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The resilience of pollination interactions: importance of temporal phases

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Abstract

Aims

The loss of species that engage in close ecological interactions, such as pollination, has been shown to lead to secondary extinctions, ultimately threatening the overall ecosystem stability and functioning. Pollination studies are currently flourishing at all possible levels of interaction organization (i.e., species, guild, group and network), and different methodological protocols aimed to define the resilience of pollination interactions have been proposed. However, the temporal dimension of the resilience of pollination interactions has been often overlooked. In the light of these considerations, we addressed the following questions: does a temporal approach help to reveal critical moments during the flowering season, when pollination interactions are less resilient to perturbations? Do pollination interactions evaluated at species, guild, group and network level show different patterns when assessed through time?

Methods

We monitored contacts between plant and pollinator species in dry grassland communities every 15 days during the overall community flowering season (12 surveys). For each survey, we built a quantitative plant–pollinator interaction matrix and we calculated two sets of metrics characterizing, respectively, the diversity and the distribution of interactions across hierarchical levels. To describe the diversity of interactions, we calculated partner diversity (PD) at the species level, vulnerability/generality (V/G) at the guild level, and interaction diversity and evenness at the network level. The distribution of interactions was characterized by calculating selectiveness at the species and the network level, and modularity at the group level. We assessed the temporal variation of PD, V/G at the level of plants and pollinators, and species selectiveness, by means of Linear Mixed Models (LMMs). To investigate the temporal variation of indexes calculated at group and network level, we applied simple linear and quadratic regressions after checking for temporal autocorrelation in residuals.

Important Findings

When taking into account the temporal dimension of interactions, the diversity of interactions showed different patterns at different levels of organization. At the species level, no relationship was disclosed between PD and time, when assessing the temporal trend of V/G separately for the guild of plants and pollinators we observed an asymmetric structure of interactions. Pollination interactions showed to be asymmetric throughout the flowering season; however, evenness of interactions and network selectiveness showed significant positive relationships with time, revealing a poorer network of interactions during the end of the flowering season. The temporal analysis of pollination interactions revealed a stronger risk of secondary extinctions at the end of the flowering season, due to a lower degree of redundancy and thus of resilience of the overall network of interactions.

Keywords: asymmetry, complementarity, ecosystems' resilience, redundancy, species-rich ecosystems

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INTRODUCTION

The interactions between plant species and wild animals for pollination are currently an issue of increasing interest worldwide. This essential process is considered one of the key ecosystem functions, necessary to preserve biodiversity and the functioning of both natural terrestrial ecosystems and crops (Fontaine *et al.* 2006; Ollerton *et al.* 2011). In addition, together with other biotic and abiotic factors, pollination interactions can contribute to define plant communities structure and composition (Dante *et al.* 2013; Fantinato *et al.* 2016a, 2017a), thus influencing ecosystem properties.

Mounting evidence exists that pollinators are declining as a consequence of global environmental changes and degradation (Biesmeijer *et al.* 2006; Potts *et al.* 2010; Winfree *et al.* 2009). Anthropogenic changes in land use (e.g. agriculture, industry and urbanization) are ranked among the most important pressures, typically resulting in the loss of native vegetation and changes to its spatial distribution, deterioration of vegetation structure, reduction of species richness and abundance, and changes in species composition (Del Vecchio *et al.* 2016; Fahrig 2003; Fischer and Lindenmeyer 2007). As for pollinators, the destruction and fragmentation of natural or semi-natural habitats is expected to cause the loss of forage and breeding habitats, or at least less floral forage over shorter periods of time (Hall *et al.* 2016), population subdivision and the consequent demographic and genetic stochasticity (Fischer and Lindenmayer 2007).

Under human-induced land use changes, several pollination interaction attributes have been recognized to deeply influence the resilience of pollination interactions to perturbations (e.g., the degree of pollination specialization; Blüthgen and Klein 2011; Fantinato *et al.* 2017b; Kaiser-Bunbury and Blüthgen 2015; Thébault *et al.* 2010; Vázquez and Aizen 2004). Pollination studies are currently flourishing at all possible levels of organization (i.e., species, guild, group and network), and different methodological protocols aimed to define the resilience of pollination interactions have been proposed (e.g., Biella *et al.* 2017; Kaiser-Bunbury *et al.* 2010; Thébault and Fontaine 2010; Tylianakis *et al.* 2010). Especially, Kaiser-Bunbury and Blüthgen (2015) introduced a set of metrics describing the diversity and the distribution of pollination interactions at different hierarchical levels, highlighting their effectiveness in defining the resilience of pollination interactions to perturbations.

