymus pulegioides	28.20 ± 13.59	0.67 ± 0.05	398.00 ± 143.42
Trifolium campestre	28.40 ± 3.51	0.01*	722.00 ± 450.63

TABLE 2 Statistics of the relationships between the volume of nectar (μl) (log10-transformed), the number of pollen grains (log10-transformed) and the number of flowers (log10-transformed), the per-grassland visitation rate of pollinators (i.e. the number of flower visits observed in a grassland during one survey), and descriptors of network structure and robustness. Statistically significant results ($p < 0.05$) are highlighted in bold

Dependent variable	Explanatory variable	Estimated coefficient	*SE*	*p*	AIC	χ^2	R^2_m	R^2_c
Visitation rate	Nectar volume (log 10-transformed)^2	−0.037	0.004	**<0.001**	1,215.200	73.497	0.886	0.974
	Number of pollen grains (log 10-transformed)^2	−0.347	0.030	**<0.001**	1,216.700	169.880	0.950	0.990
	Number of flowers (log 10-transformed)^2	−0.103	0.008	**<0.001**	1,281.700	191.960	0.890	0.976
Network connectance (*C*)	Nectar volume (log 10-transformed)^2	5.709	1.609	**<0.001**	−95.921	11.062	0.723	0.739
	Network size	−2.451	0.338	<0.001				
	Number of pollen grains (log 10-transformed)	−0.531	0.397	0.091	−86.232	2.851	0.629	0.651
	Network size	−2.209	0.308	<0.001				
	Number of flowers (log 10-transformed)^2	3.662	2.583	0.147	−87.493	2.096	0.652	0.667
	Network size	−2.019	0.326	<0.001				
Complemetary specialisation (H_2')	Nectar volume (log 10-transformed)	−0.061	0.230	0.791	−8.305	0.069	0.461	0.469
	Network size	−0.918	0.242	<0.001				
	Number of pollen grains (log 10-transformed)	−0.130	0.203	0.521	−8.646	0.410	0.477	0.480
	Network size	−0.935	0.217	<0.001				
	Number of flowers (log 10-transformed)	−0.087	0.200	0.663	−8.425	0.190	0.459	0.469
	Network size	−0.923	0.219	<0.001				
Weighted nestedness (wNODF)	Nectar volume (log 10-transformed)^2	−0.708	0.235	**0.010**	74.962	6.550	0.213	0.213
	Network size	0.055	0.052	0.258				
	Number of pollen grains (log 10-transformed)^2	−1.606	1.123	0.163	80.388	1.940	0.119	0.119
	Network size	0.056	0.062	0.318				
	Number of flowers (log 10-transformed)^2	−0.343	0.362	0.351	80.934	0.867	0.067	0.067
	Network size	0.042	0.063	0.448				
Network modularity (*Q*)	Nectar volume (log 10-transformed)	0.333	0.201	0.090	−57.070	2.866	0.076	0.076
	Network size	−0.111	0.201	0.574				
	Number of pollen grains (log 10-transformed)	0.322	0.168	0.051	−57.998	3.794	0.098	0.098
	Network size	−0.006	0.168	0.948				
	Number of flowers (log 10-transformed)	0.262	0.172	0.119	−56.633	2.429	0.065	0.065
	Network size	0.005	0.172	0.974				
Network robustness (TCM model)	Nectar volume (log 10-transformed)^2	−1.982	0.917	**0.026**	−97.870	4.897	0.263	0.263
	Network size	−0.360	0.194	0.055				
	Number of pollen grains (log 10-transformed)^2	1.655	3.240	0.589	−90.939	0.291	0.123	0.123
	Network size	−0.352	0.171	0.034				
	Number of flowers (log 10-transformed)	0.209	0.164	0.187	−94.054	1.737	0.151	0.151
	Network size	−0.403	0.164	0.013				

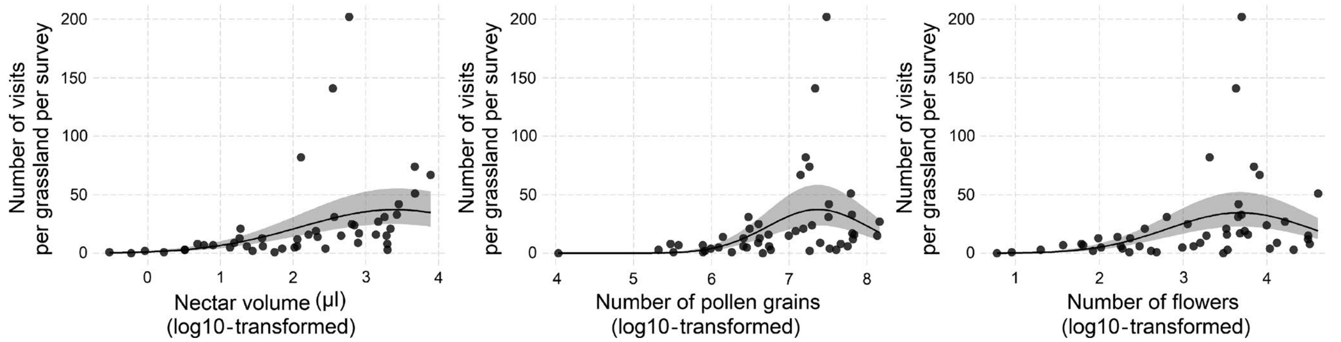

FIGURE 1 Relationship between the volume of nectar (μl) (log10-transformed), the number of pollen grains (log10-transformed) and the number of flowers (log10-transformed), and the visitation rate of pollinators (i.e. the number of flower visits observed in a grassland during one survey). Lines represent the estimates of the generalised linear mixed models. Black points are original data points, while the grey band represents 95% confidence interval around the regression line

