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Authors' contributions

LG, AM, EK and KB conceived the idea and designed the experiment. LG, AM and EK collected the data. LG analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave their final approval for publication.

Data availability statement

Data available on UMR ABSYS Dataverse: https://doi.org/10.18167/DVN1/B9HXLE

(temporary link: https://dataverse.cirad.fr/dataset.xhtml;jsessionid=d1fe6f791a3566c0ca444ff52930?persistentId=doi%3A10.18167%2FDVN1%2FB9HXLE&version=DRAFT)

Declaration of competing interest

The authors declare no conflict of interest.

Abstract

Lack of floral resources is suspected to be one of the factors involved in flower-visiting insect declines. Because agricultural landscapes are often poor in flowers, it seems crucial to assess weeds as floral resources to feed flower-visiting insects and to identify the factors that drive floral productivity, defined as floral biomass produced by the weed community. We monitored floral presence, productivity and traits in 16 olive groves from September 2021 to June 2022. The objectives were to understand to which extinct abiotic factors, among agricultural practices, pedoclimate and weather, determine floral productivity and to analyse the relationships between floral traits, floral presence and productivity. We found mowing frequency (2 to 3 per year on average) increased mean floral area and height, advanced flowering onset, and increased floral functional diversity and flowering species richness, which in turn increased floral presence and productivity.

Keywords

Floral productivity; floral resources; floral traits; woody agroecosystem; mowing

1. Introduction

Since nectar and pollen are the main food resources for pollinating insects (Roulston and Goodell, 2011), the lack of floral resources is one of the major causes of decreasing pollinating insect populations (Goulson et al., 2015; Potts et al., 2010; Scheper et al., 2014). In agroecosystems, species-rich weed communities support populations of insect natural enemies and pollinators (Aviron et al., 2023), thereby contributing to biodiversity conservation, biological control and entomophilous pollination. Insect visitation depends on traits linked to floral resources (nectar, pollen) or morphology (flower area height, number of flowers etc.) , driving the quality of plants as floral resources (Fornoff et al., 2017; Hatt et al., 2019; Hegland & Totland, 2005; Rowe et al., 2020). Besides, weed communities with high taxonomic and functional diversity enhance diversity across trophic levels (Lefcheck et al. 2015). High functional diversity in weed communities should support more populous and diverse insect communities by multiplying ecological niches for the first trophic level of consumers with various ecological requirements (Potts et al., 2010). However, intensive agricultural practices in Europe since 1945 curtailed weed diversity and abundance (Andreasen et al., 1996; Baessler & Klotz, 2006; Meyer et al., 2013), and hence floral resources in landscapes (Bretagnolle & Gaba, 2015; Richner et al., 2015).

In woody agroecosystems, weeds are a biodiversity component contributing to inter-row ground cover and can be managed in a biodiversity-friendly way by cover cropping or mowing, which maintain higher plant and insect richness and abundance than tillage or herbicide spraying (Carpio et al., 2019 ; Kratschmer et al., 2019 ; Kazakou et al., 2016). Low-intensity management such as moderate mowing (once or twice a year) maintain soil cover and insect-pollinated weeds throughout the year (Tarifa et al., 2021), especially when fewer flowers are available in surrounding semi-natural environments and insects need food resources (Rundlöf et al., 2014).

Few studies have evaluated the potential of weeds for providing floral resources to insects in woody agroecosystems, by assessing their floral traits or their floral productivity, that we defined as floral biomass produced by the weed community, and even fewer have monitored weed floral resources diachronically over the year. Weeds are unstable communities mostly composed of annual species, and change considerably within one year, both taxonomically and functionally. Because floral traits vary significantly among weed species, floral resources in agroecosystems are very diverse. Common weed species can be very attractive to insects, such as *Picris hieracioides* L., *Taraxacum sp* or *Echium vulgare* L. (Balfour & Ratnieks, 2022; Hernández-Villa et al., 2020; Kuppler et al., 2023), unlike others such as *Chenopodium album* L., *Amaranthus spp.* or *Rumex spp.*, (Kuppler et al. 2023). In addition, the timing of flowering is crucial for many insects, whose requirements peak at specific periods of the year depending on their life cycle. Previous studies have shown that anthesis occurs earlier and lasts longer in weeds (Bourgeois et al., 2019). However, the impacts of agricultural practices on the floral traits and productivity of weeds are poorly known because weed studies have mostly focused on resource-use ecological strategies and effects on crops.