However, the temporal dimension of the resilience of pollination interactions has been often overlooked (Willmer 2011). Nonetheless, all studies that have explored the temporal dynamics of pollination interactions (e.g., Basilio *et al.* 2006; Lundgren and Olesen 2005; Medan *et al.* 2002; 2006; Olesen *et al.* 2008) evidenced that pollination interactions can strongly change through time. Arguably, pollination interactions can greatly vary during the community flowering season due to changes in both environmental, ecological, biotic and anthropogenic features (e.g., temperature, resources availability, community composition, disturbance etc.), possibly leading to temporal fluctuations of the resilience of mutualistic communities (Thébault *et al.* 2010; Vázquez and Aizen 2004).

In the light of these considerations, we addressed the following questions: does a temporal approach help to reveal critical moments during the flowering season, when pollination interactions are less resilient to perturbations? Do pollination interactions evaluated at species, guild, group and network level show different patterns when assessed through time?

We addressed the problem by assessing the temporal dynamic of pollination interactions in dry grassland communities. Dry grasslands are one of the most important semi-natural habitat in Europe (Dengler *et al.* 2014; Habel *et al.* 2013). They have great conservation value (Wellstein *et al.* 2014) for their high biological diversity which includes a variety of rare species from different taxonomic groups, including plants, butterflies and other invertebrates (Bobbink and Willems 1988; Fantinato *et al.* 2016b; Ssymank *et al.* 1998; Van Swaay 2002; Wellstein *et al.* 2014). Dry grasslands are severely endangered by threats that apply to many other plant communities: changes in land use, through intensification of agriculture as well as abandonment followed by bush encroachment, fragmentation, decreased habitat quality, and the consequent decline of the biodiversity they host (Dengler *et al.* 2014; Godó *et al.* 2017; Luoto *et al.* 2003; Török *et al.* 2011). Furthermore, being characteristic of pastoral and low-intensity managed landscapes (Wellestein *et al.* 2014), dry grasslands can crucially contribute to biodiversity and pollination service retention in agricultural landscapes (Fantinato *et al.* 2017a). Therefore, the assessment of the resilience of pollination interactions to perturbations represents an important step for the maintenance of functioning of dry grassland communities, and of the pollination service they provide.

MATERIALS AND METHODS

Site selection and data collection

Field sampling was carried out on semi-natural, oligo- to mesotrophic, *Bromus erectus*-dominated dry grasslands in the Euganean Hills (NE Italy; Fantinato *et al.* 2016b). They establish on middle-altitude limestone slopes, on sites characterized by poorly developed, shallow and skeletal calcareous soils, with an average pH of 7.5 (Bini 2001; Slaviero *et al.* 2016). They are scattered and fragmented in a patchy landscape of arable fields, vineyards and olive groves, intermingled with low-intensive mowed mesophilous grasslands and forests. Local climate data reveal an average annual rainfall of 720 mm (Kaltenrieder *et al.* 2010), with two maximum peaks in April and September and two minimum peaks in July and December. Annual mean temperature is 13.0°C, with a peak mean high temperature in July and a low in January.

Within an area of 16 ha, we randomly placed 26 permanent plots of 2 m × 2 m. In each plot, animal-pollinated species presence was recorded and their flowering phenology was monitored every 15 days, from 1 April to 30 September in 2016, for a total of 12 surveys. The 12 surveys were carried out in warm and sunny days (e.g., Goverde *et al.* 2002; Ghazoul *et al.* 2006; Rodriguez-Perez and Traveset 2016). Flowering monitoring started at the opening of the first flower (Pleasants 1980) and ended when individual plants no longer possessed any flower with anthers (Dante *et al.* 2013). Plant species nomenclature follows Conti *et al.* (2005).

Furthermore, during each survey, we recorded visiting insects. The visitation frequency was monitored by counting the number of visits to each plant species during 14 min. The observation period was split in 7-min sets distributed during two daily intervals (from 10 a.m. to 1 p.m.; from 1 p.m. to 4 p.m.) to ensure the observation of pollinators showing different daily periods of activity. We considered and counted as pollinators only those insects landing on the flower, visiting it for >1 s, and getting in direct contact with the floral reproductive organs (Hegland and Totland 2005). Floral visitors were identified at the level of species or morphospecies (Memmott 1999). Bush-crickets were included as pollinators because juveniles were observed to land on flowers and to carry pollen accidently on their legs and make contact with the floral reproductive organs.

