Management linked to ecological intensification supports pollinator abundance in Iberian wood-pastures

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Abstract

Context

Iberian wood-pastures (*dehesas*) constitute important habitats for flower-visiting insects, thus supporting the delivery of essential ecosystem services. However, dehesas have been experiencing increasing degradation either by farming intensification or abandonment.

Objectives

We assess if alternative management strategies linked to ecological intensification, designed to maximize productivity in Iberian dehesas, are also favorable for biodiversity, specifically pollinators.

Methods

We carried surveys in nine dehesas located across western and southwestern Spain. Each site comprised five paddocks under different management: conventional grazing, alternative systems linked to ecological intensification (rotational grazing, legume-enriched young and old pastures) and abandonment. We surveyed bees and hoverflies along fixed transects, together with flower cover and botanical composition, and we assessed landscape configuration.

Results

Results showed that rotational grazing, legume-enriched and abandonment enhanced pollinator abundance compared to conventional management, but practices linked to ecological intensification were more beneficial. Flower cover, together with plant diversity and landscape composition, were important drivers of pollinator abundance, richness and diversity. These patterns varied among pollinator groups, e.g., hoverflies were less impacted by management than bees, while being more affected by plant diversity.

Conclusions

Our findings suggest that alternative management linked to ecological intensification has potential in low-input farming systems such as Iberian dehesas. These measures can help to maximize productivity, whilst preserving biodiversity and essential ecosystem services such as pollination. Complementary measures, including the preservation or restoration of marginal landscape elements and semi-natural habitats, which ensure abundant feeding and nesting resources, also appear to be crucial for effectively safeguarding pollinating insects in this High Nature Value farming system.

1. Introduction

The simplification of habitats and landscapes resulting from agricultural intensification has led to a widespread decline in farmland biodiversity across many different taxa (Benton et al., 2003; Kleijn et al., 2011), with increasing evidence on the decline of bees and other pollinating insects (Potts et al., 2010; Wagner, 2020). However, farmland habitats still host many species that depend on appropriate agricultural management for their survival (Kleijn and Sutherland, 2003). Amongst these, semi-natural pastures grazed by domestic livestock are recognized for hosting high species richness (WallisDeVries et al., 2002), which critically depend on appropriate management. Understanding the overall effects of livestock grazing on ecosystems in relation to biodiversity is of paramount importance to meet future goals of food security and conservation (Filazzola et al., 2020). Additionally, it is of utmost importance to explore novel management strategies focused on ecological intensification, which can maintain a high level of food production while improving positive secondary effects on ecosystem services (Bommarco et al., 2013). Although ecological intensification strategies have mostly concerned intensive agriculture, they can also be applied to more extensive production systems like livestock rearing relying on semi-natural grasslands (Loucougaray et al., 2015).

Much research has been conducted on the effects of livestock grazing on plants, from the individual to community level (Herrero-Juregui and Oesterheld, 2018). However, the cascading plant-mediated effects of grazing on higher trophic levels have been less studied, especially the effects on herbivorous ecosystem service providers, which rely on, or are directly affected by, plant communities (Shapira et al., 2020). Management and livestock pressure intensity in pastures are expected to have an important effect on the vegetation and consequently on flower-visiting insects, through a modification of the abiotic conditions and of the overall availability, quality, and phenology of pollinators' floral and nesting resources in the landscape (van Klink et al., 2015). Flower-visiting insects, particularly bees, which are focal pollinators in most ecosystems, are crucial for maintaining natural ecosystems: an estimated 88% of all angiosperm species, including main livestock pasture species, are animal-pollinated (Ollerton et al., 2011). Most of the research on the effects of management and livestock pressure on pollinating insects have been conducted in

temperate grasslands. Many of these studies have found negative effects of increased grazing on insect pollinators due to decreased flower diversity and altered plant species composition (Kruess and Tscharntke, 2002; Minckley, 2014; Sjödin et al., 2008; Tadey, 2015), while others have shown instead positive impacts of increased grazing intensity compared to low or no-grazing sites (Carvell, 2002; Öckinger et al., 2006; van Klink et al., 2016). In the Mediterranean region, the few existing studies have shown that intermediate levels of grazing favored either pollinator abundance and richness or pollinator foraging resources (Lázaro et al., 2016; Shapira et al., 2020). Discrepancies among studies are likely the result of differences in habitat types and land-use histories, grazing level, and additional interacting management practices. In addition, effects may only be evident over medium or long periods of time. For instance, some insect groups such as butterflies and bumblebees may first increase when grazing is ceased or its intensity is reduced, as a result of a taller turf and a more heterogeneous vegetation structure. However, long-term grassland abandonment has been shown to decrease the number of grassland species, including pollinators, as the succession proceeds and the grasslands are increasingly covered with shrubs and trees (Öckinger et al., 2006). The few existing studies addressing the effect of alternative management linked to ecological intensification such as rotational grazing in mountain pastures have showed a general positive effect compared to continuous grazing on flower-visiting insects such as bumblebees and butterflies (Enri et al., 2017; Scohier et al., 2013). These studies suggest that in order to maintain a high species richness of plants and insect species dependent on pastureland it may be necessary to ensure that these grasslands are appropriately managed.

Extensive pastureland, which consist of mixtures of grassland, scrub and/or woodland used for raising livestock, dominates current European lists and maps of High Nature Value Farming Systems (Paracchini et al., 2008). An example of extensive pastureland that covers over 4.5 million hectares in the Iberian Peninsula are oak dehesas; semi-natural savanna-like open woodlands with scattered oak trees and extensive grazed grasslands (Moreno and Pulido, 2009; Plieninger et al., 2015). The main activity in this low input system typically consists of livestock rearing at low stocking densities and careful exploitation of evergreen oaks (Moreno et al., 2016). This system maintains outstanding levels of biodiversity (Moreno et al., 2016), to the point of being considered as habitats to be protected under the European Habitats Directive (EEC, 1992). Nevertheless, Iberian dehesas have been experiencing an increasing degradation over the last few decades (e.g., land abandonment, soil erosion, lack of tree regeneration and decay), mostly linked to the intensification of dehesa management and loss of traditional multiple uses and management practices due to its low profitability (Moreno and Pulido, 2009). With the aim of tackling dehesa degradation whilst enhancing overall profitability, alternative management strategies linked to ecological intensification, such as rotational grazing or sowing of legume-rich mixtures, are increasingly being implemented in Iberian dehesas. Rotational grazing (consisting of short intensive grazing periods followed by long enough recovery times) is expected to avoid plant overgrazing and help tree regeneration (López-Sánchez et al., 2016), and it has been often recommended for insect conservation (Goulson et al., 2008). On the other hand, sowing of legume-rich mixtures is a strategy frequently used by farmers to increases forage yield and protein content, besides increasing soil nitrogen content. It can be a cost-efficient way of meeting farmers' needs while maintaining high-levels of (Hernández-Esteban et al., 2019). Previous studies in Iberian dehesas have shown that landscape heterogeneity and habitat mosaic were important at determining the abundance and diversity of insect pollinators like solitary bees and bumblebees (Moreno et al., 2016). However, to our knowledge, no studies have addressed the effect of diverse management, particularly strategies linked to ecological intensification, on pollinating insects.

