Management linked to ecological intensification supports insect pollinators 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. Yet, ecological intensification practices were the most beneficial, showing a positive impact also on pollinator richness. Flower cover, together with plant diversity and landscape composition, were important drivers of pollinator diversity metrics. 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, such as the preservation or restoration of semi-natural habitats, also appear to be crucial for effectively safeguarding pollinating insects in this High Nature Value farming system.

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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 focusing on maximizing productivity while reducing the impact on the environment and improving positive secondary effects on ecosystem services delivery. This approach has been termed "ecological intensification" and it is defined as using natural processes to replace human-produced inputs like pesticides and fertilizers, while maintaining or increasing food production per unit area (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 important livestock pasture species such as legumes and other forbs, 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; Sjödin et al. 2008; Minckley 2014; 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 (Scohier et al. 2013; Enri et al. 2017). 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), with average stocking rates of 0.7 LU ha-1 (Reyes-Palomo et al. 2022). Dehesas are multipurpose systems, being tree products, hunting and livestock rearing the main economic activities (Campos et al. 2020). 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 plant biodiversity (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 (wild bees and hoverflies).

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.

Methods

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 ºC and annual precipitation 513, 747 and 490 mm in Badajoz, Cáceres and Salamanca respectively. Exact location details of sites can be found in Table S1. The vegetation of each site was characterized by wood pastures (dehesas), dominated by holm oaks (*Quercus ilex*) in Badajoz and Cáceres and a mixture of holm oaks and pyrenean oak (*Quercus pyrenaica*) in Salamanca. The herbaceous understory of the studied sites is highly diverse and dominated by annual species, such as *Bromus hordeaceus*, *Hordeum murinum*, *Tolpis barbata*, *Vulpia geniculata*, *Trifolium subterraneum*, *Plantago lagopus* or *Echium plantagineum* (see Table S2 for the full list of plant species surveyed together with their life cycle, flower color and relative abundance).

In each site we located five paddocks that have been exposed to different management regimes and that comprise the five treatments of the study: control, abandoned, and the three alternative schemes focused on ecological intensification which are legume-rich young, legume-rich old and rotational grazing. We interviewed the farmers of each site to locate each treatment and to assess its current and
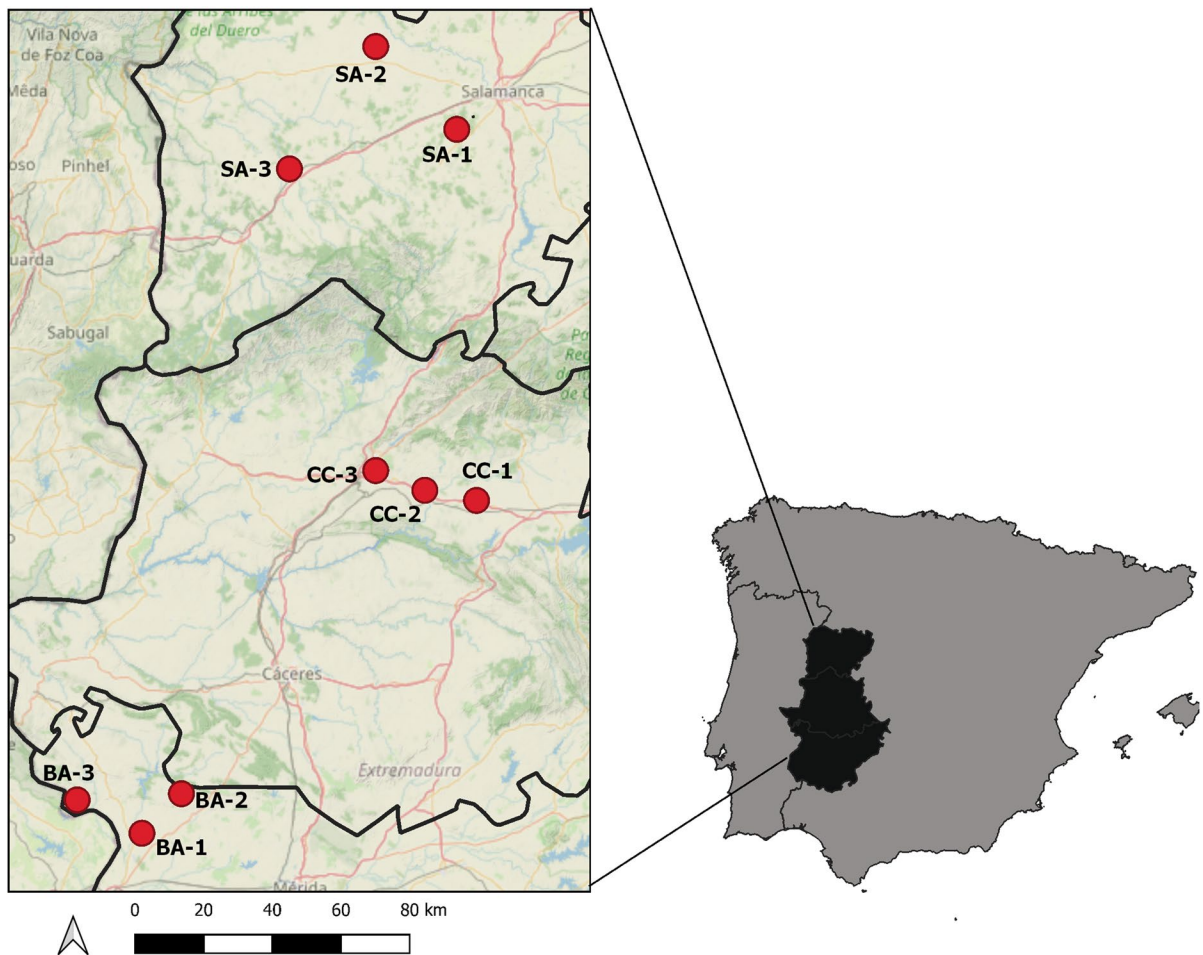
Fig. 1 Location of the nine study sites (red dots) in wood-pasture habitats across Western and Southwestern Spain

