RESEARCH ARTICLE

Using the response–effect trait framework to quantify the value of fallow patches in agricultural landscapes to pollinators

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Abstract

Questions: What is the role of managed fallow habitats in providing resources for pollination services in agricultural landscapes? How is resource provision affected by fallow management and landscape structure? Can the resulting variation in the value of fallows to pollinators be explained using the response-and-effect trait framework?

Location: Four semi-arid Mediterranean agricultural regions (NE Iberian Peninsula).

Methods: Landscape complexity, fallow field age and management practices were identified as the explanatory factors that interact which each other and affect the provision of resource for pollination communities. A trait-based approach was taken to model the system. Plant traits were selected on the basis of their response to abiotic factors (response traits) and those that influence the interaction with pollinators (effect traits). Plant community characterization was calculated based on both taxonomic and functional indices. The linkages between the selected plant traits on contrasting fallows were analysed using community-weighted mean redundancy analysis (CWM-RDA).

Results: The presence of semi-natural areas in the landscape was shown to enhance the value of fallows for pollinators, providing a source of diverse flower forms. In contrast, we found that field edges act as a relatively poor reservoir for flowering plant species in these areas. Land-use practices promoting mid-successional plant communities that support the coexistence of diverse life forms with overlapping flowering periods and a range of flower morphologies had the greatest potential to support a diverse pollinator community.

Conclusions: Early herbicide application (Feb) combined with shredding were identified as the best fallow practices for enhancing resources for pollinators. The construction of our framework will help policy makers to identify management recommendations that will result in the most beneficial plant communities for pollinators in fallows.

KEYWORDS
agri-environmental schemes, ecosystem services, environmental filters, fallow lands, functional traits, pollinator attractiveness

1 | INTRODUCTION

In recognition of the unintended environmental consequences of the drive for increased productivity of agricultural land, the European Union's Agri-Environmental Regulation Initiative has promoted various Agri-Environmental Schemes (AES) to enhance levels of biodiversity on farmland (Whittingham, 2011). Leaving land fallow is one option available in these schemes and is one of the most promising approaches

for supporting and enhancing biodiversity in agro-ecosystems (Ma & Herzon, 2014; Toivonen, Herzon, & Helenius, 2013). In contrast to perennial field margins, fallows present the opportunity to manage large areas in field centres that provide a habitat for species adapted to disturbed environments (Butler et al., 2009). Although the management of fallows has tended not to be primarily driven by the delivery of ecosystem services, these non-crop habitats are important landscape elements which may reinforce key ecosystem services such as pollination or biological control in the context of optimizing the multi-functionality of AES habitats (Kuussaari, Hyvönen, & Härmä, 2011; Toivonen et al., 2013).

Because fallows are located in the main area of crop fields, characterized by regular disturbance, they provide a habitat for arable plant species that are functionally distinct from the more generalist species that tend to be found in the boundary features of arable landscapes. These arable plants (including many that could be classified as weeds) are more sensitive to perturbations and may also have a high intrinsic value as a component of biodiversity that provides distinct resources and functions in agroecosystems (Rotchés-Ribalta, Blanco-Moreno, Armengot, José-María, & Sans, 2015). The value of these floras on fallow lands will be influenced by the historical management pressure imposed on the field crop and on the specific conditions generated by the management of the fallow. A poor seed bank resulting from intensively managed land will require seeds from outside the field to increase plant diversity; therefore the surrounding landscape may also play a key role, acting as a reservoir for propagules (Kohler, Verhulst, Van Klink, & Kleijn, 2008). A complex landscape, with a high percentage of natural and semi-natural habitats, is likely to act as a refuge for weed species that are most sensitive to intensive agriculture and also offer a large amount of resources for pollinator insects (Gaba, Chauvel, Dessaint, Bretagnolle, & Petit, 2010; Smart, Bunce, Firbank, & Coward, 2002; Solé-Senan et al., 2014).

Declining weed abundance has been identified as a driver of both pollinator declines and losses of pollination services (Nicholls & Altieri, 2012; Steffan-Dewenter & Westphal, 2008). Therefore, providing greater plant biodiversity on farmland through the provision of areas of land managed specifically for this aim is likely to increase the provision of a range of ecosystem services, and utilizing fallow land avoids the negative impact arable weeds have on crop yield. However, it is difficult to quantify the enhancement of pollinator habitat (Whittingham, 2011; Wratten, Gillespie, Decourtye, Mader, & Desneux, 2012) – all plant species do not contribute equally to the delivery of varied ecosystem processes, and the sustainability and resilience of these processes may depend on aspects of diversity beyond the number of species present in a community (Stuart-Smith et al., 2013). Different pollinators promote selection for diverse floral forms that produce an array of "pollination syndromes", defined as a suite of floral traits that function as an advertisement and reward for pollinators (Fenster et al., 2004; Poveda, Steffan-Dewenter, Scheu, & Tscharntke, 2005). Changes in floral characters such as morphology, colour and odour or food quality can influence pollinator visits (Ricou, Schneller, Amiaud, Plantureux, & Bockstaller, 2014; Wratten et al., 2012). Developing models for quantifying the relative value of different habitats in the