In this study, we assess the effect of diverse management strategies in Iberian dehesas on the abundance and diversity of insect pollinators, namely wild bees and hoverflies. We also evaluate the effect of landscape composition and flower resource availability on pollinator diversity metrics. Considering different insect taxa is essential as these effects may differ among pollinator groups (Sjödin et al., 2008). Specifically, we tested whether: i) alternative management linked to ecological intensification (rotational, legume-rich sown pastures), designed to maximize productivity, favored the abundance, richness and diversity (taxonomic and functional) of flower-visiting insects, ii) alternative management strategies were more beneficial for insect pollinators than abandonment or renaturalization, iii) local floral resources and landscape composition had a major role at determining pollinator diversity metrics and iv) these effects varied among pollinator groups.

2. Methods

2.1. Study area

We carried out biodiversity surveys at nine sites located across three distinctive areas (Badajoz, Cáceres and Salamanca provinces), stretching along 300 km of western and southwestern Spain (Fig. 1). Each area was characterized by contrasting climatological conditions. Mean annual temperature is 16.6, 16.7 and 11.1 °C and annual precipitation 513, 747 and 490 mm in Badajoz, Cáceres and Salamanca. The vegetation of each site was characterized by wood pastures (dehesas), dominated by holm oaks in Extremadura and a mixture of holm oaks and pyrenean oak (*Quercus pyrenaica*) in Salamanca. The understory of this system is highly diverse and dominated by annual herbaceous species. Each site comprised five different paddocks under different management regimes: conventional grazing system (control, CT, where livestock graze all year round), alternative schemes focused on ecological intensification which includes three systems; rotational grazing (ROT, grazed intensely during short periods followed by long resting periods), legume-rich young (LY, enriched with a mixture of leguminous species in the last five years) and legume-rich old (LO, similar than the previous one but leguminous species sown more than 10 years ago), and finally abandonment (AB, not grazed at least during the last ten years). All sites were grazed mostly by cattle and occasionally by sheep. Exact location details of sites can be found in Table S1.

Within each area, sites were located at least 10 km apart from each other to ensure a sampling of different species pools. In each site, the five treatments were located close enough to have the same species pool but separated enough to ensure that most individual insects would not fly readily between sites (> 500 m). This minimum distance was considered greater than the average foraging range of most solitary bees (Gathmann and Tscharntke, 2002; Zurbuchen et al., 2010).

2.2. Pollinator field surveys and taxonomical identification

We surveyed flower-visiting bees (Hymenoptera: Apoidea) and hoverflies (Diptera: Syrphidae) using the 'Pollard walk' (Pollard and Yates, 1994) along 100m long by 2m wide fixed transects, one per site. While walking, the surveyor collected all individual bees and hoverflies (only individuals which the surveyor was not able to recognize directly in the field) seen within the 2 m wide 'belt' with a standard entomological aerial net and transferred to a tube with ethanol at 70%. *Apis mellifera* individuals were not captured, but counted in the field. The surveys were made between 10 a.m. and 5 p.m., under good weather conditions (temperature > + 15 C, gentle wind, cloudless sky) and were repeated twice at 2- or 3-week intervals between late April and early June 2021, corresponding with the peak of flight activity for most species.

Specimens collected were identified to the lowest taxonomic unit possible with the help of taxonomic keys and reference entomological collections for the region, under the supervision of entomology experts. The entomological collection for bees was compiled for the past EU project BioBio by bee taxonomist Francisco Javier Ortiz, while for hoverflies the collection was compiled by A. Gaytan and G. González-Bornay. When species-level identification could not be resolved, individuals were identified to the lowest taxonomic unit possible (genus level, especially in the case of problematic bee families such as *Andrenidae*). All species were additionally classified on the basis of their functional traits. For bees the functional traits included nesting type (soil, plant stems, existing cavities underground, existing cavities in wood, walls or hollow stems), sociality (eusocial, primitively eusocial, solitary, klepto-parasitic) and pollen transportation (abdomen, legs, legs and body, corbiculae, accidental). Hoverflies functional traits included larval feeding mode (phytophagous, zoophagous or saprophagous), larval microhabitat (aquatic, bulbs, decaying matter, terrestrial, tree roots and cavities), wing length (mm) and flight mode (arboreal or near the ground). See Table S2 in appendix for the functional traits gathered for each species. Functional diversity (FD from here onwards) of bees and hoverflies was calculated using Petchey and Gaston' dendrogram-based index (Petchey and Gaston, 2002).

2.3. Flower cover, plant diversity and landscape composition

During the flowering peak (May 2021), the flower cover percentage was visually estimated once by the same observer in ten 50x50 cm squares along the 100 m pollinator transect (one square each 10 m). The percentage cover of yellow, white and purple-pink flowers in each square was noted during each observation and then used to calculate an overall flower cover percentage.