past management. The size of the paddocks varied across sites, ranging between 2 and 80 ha. All treatments were grazed by cattle or occasionally by sheep except for the abandoned treatment (AB) where no grazing has occurred in at least the last ten years. The stocking rate is similar among all grazed treatments (around 0.3-0-4 LU ha-1), but differing in the frequency of grazing during the year. The control treatment (CT) represents the conventional grazing practices in the studied systems, livestock can freely access this area and can graze on it all year round. The legume-rich treatment, both young and old, are similar to the control treatment in terms of grazing frequency but not in the pasture management. In legume-rich treatments pastures have been sown with a mixture of leguminous species either in the last five years (legume-rich young; LY) or more than ten years ago (legume-rich old; LO), to enhance pasture quality and quantity, a practice commonly undertaken by farmers in the studied system (Moreno et al. 2018; Hernández-Esteban et al. 2019). In contrast, in the rotational grazing treatment (ROT), livestock can only graze during a short period of time (a few days), allowing long periods of resting (some months) in between grazing episodes (Augustine et al. 2020).

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).

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 100 m long by 2 m wide fixed transects, one per treatment. Transects were located randomly starting near the center of the treatment, recorded with a GPS and established for the duration of the study. 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, which were gathered from the literature (Van Veen 2010; Ball and Morris 2015; Falk 2019). 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 S4 in appendix for the functional traits gathered for each pollinator species. Functional diversity (FD from here onwards) of bees and hoverflies was calculated using Petchey and Gaston' dendrogram-based index (Petchey and Gaston 2002).

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 50×50 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. We focused on yellow, white and purple-pink flowers as they were predominant in our study sites (see Table S2 for a full list of plant species, their relative abundances and color of the flowers).

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 intervals along four 25 m transects per treatment. In each sampling point the dominant individual was surveyed, and in total 100 plants were collected for each treatment. 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 all sampled species (forbs, legumes and grasses). 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 treatment 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 treatment within buffers of 250 m, 500 m and 1000 m of radius, based on 44 land use categories mapped by the CORINE 2018 land cover dataset (EEA 2019). Landscape diversity at 500 m 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.

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 visually compared 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. NMDS was also used to visually compare differences in plant composition across treatments. We additionally tested the effects of management and region on pollinator and plant species composition by using Multi Response Permutation Procedures (MRPP), a multivariate, nonparametric method for testing differences among predefined groups (Zimmerman et al. 1985). The MRPP statistic is based on the average

within-group distances and is tested against a distribution determined by randomly reassigning the data into the groups many times. The MRPP test was carried out using the function *mrpp* from the "vegan" package in R.