context of these floral traits is a clear research need for assessing contrasting habitats and management recommendations. Although the most often used management techniques to enhance pollinator habitat on farmland consists of field margin manipulation, the role of fallow land as a temporary patch habitat in dryland Mediterranean systems has seldom been explored.

The use of functional traits has been an important conceptual advance in linking biodiversity with ecosystem processes and associated services (Ma & Herzon, 2014). A conceptual framework has been developed by Lavorel and Garnier (2002) that differentiates traits associated with response to environmental and management filters – response traits – from those that determine the effect of that change in the functional signature of the plant community on ecosystem services – predicted by effect traits. The overlaps or correlation between relevant response and effect traits will determine the extent to which an environmental or management driver will impact ecosystem functioning. This framework has recently been extended to systems where services are delivered through higher trophic groups (Lavorel et al., 2013; Solé-Senan, Juárez-Escario, Robleño, Conesa, & Recasens, 2017).

The goal of this study was to populate this framework based on plant species abundance measured in experimental fallows in four semi-arid regions of the NE Iberian Peninsula, modelling the effects of landscape, age of fallow and field management as a series of filters acting on plant biodiversity and pollinator insects. By selecting target traits, we set out to (1) examine the response of plant vegetation traits to environment and management factors and (2) explore the overlap and interaction with plant 'effect' traits to predict the potential impact of changes in management in contrasting landscapes on the potential value of the fallows to pollinators.

2 | METHODS

2.1 | Study area and experimental design

Trials were located in the Catalan part of the Ebro basin (NE Iberian Peninsula), an area with a flat or slightly undulating topography, mediterranean continental climate and average annual rainfall of 350 mm. A total of four separate fallow lands with different ages were selected as study areas: Montcortes (41°42′35.22″N, 1°13′52.33″E) and Ballobar (41°32′55.37″N, 0°5′59.06″E), were new fallows following an annual crop rotation, and Balaguer (41°44′38.92″N, 0°45′21.63″E) and Mas de Melons (41°30′14.26″N, 0°42′40.18″E) have remained as fallows for 5 and 4 years before the start of the experiment, respectively. All the study sites were selected because they were located in areas dominated by dryland cereal crops but represented different degrees of landscape complexity, from structurally simple –with a high percentage of arable land – to more complex ones – with a high percentage of semi-natural patches- (Appendix S1). All are also included in a special protection area of the Natura 2000 network, a key policy instrument for continental-wide biodiversity protection in Europe.

We conducted a 3-years field experiment (over the 2012, 2013 and 2014 agronomic seasons, from Oct to Jun–Jul) to examine the succession of plant communities on fallow lands and the impact of

contrasting management. The different starting points of the fallow fields allowed us to test the impact of management in the context of different natural successional stages, from more ruderal to more competitive communities. In each of the four study sites, one fallow field was divided into 21 plots of 200 m² as a randomized complete block design with three replicates for each of the treatments, which reproduce some of the most common cultural practices carried out in fallow lands. The following treatments were applied: (1) chisel plough – a minimum tillage resulting in soil disturbance down to 10 cm, (2) shredding – cutting and removal of the biomass, (3) herbicide spray – glyphosate at 1.5 lha^{-1} dose, and (4) alfalfa sowing. The treatments had different timings: "early dates" – Feb, for chisel and herbicide, "late dates" –Apr, again for chisel, herbicide and shredding, and Oct for alfalfa sowing. Additionally, some plots were untreated (control), giving a total of seven treatments repeated three times in each study area: early chisel, late chisel, early herbicide, late herbicide, late shredding, early alfalfa and untreated control. At the end of each agronomic season (Oct), the vegetation of all experimental plots was cut in order to remove an excess of organic matter while maintaining the cumulative effect of the previous treatments.

2.2 | Vegetation sampling

Plant data were collected from five quadrats of 0.25 m² located on each experimental plot in May, 15–20 days after the last management was done and when AES restrictions came into force. Coverage of each species was visually estimated as a percentage of the area of the entire quadrat (Appendix S2). Vegetation richness was recorded as the number of plant species identified in each quadrat.