Data analysis

We built a quantitative plant–pollinator interaction matrix for each survey (12). As interaction weight, we used the visitation frequency, expressed as the number of contacts between each plant and pollinator species during a census. To define the resilience of dry grassland pollination interactions, we followed Kaiser-Bunbury and Blüthgen (2015). We used the *bipartite* package (Dormann *et al.* 2008) run in R to obtain all the metrics calculated in this study. The pollination interactions attributes were described through two sets of metrics characterizing, respectively, the diversity and the distribution of interactions across hierarchical levels (i.e., species, guild, group and network level). To describe the diversity of interactions, we calculated partner diversity (PD) at the species level, vulnerability/generality (V/G; i.e., mean PD across (i) plant and (ii) pollinator species) at the guild level, and interaction diversity (ID) and evenness (IE) at the network level. The distribution of interactions was characterized by calculating selectiveness at the species and the network level (d′ and H'_2, respectively; Blüthgen *et al.* 2006), and modularity at the group level (Q; Dormann and Strauss 2014). For a detailed description of the metrics see Kaiser-Bunbury and Blüthgen (2015). Since modularity (Q) strongly depends on network size, to ensure that the comparison of modularity (Q) was between the most unbiased estimates (Lazaro *et al.* 2016; Traveset *et al.* 2017), we corrected observed modularity (Q) for the mean of values resulting from 1000 randomly generated matrices of the same size as the focal one, using a null model that fixes total number of interactions (function null model; method; r2d; R-based package *bipartite*; Ballantyne *et al.* 2017). Standardized *z*-scores were calculated for each group and network level metric (z = [observed − null mean]/null σ) to test for significant difference from the null model distribution.

We assessed the temporal variation of PD, V/G at the levels of plants and pollinators, and species selectiveness (d′) by means of LMMs (R-based package *nlme*). We regressed each metric with respect to a quadratic trend and a random factor represented by the identity of species. Possible temporal dependences among the different surveys were taken into account using a first order autoregressive model for the random errors.

To investigate the temporal variation of indexes calculated at group and network level, we applied simple linear and quadratic regressions. Specifically, we applied simple linear regressions to assess the temporal variation of IE, corrected modularity (Q) and network selectiveness (H'_2); while a simple quadratic regression was calculated to assess the temporal variation of ID. Simple linear regressions and the quadratic model were firstly checked for temporal autocorrelation in residuals by performing a Durbin–Watson test (function durbinWatsonTest; library-based package *car*).

RESULTS

Diversity of interactions

Overall, we identified 34 plant and 77 pollinator species. At the species level, PD did not show a significant relationship with time (PD; $t = -0.321$; $P = 0.748$; Fig. 1A). At the guild level, V/G of plants showed a significant U-shaped relationship with time (V/G; $t = 2.056$; $P = 0.046$; Fig. 1B); while, V/G of pollinators showed a significant hump-shaped trend (V/G; $t = -2.439$; $P = 0.016$; Fig. 1C). Values of ID (Table 1) and IE (Table 1) did not show temporal autocorrelation in residuals (ID; $P = 0.06$; IE; $P = 0.756$). ID showed a significant hump-shaped relationship with time ($R^2 = 0.498$; $P = 0.044$), while IE increased significantly through time ($R^2 = 0.356$; $P = 0.040$).

Distribution of interactions

The degree of species selectiveness (d′) did not show a significant relationship with time ($t = -1.774$; $P = 0.078$; Fig. 1D). Values of corrected modularity (Q; Table 1) and network selectiveness (H'_2; Table 1) did not show temporal autocorrelation in residuals (Q; $P = 0.98$; H'_2; $P = 0.089$). No significant relationship could be detect between corrected modularity and time ($R^2 = 0.034$; $P = 0.56$). Contrarily, network selectiveness (H'_2) followed a significant positive trend ($R^2 = 0.546$; $P = 0.001$).

DISCUSSION

Pollination interactions in dry grassland communities showed to have a strong temporal dynamic. The application of Kaiser-Bunbury and Blüthgen (2015) methodology on a time series of pollination interactions allowed us to highlight critical moments, in which pollination interactions resulted more vulnerable and less resilient to perturbations.