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".

Results

Description of pollinator assemblages

A total of 547 bees (Hymenoptera) from 80 different species and morphospecies were sampled (table S5 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 across management: in the control (CT) treatment the most abundant was *P. calcaratus*, in the legume-rich old (LO) it was *P. perezi* instead, in the legume-rich young (LY) and abandonment (AB) the most abundant species was *A. mellifera*, whereas for the rotational (ROT) it was *Lasioglossum* sp. Hoverfly (Diptera: Syrphidae) abundance amounted to

204 individuals, belonging to 18 different species (table S5). 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, for the NMDS showing the five distinct treatment groups see Fig. S2 in the appendix). This result was confirmed by the MRPP test, which showed non-significant differences across management (MRPP, P=0.767). We did not find a clear differentiation in species composition across study regions from the NMDS (Fig. 2B).
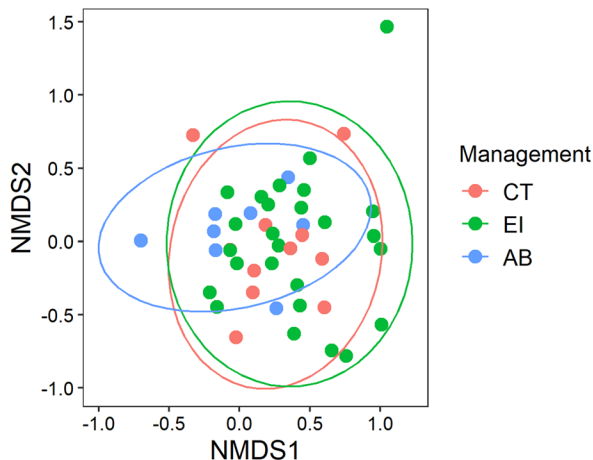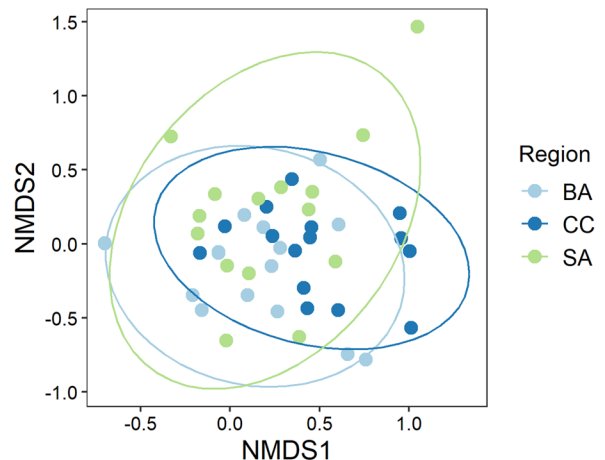
However, the MRPP test showed significant differences in pollinator community composition across regions (MRPP, P=0.001).

Plant composition, flower cover and pollinator diversity across treatments

Plant species composition differed among treatments as shown by the NMDS ordination technique (Fig. S3 appendix), which was confirmed by the MRPP test (MRPP, P=0.004). Mean plant richness and diversity were significantly higher in the abandonment system with respect to the rotational and legume-rich young, whereas mean flower cover differences were not statistically significant across management (Table 1). The relative abundance of legumes was significantly higher in the legume-rich young treatment with respect to control and abandonment, as theoretically expected (Table 1). Both legume-rich systems showed an overall higher proportion of legumes (dominated by *Trifolium michelianum* and *T. subterraneum*) than the other treatments. Rotational grazing system exhibited a dominance of grasses (most abundant species *Vulpia geniculata, Bromus hordeaceus* and *Hordeum murinum*) with respect to forbs and legumes. In control and abandonment treatments forbs were dominant, with *Tolpis barbata* being the most abundant species (see table S2 for the full list of plant species and table S3 for the relative abundance of

Fig. 2 NMDS analysis of pollinator species composition across treatments 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, *CC* Caceres, *SA* Salamanca). The 95% confidence interval ellipse for each category group is shown

Table 1 Plant diversity metrics and pollinator abundance, richness and diversity (taxonomic and functional) according to management (*CT* control, *LO* legume-rich old, *LY* legume-rich young, *ROT* rotational, *AB* abandonment)