2.3 | Landscape/habitat information

Data on landscape structure variables were obtained from an aerial orthophoto SIGPAC (http://sigpac.mapa.es/fega/visor/) taken during the experimental period and measured within circles with a radius of 500 m around the centre of each experimental field, identified as the appropriate scale at which weeds are most strongly associated with landscape structure (Gaba et al., 2010; Marshall, West, & Kleijn, 2006). After checking that the non-crop elements of the landscape had not changed substantially during the study period, two landscape variables were calculated: percentage of semi-natural habitats and length of field edges, which previous studies have shown are relevant to plant diversity and weed community composition in the study area, providing quantified information regarding the surrounding habitat (Solé-Senan et al., 2014). Semi-natural habitats were identified as all non-cropped land uses, and edge length was calculated by summing all the boundaries of the fields in that area.

2.4 | Selection of plant traits

According to the model proposed by Lavorel et al. (2013), we first identified the plant traits that we expected to respond directly to the environmental and management drivers described above (response

traits; Appendix S3). Growth form and flowering onset were included as they have been associated with persistence in disturbed habitats (Cornelissen et al., 2003; Gunton, Petit, & Gaba, 2011; McIntyre, Lavorel, & Tremont, 1995) and have been related to management practices, specifically the intensity of tillage (Fried, Kazakou, & Gaba, 2012). Seed dispersal plays an important role as it affects plant colonization, related to landscape structure and disturbance level, therefore modulating community assembly in space and time (Critchley, Allen, Fowbert, Mole, & Gundrey, 2004; McIntyre et al., 1995). Plant height and Specific Leaf Area (SLA, the ratio of leaf surface to leaf dry mass) were both expected to respond to intensity of disturbance, with disturbed environments being characterized by shorter plants with higher SLA, associated with faster resource use strategies sensu Westoby (1998). Plant height and SLA are also related to plant competition, which will vary with the succession stage.

Second, we classified the plant traits that can influence interactions with pollinator communities (effect traits) in the context of the traits of the pollinators themselves (trophic response traits, sensu Lavorel et al., 2013; Appendix S3). It has long been noted that changes in floral features are highly linked with this function (Ricou et al., 2014; Wratten et al., 2012); so-called "pollination syndromes" (Fenster et al., 2004), such as corolla morphology and colour. These were therefore selected as traits that determine pollinator response. Discrimination between different corolla shapes is associated with accessibility (Gómez et al., 2008), distinguishing among generalists (pollinated by several to many animal species from different taxa) and specialist (pollinated by one or a few taxonomically similar animal species) flowers (Ashworth, Aguilar, & Galetto, 2004). This is likely to be correlated with morphometric parameters of pollinators (body size and mouthparts length; Fenster et al., 2004). Flower colour is also a plant effect trait that will determine pollinator response. It is related to UV reflection and the ability of perception, thus it is associated with visual attractiveness (Menzel & Shmida, 1993; Ricou et al., 2014). Finally, flowering duration also influences pollination visitation, determining reward (nectar and/or pollen) availability period (Bosch, Retana, & Cerdá, 1997).

Trait values for each of the species were obtained from the literature and from open access databases (Appendix S3). We acknowledge the potential importance of intraspecific variability in determining functional diversity (Albrecht, Schmid, Hautier, Mueller, & Müller, 2012) and the benefit of measuring traits directly in the contrasting treatments. However, although this may affect the conclusions based on plastic traits such as SLA and height, many of the traits we included in our analysis (such as flower morphology and growth form) are categorical and will be largely unaffected by intraspecific differences.

Plant community characterization was calculated based on taxonomic and functional indices. Two taxonomic metrics were selected: the total species richness (S) and the Shannon entropy index (H), presented as the exponential of Shannon-Weaver index. With this transformation, species are weighted in proportion to their frequency in the sampled community (Appendix S2) and thus it can be interpreted as an equivalent number of species in the community if they were all equally common and facilitates the interpretation and comparison of diversity among communities (Jost, 2006). To assess the functional

TABLE 1 General linear mixed model (GLMM) of changes in species richness, Shannon diversity index (*H*) and functional diversity index (Rao) in relation to landscape features (percentage of semi-natural habitat and length of field edges) and age since fallow using Poison error distribution and including location and plot as random factors

Environmental factors	Indices	F
Semi-natural habitat	Richness	7.75***
	H	5.74**
	FD (Rao)	3.14
Edges length	Richness	0.01
	H	0.18
	FD (Rao)	0.27
Age since fallow	Richness	1.18*
	H	1.41*
	FD (Rao)	2.97*

*p < .05; **p < .01; ***p < .001.

approach we used the CWM trait value (Garnier et al., 2004), which expresses the mean trait value in the community weighted by the relative abundance of the species. Furthermore, as a complementary metric, we quantified the degree to which trait values differ in a community by functional diversity (FD). We measured the variation in traits using Rao's quadratic diversity, combining multiple traits into one FD index (Moretti et al., 2013). Unlike CWM, which is calculated per each trait separately, FD is based on multiple traits. The Rao coefficient has recently been identified as a useful metric for comparing functional studies of contrasting biological communities and has the flexibility to combine dissimilarity data from single traits into a compound value from multivariate analysis of multiple traits (Ricotta & Moretti, 2011).