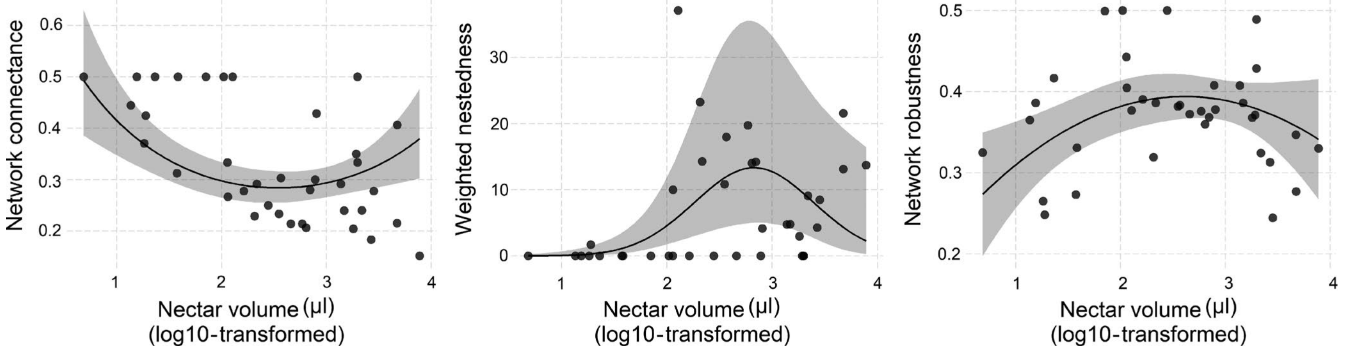

FIGURE 2 Relationship between the volume of nectar (μl) (log10-transformed), and the per-grassland network connectance (*C*), weighted nestedness (wNODF) and robustness (TCM model). Lines represent the estimates of the generalised linear mixed models. Black points are original data points, while the grey band represents 95% confidence interval around the regression line. Only significant results are shown in the figure

descriptors of network structure (i.e. network connectance, complementary specialisation, weighted nestedness and network modularity) and the network robustness, we used generalised linear mixed models (GLMMs, R version 3.4.3; package lme4). Specifically, each model included the grassland quantity of floral resources (i.e. volume of nectar, number of pollen grains or total number of flowers, log10-transformed) as explanatory variable, the visitation rate of pollinators per grassland, network connectance (*C*), complementary specialisation (H_2'), weighted nestedness (wNODF), network modularity (*Q*) and network robustness (TCM) as dependent variables and the grassland identity as random factor. Moreover, we included the quadratic term of floral resources in the GLMMs to account for possible nonlinear relationships (without removing the linear term). Since descriptors of network structure and robustness can be sensitive to the network size (total number of plant species × total number of pollinator species), we included this term in the models to account for its possible effects (Biella et al., 2020; Olesen & Jordano, 2002). Pollination networks too small for the quantification of descriptors of network structure and robustness (i.e. pollination networks with a number of plant or pollinator species equal to one) were excluded from the analyses. We compared linear and quadratic models based on their AIC values. We considered the best models as those with the lowest AIC (Akaike's information criterion) score. We performed GLMMs using (a) Poisson error distribution and log link functions for the visitation rate of pollinators per grassland; (b) Gamma error distribution and log link function for network connectance, complementary specialisation and weighted nestedness; (c) Gaussian error distribution and identity link function for network modularity and robustness. As the variables were in different units, estimates of regression coefficients were standardised. The significance of models was based on likelihood ratio tests (LRT; drop1 function; package stats) and the conditional and marginal coefficients of determination (R^2_c and R^2_m) for the GLMM models were calculated (r.squared function; package MuMIn; Barton, 2015). R^2_c shows the model variance explained by both fixed and random factors, while R^2_m represents the variance explained by fixed factors alone.

3 | RESULTS

3.1 | Floral resources

Nectar was detected for 22 plant species (52.3% of all species, Table 1). The lowest nectar volume was recorded in *Lotus herbaceus*

(Vill.) Jauzein, and in *Trifolium campestre* Schreb., with 0.01 µl per flower, and in *Bupleurum baldense* Turra (0.06 ± 0.00 µl; *M* ± *SD*). The highest volume of nectar was measured in *Cytisus hirsutus* L. (1.68 ± 0.31 µl). Except for orchid species, all plant species produced pollen grains that can be collected by pollinators (35 species, Table 1). The lowest number of pollen grains produced by a single flower was detected in *Thymus pulegioides* and *T. oenipontanus* H. Braun., with 398 ± 143.42 and 496 ± 174.15 pollen grains. The plant species with the highest number of pollen grains was *Spartium junceum* L., with 104,300 ± 20,099 pollen grains per flower. At the grassland scale, the total volume of nectar quantified during one survey varied from 0 to 7,762 µl, the total number of pollen grains from 10,800 to 144,501,208, while the number of flowers varied from 6 to 40,626.