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	25.00 ± 1.85^a	$23.78 \pm 2.53a$	$22.78 \pm 2.34ab$	$21.11 \pm 1.62abc$	$30.25 \pm 2.37ad$	40	**3.667****
Plant diversity	$2.65 \pm 0.12a$	$2.65 \pm 0.12a$	$2.48 \pm 0.14ab$	$2.47 \pm 0.12abc$	$3.00 \pm 0.08ad$	40	**2.991***
Legumes rel. abundance	0.12 ± 0.02^a	$0.17 \pm 0.03abc$	$0.26 \pm 0.04b$	$0.14 \pm 0.04abc$	$0.09 \pm 0.03ac$	40	**3.892***
Plant phylogenetic div	98.49 ± 1.79	94.5 ± 5.29	89.83 ± 7.32	87.26 ± 9.04	96.47 ± 2.52	40	0.791 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

Means $\pm$ SE. Means followed by different letters are significantly different in *t*-tests of least square-means (LSM) after fitting GLMMs, with site as a random factor. Significance levels (*p*) are * < 0.05, ** < 0.01, *** < 0.001, NS denote non-significant differences

Bold font indicates statistical significance

forbs, legumes and grasses across treatments). 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 (CT) showed higher bee and hoverfly FD values, but these differences were not statistically significant (Table 1).

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 ($\chi^2 = 21.325$, df = 4, p < 0.001), Andrenidae reached higher abundances in the LO treatment ($\chi^2 = 25.471$, 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 ($\chi^2 = 27.178$, 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 ($\chi^2 = 12.722$, df = 4, p = 0.013). The abundance of Syrphidae was not significantly different across treatments ($\chi^2 = 4.858$, df = 4, p = 0.013, p = 0.302).

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 to a less extent on richness, while 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

Fig. 3 Total abundance
of pollinators belonging to
different taxonomic families
across management (*CT*
control, *LO* legume-rich
old, *LY* legume-rich young,
ROT rotational, *AB* aban-
donment)
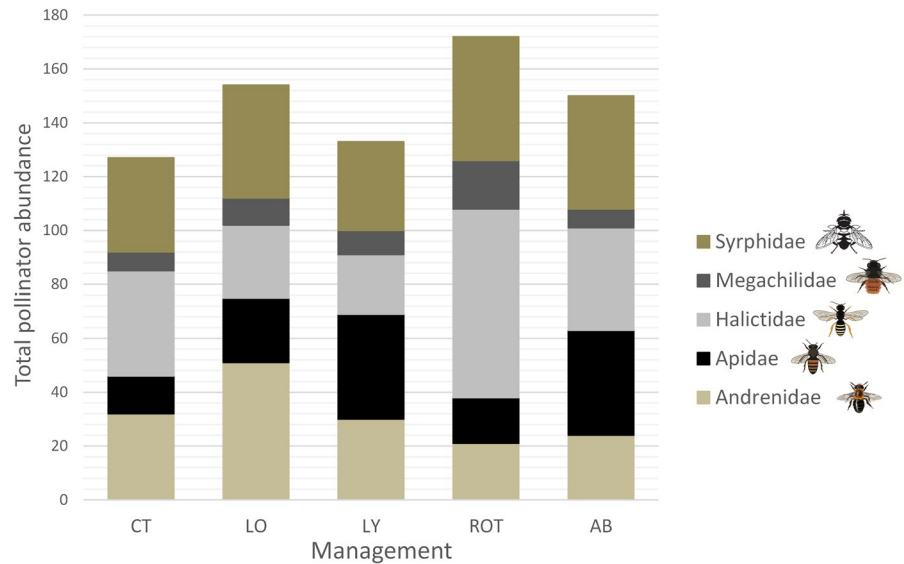
showed higher total pollinator abundance (and rich-
ness in the case of the rotational) than the control
treatment when accounting for the random effect of
the site (Table 2).

Regarding bee diversity metrics, flower cover
showed the most significant positive effect on bee
abundance, whilst it was not significant on bee rich-
ness (Table 2; Fig. 4), followed by plant phylogenetic
diversity. Plant phylogenetic diversity also showed
a marginally significant positive effect on bee rich-
ness, whereas plant diversity had a marginally nega-
tive effect on bee abundance (Table 2; Fig. 4). In
accordance with the results for total pollinator abun-
dance, 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).