2.5 | Statistical analysis

Species richness, *H* and FD (Rao) indices were used to explain variation in plant communities between the different habitats and landscapes (Appendix S4). We performed GLMM with Poisson error distribution to investigate the relationship with landscape features and fallow age taking into account only data from control plots. The effects of field treatments on diversity and species richness were tested, using all data, with a LMM, and a post-hoc Tukey's pair-wise comparison was utilized to determine differences among treatments. Locality and plot were included as random factors in both analysis to control for the different historical management and the independence of the samples.

To quantify the innate correspondence between response–effect trait values in the study species pool, a PCA was carried out to characterize the patterns of correlations among them. Variance in trait values between species was standardized to zero mean and unit *SD* to give them all equal weight in the analysis before performing the PCA. To assess how the variability of individual traits changes along the environmental factors (effects of landscape, age since fallow and field treatments) we performed a CWM-RDA analysis following Kleyer et al. (2012). This technique uses multiple linear regressions (ordinary

least squares) among response variables (traits) and predictors (environmental data). Because *Medicago sativa* was sown in some treatments, this species was excluded from the analysis in alfalfa plots, therefore only testing the indirect effect of the cultivation and additional competition on the background flora. Locality and plot were included as covariables.

The *t*-value biplots were constructed from the CWM-RDA analysis for each of the explanatory variables (effects of landscape, age since fallow and field treatments) using the Van Dobben method (terBraak & Looman 1994). Previous studies have used these ordination diagrams to disentangle plant species relationships (Madrigal, Kelt, Meserve, Gutierrez, & Squeo, 2011; Schmitt, Denich, Demissew, Friis, & Boehmer, 2010). The ordination is based on reduced-rank regression, combining multiple regressions between species traits and a particular site factor, and the model defined by the CWM-RDA. Van Dobben circles indicate those traits with a strong relation to the explanatory variables tested (*t*-value < |2|).

Statistical analyses were performed with the R program, 3.0.2 (R Foundation for Statistical Computing, Vienna, Austria) with the lme4 package (http://CRAN.R-project.org/package=lme4) and with CANOCO 5.0 for Windows (Microcomputer Power, Ithaca, NY, USA).

3 | RESULTS

An increase of Shannon entropy index (*H*) and species richness was observed as the percentage of semi-natural habitat in the landscape increased and the fallows became older, in this case also for FD (Rao); there was no relationship with total length of field boundary (Table 1). Post-hoc Tukey test results from LMM analysis did not find any association for either the taxonomical indices (*H* and species richness) or for the functional diversity index (FD Rao) between different treatments (data not shown). However, the late management interventions (chisel and herbicide) resulted in lower values of *H* and richness. In contrast, shredding and early herbicide were the treatments with highest values, more similar to those of the control. Regarding FD, the highest values were related to early herbicide and late chisel treatments (Figure 1).