Floral traits are mostly studied as determinants of insect presence as they drive insect visitation and richness at the community scale (Fornoff et al., 2017; Rowe et al., 2020). However, their community-scale responses to environmental factors are rarely investigated (Vojtko et al., 2020), and only in grasslands or semi-natural environments., A previous study showed that floral functional diversity responds to soil characteristics in French grasslands (Goulnik et al. 2021). Another recent work investigates the effects of water deficit on floral traits, which reduces flower size and number, and nectar volume (Kuppler & Kotowska, 2021). Dry Mediterranean conditions select for mostly small or short-lived flowers (Teixido and

Valladares, 2014) so as to maintain a positive water balance at the flower scale (Roddy et al., 2023). However, weed floral traits response to the environment, pedoclimatic conditions or agricultural practices, are almost unknown. At the species level, weed floral traits are linked to Grime's CSR strategies (Genty et al., 2023), suggesting that they could be sensitive to management and disturbance. One recent study showed that organic farming increases functional richness and the number of red and zygomorphic flowers in weed communities (Rotchés-Ribalta et al., 2023), but how other floral traits linked to insects respond to agricultural practices is not known.

Flower abundance, usually measured as the flower cover, is another factor of insect visitation (Hegland and Boeke, 2006; Wray et al., 2014). However, which practices determine floral resources abundance, composition, and above all, dynamics, in agroecosystems is scarcely studied. We suppose that low-disturbance practices should allow greater weed flower production than intensive practices (Kratschmer et al., 2019). In addition, species richness, especially of flowering species, should increase flower abundance and productivity. The relationships between plant traits (Pontes et al., 2007) and productivity of vegetative biomass, as well as those between diversity and -productivity (Lehman and Tillman, 2000) are well studied. They indicate that more diverse plant communities with specific values for vegetative traits are also more productive, however, these relationships this remains largely unexplored for floral productivity.

In this study, we explored how agricultural practices, weather and pedoclimatic conditions affected weed communities and flowers over one agricultural year in extensive olive groves in southern France, focusing on optimising weed floral resources for insects. Our hypotheses were that species richness and functional structure of weed communities (1) are affected both by agricultural and pedoclimatic variables, in particular that low-disturbance inter-row management practices (e.g. mowing), water availability and soil fertility would enhance species richness and floral trait diversity, and (2) have a positive effect on floral productivity *via* their effects on traits and richness that could drive temporal niche partitioning. Weeds flowering earlier can be visited by different insects than those flowering later, thus decreasing competition to attract pollinators and improving flower production. Greater diversity in morphological floral traits in the community could increase flower-visiting insect richness because different floral morphologies attract different insects. More flowers per plant on average and longer mean flowering duration should increase floral productivity over the entire year by extending the period during which flowers are present.