The detailed botanical composition of the sites was recorded once in April-May 2021 during the flowering peak, i.e., at the maximum trophic availability for flower-visiting insects. In each treatment, species composition was recorded following the Point Transect method (Kent, 2011). Sampling points were taken at 100 cm along four 25m transects per plot. In total 100 plants were collected in each plot. The relative abundance of each species was computed as the number of times that it appears in the four transects. The total inventory in the nine sites included 193 species and 4500 sampled individuals. Plant diversity metrics were calculated taking into account only forbs and legumes species (excluding grasses which are less relevant resources for pollinators). In addition to plant richness and diversity (Shannon), phylogenetic diversity of plants was computed. Phylogenetically distinct species are likely to have distinct functional traits and therefore phylogenetic diversity is often used as a proxy for FD (Winter et al., 2013). The phylogenetic tree of the vegetation (Figure S1 appendix) was constructed using the phylogeny derived from the GBOTB mega-tree for seed plants developed by Smith and Brown (2018). From the matrix of species abundances in each plot and our phylogenetic tree, we computed the Rao index (Rao, 1982) as an approximation to the phylogenetic diversity, which is calculated taking into account the relative abundances of the species, making this index more independent of species richness (Winter et al., 2013).

Shannon's landscape diversity index was characterized for every study paddock within buffers of 250m, 500m and 1000m of radius, based on 44 land use categories mapped by the CORINE 2018 land cover dataset (EEA, 2019). Landscape diversity at 500m radius buffer showed the highest correlation with pollinator species richness and diversity, as well as with FD of bees and hoverflies. Therefore, it was subsequently used for the statistical models. In addition to landscape diversity, the percentages of agricultural land and of semi-natural areas (natural open grasslands, sclerophyllous vegetation and broad-leaved forests) were also extracted from CORINE and subsequently used as additional explanatory variables in the statistical models.

2.4. Statistical analyses

Generalized linear mixed models (GLMMs) were applied to test for differences in flower cover, plant diversity and pollinator metrics across management treatments. Study site (nested within area) was included as a random effect in the models. We also applied GLMMs to test for differences in the abundance of each distinct pollinator family (Andrenidae, Apidae, Halictidae, Megachilidae and Syrphidae) across management treatments. In addition to the direct comparisons, differences in species composition across management and across study regions were tested by Non-metric multidimensional scaling (NMDS) models using the *metaMDS* function of the "vegan" package in R. NMDS is an ordination technique that uses a Bray–Curtis matrix of ranked similarities and displays samples in low-dimensional space while retaining as nearly as possible the similarity rankings between samples. To assess the effect of multiple drivers along with management (including landscape composition, plant

diversity and flower cover) on pollinator diversity, both taxonomic (computed as the Shannon index) and functional, we applied GLMMs with the same random effect structure as above. GLMMs with a Poisson distribution were used instead to test the effect of the same predictors on pollinator abundance and richness. Diversity (Shannon) of total pollinators, bees and hoverflies separately and plants was calculated using the function *diversity* from the "vegan" package. FD of bees and hoverflies was calculated with the function *FD_dendro* from the "fundiv" package (https://github.com/ibartomeus/fundiv), which calculates dendrogram-based Functional Diversity Indices for a set of communities using Petchey and Gaston' index (Petchey and Gaston, 2002) and its weighted version (Gagic et al., 2015). We built the plant phylogenetic tree using the package "V. PhyloMaker" (Jin and Qian, 2019), and the chosen phylogenetic index (Rao) was obtained with the "spicy" package. All statistical analyses were performed in R version 5.3.1, using the packages "lme4", "nlme", "vegan", "fundiv", "V. PhyloMaker" and "spicy".

3. Results

3.1. Description of pollinator assemblages

A total of 547 bees (Hymenoptera) from 80 different species and morphospecies were sampled (table S3 in appendix). The most common bee species surveyed belonged to the genus *Lasioglossum* (17.4%, Halictidae), followed by *Apis mellifera* (15%, Apidae) and *Panurgus calcaratus* (7.3%, Andrenidae). Relative bee species abundances showed some differences among treatments: in the CT treatment the most abundant was *P. calcaratus*, in the LO it was *P. perezi* instead, in the LY and AB the most abundant species was *A. mellifera*, whereas for ROT it was *Lasioglossum* sp. Hoverfly (Diptera: Syrphidae) abundance amounted to 204 individuals, belonging to 18 different species (table S3). The most common species was *Sphaerophoria scripta* (61.8%), followed by *Eristalis tenax* (12.8%) and *Eupeodes corollae* (7.4%). The most common hoverfly species across all treatments was *Sphaerophoria scripta*, whereas the second most abundant species varied across treatments; in the CT, AB and ROT it was *Eristalis tenax*, whereas in the LO treatment it was *Melanostoma scalare* and in the LY treatment it was *Eupeodes corollae*, followed closely by *Melanostoma sp.* and *Episyrphus balteatus*. With respect to functional traits, bees sampled were predominantly soil nesting species, solitary and species that carried pollen on their legs (table S1A). Hoverflies species sampled were mostly zoophagous regarding larval feeding mode, with terrestrial larval microhabitat, medium wing length (5–7 mm), and arboreal height of flight (table S1B). Non-metric multidimensional scaling (NMDS) analysis showed that the overall composition of the pollinator community did not strongly differ across management (grouping management in three categories conventional, ecological intensification and abandonment, Fig. 2A). Similarly, there was not a strong differentiation in species composition across study regions (Fig. 2B).

3.2. Plant diversity, flower cover and pollinator diversity across treatments

Mean flower cover, together with plant richness and diversity showed higher mean values in the abandonment (AB) treatment, although differences were not statistically significant across treatments (Table 1). The relative abundance of legumes was significantly higher in the legume-rich young treatment with respect to the control and abandoned treatments, as theoretically expected. Plant phylogenetic diversity showed higher mean values in the control treatment instead, although we did not find significant differences among treatments. With regards to pollinator diversity metrics, total pollinator abundance as well as bee abundance were significantly higher in the rotational, legume-rich old and abandonment treatments with respect to the control (Table 1). Total pollinator richness and diversity, as well as mean hoverfly abundance, richness and taxonomic diversity showed mean higher values in the abandoned treatment, but no statistically significant differences were found. Lastly, the conventional grazing system (control, CT) showed higher bee and hoverfly FD values, but again these differences were not statistically significant (Table 1).