The first PCA axis accounted for 26.23% of the variance and identified a trade-off between plant traits that were related to a successional gradient from more ruderal to competitive plant strategies (Figure 2). Species with a low PCA1 score were characterized as having a high SLA, early flowering or annual life cycle, graminoid forms, white-greenish-brownish flower colours with anemophilous and open entomophilous shapes. In contrast, species with a high PCA1 score had a perennial life form, late flowering time, tall stature, autochory seed dispersal, zygomorphic and tubular corollas, and yellow and blue flower colours. The contrasting plant strategies reflected in the multivariate analysis provide a useful framework for interpreting the response of the plant communities to different management treatments and potential value to pollinators. Trait relationships from Van Dobben circle results have been summarized in Table 2 for those plant traits which response to the environmental factors (response traits), and in Table 3 for the traits underpinning
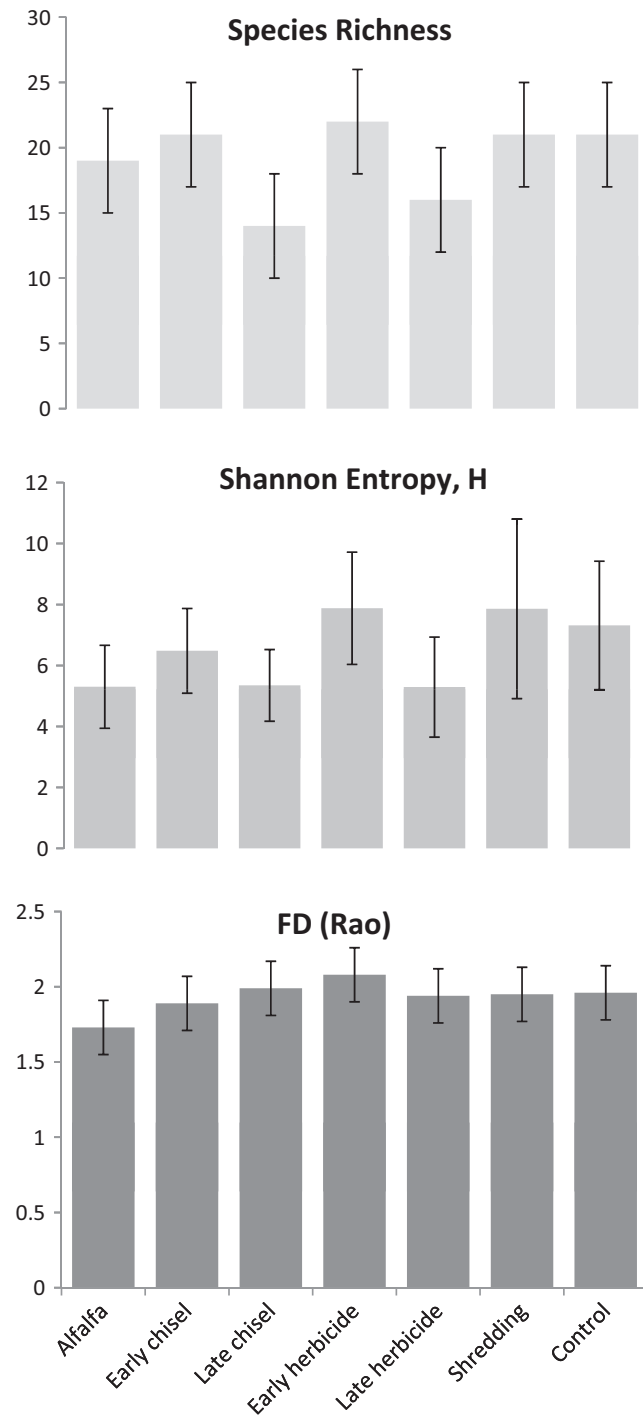
FIGURE 1 Mean of species richness, Shannon entropy index (*H*) and Functional diversity index (Rao) per field treatment. Error bars ± *SE*

interactions between plants and pollinators (effect traits/trophic response traits). The results are summarized in the following sections.

3.1 | Landscape features and age since fallow

Fallows within landscapes with a high percentage of semi-natural habitats had a community with a higher proportion of legumes, autochory
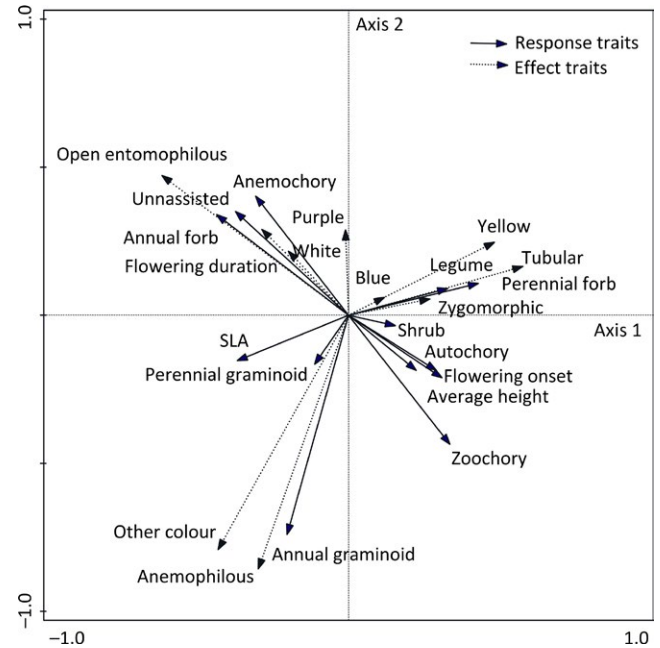
FIGURE 2 Correlation among plant functional traits represented by a PCA. Percentage variance accounted for in first two axes = 36.3%. Primary axis for the response traits represents trade-off between ruderal traits (fast life cycle, high SLA, annual) and competitive traits (late flowering time, perennial life forms, tall stature) and for the effect traits is associated with the complexity of floral structures, traits related to generalist pollinators (white-greenish-brownish flower colours, anemophilous, open entomophilous corollas) and traits linked with more specialists insects (yellow and blue flower colours, zygomorphic and tubular corollas)