2. Material and methods

2.1. Sampled fields

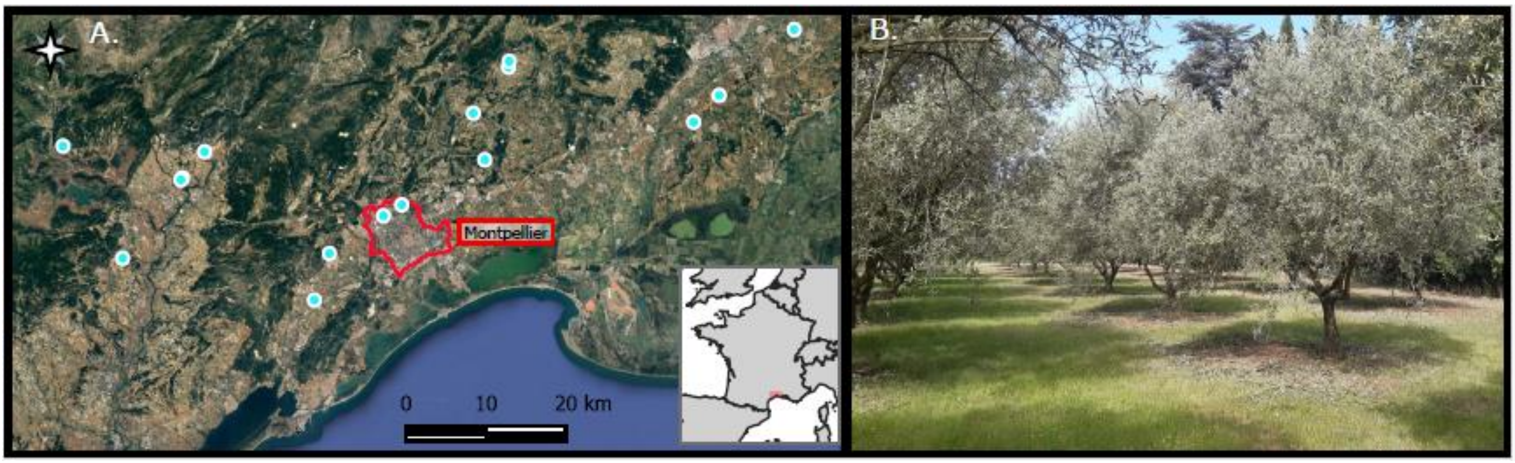

Figure 1. A. Locations of the sampled olive groves (Google©, 2022) in the Mediterranean part of the Occitanie region, France. B. One example of surveyed grove in Spring 2022.

We surveyed 16 olive groves in the hinterland of Montpellier, southern France, in a Mediterranean climatic area (Figure 1). Agricultural practices were assessed by interviewing farmers in 2021 and 2022, focusing on inter-row management (Genty et al., 2023). Mowing was the only management practice used to control weeds and was described using the mean number of mowing interventions per year (1-5)(('mowing'). We also recorded the yearly amount of water used for irrigation ('irrig')(0-190 mm) and inorganic and organic nitrogen (N) applied for fertilisation and amendments (0-641 kg of N/ha) ('N fertilization"),.

2.2. Pedoclimatic conditions

We used the data from six weather stations of the national meteorological network (Météo France), located 0.5-19.7 km from the 16 surveyed olive groves, to describe the long-term climatic trends (1980-2021). We calculated six climatic variables describing seasonal trends using the 'biovars' function from the R package *dismo* (Hijmans et al., 2017): mean annual temperature (15.3±0.33°C, mean±SD), annual rainfall (704±124mm), rainfall in the driest month (6.06±1.84mm), maximum temperature of the warmest month (36.8±1.1°C), annual temperature range (41.8±15.8°C) and rainfall coefficient of variation (89.6±2.25mm). In addition, we recorded rainfalls ('$\text{Rainfalls}_{\text{sampl'}}$') and mean temperature ('Mean $\text{Temp}_{\text{sampl}}$') between successive sampling dates to assess short-term weather effects at the monthly scale. We also calculated the rainfall over the agricultural year ('$\text{Rainfalls}_{\text{year}}$') and the annual minimum temperature ('Temp min_{year}') to describe weather effects at the yearly scale (Table S5). Soil pH (NF ISO10390), nitrogen content, total organic matter content (NF ISO 14235), cation-exchange capacity (CEC) and texture (NF X 31-107 method) were determined for each olive grove on a 20-cm-deep composite soil sample. More informations on the soil analyses can be found in Genty et al. (2022).