3.2 | Relationships between floral resources and pollinator visitation rate

Overall, we registered 1,122 interactions between 42 plant and 90 pollinator species. The number of plant–pollinator interactions observed in a grassland during one survey varied from 0 to 202. The total number of flower visits observed in a grassland during one survey showed a statistically significant hump-shaped relationship with the volume of nectar (Table 2; Figure 1), the number of pollen grains (Table 2; Figure 1) and the number of flowers (Table 2; Figure 1). Results were consistent also when addressing the relationship between the visitation rate per flower (i.e. the number of flower visits per flower per 14 min) and the quantity of floral resources (i.e. volume of nectar, number of pollen grains, total number of flowers) per plot (see Appendix S4).

3.3 | Relationships between floral resources and network structure and robustness

Descriptors of network structure, such as network connectance (*C*), complementary specialisation (H_2'), weighted nestedness (wNODF) and modularity (*Q*), were significantly different from random values during all the monitoring surveys (*C*; H_2'; wNODF; *Q*; $p < 0.001$).

Network connectance showed a positive quadratic relationship with the volume of nectar (Table 2; Figure 2). This means that, at intermediate levels of nectar volume, the realised proportion of possible interactions in pollination networks was the lowest (Table 2; Figure 2). There were no significant relationships between network connectance, the number of pollen grains and the number of flowers (Table 2).

Network weighted nestedness showed a significant hump-shaped relationship with the volume of nectar (Table 2; Figure 2), indicating that, at intermediate levels of nectar volume, specialist species interact with generalist species more than at low and high levels of nectar volume. There were no significant relationships between network weighted nestedness, the number of pollen grains and the number of flowers.

No significant relationships were found between network complementary specialisation and modularity, and the different types of floral resources (Table 2).

Lastly, we found a significant hump-shaped relationship between network robustness and the volume of nectar (Table 2). In other words, at intermediate levels of nectar volume, rates of species co-extinctions were slower than at low and high levels of nectar volume. No significant relationships were observed between network robustness, the number of pollen grains and the number of flowers.

4 | DISCUSSION

4.1 | Relationships between floral resources and pollinator visitation rates

We found a significant hump-shaped relationship between the visitation rate of pollinators and the total quantity of floral resources at the community level. The observed hump-shaped pattern resembles the relationship previously found between the quantity of floral resources of a given plant species and its visitation rate per flower (Benadi & Pauw, 2018). In generalised pollination systems, interspecific competition for pollinators can cause a decrease in pollinator availability at the community level, which can result in a negative relationship between the quantity of floral resources and the visitation rate of pollinators (Totland & Matthews, 1998; Veddeler et al., 2006). Given that the studied range of floral resource quantity can substantially influence the observed relationship between visitation rate and the quantity of floral resources (Essenberg, 2012; Totland & Matthews, 1998), previous studies that found a positive or negative linear relationship in generalised pollination systems may have in fact observed part of a hump-shaped curve (Dauber et al., 2010; Ebeling et al., 2008; Seifan et al., 2014; Veddeler et al., 2006). In other words, large quantities of floral resources may attract more pollinators up to a certain threshold, after which the visitation rate may decrease as the pool of available pollinators may be saturated (Totland & Matthews, 1998). This saturation may likely be due to interspecific competition for pollinators.

4.2 | Relationship between floral resources and network structure and robustness

Although the visitation rate of pollinators peaked at intermediate levels of floral resources (irrespective of the type of resource), the relationship between the quantity of floral resources and the network structure and robustness was not consistent among different types of floral resources. High rates of pollinator visitation are expected to enhance the opportunities of interaction, ultimately improving the network structure and robustness (e.g. Vázquez et al., 2009). However, our study showed that only nectar volume explained most of the patterns in network structure (i.e. network connectance and weighted nestedness) and robustness (based on the topological co-extinction model).

Our models revealed that intermediate levels of nectar volume were associated with low values of network connectance. This outcome seems to contradict our previous result, in which intermediate levels of nectar volume were associated with high rates of pollinator visitation. Indeed, under increased rates of pollinator visitation, we should expect higher values of network connectance, because of the higher probability for different interactions to establish. However, network connectance is especially influenced by the network size, with values of network connectance increasing as the size of the network decreases (Valdovinos et al., 2009). Thus, if we assume that higher rates of pollinator visitation are associated with larger networks, then the probability for all possible interactions to occur would decrease. Moreover, network connectance quantification ignores interaction strength among species. These properties, coupled with the contradictory findings in the literature (e.g. Memmott et al., 2004; Vieira & Almeida-Neto, 2015), led authors to claim caution when interpreting patterns of network connectance (Blüthgen et al., 2006; Valdovinos et al., 2009). According to Heleno et al. (2012), network connectance applied on its own may be misleading and it should be integrated with other descriptors of network structure. In particular, the relationship between network connectance and robustness has not been yet clarified (Valdovinos, 2019) since high values of connectance may reflect either high (Memmott et al., 2004) or low levels of network robustness (Vieira & Almeida-Neto, 2015). In our study, intermediate levels of nectar volume were also associated with high values of weighted nestedness, thereby indicating that at intermediate levels of nectar volume the tendency of specialist species to interact with generalist species was higher. Such attributes may, in turn, improve network robustness in the face of local species extinctions (Bastolla et al., 2009). In nested networks, the loss of extinction-prone specialists is less likely to trigger the extinction of other specialists (Thébault & Fontaine, 2010; Vázquez & Aizen, 2004). The more direct descriptor of network robustness (TCM model) supported the insights on network robustness arising with patterns of weighted nestedness. Indeed, the TCM model revealed that the rates of secondary extinctions due to the loss of interaction partners were slower at intermediate levels of nectar volume.