Variable	CT	LO	LY	ROT	AB	df	F
Flower cover (%)	10.73 ± 2.43	9.26 ± 2.52	12.91 ± 2.93	8.97 ± 3.33	17.07 ± 2.96	40	1.277 NS
Plant richness	17.89 ± 1.24	17.11 ± 2.07	17.11 ± 1.93	15.11 ± 2.1	21.38 ± 2.34	40	2.272 NS
Plant diversity	2.32 ± 0.09	2.25 ± 0.18	2.32 ± 0.13	2.20 ± 0.14	2.68 ± 0.1	40	1.985 NS
Legumes rel. abundance	0.12 ± 0.02 a	0.17 ± 0.03 abc	0.26 ± 0.04 b	0.14 ± 0.04abc	0.09 ± 0.03 ac	40	**3.892 ***
Plant phylogenetic div.	93.58 ± 1.48	85.45 ± 6.02	86.13 ± 2.42	87.48 ± 3.86	88.97 ± 1.73	40	1.054 NS
Total pollinator abundance	12.73 ± 2.14 a	17.22 ± 4.8 b	14.89 ± 3.94 abcd	19.11 ± 6.76 bc	18.75 ± 1.9 bcd	40	**3.559 ** **
Total pollinator richness	6.45 ± 1.11	5.89 ± 1.26	7.56 ± 2.04	8.22 ± 1.45	8.63 ± 1.16	40	1.705 NS
Total pollinator diversity	1.43 ± 0.19	1.17 ± 0.21	1.37 ± 0.25	1.64 ± 0.25	1.75 ± 0.14	40	1.880 NS
Bee abundance	9.00 ± 2.14 a	12.56 ± 3.87 b	11.22 ± 2.96 abcd	14.00 ± 5.69 bc	13.50 ± 1.98 bcd	40	**2.704 ***
Bee richness	5.40 ± 1.06	4.00 ± 1.11	6.75 ± 1.81	5.78 ± 1.4	5.63 ± 1.08	40	1.275 NS
Bee diversity	1.26 ± 0.2	0.73 ± 0.27	1.33 ± 0.2	1.24 ± 0.29	1.31 ± 0.18	40	1.924 NS
Bee functional div.	3.39 ± 0.5	3.11 ± 0.48	2.70 ± 0.31	3.03 ± 0.34	3.08 ± 0.73	40	0.269 NS
Hoverfly abundance	3.73 ± 0.75	4.67 ± 1.86	3.67 ± 1.72	5.11 ± 1.35	5.25 ± 1.01	40	1.058 NS
Hoverfly richness	1.55 ± 0.16	1.88 ± 0.4	2.33 ± 0.67	2.63 ± 0.63	3.00 ± 0.5	40	1.344 NS
Hoverfly diversity	0.26 ± 0.09	0.37 ± 0.16	0.48 ± 0.27	0.64 ± 0.23	0.68 ± 0.18	40	1.211 NS
Hoverfly functional div.	2.07 ± 0.36	1.53 ± 0.35	1.51 ± 0.31	1.30 ± 0.15	1.63 ± 0.26	40	1.054 NS

When analysing distinct pollinator families separately (the four main bee families and hoverflies), we found some differences in the total abundance of individuals across treatments (Fig. 3). Halictidae was most abundant in the ROT treatment (χ^2 = 21.325, df = 4, p < 0.001), Andrenidae reached higher abundances in the LO treatment (χ^2 = 25.471, df = 4, p < 0.001) while Apidae was relatively more abundant in the LY, AB and LO treatments with respect to the CT and ROT (χ^2 = 27.178, df = 4, p < 0.001). Although the abundance of Megachilidae was generally very low across all treatments, it showed significantly higher values in the ROT and LO treatment (χ^2 = 12.722, df = 4, p = 0.013). The abundance of Syrphidae was not significantly different across treatments (χ^2 = 4.858, df = 4, p = 0.013, p = 0.302).

3.3. Drivers of pollinator diversity metrics

Results from the GLMMs models, which include the effect of multiple explanatory variables (management, plant diversity and phylogenetic diversity, flower cover, landscape diversity, percentage of agricultural land and percentage of semi-natural habitat) on pollinator diversity metrics, are shown in Table 2. Flower cover showed a strong significant positive effect on total pollinator abundance and richness, while both landscape diversity and percentage of semi-natural habitats showed a positive effect on total pollinator abundance (Table 2). Regarding management, both the rotational grazing and legume-rich old treatments showed higher total pollinator abundance than the control treatment when accounting for the random effect of the site (Table 2).

Table 2
Results of the GLMMs analysing the effect of multiple explanatory variables on pollinator diversity metrics. Site was included as a random factor. Significance levels (P) are *< 0.05, **< 0.01, ***< 0.001, and (.) marginally significant with p < 0.1.

		Total pollinators			Bees				Hoverflies			
		Abund.	Rich.	Div.	Abund.	Rich.	Div.	FD	Abund.	Rich.	Div.	FD
Management	LO	0.396**	-0.028	-0.119	0.521**	-0.171	-0.315	-0.06	0.255	0.268	0.143	-0.449
	LY	0.034	0.12	0.021	0.219	0.225	0.216	-0.417	-0.388	0.339	0.234	-0.854(.)
	ROT	0.373**	0.33 (.)	0.327	0.445**	0.234	0.178	-0.148	0.343	0.553	0.396	-0.692
	AB	0.174	0.102	0.308	0.412*	-0.055	0.181	0.047	-0.433	0.199	0.184	-1.254*
Flower cover		0.04***	0.017*	0.0008	0.031***	0.015(.)	-0.002	-0.047	0.059***	0.008	-0.004	0.017
Plant diversity		0.077	0.17	0.171	-0.325	-0.045	-0.047	-0.346	0.994**	0.759(.)	0.632*	0.581
Plant phylogenetic div.		0.006	0.008	0.008	0.016*	0.015	0.017	0.0001	-0.013	-0.009	-0.007	-0.02
Landscape div.		0.342(.)	0.195	0.247	0.361	0.316	0.326	1.41	0.555(.)	0.286	-0.031	1.372*
% Agriculture		-0.0004	-0.0002	-0.0003	-0.005(.)	-0.005	-0.005	-0.013	0.006(.)	0.005	0.005	-0.005
% Semi-natural		0.004*	-0.002	0.0007	0.002	-0.005	-0.003	-0.001	0.005	0.002	0.003	-0.012*

Regarding bee diversity metrics, flower cover showed the most significant positive effect on bee abundance and bee richness (although marginally significant for the latter, Table 2 and Fig. 4). In accordance with the results for total pollinator abundance, the legume-rich old and the rotational grazing, together with the abandonment treatment in this case, showed a higher total bee abundance than the control treatment (Table 2). We also observed a positive significant effect of plant phylogenetic diversity and a marginally negative effect of agricultural land cover on bee abundance (Table 2).