When taking into account the temporal dimension of interactions, the diversity of interactions showed different and even contrasting patterns at different levels of organization (species, guild and network). If, at the species level, no relationship was disclosed between PD and time, when assessing the temporal trend of PD separately for the guilds of plants and pollinators (i.e., V/G) we could observe two opposite temporal trends. Generalist plants (i.e., plant species interacting with a

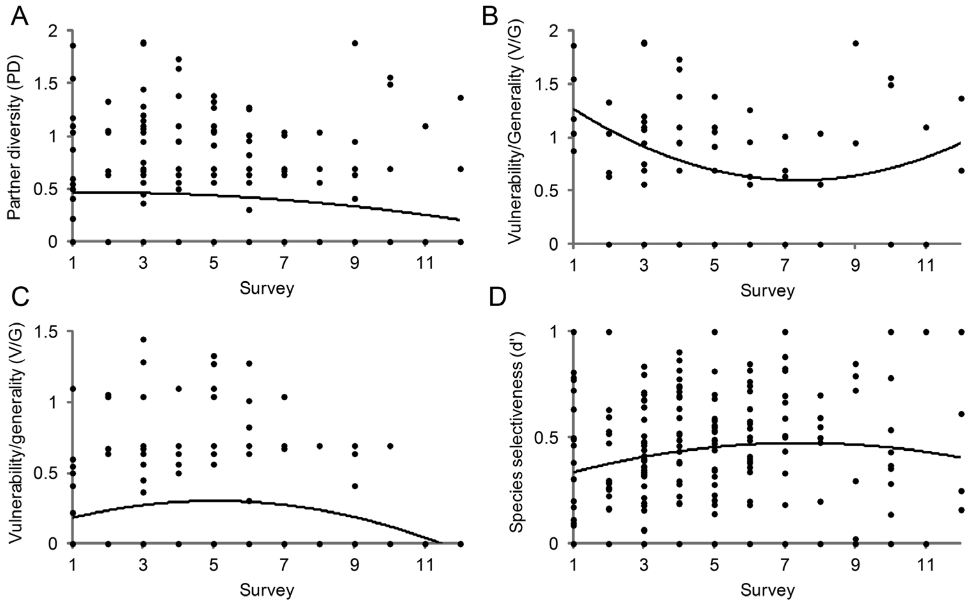

Figure 1: relationships between time and (**a**) species partner diversity (PD), (**b**) plant species vulnerability/generality (V/G), (**c**) pollinator species V/G and (**d**) species selectiveness (d′). Lines represent the estimates of the models corrected from temporal dependences among the different surveys.

broad range of pollinator species) prevailed during the start and the end of the community flowering season and were pollinated by specialist pollinators (i.e., pollinator species interacting with a few plant species), while specialist plants (i.e., plant species interacting with a few pollinator species) flowered during the peak of the community flowering season, and were pollinated by generalist pollinators (i.e., pollinator species interacting with a broad range of plant species), resulting in an asymmetric structure of interactions. An asymmetric structure has been proven to have important implications for mutualistic communities (Abramson *et al.* 2011; Thébault *et al.* 2010; Vázquez and Aizen 2006). The way in which pollination interactions are structured, i.e. the type of interactions developed among species (symmetric or asymmetric), might affect their own stability and function, communities organization as well as the entire ecosystem functioning (Bascompte and Jordano 2013; Krause *et al.* 2003; McCann *et al.* 2005). The structure of interactions is also supposed to influence the mutualistic communities responses to disruptions, i.e. resilience to perturbations such as the extinction of species if, for example, generalist partners buffer the loss of specialist ones (Memmott *et al.* 2004) or, conversely, fragility, if the most-connected partners disappear. Contrarily to symmetry, asymmetry in species interactions has been proven to confer higher resilience to mutualistic communities, preventing the occurrence of secondary extinctions (Thébault *et al.* 2010; Vázquez and Aizen 2004). Furthermore, Ashworth *et al.* (2004) theorized that asymmetric interactions would mitigate the effects of habitat destruction and fragmentation on the reproductive success of specialist plants, which have been predicted to be more sensitive to the loss of their specific mutualist partners than generalist ones.