seed dispersal and later flowering species, characteristics correlated with zygomorphic corolla and blue flower colour (Tables 2 and 3). A longer length of field edges promoted a community dominated by annual graminoid species and anemochory and unassisted seed dispersal, related positively with characteristics as white-greenish-brownish flower colours and negatively with purple and yellow corollas and long flowering duration. A successional pattern was evident in that older fallows had plant communities more dominated by perennial forbs, such as hemicryptophytes and geophytes, and species with autochoric seed dispersal. These traits in turn were positively correlated with tubular corollas and yellow flower colour, and negatively correlated with open entomophilous corollas and purple colour.

3.2 | Field management practices

Among field management treatments, a promotion of annual plants by early interventions was observed together with the presence of shrubs on the early herbicide treatment (Tables 2 and 3). Late herbicide and shredding increased the presence of perennial forms (mainly hemicryptophytes). Graminoid forms were more prevalent on early chisel and alfalfa treatments than forbs. A late flowering onset was observed on the early herbicide practices, while in late herbicide treatments, a positive relation with taller plants and early flowering time was observed. The characteristics of plant communities resulting from

TABLE 2 Summary of Van Dobben circle results for response plant traits, representing the positive (represented as +) or negative (represented as −) relation to the abiotic variables. Traits not acting in response to the abiotic filters according to the framework described in Appendix S5 are represented as grey blocks

| | | Abiotic filters | | | | | | | | |
| | | Landscape features | | | Field managements | | | | | |
		Semi-natural habitats	Length of field edges	Age of fallow	Alfalfa	Early chisel	Late chisel	Early herbicide	Late herbicide	Shredding
Growth form	Annual forbs							+	−	
	Perennial forbs		−	+	−	−			+	+
	Annual graminoids		+	−	+	+				
	Perennial graminoids						+			
	Legumes	+								
	Shrubs							+		
Seed dispersal	Anemochory		+	−						
	Autochory	+		+						
	Zoochory									
	Unassisted		+							
	Average height								+	
	SLA			−						
	Flowering onset	+							−	

TABLE 3 Summary of Van Dobben circle results for effect plant traits, representing the positive (represented as +) or negative (represented as −) relation to the abiotic variables

| | | Abiotic filters | | | | | | | | |
| | | Landscape features | | | Field managements | | | | | |
		Semi-natural habitats	Length of field edges	Age of fallow	Alfalfa	Early chisel	Late chisel	Early herbicide	Late herbicide	Shredding
Corolla shape	Anemophilous		+		+	+	+			+
	Open entomophilous			−				+		+
	Tubular			+	−	−		−		
	Zygomorphic	+								
Flower colour	Purple		−	−						
	Blue	+								
	Yellow		−	+					+	
	White		+							
	Other colour		+		+	+	+			+
	Flowering duration		−				+	+		

the different field treatments were correlated with traits which are likely to determine pollinator interaction such as anemophilous corollas, positively related with alfalfa, chisel and shredding practices. Early herbicide and shredding treatments were positively correlated with open entomophilous corollas and negatively with tubular ones, as was observed in alfalfa and early chisel treatments. Yellow flowers showed a positive correlation to late herbicide, and other flower colours (such as greenish and brownish) were positive correlated with alfalfa, chisel treatments and shredding. Finally, a longer period of flowering was related to late chisel and early herbicide treatments.

4 | DISCUSSION

We aimed to better understand how altering fallow habitats by environmental or human-associated disturbances could influence the functional trait composition of the vegetation, selecting between different plant ecological strategies. From the shifts in response and effect traits we predicted changes in the attractiveness for pollinators. Following the response–effect framework (Appendix S5), we now discuss: (1) the functional response of plant communities to environmental and management drivers and (2) the overlap with flowering traits that determine the value of fallows for pollinators.

4.1 | Response of fallow plant communities to environmental and management drivers

Understanding the processes determining the variation of biological communities in habitats managed as part of agri-environment schemes requires analyses at multiple scales. Although particular management strategies may benefit certain species, it has been shown that landscape characteristics also play an important role in determining plant and pollinator diversity in managed ecosystems (Carvalheiro et al., 2011). Any change in species composition also needs to be related to functional characteristics, since a reduction in functional diversity implies a substitution of specialist species by generalists, leading to a functional homogenization of the communities and a potential increase in competition among pollinators for resources (Clavel, Julliard, & Devictor, 2010; Tadey, 2015).