2.3. Botanical survey of flower cover

Five permanent quadrats of 0.25 m^2 were randomly placed in the inter-rows of each olive grove (n = 80 quadrats), keeping a minimum distance of two metres from the field edge. We sampled each quadrat seven times over the entire agricultural year 2021-2022 (n = 560 surveys: 17-09-

2021; 14-10-2021; 27-01-2022; 01-03-2022; 04-04-2022; 04-05-2022; 06-06-2022). On each date and for each quadrat we recorded the latest mowing date ('last mowing') and visually recorded the phenological stage and flower cover per species as the total percentage of the ground covered by open flowers and flower buds in each quadrat. We also recorded the number of species at the flowering stage ('floral richness') in each quadrat, and the total species richness of each field based on sampling from Genty et al., 2023. Recorded data concerned insect-pollinated species exclusively.

2.4. Indicators of floral productivity at the year scale

We used a loess regression to model flower cover dynamics over the year (Cleveland & Devlin, 1988) for each quadrat based on the seven samplings. We extracted four indicators of floral productivity (Figures 2 and 3): (1) annual flower cover, calculated as the normalised integral of the regression curve ('annual flower cover'); (2) flower cover maximum value in % of surface ('max flower cover'); (3) date of the flower cover maximum ('max flower cover date'), expressed as the number of days since the beginning of the sampling (17th of September 2021); and (4) number of days during which the flower cover reached or exceeded 80% of its flower cover maximum, representing the period of abundant flower presence in the field ('flower cover peak duration'). For flower cover peak duration, we excluded nine quadrats in which 80% of the max flower cover was under 1% (Table S1). The four indicators were measured at the year scale (n = 80) by pooling the data of the seven surveys, considering each quadrat survey as one community composed of all the sampled species proportionally. We recorded the species richness of flowering weeds in each community over the full season.