As the Optimal Foraging Theory (Pyke, 1984) predicts, pollinators can adapt their foraging behaviour according to the available resources and their distribution in space and time, meaning that a decreased efficiency of resource collection may lead to lower rates of pollinator visitation (Cakmak et al., 2009). Intermediate levels of nectar volume might be abundant enough to attract pollinators at a sufficient rate, but small enough to force pollinators to visit different flowering species (e.g. Pyke, 1984; Vandelook et al., 2019). This would promote the opportunities of interaction between plants and pollinators, as well as among plants via shared pollinators, ultimately improving the robustness of pollination networks. Conversely, both large and small volumes of nectar were associated with low values of weighted nestedness. With small volumes of nectar, pollination contacts might be highly stochastic; on the other hand, large volumes of nectar may result in higher levels of interspecific competition among plants for pollinators (Bergamo et al., 2020). In both cases, the development of nested interactions would be less probable, resulting in low robustness of pollination networks.

Interestingly, no significant relationship could be observed between the total number of pollen grains and network structure and robustness. Differences in the time spent per flower and in the floral constancy between nectar- and pollen-seeking pollinators might explain the contrasting results obtained when considering the nectar volume and the number of pollen grains as target resource. According to Nicholls and Hempel de Ibarra (2017), nectar location and extraction takes less time than pollen handling. Therefore, longer times spent on flowers by pollen-seeking pollinators might have prevented us from recording their movements on different plant species (but see Buchmann & Shipman, 1990), resulting in less clear relationships between the number of pollen grains and descriptors of network structure and robustness. Moreover, pollen-seeking pollinators can develop high flower constancy (e.g. Heinrich, 1979; Minckley & Roulston, 2006); in other words, they can restrict consecutive visits to a single species (Kearns & Inouye, 1993). If we assume flower constancy being more frequent among pollen-seeking than nectar-seeking pollinators, then flower constancy may contribute to explaining the absence of a clear relationship between the number of pollen grains and network parameters. Clearly, additional experiments are needed to support these speculations.

Considering the number of flowers, we assume that this might be a too vague measure of floral resources to highlight patterns in pollination network structure and robustness. Although different types of floral resources induced very similar patterns in pollinator visitation rates, only nectar volume was significantly related to most of the descriptors of network structure and robustness. From the methodological point of view, using the number of flowers as a proxy of floral resources (i.e. nectar and pollen) has been repeatedly criticised (e.g. Benadi et al., 2014; Zimmerman & Pleasants, 1982). It is claimed that the number of flowers can be considered a valid measure of resource availability only when species have equal production rates of nectar and pollen (Zimmerman & Pleasants, 1982). Even with equal production rates of nectar and pollen, their nutritional value (depending on the composition and concentration of sugars, amino acids, etc.) can considerably differ between plant species, which, in turn, can affect pollination interactions (Cnaani et al., 2006; Somme et al., 2015). However, since the analysis of the composition of nectar and pollen is even more challenging than the quantification of their production, studies on floral resource availability rarely consider their nutritional value (Szigeti et al., 2016).

Our results revealed that the number of flowers can be a reliable proxy for the quantity of floral resources when assessing its relationship with pollinator visitation rate, supporting the reasoning of Hegland and Totland (2005), and justifying studies in which floral resources were quantified by counting the number of flowers (e.g. Benadi & Pauw, 2018; Bergamo et al., 2020). On the other hand, our results also highlighted that, when the aim is to investigate the relationship between floral resources and network structure and robustness, the number of flowers may fail in revealing possible outcomes of pollination-related processes. Moreover, it is worth noting that in this study we quantified nectar and pollen as standing crop (similarly to e.g. Lichtenberg et al., 2020; Pyke et al., 2020), but other approaches also exist for the quantification of nectar and pollen, such as quantifying daily production of nectar and harvesting pollen using sonication (e.g. Hicks et al., 2016), and differences in the quantification of nectar and pollen production may result in different relationships between floral resources and pollinator visitation, which is an issue that requires further investigation.

5 | CONCLUSIONS

In the studied species-rich grassland ecosystem, pollinator visitation rates displayed a hump-shaped relationship with the community-level quantity of floral resources. This observed relationship shows that communities with a larger quantity of floral resources attract more pollinators up to a certain threshold, after which the visitation rate may decrease as the pool of available pollinators becomes saturated, most probably due to competitive interactions for pollinators. Although pollinator visitation rates displayed a hump-shaped relationship with the quantity of floral resources, the relationship between floral resources and network structure and robustness was not consistent among different types of floral resources. Our results highlighted that, by using specific types of floral resources like the volume of nectar, we can reveal a series of possible ecological processes that would be masked by using the number of flowers as the sole measure of floral resource.