Areas of semi-natural habitat and field margins represent areas of least disturbance within arable systems, acting as a sink that provides shelter and refugia for plant species which are unable to persist in the harsh conditions of intensely cultivated habitats (Fried, Petit, Dessaint, & Reboud, 2009), and as a source, allowing immigration of plant species either to crop fields or new uncultivated patches such as fallow lands (Gabriel, Thies, & Tscharntke, 2005; Kleijn, Rundlöf, Scheper, Smith, & Tscharntke, 2011; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). These habitats generally have lower fertility than fertilized arable fields and are more likely to harbour legumes, a plant morphology which is predicted to increase under these conditions (van Elsen, 2000); in our study, legume species of the *Coronilla*, *Medicago* or *Retama* genera were found at higher frequency in landscapes with a larger proportion of semi-natural habitat. The relative

ecological stability of semi-natural areas is also reflected in the presence of species with late time of first flowering (Pinke & Gunton, 2014) or autochory seed dispersal. Autochory is a short-distance dispersal mechanism, and the low colonizing capacity over space suggests that species are in an optimal area. An increased proportion of semi-natural habitat in the landscape surrounding the fallows was reflected in a greater representation of these traits in the field centres and an overall increase in taxonomic and functional diversity. Contrary to our expectation and to the trend with an increase of semi- natural areas around fallow-fields, more field edges in the landscape did not show any relation either with the taxonomic indices or with the functional diversity (FD (Rao)). In our study system, field edges were not managed for biodiversity and only provided extremely narrow boundaries with no capacity to buffer negative effects from neighbouring areas due to the high intensity of agricultural practices (Aavik & Liira, 2010; Ma, Tarmi, & Helenius, 2002), resulting in a dominance of annual grasses. There may, therefore, be potential to combine improved field margin management with the appropriate management of fallows to add value to both components of the agricultural landscape.

Studies of successional dynamics in managed ecosystems have highlighted that old communities tend to be more competitive, leading to uniform landscapes which provide fewer niches for weeds or insects (Kuussaari et al., 2011; Lososová et al., 2006). Our results show a contrasting trend, with older fallows having a higher taxonomic and functional diversity and coexistence of species with dissimilar functionality. Low disturbance rates, the chance to develop different resource acquisition strategies or unpredictable natural regeneration have all been suggested as causes of the persistence of a diversity of flower species with high resource value (Wratten et al., 2012). It may be, however, that as the fallows age further, the dominance of a few, more competitive species may increase and that we mainly observed mid-successional communities with a combination of earlier ruderal and later competitive strategies. Succession of the vegetation with fallow age also revealed a gradient of plant strategies as noted by Garnier et al. (2004). Early fallow stages, immediately following agricultural disturbances, had a community dominated by opportunistic ruderal species with traits associated with fast growth, annual life cycle and high SLA. Anemochory seed dispersal is related most strongly to the ability of a species to colonize new patches that may be a long distance from the source population (Dupré & Ehrlén, 2002; Kohler et al., 2008). Hemicryptophytes and geophytes appear as the dominant life forms on late successional fallow stages, mainly represented by Asterceae (*Crepis*, *Silybum* or *Carduus*) and autochory seed dispersal, indicative of competitive plant communities.

Among the management regimens tested in this study, early herbicide application is the one that led to a habitat occupied by both annual and woody plants, diversifying vegetation structures and so, ecological strategies. Glyphosate is a non-selective contact herbicide that controls a wide range of weeds. However, phanerophytes, chamaephytes and most of the hemicryptophytes are the least harmed, leading to a more heterogeneous habitat. The role of these biological forms, in contrast to annual herbaceous plants, resulted

in a sparse and patchy habitat with a lower density of vegetation. Previous studies have shown that periodicity of flowering is adapted to the intensity and frequency of soil disturbances in herbicide treatments (Gaba, Fried, Kazakou, Chauvel, & Navas, 2013). Tillage promoted pioneer annual plants with fast life cycles (Sojneková & Chytrý, 2015). It is also noteworthy that the annual graminoid dominance on alfalfa and early chisel was related to early soil disturbance, while late chisel managements were characterized by a predominance of perennial rhizomatous/stoloniferous graminoids such as *Cynodon dactylon*, which permit an effective colonization of bare ground sites (Kahmen, Poschlod, & Schreiber, 2002). Although we have shown that the effect of herbicides can be interpreted in the context of a disturbance regime and so related to plant traits, it is also the case that herbicide selectivity will play a major part in the structuring of communities in agricultural landscapes. These effects may ultimately have to be modelled at the level of individual species.