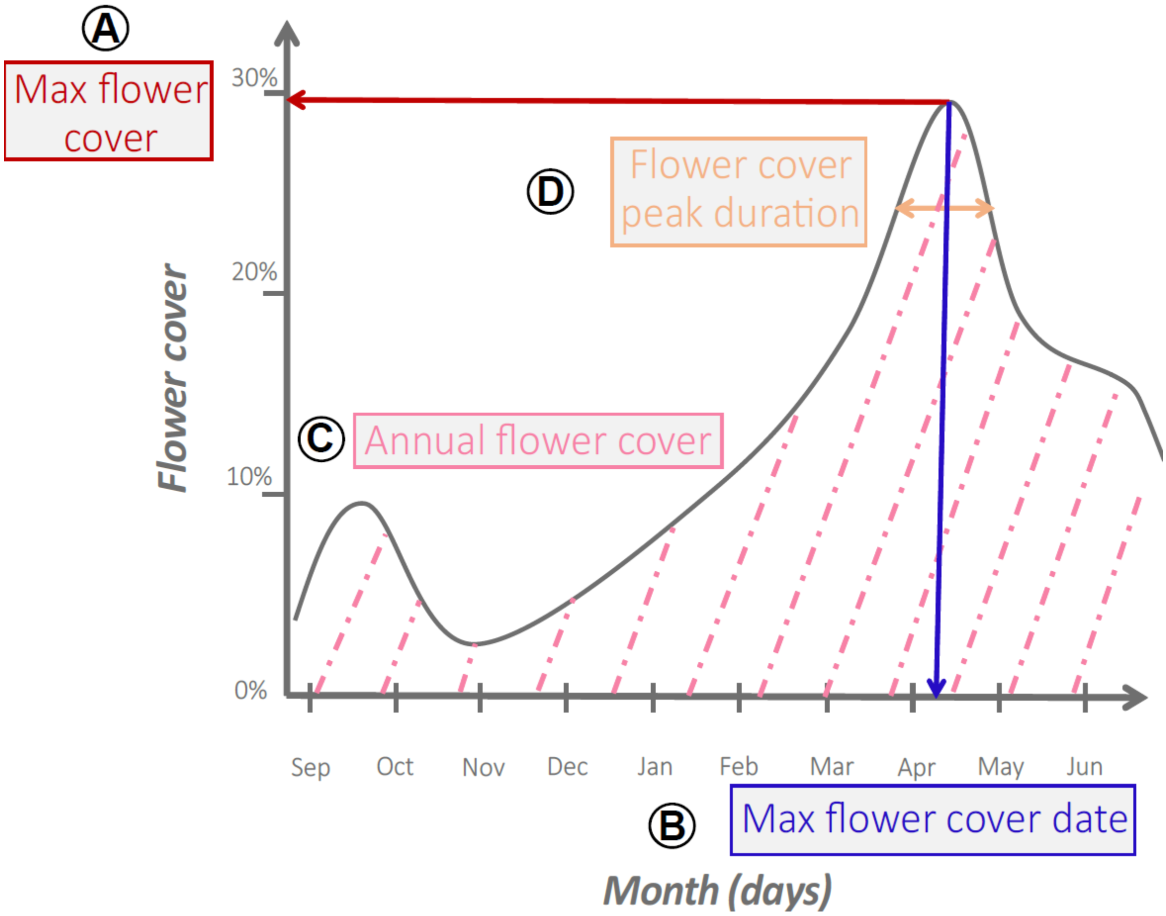

Figure 2. Dynamics of flower cover throughout the year, presenting the four floral productivity indicators: A. Max flower cover (flower cover maximum value in %), B. Max flower cover date (number of days since the start of the sampling, on 17-09-2021), C. Annual flower cover (% calculated as the normalised integral of the regression curve), and D. Flower cover peak duration (number of days with flower cover ≥ 80% of flower cover maximum).