With respect to hoverfly diversity metrics, we
found a strong positive effect of flower cover on
hoverfly abundance and not in hoverfly richness,
in accordance with the results for bees (Table 2 and
Fig. 4). In contrast to the results for bees, the effect
of plant diversity had a positive effect on hoverfly
abundance (Fig. 4), richness and diversity (Table 2).
Alternative management showed a weaker effect on
hoverfly abundance with respect to bees, with higher
abundances only observed in the rotational treatment.
The rotational grazing also showed a marginally
higher hoverfly richness and diversity. Instead, hov-
erfly functional diversity was marginally lower in the

abandonment and legume-rich young treatments with
respect to the control (Table 2). We also found a sig-
nificant positive effect of landscape diversity on hov-
erfly abundance and FD. Unexpectedly, the percent-
age of semi-natural areas showed a negative effect on
hoverfly FD (Table 2).

Discussion

Effects of management on pollinator abundance and diversity

Our findings showed that non-conventional manage-
ment in Iberian dehesas supports pollinator abun-
dance and to a lesser extent also species richness. A
high abundance of the dominant pollinating species is
known to be strongly correlated with pollination ser-
vice potential and helps to buffer the effect of envi-
ronmental 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 sys-
tem. 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

Table 2 Results of the GLMMs analysing the effect of multiple explanatory variables on pollinator diversity metrics

		Total pollinators			Bees				Hoverflies			
		Abund	Rich	Div	Abund	Rich	Div	FD	Abund	Rich	Div	FD
Management	LO	**0.348****	− 0.085	− 0.741	**0.392****	− 0.265	− 1.549	− 0.06	0.314	0.256	0.552	− 0.855
	LY	0.038	0.122	0.185	0.108	0.128	0.3	− 0.575	− 0.224	0.487	1.443	− 1.443
	ROT	**0.387****	**0.345***	1.351	**0.397****	0.215	0.52	− 0.132	**0.472***	**0.608**(.)	**1.85**(.)	− 1.371
	AB	0.158	0.08	0.742	**0.464***	− 0.019	0.345	− 0.065	**−0.51**(.)	0.173	0.811	**− 1.907**(.)
Flower cover		**0.035** ***	**0.014**(.)	− 0.111	**0.026*****	0.013	− 0.082	− 1.58	**0.059*****	0.006	− 0.682	0.817
Plant diversity		0.155	0.261	0.883	**− 0.451**(.)	− 0.169	− 0.195	− 0.055	**1.419*****	**0.928**(.)	**1.884**(.)	0.335
Plant phylogenetic div		0.007	0.006	0.288	**0.018****	**0.015**(.)	0.739	0.195	**−0.016**(.)	− 0.006	− 0.091	− 0.291
Landscape div		0.291	0.149	0.703	0.166	0.203	0.844	1.476	**0.685***	0.322	− 0.11	**2.172***
% Agriculture		0.0006	0.001	0.053	− 0.003	− 0.003	− 1.172	− 1.255	**0.006**(.)	0.006	1.679	− 0.784
% Semi-natural		**0.004***	− 0.001	0.284	0.003	− 0.005	− 0.803	− 0.218	**0.006**(.)	0.003	1.183	**− 2.191***

Site was included as a random factor. Estimates are shown together with significance levels (*P*) as follows: * <0.05, ** <0.01, *** <0.001, and (.) marginally significant with p<0.1

Bold font indicates statistical significance

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 in Iberian wood-pastures do not damage pollinator communities and can be even more beneficial than abandonment or renaturalization. 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). Compared to the results for abundance, alternative management had an overall weaker effect on pollinator richness and taxonomic or functional diversity. Only the rotational grazing system showed a positive effect on total pollinator richness, together with marginal positive effect on hoverfly richness and diversity when considered separately from bees, which suggests that this system can potentially have the most benefits for flower-visiting insects in Iberian dehesas. This result would be in line with the findings of previous studies for mountain pastures (Scohier et al. 2013; Enri et al. 2017).