4.2 | Interaction of response and effect traits

Identifying key plant traits which influence the interaction with pollinators will be useful for understanding the effect of the responses of communities to environment and management discussed above for pollination services. Pollinators were not directly measured in this study; however, well-established published relationships between flowering traits and attractiveness to pollinators allow us to predict the impact of the landscape and treatments on the value for different plant communities to pollinators.

In our study, the increase of legumes on fallows in landscapes with a higher proportion of semi-natural habitats was linked with zygomorphic corolla and blue flower colour, well-known syndromes of complex flowers that are associated with pollination by long-tongued bees (Corbet, 1995; Fenster et al., 2004). However, the high functional divergence on these fallows may indicate that, although pollinators specializing in zygomorphic flowers would be expected to be promoted, these fallows also support plants that provide resources to generalist pollinators. The presence of these patches of relatively high-contrast habitat types, or 'ecotones', is predicted to enhance the value of managed fallows for pollinators. Moreover, semi-natural habitats provide a place to nest and hibernate for the major pollinator groups (Batáry, Báldi, Kleijn, & Tscharntke, 2011), making them an essential element in the landscape. But, not all the so-called ecotone′ elements in the landscape were acting in the same way on the fallow floras, with a high proportion of field boundaries having a deleterious effect on resource provision for pollinators. The high level of disturbance generated by the farm practices has led to an impoverishment of the habitat value of field edges, acting as a source of undesirable species such as graminoids. The Poaceae family is considered to be inaccessible and so less frequently visited by pollinators (Ricou et al., 2014), leading to a reduction of flower features that promote pollinator–plant interactions (Fenster et al., 2004).

Along the age–gradient succession, the dominance of more generalist flower features in early stages such as open entomophilous corollas is notable and suggests that, at this stage, all pollinator fauna

may be functionally equivalent (Fenster et al., 2004). As expected, different successional stages were not functionally equivalent and one approach to management would be to design interventions that aim to maintain communities in the successional stage that delivers the most value to pollinators. We suggest maintaining mid-successional communities would be optimal for supporting a wide range of pollinators in our system. To achieve this type of habitat, intermediate levels of disturbance may be required (Wratten et al., 2012). In this regard, early herbicide treatments were beneficial because they promoted a heterogeneous habitat structure allowing a high coexistence of life forms and so an overlap of flowering periods. The increased abundance of flowers with open entomophilous corollas as opposed to anemophilous ones (which tended to dominate in other management treatments) was another important component of the floras adapted to this treatment. However, the role of pesticides in agriculture in causing pollinator declines is well documented, especially where spraying time coincides with flowering time (Nicholls & Altieri, 2012). Here the application was made in early February, out of the flowering peaks of most of the species. Open entomophilous and anemophilous corollas were promoted by shredding management, while anemophilous ones dominated in chisel and alfalfa treatments, resulting in poor habitat quality in terms of attractiveness for pollination. Alfalfa is generally considered as a temporary pollinator-friendly cover crop (Wratten et al., 2012) because of its beneficial flower features. Nevertheless, this area presents a low productivity index (Oñate, Atance, Bardají, & Llusia, 2007), and alfalfa crops without an irrigation supply often fail. At the same time, the early soil removal caused by the alfalfa sowing favours the development of Poaceae species, the least attractive family for insects.

A landscape perspective is needed to achieve conservation goals on fallow lands. While local effects of management can be detected over small scales that share a similar environment, deriving more general rules of plant community assembly in fallows is dependent upon regional scales that aggregate environmental heterogeneity. In order to achieve this, an important distinction between the landscape elements must be made. As a next step to further assess ways to enhance pollinator habitats in fallow lands, a validation of the results of the study would be desirable to determine the relationships between our predictions and information on insect species′ abundance and diversity. Also, here we have tested the field practices that are most commonly developed in these non-crop habitats; however other management options could also be applied. Since livestock tend to promote vegetation heterogeneity, selective grazing could be suggested as an alternative management practice in fallows. If sowing is an option, an important issue to take into account to enhance its efficiency is to have a good knowledge about the abundance and diversity of groups of pollinator in the region before choosing plant species (Pywell et al., 2011). The use of herbicides in a conservation study often causes controversy and, although chemical application could presumably be beneficial for some target species, future assessment of its potential damage to insects or wildlife in general is first required.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1 Summary of the site characteristics

APPENDIX S2 List of species encountered and average abundance in relation to field practices applied in the study

APPENDIX S3 Summary of plant response and effect traits used in the analysis

APPENDIX S4 Summary of the mean species richness, Shannon diversity index (*H*) and functional diversity index (Rao) (± *SE*) per field treatment

APPENDIX S5 The response–effect trait framework based on Lavorel et al. (2013)