ACKNOWLEDGEMENTS

The authors were supported by the Ca' Foscari University of Venice and MIUR (E.F. and G.B.), and by NKFI K119225 and NKFI KH129483 (J.S. and P.T.).

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHORS' CONTRIBUTIONS

E.F. formulated the study design, conducted the fieldwork and analysed the data. All the authors improved the study design and wrote the manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.3n5tb2rjc (Fantinato et al., 2021).

ORCID

Edy Fantinato https://orcid.org/0000-0003-0114-4738
Judit Sonkoly https://orcid.org/0000-0002-4301-5240
Péter Török https://orcid.org/0000-0002-4428-3327
Gabriella Buffa https://orcid.org/0000-0002-0862-637X

REFERENCES

Akter, A., Biella, P., & Klecka, J. (2017). Effects of small-scale clustering of flowers on pollinator foraging behaviour and flower visitation rate. *PLoS ONE*, *12*, e0187976. https://doi.org/10.1371/journal.pone.0187976

Barton, K. (2015). *MuMIn: Multi-model inference*. R package version 1.43.17. Retrieved from https://CRAN.R-project.org/package=MuMIn

Bastolla, U., Fortuna, M. A., Pascual-García, A., Ferrera, A., Luque, B., & Bascompte, J. (2009). The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature*, *458*, 1018–1020. https://doi.org/10.1038/nature07950

Benadi, G., Hovestadt, T., Poethke, H.-J., & Blüthgen, N. (2014). Specialisation and phenological synchrony of plant-pollinator interactions along an altitudinal gradient. *Journal of Animal Ecology*, *83*, 639–650. https://doi.org/10.1111/1365-2656.12158

Benadi, G., & Pauw, A. (2018). Frequency dependence of pollinator visitation rates suggests that pollination niches can allow plant species coexistence. *Journal of Ecology*, *106*, 1982–1901. https://doi.org/10.1111/1365-2745.13025

Bergamo, P. J., Susin Streher, N., Traveset, A., Wolowski, M., & Sazima, M. (2020). Pollination outcomes reveal negative density-dependence coupled with interspecific facilitation among plants. *Ecology Letters*, *23*, 129–139. https://doi.org/10.1111/ele.13415

Biella, P., Akter, A., Ollerton, J., Nielsen, A., & Klecka, J. (2020). An empirical attack tolerance test alters the structure and species richness of plant–pollinator networks. *Functional Ecology*, *34*(11), 2246–2258. https://doi.org/10.1111/1365-2435.13642

Biella, P., Akter, A., Ollerton, J., Tarrant, S., Janeček, Š., Jersáková, J., & Klecka, J. (2019). Experimental loss of generalist plants reveals alterations in plant-pollinator interactions and a constrained flexibility of foraging. *Scientific Reports*, *9*, 1–13. https://doi.org/10.1038/s41598-019-43553-4

Biesmeijer, J. C., Roberts, S. P., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A. P., Potts, S. G., Kleukers, R., Thomas, C. D., Settele, J., & Kunin, W. E. (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, *313*, 351–354. https://doi.org/10.1126/science.1127863

Blüthgen, N., & Klein, A. M. (2011). Functional complementarity and specialisation: The role of biodiversity in plant-pollinator interactions. *Basic and Applied Ecology*, *12*(4), 282–291. https://doi.org/10.1016/j.baae.2010.11.001

Blüthgen, N., Menzel, F., & Blüthgen, N. (2006). Measuring specialization in species interaction networks. *BMC Ecology*, *6*, 9. https://doi.org/10.1186/1472-6785-6-9

Braun, J., & Lortie, C. J. (2019). Finding the bees knees: A conceptual framework and systematic review of the mechanisms of pollinator-mediated facilitation. *Perspectives in Plant Ecology, Evolution and Systematics*, *36*, 33–40. https://doi.org/10.1016/j.ppees.2018.12.003

Brosi, B. J., Niezgoda, K., & Briggs, H. M. (2017). Experimental species removals impact the architecture of pollination networks. *Biology Letters*, *13*, 20170243. https://doi.org/10.1098/rsbl.2017.0243

Buchmann, S. L., & Shipman, C. W. (1990). Pollen harvesting rates for *Apis mellifera* L. on *Gossypium* (Malvaceae) flowers. *Journal of the Kansas Entomological Society*, *63*, 92–100.

Burgos, E., Ceva, H., Perazzo, R. P. J., Devoto, M., Medan, D., Zimmermann, M., & María Delbue, A. (2007). Why nestedness in mutualistic networks? *Journal of Theoretical Biology*, *249*(2), 307–313. https://doi.org/10.1016/j.jtbi.2007.07.030

Cakmak, I., Sanderson, C., Blocker, T. D., Lisa Pham, L., Checotah, S., Norman, A. A., Harader-Pate, B. K., Tyler Reidenbaugh, R., Nenchev, P., Barthell, J. F., & Wells, H. (2009). Different solutions by bees to a foraging problem. *Animal Behaviour*, *77*(5), 1273–1280. https://doi.org/10.1016/j.anbehav.2009.01.032

Cnaani, J., Thomson, J. D., & Papaj, D. R. (2006). Flower choice and learning in foraging bumblebees: Effects of variation in nectar volume and concentration. *Ethology*, *112*, 278–285. https://doi.org/10.1111/j.1439-0310.2006.01174.x