With respect to hoverfly diversity metrics, we found a strong positive effect of flower cover on hoverfly abundance, in accordance with the results for bee abundance (Table 2 and Fig. 4). In addition to flower cover, the effect of plant diversity had a positive effect on hoverfly abundance, richness and diversity (but not for bees, Table 2, Fig. 4). Contrary to the results for bees, we did not find an effect of management on hoverfly abundance. Instead, management showed a negative effect on hoverfly FD; lower FD in the legume-rich young and abandonment treatments with respect to the control treatment (Table 2). We also found a marginally significant positive effect of landscape diversity and of percentage of agricultural areas on hoverfly abundance. Landscape diversity also showed a positive effect on hoverfly FD. Unexpectedly, the percentage of semi-natural areas showed a negative effect on hoverfly FD (Table 2).

4. Discussion

4.1. Effects of management on pollinator abundance and diversity

Our findings showed that non-conventional management in Iberian dehesas supports pollinator abundance and marginally species richness, while it did not show a strong effect on overall community composition. A high abundance of the dominant pollinating species is known to be strongly correlated with pollination service potential and helps to buffer the effect of environmental change on pollination services (Hoehn et al., 2008; Winfree et al., 2015). We additionally found that, compared to the conventional grazing, the abundance of pollinators and in particular bees, increased more significantly in the alternative systems linked to ecological intensification (rotational grazing and legume-rich old) than in the abandonment system. The relative abundances of distinct bee families also varied across management; Halictidae was most abundant in the rotational system while Andrenidae abundances were larger in the legume-rich old with respect to other systems. Bee families usually comprise species with broadly similar foraging and nesting habits and thus are likely to be linked to particular habitat types (Potts et al., 2003). These results show support for the potential of ecological intensification even in low-input farming systems (Loucougaray et al., 2015), indicating that strategies designed to increase productivity in a sustainable manner do not damage pollinator communities and can be even more beneficial than abandonment or renaturalization in Iberian wood-pastures. Although short-term benefits for flower-visiting insects have been recorded after grassland abandonment (Sjödin et al., 2008), in the long-term this system could lead to the decrease of pollinators as the succession proceeds and the grasslands are increasingly covered with shrubs and trees (Öckinger et al., 2006). Nevertheless, alternative management had an overall weak effect on either species richness or taxonomic and functional diversity. Only the rotational grazing system showed a minor positive effect on pollinator richness when considering bees and hoverflies together, which suggests that this system can potentially have the most benefits for flower-visiting insects in Iberian dehesas, in line with the findings of previous studies for mountain pastures (Enri et al., 2017; Scohier et al., 2013). The limited effect of management on overall pollinator community composition could be explained by the lack of substantial differences in floral

resource availability or plant diversity across management systems. Mediterranean native pastures are characterized by a high taxonomic diversity and, thanks to the presence of species with persistent or semi-persistent seed banks, a high resilience against human disturbances such as a more intensive grazing regime (Hernández-Esteban et al., 2019). Similar to flower cover and plant diversity, landscape diversity around surveyed paddocks was not significantly different across treatments, which excludes the possible confounding effect of landscape composition with that of management.

The drivers behind the observed benefits of the rotational and legume-rich management systems for pollinators may be related to differences in the specific types of flowering plants. The legume-rich old system, together with the legume-rich young, showed a higher percentage of leguminous plant species as theoretically expected, which are particularly favored by bees for their protein-rich pollen (Campbell et al., 2012). Both legume-rich management systems showed a higher proportion of white flowers (dominated by clover *Trifolium* sp., which is highly valuable as pollen source particularly for long-tongued bees) with respect to yellow flowers (dominated by Asteraceae) or pink/purple flowers (mostly dominated by *Echium* sp.). By contrast, plant species composition was not particularly favourable for pollinators in the case of dehesas under rotational grazing system, which exhibited a dominance of grasses with respect to forbs and legumes. The enhancement of bee abundance and richness in this system could tentatively be linked to better nesting conditions for ground-dwelling wild bees, as a result of lack of livestock disturbances, such as grazing and trampling, during cattle exclusion periods (Sjödin et al., 2008). Temporarily excluding grazing livestock from pastures, particularly during the peak flowering period, has shown to offer an opportunity to preserve the diversity of flower-visiting insects (Franzén and Nilsson, 2008; Scohier et al., 2013), through the avoidance of direct or indirect disturbances.

4.2. Effects of local floral resources and landscape drivers on pollinator abundance and diversity

Our findings evidenced that flower abundance and the diversity of forbs and legumes, together with the composition of the surrounding landscape, were important drivers of pollinator diversity metrics in the studied dehesas. Floral resource abundance is critical to maintain strong pollinator communities; for instance, flower-rich local habitats can support large population of small bees species which are dependent on floral resources close to the nest while attracting large bees species with longer flying ranges which may aggregate in flower-rich patches (Gathmann and Tscharntke, 2002). Flowering plant diversity can support a variety of pollinator species that differ in floral preferences and level of specialization, as well as individual pollinator species with long flight periods that outlast the floral period of any one of their plant host species (Isbell et al., 2017). Flowering plant diversity showed a strong positive effect on hoverfly abundance, richness and diversity in this study, but surprisingly not on bees. We found instead a positive significant effect of plant phylogenetic diversity on bee abundance. Plant phylogenetic diversity is often used as a proxy of functional diversity, and the diversity of functional flower traits frequently predicts the diversity of animal species that consume floral resources. However, these metrics are not always correlated due to convergences and divergences in traits, meaning that the functional dissimilarity of plant species is not always correlated to the time since the species diverged (Junker et al., 2015). In addition to local floral abundance and richness, the presence of semi-natural habitats in the wider surrounding landscape showed a positive effect on total pollinator abundance, while landscape diversity positively affected hoverfly functional diversity and abundance. Many studies have shown that patches of semi-natural habitats within farming landscapes are vital for the conservation of pollinators as they provide nesting and alternative foraging resources, sustaining pollination services in human-modified landscapes (Kennedy et al., 2013). Our findings add support to the pressing need of guaranteeing a diverse landscape to halt current biodiversity and ecosystem services losses in agricultural systems (Kennedy et al., 2013). These results call for specific measures in Iberian dehesas, complementary to the main management system, that ensure abundant and varied floral resources and sufficient landscape heterogeneity. Preserving or restoring marginal habitats such as hedges with flowering shrubs, woodlots, or boundary strips could be extremely important to ensure phenological complementarity of floral resources for insect species that can provide pollination and pest control services. Previous studies in Iberian dehesas (Moreno et al., 2016) have shown that one third of the species of bees were associated to marginal habitats (e.g. shrubby patches, wood lines). At the landscape scale, it has been shown that the conservation of semi-natural patches and the maintenance of a diversity of farming activities in extensive rangelands would guarantee the conservation of habitat diversity (Concepción et al., 2012). In Iberian dehesas, the mix of wood pastures with open pastures at different spatial scales and the preservation of the traditional habitat mosaic seems essential for the conservation of pollinating insects (Moreno et al., 2016).