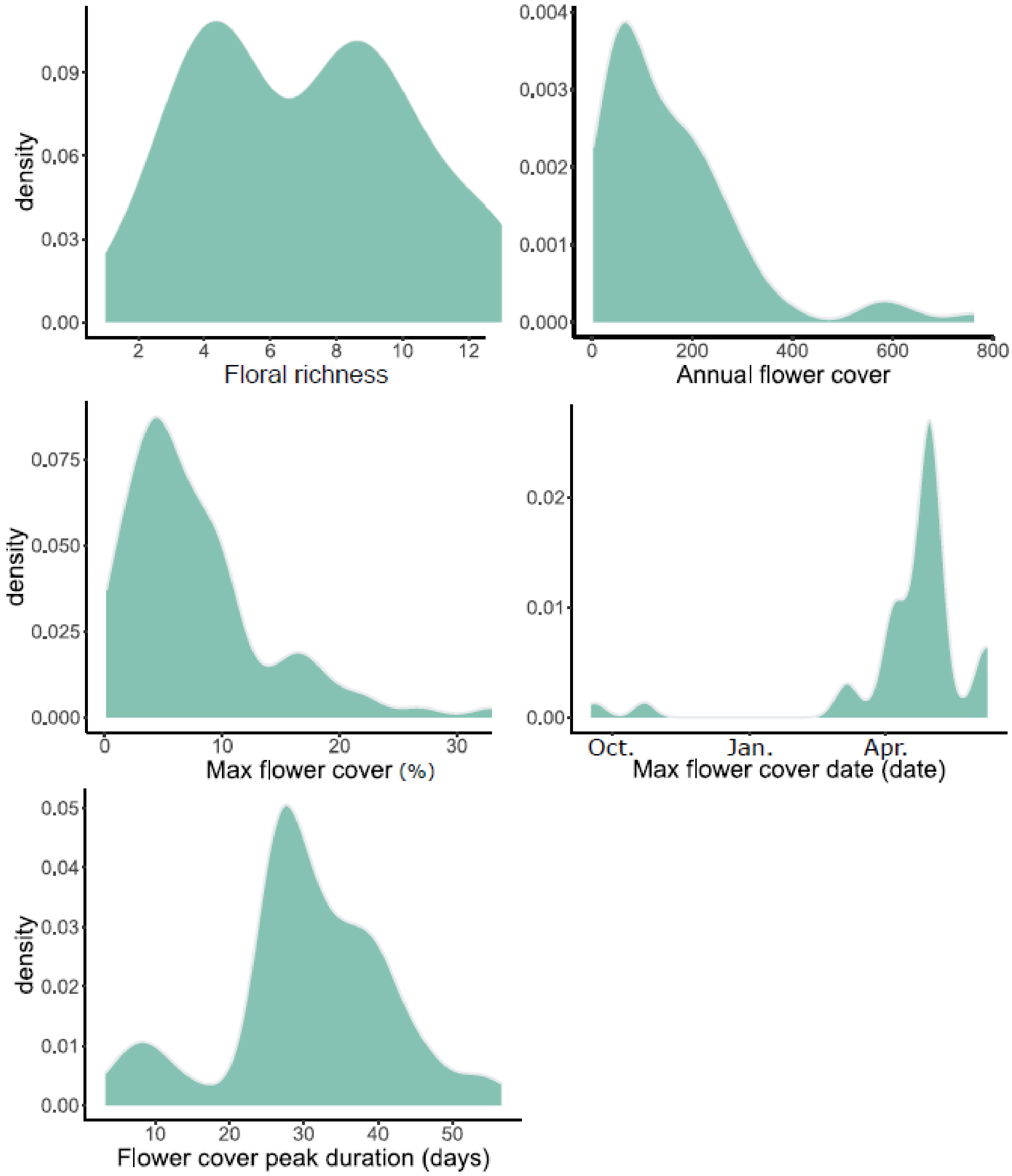

Figure 3. Distribution of floral richness, annual flower cover, max flower cover, max flower cover date and flower cover peak duration among weed communities (n=80).

2.5. Trait measurements and functional indices at the community level

Seven floral traits linked to insect attraction (Table S2) were measured for 17 common weed species in olive grove (Table S3) in a greenhouse experiment during the spring and summer of 2022 (Genty et al., 2023b): pollen volume (‘pollen’), nectar sugar content (‘nectar’), number of floral units per plant (‘floral unit number’), reproductive height (‘height’), flower area (‘area’), flowering duration (‘duration’) and flowering onset (‘onset’).