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., Steege, H. T., Morgan, H. D., Heijden, M. G. A. V. D., Pausas, J. G., & Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, *51*, 335–380. https://doi.org/10.1071/BT02124

Dauber, J., Biesmeijer, J. C., Gabriel, D., Kunin, W. E., Lamborn, E., Meyer, B., Nielsen, A., Potts, S. G., Roberts, S. P. M., SÃµber, V., Settele, J., Steffan-Dewenter, I., Stout, J. C., Teder, T., Tscheulin, T., Vivarelli, D., & Petanidou, T. (2010). Effects of patch size and density on flower visitation and seed set of wild plants: A pan-European approach. *Journal of Ecology*, *98*, 188–196. https://doi.org/10.1111/j.1365-2745.2009.01590.x

Dormann, C. F., Gruber, B., & Fründ, J. (2008). Introducing the bipartite package: Analysing ecological networks. *R News*, *8*, 8–11.

Dormann, C. F., & Strauss, R. (2014). A method for detecting modules in quantitative bipartite networks. *Methods in Ecology and Evolution*, *5*, 90–98. https://doi.org/10.1111/2041-210X.12139

Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Food-web structure and network theory: The role of connectance and size. *Proceedings of the National Academy of Sciences of the United States of America*, *99*, 12917–12922. https://doi.org/10.1073/pnas.192407699

Ebeling, A., Klein, A. M., Schumacher, J., Weisser, W. W., & Tscharntke, T. (2008). How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos*, *117*, 1808–1815. https://doi.org/10.1111/j.1600-0706.2008.16819.x

Essenberg, C. J. (2012). Explaining variation in the effect of floral density on pollinator visitation. *The American Naturalist*, *180*, 153–166. https://doi.org/10.1086/666610

Fantinato, E. (2019). The impact of (mass) tourism on coastal dune pollination networks. *Biological Conservation*, *236*, 70–78. https://doi.org/10.1016/j.biocon.2019.05.037

Fantinato, E., Del Vecchio, S., & Buffa, G. (2019b). The co-occurrence of different grassland communities increases the stability of pollination networks. *Flora*, *255*, 11–17. https://doi.org/10.1016/j.flora.2019.03.017

Fantinato, E., Del Vecchio, S., Gaetan, C., & Buffa, G. (2019a). The resilience of pollination interactions: Importance of temporal phases. *Journal of Plant Ecology*, *12*, 157–162. https://doi.org/10.1093/jpe/rty005

Fantinato, E., Del Vecchio, S., Giovanetti, M., Acosta, A. T. R., & Buffa, G. (2018). New insights into plants co-existence in species-rich communities: The pollination interaction perspective. *Journal of Vegetation Science*, *29*, 6–14. https://doi.org/10.1111/jvs.12592

Fantinato, E., Sonkoly, J., Török, P., & Buffa, G. (2021). Data from: Patterns of pollination interactions at community-level are related to the type and quantity of floral resources. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.3n5tb2rjc

Fenster, C. B., Armbruster, W. S., Wilson, P., Dudash, M. R., & Thomson, J. D. (2004). Pollination syndromes and floral specialisation. *Annual Review of Ecology Evolution and Systematics*, *35*, 375–403. https://doi.org/10.1146/annurev.ecolsys.34.011802.132347

Fowler, R. E., Rotheray, E. L., & Goulson, D. (2016). Floral abundance and resource quality influence pollinator choice. *Insect Conservation and Diversity*, *9*, 481–494. https://doi.org/10.1111/icad.12197

Galeano, J., Pastor, J. M., & Iriondo, J. M. (2009). Weighted-interaction nestedness estimator (WINE): A new estimator to calculate over frequency matrices. *Environmental Modelling & Software*, *24*, 1342–1346. https://doi.org/10.1016/j.envsoft.2009.05.014

Goldstein, J., & Zych, M. (2016). What if we lose a hub? Experimental testing of pollination network resilience to removal of keystone floral resources. *Arthropod–Plant Interactions*, *10*, 263–271. https://doi.org/10.1007/s11829-016-9431-2

Hegland, S. J., & Totland, Ø. (2005). Relationships between species' floral traits and pollinator visitation in a temperate grassland. *Oecologia*, *145*, 586–594. https://doi.org/10.1007/s00442-005-0165-6

Heinrich, B. (1979). Resource heterogeneity and patterns of movement in foraging bumblebees. *Oecologia*, *40*, 235–245. https://doi.org/10.1007/BF00345321

Heleno, R., Devoto, M., & Pocock, M. (2012). Connectance of species interaction networks and conservation value: Is it any good to be well connected? *Ecological Indicators*, *14*, 7–10. https://doi.org/10.1016/j.ecolind.2011.06.032

Hicks, D. M., Ouvrard, P., Baldock, K. C. R., Baude, M., Goddard, M. A., Kunin, W. E., Mitschunas, N., Memmott, J., Morse, H., Nikolitsi, M., Osgathorpe, L. M., Potts, S. G., Robertson, K. M., Scott, A. V., Sinclair, F., Westbury, D. B., & Stone, G. N. (2016). Food for pollinators: Quantifying the nectar and pollen resources of urban flower meadows. *PLoS ONE*, *11*, e0158117. https://doi.org/10.1371/journal.pone.0158117