Table 1: group and network level metrics. Q, modularity; ID, interaction diversity; IE, interaction evenness; H′$_2$, network selectiveness

	Group level metrics		Network level metrics		
Survey	Observed Q	Corrected Q	ID	IE	H′$_2$
1	**0.416**	0.371	**1.798**	**0.417**	**0.394**
2	**0.574**	0.334	**2.968**	**0.638**	**0.226**
3	**0.562**	0.402	**3.464**	**0.585**	**0.392**
4	**0.746**	0.594	**3.345**	**0.610**	**0.467**
5	**0.548**	0.343	**3.364**	**0.620**	**0.217**
6	**0.587**	0.382	**2.967**	**0.583**	**0.384**
7	**0.646**	0.410	**2.328**	**0.547**	**0.604**
8	**0.518**	0.153	**1.977**	**0.619**	**0.393**
9	**0.442**	0.172	**2.112**	**0.800**	**0.543**
10	**0.506**	0.065	**2.303**	**0.677**	**0.451**
11	**1.000**	0.799	**2.043**	**0.590**	**0.812**
12	**1.000**	0.748	**1.778**	**0.716**	**0.747**

Significant differences of observed values from null model predictions were indicated in bold ($P < 0.001$).

Despite pollination interactions in dry grasslands showed to be asymmetric throughout the flowering season, ID at the network level followed a significant hump-shaped trend. Lower values of ID during the start and the end of the community flowering season may imply a lower network resilience (Blüthgen *et al.* 2008; Lazaro *et al.* 2016; Traveset *et al.* 2017). However, given the positive trend of IE, we expect that the resilience of the pollination network might be especially low at the end of the community flowering season. In fact, according to Kaiser-Bunbury and Blüthgen (2015) when high values of IE are coupled with low values of ID, they may not represent the spread of more uniform connections among plants and pollinators but rather the development of a poorer network of interactions.

Interaction distributions evaluated at the network level through the analysis of network selectiveness (H'_2), confirmed the pattern of vulnerability arose from the temporal assessment of the network diversity of interactions. A high degree of selectiveness in pollination networks occurs when two or more species improve the overall pollination network by adding further original interactions (Blüthgen *et al.* 2006). High selectiveness requires a certain degree of specialization of each interaction, while high generalization is associated with high pollinator sharing and thus redundancy. Redundancy implies that species are mutually substitutable in terms of a given ecological function (Mouillot *et al.* 2013). In a mutualistic community, it confers a high resilience, acting as a buffer against species loss (Memmott *et al*. 2004). Conversely, a high selectiveness entails a high dependence of plant diversity to flower visitor diversity (and vice versa), thereby resulting in less resilience to perturbations (Blüthgen and Klein 2011).

Thus, despite a comparable functional composition of generalist plant and specialized pollinator species at the start and at the end of the flowering season, the degree of selectiveness of the pollination network revealed a stronger risk of secondary extinctions during the end of the flowering season, due to a lower degree of redundancy and resilience of the overall network.

From a conservation perspective, this implies that the loss of plant species flowering at the end of the community flowering season can put the ecosystem functioning more in danger than the loss of plant species flowering during the start and at the peak of the community flowering season. In natural landscapes, the loss of one of them may force the related pollinator species to forage elsewhere, damaging the integrity of the pollination network. However, in fragmented habitats surrounded by a hostile matrix, which represents an increasingly common situation for dry grasslands, effects may be even more pronounced. The loss of one of the late flowering plant species would indeed lead to the secondary extinction of specialized pollinators observed to forage exclusively on them, because incapable to find foraging habitats nearby, ultimately compromising the integrity of the mutualistic community also for the upcoming flowering seasons.

Conflict of interest statement. None declared.

REFERENCES

Abramson G, Soto CAT, Oña L (2011) The role of asymmetric interactions on the effect of habitat destruction in mutualistic networks. *PLOS ONE* **6**:e21028.

Ashworth L, Aguilar R, Galetto L, Aizen MA (2004) Why do pollination generalist and specialist plant species show similar reproductive susceptibility to habitat fragmentation? *J Ecol* **92**:717–19.

Ballantyne G, Baldock KCR, Rendell L, Willmer PG (2017) Pollinator importance networks illustrate the crucial value of bees in a highly speciose plant community. *Sci Rep* **7**:8389.

Bascompte J, Jordano P (2013) *Mutualistic Networks*. Princeton Univ Press

Basilio AM, Medan D, Torretta JP, *et al.* (2006) A year-long plant–pollinator network. *Austral Ecol* **31**:975–83.