4.3. Response of different pollinator groups

The responses to management and additional local and landscape drivers varied between pollinator groups. For instance, contrary to the pattern found for bees, alternative management systems did not support the abundance or richness of hoverflies, whilst they negatively affected their functional diversity. Such contrasting effects may be related to species-specific differences in foraging and nesting requirements (Lázaro et al., 2016). Syrphids may be less impacted by the rotational or legume-rich managements as a result of their nesting sites experiencing less disturbances from grazing cattle or due to a lower gain from certain flowering plant species like legumes. The specific ecological traits of hoverflies could also influence their unique responses to floral resource availability and landscape composition. Floral abundance was more determinant for bees than for hoverflies, as bees depend entirely on nectar for energy and on pollen for protein and to feed their larvae, while hoverflies depend on pollen and nectar only in their adult phase. Hoverfly larvae have extremely diverse diets, feeding on underground and aerial parts of live plants, other insects or decaying material (Thompson and Rotheray, 1998). Hoverflies may aggregate in relation to specific plant species associated with adult feeding sites or larval habitats rather than total flower abundance (Sjödin et al., 2008). We also observed an

unexpected negative effect of seminatural areas on hoverfly functional diversity. Natural habitats such as forests, where structural complexity is very high, support the greatest diversity of syrphid species (Meyer et al., 2009). Hoverfly diversity in Mediterranean woodlands has been shown to be higher than in purely grassland sites (Gaytán et al., 2020), due to the higher variety of developmental sites for larvae of phytophagous and saprophagous species. Seminatural areas around our studied dehesas are mostly composed of open natural grasslands and sclerophyllous vegetation, which may represent less favourable habitats for species associated with trees and could even lead to a decrease in the availability of developmental sites for different hoverfly functional groups.

5. Conclusions

In conclusion, this study showed that, in Iberian dehesas, alternative management linked to ecological intensification enhanced pollinator abundance and, to a certain extent, species richness. Moreover, we found that the effectiveness of alternative management for supporting pollinators was higher than that of abandonment or renaturalization, stressing the need of appropriate landscape-scale management in this extensive farming system. Distinct patterns between bees and hoverflies, related to species-specific differences in foraging and nesting requirements, stresses the importance of considering different pollinator guilds in the assessment of best management practices for pollinating insects in permanent pastures. Due to inter-annual variations in Mediterranean climatic conditions, longer monitoring periods would be necessary to discriminate if the observed patterns are sustained over time. Nevertheless, these results represent a first valuable assessment that can help to inform guidelines for a more biodiversity-friendly management of dehesa ecosystems. These findings support the notion that ecological intensification strategies, implemented at the regional scale, have potential also in low-input farming systems, where they can help to maximize productivity whilst preserving biodiversity and essential ecosystem services such as pollination. The implementation of such alternative management strategies can deliver further recognised benefits such as the improvement of pasture production, soil quality and carbon sequestration, which are essential for overall dehesa profitability and long-term sustainability. Because of the major importance of varied and abundant local floral resources on pollinators, together with the presence of semi-natural areas and landscape diversity, preserving or restoring marginal landscape elements and semi-natural patches are additional practices that may be pivotal for safeguarding flower-visiting insects in Iberian dehesas.

Declarations

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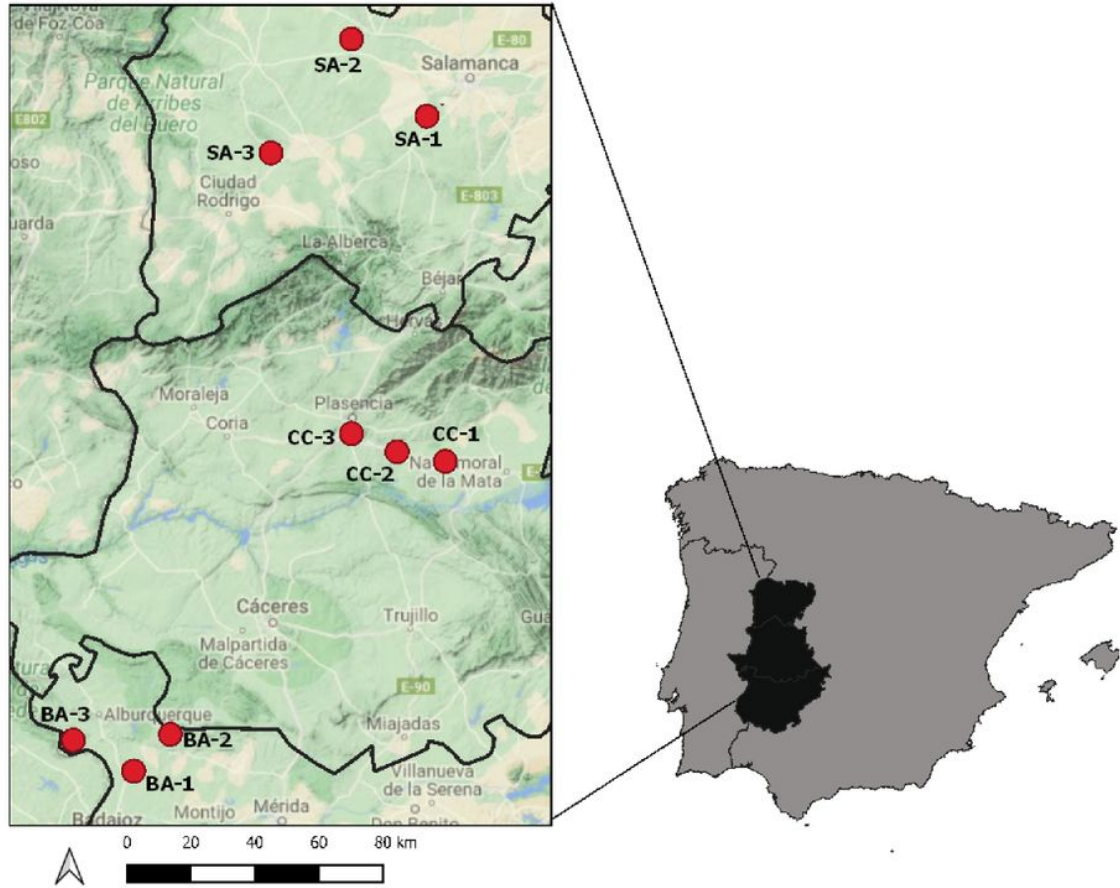
Figures