Hoyle, H., Norton, B., Dunnett, N., Richards, J. P., Russell, J. M., & Warren, P. (2018). Plant species or flower colour diversity? Identifying the drivers of public and invertebrate response to designed annual meadows. *Landscape and Urban Planning*, *180*, 103–113. https://doi.org/10.1016/j.landurbplan.2018.08.017

Jordano, P. (2016). Sampling networks of ecological interactions. *Functional Ecology*, *30*, 1883–1893. https://doi.org/10.1111/1365-2435.12763

Justino, D. G., Maruyama, P. K., & Oliveira, P. E. (2012). Floral resource availability and hummingbird territorial behaviour on a Neotropical savanna shrub. *Journal of Ornithology*, *153*, 189–197. https://doi.org/10.1007/s10336-011-0726-x

Kaiser-Bunbury, C. N., & Blüthgen, N. (2015). Integrating network ecology with applied conservation: A synthesis and guide to implementation. *AoB Plants*, *7*, plv076. https://doi.org/10.1093/aobpla/plv076

Kaltenrieder, P., Procacci, G., Vannière, B., & Tinner, W. (2010). Vegetation and fire history of the Euganean Hills (Colli Euganei) as recorded by Lateglacial and Holocene sedimentary series from Lago della Costa (northeastern Italy). *The Holocene*, *20*, 679–695. https://doi.org/10.1177/0959683609358911

Kearns, C. A., & Inouye, D. W. (1993). *Techniques for pollination biologists*. University Press of Colorado.

Klumpers, S. G., Stang, M., & Klinkhamer, P. G. (2019). Foraging efficiency and size matching in a plant–pollinator community: The importance of sugar content and tongue length. *Ecology Letters*, *22*, 469–479. https://doi.org/10.1111/ele.13204

Lázaro, A., Tscheulin, T., Devalez, J., Nakas, G., & Petanidou, T. (2016). Effects of grazing intensity on pollinator abundance and diversity, and on pollination services. *Ecological Entomology*, *41*, 400–412. https://doi.org/10.1111/een.12310

Lichtenberg, E. M., Richman, S. K., Irwin, R. E., & Bronstein, J. L. (2020). Competition for nectar resources does not affect bee foraging tactic constancy. *Ecological Entomology*, *45*, 904–909. https://doi.org/10.1111/een.12866

Memmott, J., Waser, N. M., & Price, M. V. (2004). Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society B: Biological Sciences*, *271*(1557), 2605–2611. https://doi.org/10.1098/rspb.2004.2909

Minckley, R. L., & Roulston, T. H. (2006). Incidental mutualisms and pollen specialization among bees. In N. M. Waser, & J. Ollerton (Eds.), *Plant–pollinator interactions: From specialization to generalization* (pp. 69–98). The University of Chicago Press.

Nicholls, E., & Hempel de Ibarra, N. (2017). Assessment of pollen rewards by foraging bees. *Functional Ecology*, *31*, 76–87. https://doi.org/10.1111/1365-2435.12778

Noordijk, J., Delille, K., Schaffers, A. P., & Sýkora, K. V. (2009). Optimizing grassland management for flower-visiting insects in roadside verges. *Biological Conservation*, *142*(10), 2097–2103. https://doi.org/10.1016/j.biocon.2009.04.009

Olesen, J. M., Bascompte, J., Dupont, Y. L., Elberling, H., Rasmussen, C., & Jordano, P. (2010). Missing and forbidden links in mutualistic networks. *Proceedings of the Royal Society B: Biological Sciences*, *278*, 725–732. https://doi.org/10.1098/rspb.2010.1371

Olesen, J. M., & Jordano, P. (2002). Geographic patterns in plant–pollinator mutualistic networks. *Ecology*, *83*(9), 2416–2424. https://doi.org/10.1890/0012-9658(2002)083[2416:GPIPPM]2.0.CO;2

Petanidou, T., & Smets, E. (1995). The potential of marginal lands for bees and apiculture: Nectar secretion in Mediterranean shrublands. *Apidologie*, *26*, 39–52. https://doi.org/10.1051/apido:19950106

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology & Evolution*, *25*, 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Pyke, G. H. (1984). Optimal foraging theory: A critical review. *Annual Review of Ecology and Systematics*, *15*, 523–575. https://doi.org/10.1146/annurev.es.15.110184.002515

Pyke, G. H., Kalman, J. R., Bordin, D. M., Blanes, L., & Doble, P. A. (2020). Patterns of floral nectar standing crops allow plants to manipulate their pollinators. *Scientific Reports*, *10*(1), 1–10. https://doi.org/10.1038/s41598-020-58102-7

Quantum GIS Development Team. (2000). *QGIS Geographic Information System*. Open Source Geospatial Foundation Project. Retrieved from http://qgis.osgeo.org

Rathcke, B. (1983). Competition and facilitation among plants for pollination. *Pollination Biology*, *305*, 329. https://doi.org/10.1007/s11258-013-0274-y