Biella P, Ollerton J, Barcella M, *et al.* (2017) Network analysis of phenological units to detect important species in plant-pollinator assemblages: can it inform conservation strategies? *Community Ecol* **18**:1–10.

Biesmeijer JC, Roberts SP, Reemer M, *et al.* (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* **313**:351–4.

Bini C (2001) *I Suoli Dei Colli Euganei*. Legnaro, IT: Veneto Agricoltura.

Blüthgen N, Klein A-M (2011) Functional complementarity and specialization: the role of biodiversity in plant-pollinator interactions. *Basic Appl Ecol* **12**:282–91.

Blüthgen N, Fründ J, Vazquez DP, Menzel F (2008) What do interaction network metrics tell us about specialization and biological traits? *Ecology* 89:3387–99.

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

Bobbink R, Willems JH (1988) Effects of management and nutrient availability on vegetation structure of chalk grasslands. In: During JH, Werger MJA, Willems JH (eds). *Diversity and Pattern in Plant Communities*. The Hague: SPB Academic Publishing, 183–93.

Conti F, Abbate G, Alessandrini A, *et al.* (2005) *An Annotated Checklist of the Italian Vascular Flora*. Roma: Palombi.

Dante SK, Schamp BS, Aarssen LW (2013) Evidence of deterministic assembly according to flowering time in an old-field plant community. *Funct Ecol* **27**:555–64.

Del Vecchio S, Slaviero A, Fantinato E, *et al.* (2016) The use of plant community attributes to detect habitat quality in coastal environments. *AoB Plants* **8**:plw040.

Dengler J, Janisová M, Török P, *et al*. (2014) Biodiversity of Palaearctic grasslands: a synthesis. *Agric Ecosyst Environ* **182**:1–14.

Dormann CF, Gruber B, Fründ J (2008) Introducing the bipartite Package: analysing ecological networks. *R news* **8**:8–11.

Dormann CF, Strauss R (2014) A method for detecting modules in quantitative bipartite networks. *Methods Ecol Evol* **5**:90–8.

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Ann Rev Ecol Evol Syst* **34**:487–515.

Fantinato E, Del Vecchio S, Slaviero A, *et al.* (2016a) Does flowering synchrony contribute to the sustainment of dry grassland biodiversity? *Flora Morphol Distrib Funct Ecol Plants* **222**:96–103.

Fantinato E, Giovanetti M, Del Vecchio S, *et al.* (2016b) Altitudinal patterns of floral morphologies in dry calcareous grasslands. *Plant Sociol* **53**:83–90.

Fantinato E, Del Vecchio S, Baltieri M, *et al.* (2017b) Are food-deceptive orchid species really functionally specialized for pollinators? *Ecol Res* **32**:1–9.

Fantinato E, Del Vecchio S, Giovanetti M, *et al.* (2017a) New insights into plants coexistence in species-rich communities: the pollination interaction perspective. *J Veg Sci* doi:10.1111/jvs.12592.

Fischer J, Lindenmayer DB (2007) Landscape modification and habitat fragmentation: a synthesis. *Ann Rev Ecol Evol Syst* **16**:265–80.

Fontaine C, Dajoz I, Meriguet J, *et al.* (2006) Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. *PLOS Biol* **4**:e1.

Ghazoul J (2006) Floral diversity and the facilitation of pollination. *J Ecol* **94**:295–304.

Godó L, Valkó O, Tóthmérész B, *et al.* (2017) Scale-dependent effects of grazing on the species richness of alkaline and sand grasslands. *Tuexenia* **37**:229–46.

Goverde M, Schweizer K, Baur B, *et al.* (2002) Small-scale habitat fragmentation effects on pollinator behaviour: experimental evidence from the bumblebee *Bombus veteranus* on calcareous grasslands. *Biol Conserv* **104**:293–9.

Habel JC, Dengler J, Janišová M, *et al.* (2013) European grassland ecosystems: threatened hotspots of biodiversity. *Biodiv Conserv* **22**:2131–8.

Hall DM, Camilo GR, Tonietto RK, *et al.* (2016) The city as a refuge for insect pollinators. *Conserv Biol* **31**:24–9.

Hegland SJ, Totland Ø (2005) Relationships between species' floral traits and pollinator visitation in a temperate grassland. *Oecologia* **145**:586–94.

Kaiser-Bunbury CN, Muff S, Memmott J, Müller CB, Caflisch A (2010) The robustness of pollination networks to the loss of species and interactions: A quantitative approach incorporating pollinator behaviour. *Ecol Lett* **13**:442–52.