Figure 1

Location of the nine study sites (red dots) in wood-pasture habitats across Western and Southwestern Spain.
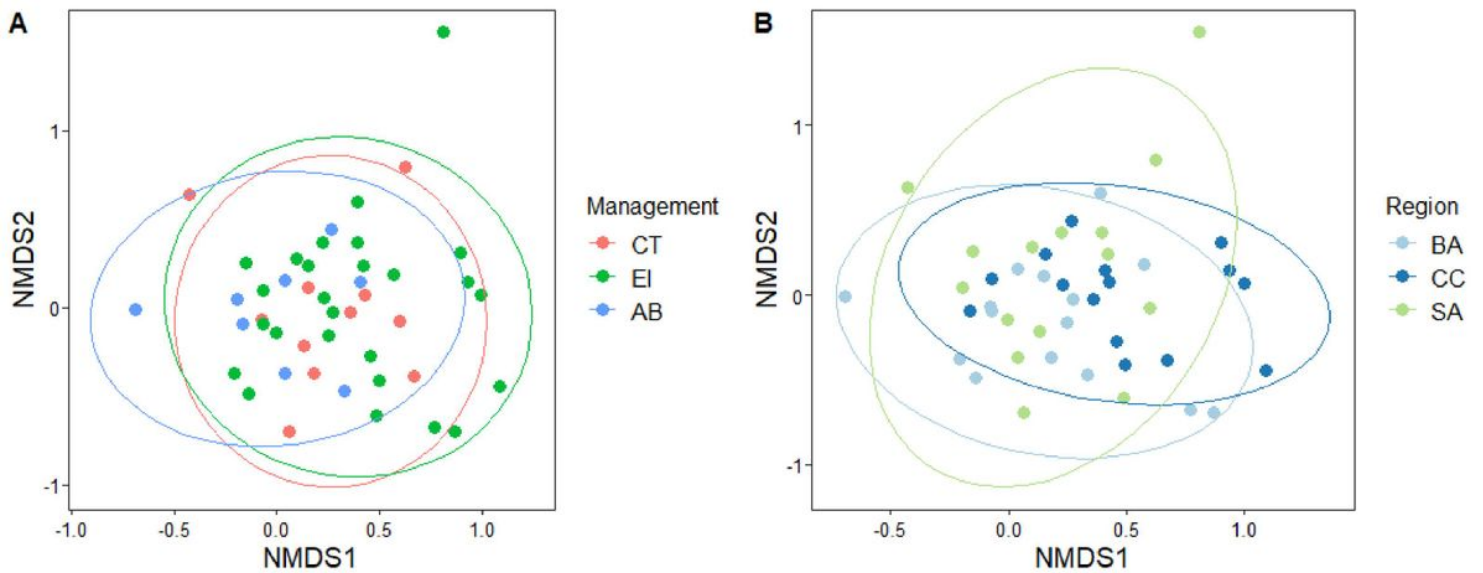