The limited effect of management on overall pollinator community composition could be explained by the lack of substantial differences in floral resource availability 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, landscape diversity around surveyed treatments was not significantly different across management, which excludes the possible confounding effect of landscape composition with that of management. On the other hand, pollinator community composition did vary across the three study regions, which reflects expected variations in the regional species pools together with climatic and soil conditions.

The drivers behind the observed benefits of the rotational and legume-rich management systems for pollinators may be related to differences in the
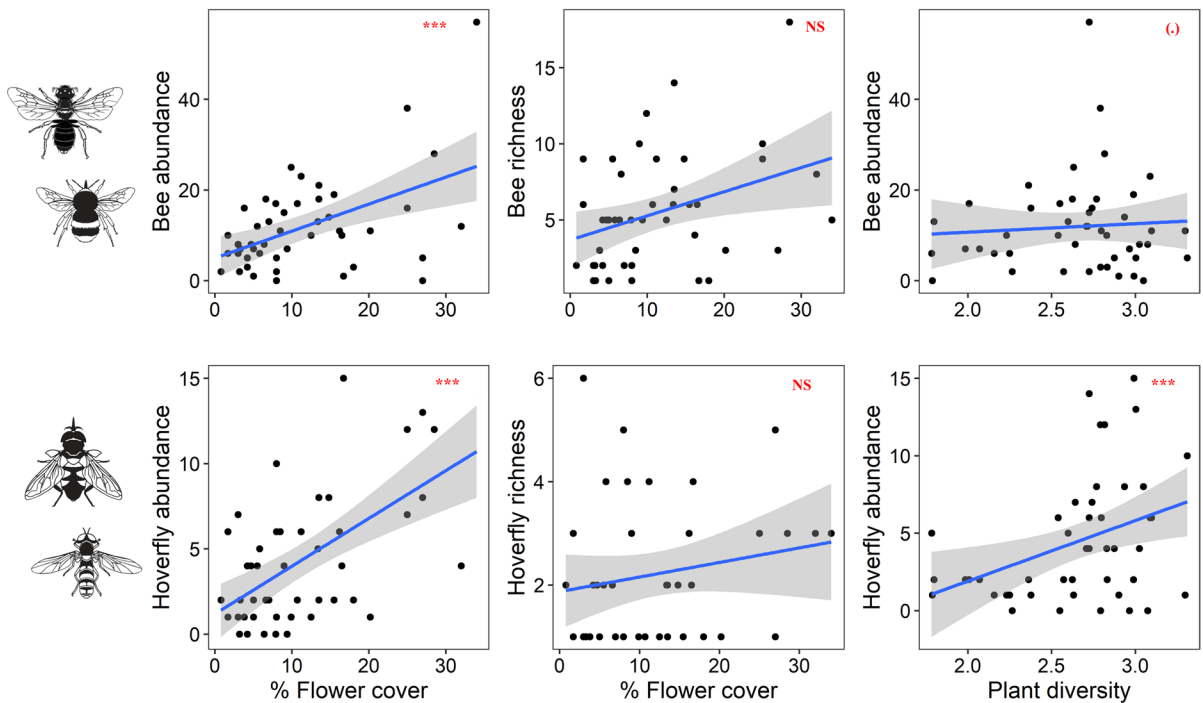
Fig. 4 Scatterplots showing the effect of flower cover and plant diversity on the abundance and richness of the two distinct pollinator groups, bees and hoverflies

specific types of flowering plants. The legume-rich old system, together with the legume-rich young, showed a larger 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, the rotational grazing system exhibited a plant composition dominated by grasses with respect to forbs and legumes, which may not be particularly favourable for pollinators. 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 long 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.

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

Our findings evidenced that flower abundance and plant diversity, 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). 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).

Response of different pollinator groups

The responses to management and additional local and landscape drivers varied between pollinator groups. For instance, opposite to the pattern found for bees, only the rotational grazing supported the abundance and diversity of hoverflies whilst other alternative management systems like abandonment negatively affected their abundance and 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 legume-rich managements as a result of 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. While, for bees, floral abundance was the most significant variable, for hoverflies plant diversity was equally or even more relevant than flower cover. 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.

Conclusions

In conclusion, this study showed that, in Iberian dehesas, alternative management linked to ecological intensification enhanced pollinator abundance and 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 semi-natural patches are additional practices that may be pivotal for safeguarding flower-visiting insects in Iberian dehesas.

Declarations

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