Reverté, S., Bosch, J., Arnan, X., Roslin, T., Stefanescu, C., Calleja, J. A., Molowny-Horas, R., Hernández-Castellano, C., & Rodrigo, A. (2019). Spatial variability in a plant–pollinator community across a continuous habitat: High heterogeneity in the face of apparent uniformity. *Ecography*, *42*(9), 1558–1568. https://doi.org/10.1111/ecog.04498

Seifan, M., Hoch, E. M., Hanoteaux, S., & Tielbörger, K. (2014). The outcome of shared pollination services is affected by the density and spatial pattern of an attractive neighbour. *Journal of Ecology*, *102*, 953–962. https://doi.org/10.1111/1365-2745.12256

Slaviero, A., Del Vecchio, S., Pierce, S., Fantinato, E., & Buffa, G. (2016). Plant community attributes affect dry grassland orchid establishment. *Plant Ecology*, *217*, 1533–1543. https://doi.org/10.1007/s11258-016-0666-x

Somme, L., Vanderplanck, M., Michez, D., Lombaerde, I., Moerman, R., Wathelet, B., Wattiez, R., Lognay, G., & Jacquemart, A.-L. (2015). Pollen and nectar quality drive the major and minor floral choices of bumble bees. *Apidologie*, *46*, 92–106. https://doi.org/10.1007/s13592-014-0307-0

Stock, M., Piot, N., Vanbesien, S., Vaissière, B., Coiffait-Gombault, C., Smagghe, G., & De Baets, B. (2020). Information content in pollination network reveals missing interactions. *Ecological Modelling*, *431*, 109161. https://doi.org/10.1016/j.ecolmodel.2020.109161

Szigeti, V., Kőrösi, Á., Harnos, A., Nagy, J., & Kis, J. (2016). Measuring floral resource availability for insect pollinators in temperate grasslands – A review. *Ecological Entomology*, *41*, 231–240. https://doi.org/10.1111/een.12298

Thébault, E., & Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, *329*, 853–856. https://doi.org/10.1126/science.1188321

Totland, Ø., & Matthews, I. (1998). Determinants of pollinator activity and flower preference in the early spring blooming *Crocus vernus*. *Acta Oecologica*, *19*, 155–165. https://doi.org/10.1016/S1146-609X(98)80019-2

Valdovinos, F. S. (2019). Mutualistic networks: Moving closer to a predictive theory. *Ecology Letters*, *22*(9), 1517–1534. https://doi.org/10.1111/ele.13279

Valdovinos, F. S., Ramos-Jiliberto, R., Flores, J. D., Espinoza, C., & López, G. (2009). Structure and dynamics of pollination networks: The role of alien plants. *Oikos*, *118*(8), 1190–1200. https://doi.org/10.1111/j.1600-0706.2009.17364.x

Vanbergen, A. J., Woodcock, B. A., Heard, M. S., & Chapman, D. S. (2017). Network size, structure and mutualism dependence affect the propensity for plant–pollinator extinction cascades. *Functional Ecology*, *31*, 1285–1293. https://doi.org/10.1111/1365-2435.12823

Vandelook, F., Janssens, S. B., Gijbels, P., Fischer, E., Van den Ende, W., Honnay, O., & Abrahamczyk, S. (2019). Nectar traits differ between pollination syndromes in Balsaminaceae. *Annals of Botany*, *20*, 1–11. https://doi.org/10.1093/aob/mcz072

Vázquez, D. P., & Aizen, M. A. (2004). Asymmetric specialization: A pervasive feature of plant–pollinator interactions. *Ecology*, *85*, 1251–1257. https://doi.org/10.1890/03-3112

Vázquez, D. P., Blüthgen, N., Cagnolo, L., & Chacoff, N. P. (2009). Uniting pattern and process in plant–animal mutualistic networks: A review. *Annals of Botany*, *103*(9), 1445–1457. https://doi.org/10.1093/aob/mcp057

Veddeler, D., Klein, A. M., & Tscharntke, T. (2006). Contrasting responses of bee communities to coffee flowering at different spatial scales. *Oikos*, *112*, 594–601. https://doi.org/10.1111/j.0030-1299.2006.14111.x

Vieira, M. C., & Almeida-Neto, M. (2015). A simple stochastic model for complex coextinctions in mutualistic networks: Robustness decreases with connectance. *Ecology Letters*, *18*(2), 144–152. https://doi.org/10.1111/ele.12394

Wang, X., Zeng, T., Wu, M., & Zhang, D. (2020). Seasonal dynamic variation of pollination network is associated with the number of species in flower in an oceanic island community. *Journal of Plant Ecology*, *13*, 657–666. https://doi.org/10.1093/jpe/rtaa054

Ye, Z. M., Dai, W. K., Jin, X. F., Gituru, R. W., Wang, Q. F., & Yang, C. F. (2014). Competition and facilitation among plants for pollination: Can pollinator abundance shift the plant–plant interactions? *Plant Ecology*, *215*, 3–13. https://doi.org/10.1007/s11258-013-0274-y

Zimmerman, M., & Pleasants, J. M. (1982). Competition among pollinators: Quantification of available resources. *Oikos*, *38*, 381–383. https://doi.org/10.2307/3544681

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Fantinato, E., Sonkoly, J., Török, P., & Buffa, G. (2021). Patterns of pollination interactions at the community level are related to the type and quantity of floral resources. *Functional Ecology*, 35, 2461–2471. https://doi.org/10.1111/1365-2435.13915