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

Kaltenrieder P, Procacci G, Vannière B, *et al.* (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). *Holocene* **20**:679–95.

Krause AE, Frank KA, Mason DM, *et al.* (2003) Compartments revealed in food-web structure. *Nature* **426**:282–5.

Lazaro A, Tscheulin T, Devalez J, *et al.* (2016) Moderation is best: effects of grazing intensity on plant–flower visitor networks in Mediterranean communities. *Ecol Appl* **26**:796–807.

Lundgren R, Olesen JM (2005) The dense and highly connected world of Greenland's plants and their pollinators. *Arct Antarct Alp Res* **37**:514–20.

Luoto M, Pykala J, Kuussaari M (2003) Decline of landscape scale habitat and species diversity after the end of cattle grazing. *J Nat Conserv* **11**:171–8.

McCann KS, Rasmussen JB, Umbanhowar J (2005) The dynamics of spatially coupled food webs. *Ecol Lett* **8**:513–23.

Memmott J (1999) The structure of a plant-pollinator food web. *Ecol Lett* **2**:276–80.

Memmott J, Waser NM, Price MV (2004) Tolerance of pollination networks to species extinctions. *Proc Biol Sci* **271**:2605–11.

Mouillot D, Bellwood DR, Baraloto C, *et al.* (2013) Rare species support vulnerable functions in high-diversity ecosystems. *PLOS Biol* **11**:e1001569.

Olesen JM, Bascompte J, Elberling H, *et al.* (2008) Temporal dynamics in a pollination network. *Ecology* **89**:1573–82.

Ollerton JM, Winfree S, Tarrant S (2011) How many flowering plants are pollinated by animals? *Oikos* **120**:321–6.

Pleasants J (1980) Competition for bumblebee pollinators in Rocky Mountain plant communities. *Ecology* **61**:1446–59.

Potts SG, Biesmeijer JC, Kremen C, *et al.* (2010) Global pollinator declines: trends, impacts and drivers. *Trends Ecol Evol* **25**:345–53.

R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rodriguez-Perez J, Traveset A (2016) Effects of flowering phenology and synchrony on the reproductive success of a long-flowering shrub. *AoB Plants* **8**:plw007.

Slaviero A, Del Vecchio S, Pierce S, *et al.* (2016) Plant community attributes affect dry grassland orchid establishment. *Plant Ecol* **217**:1533–43.

Ssymank A, Hauke U, Rückriem C, *et al.* (1998) Das europäische Schutzgebietssystem NATURA 2000 – BfNHandbuch zur Umsetzung der Fauna-Flora-Habitat-Richtlinie und der Vogelschutz-Richtlinie. *Schriftenr Landschaftspfl Natursch* **53**:1–560.

Thébault E, Fontaine C (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* **329**:853–6.

Török P, Vida E, Deák B, *et al.* (2011) Grassland restoration on former croplands in Europe: an assessment of applicability of techniques and costs. *Biodiv Conserv* **20**:2311–32.

Traveset A, Castro-Urgal R, Rotllàn-Puig X, *et al.* (2017) Effects of habitat loss on the plant–flower visitor network structure of a dune community. *Oikos* **127**:45–55.

Tylianakis JM, Laliberté E, Nielsen A, *et al.* (2010) Conservation of species interaction networks. *Biol Conserv* **143**:2270–9.

Van Swaay CAM (2002) The importance of calcareous grasslands for butterflies in Europe. *Biol Conserv* **104**:315–8.

Vázquez DP, Aizen M (2004) Asymmetric specialization: a pervasive feature of plant-pollinator interactions. *Ecology* **85**:1251–7.

Vázquez DP, Aizen M (2006) *Community-wide patterns of specialization in plant-pollinator interactions revealed by null model*. In: Waser NM, Ollerton J, (eds) *Plant-Pollinator Interactions. From Specialization to Generalization*. Chicago: University Chicago Press, 387–408.

Wellstein C, Campetella G, Spada F, *et al.* (2014) Context-dependent assembly rules and the role of dominating grasses in semi-natural abandoned sub-Mediterranean grasslands. *Agric Ecosyst Environ* **182**:113–22.

Willmer P (2011) *Pollination and Floral Ecology*. Princeton University Press, Princeton, New Jersey.

Winfree R, Aguilar R, Vázquez DP, *et al.* (2009) A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology* **90**:2068–76.