Figure 2

NMDS analysis of pollinator species composition across paddocks categorized according to A) Management (CT: control, EI: ecological intensification which includes rotational grazing, legume-rich old and legume-rich new pastures, AB: abandonment) and B) Region (BA: Badajoz,
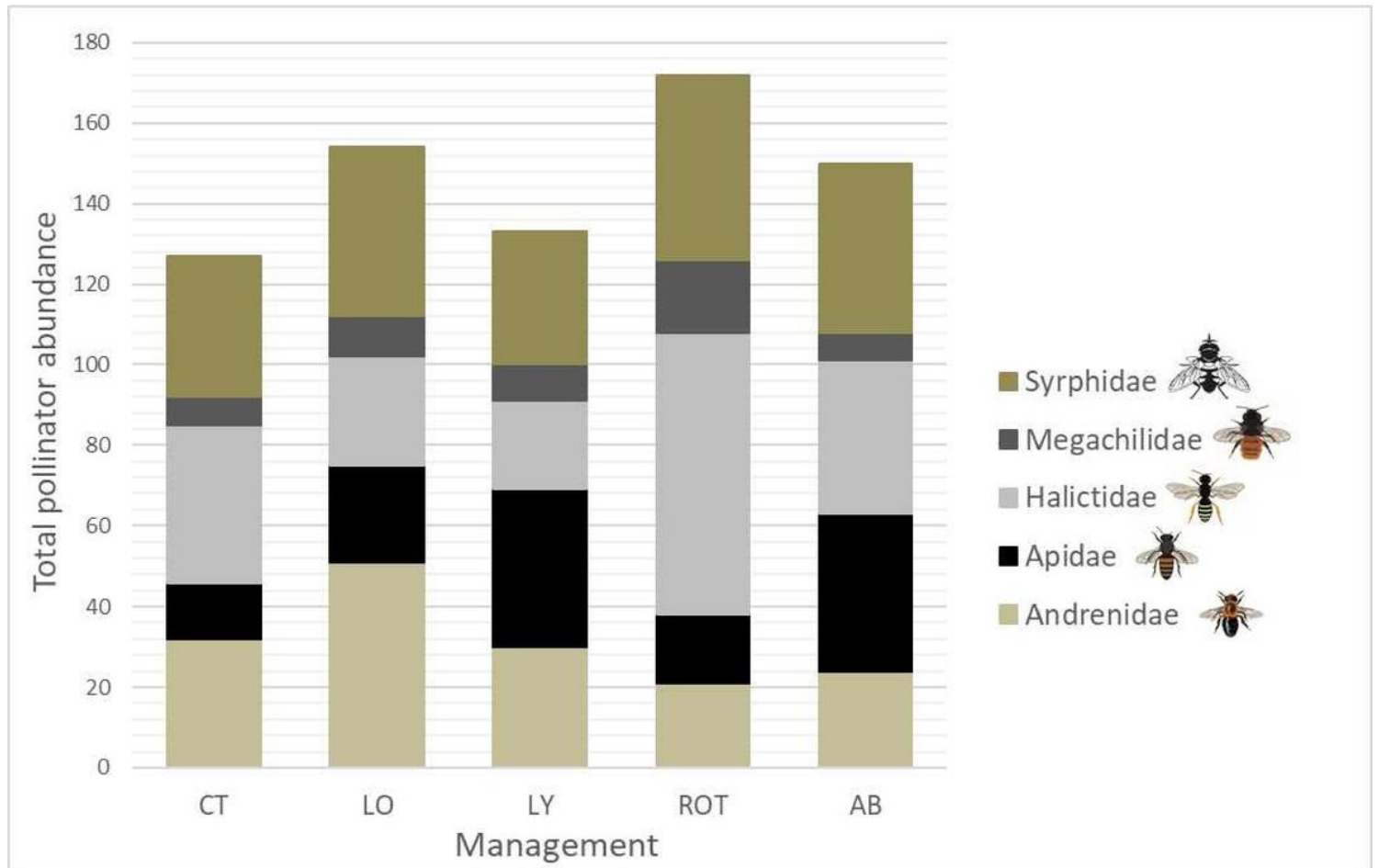
Figure 3

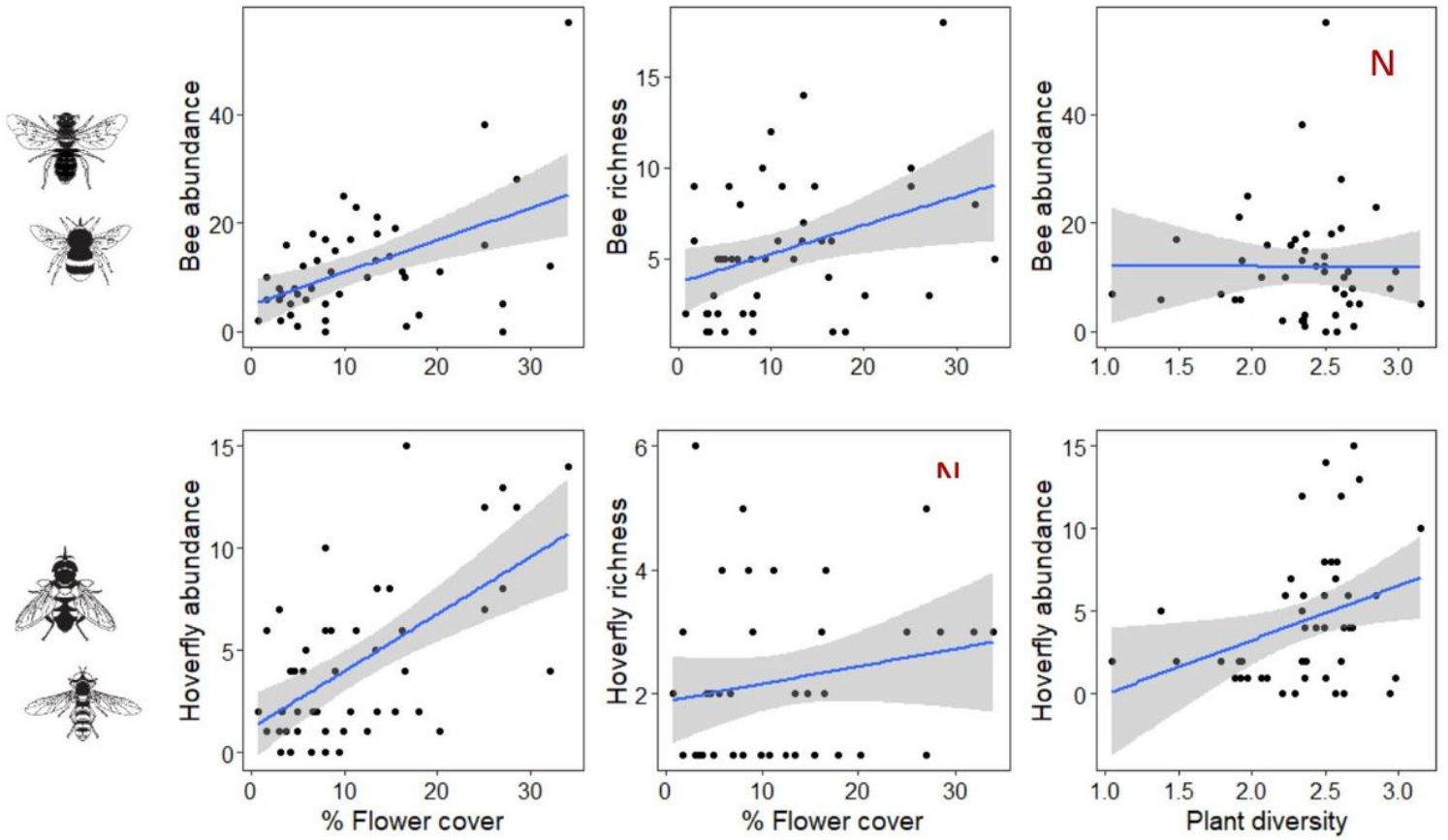Total abundance of pollinators belonging to different taxonomic families across management.

Figure 4

Scatterplots showing the effect of flower cover and plant diversity on the abundance and richness of the two distinct pollinator groups, bees and hoverflies.

Supplementary Files

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