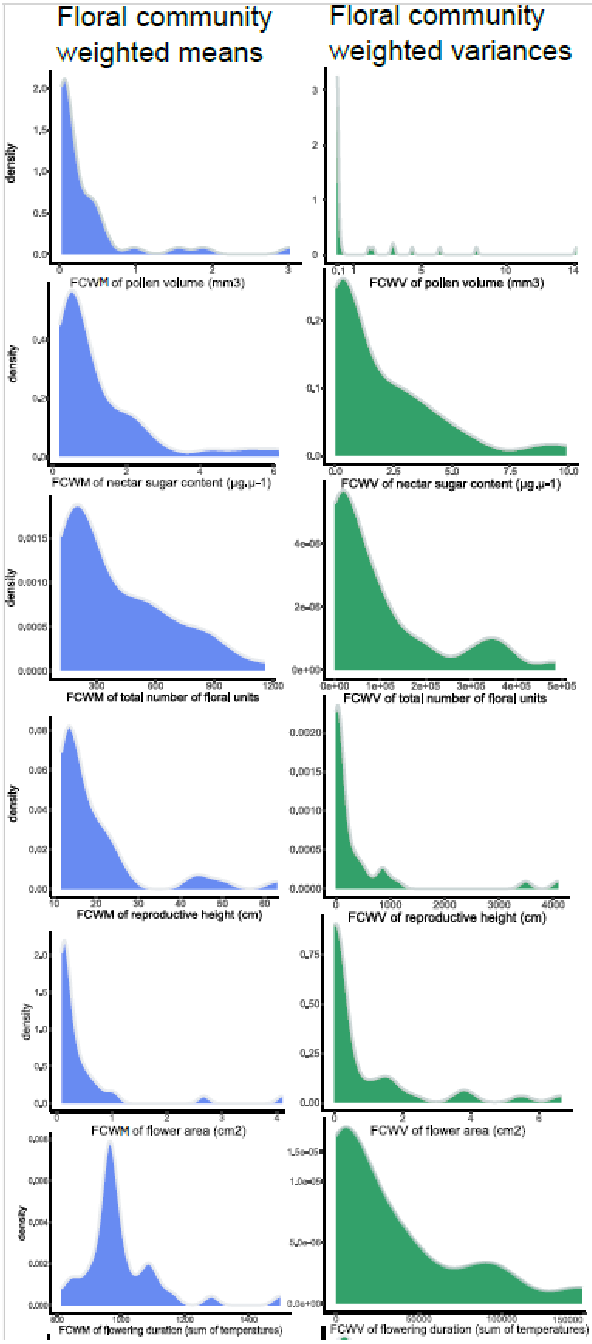

Figure 4. Distribution of community weighted means and variances of floral traits: pollen volume, nectar sugar content, total number of floral units, reproductive height, flower area, flowering duration and onset among weed communities (n=40).

We calculated the floral community-weighted mean and variance of each floral trait in all the communities (n = 40) composed of at least 60% of these species, at the year scale (Table S4), using the 'dbFD' function of the FD package. Community weighted mean is the average floral trait value of each species at the flowering stage weighted by its relative flower cover (Garnier et al., 2004). Community weighted variance quantifies the variability of each floral trait value around the average value within the floral community (Sonnier et al., 2010) (Figure 4). Because floral traits are phylogenetically conserved (Vojtko et al., 2022), we pooled trait values at the genus level for three unstudied abundant species: *Geranium molle* L., *Medicago polymorpha* L. and *Medicago rigidula* (L.) All. *G. molle* belongs to the same subgenus as *Geranium rotundifolium* L. and *Geranium dissectum* L. (Aedo et al., 1998), and *M. polymorpha* and *M. rigidula* to that of *Medicago minima* (L.) L. and *Medicago arabica* (L.) Hudson (Steele et al., 2010).

2.6. Data analysis

All statistical analyses were run using R version 4.3.1 (R Core Team, 2022), and in particular the packages *lme4* (Bates et al., 2015), *vegan* (Oksanen et al., 2007), *FD* (Villéger et al., 2008), *FactoMineR* (Lê et al., 2008), *MuMIn* (Barton, 2009), *car* (Fox et al., 2012) and *piecewiseSEM* (Lefcheck, 2016).

We ran Kruskal-Wallis' tests and pairwise Wilcoxon's tests as post-hoc analyses to test whether flowering species richness and flower cover differed between months and determine the periods of flower presence.

To summarise soil and climatic characteristics of the study sites we ran a PCA with all the pedoclimatic variables. The coordinates of each individual on the first two components were extracted and used as explanatory variables (pedoclim1 and pedoclim2).

To test whether agricultural practices and weather affected monthly flowering species richness and flower cover, we ran linear mixed models with 'last mowing', '$Rainfalls_{sampl}$' and 'Mean $Temp_{sampl}$' as fixed effects and 'month' and 'field' as random effects. To test whether they influenced annual flowering species richness, floral productivity indicators, floral community weighted means and variances, we ran linear mixed models with 'pedoclim1', 'pedoclim2', 'mowing', 'irrig', 'N fertilization', '$Rainfalls_{year}$' and 'Temp min_{year}' as fixed effects, and 'field' as random effect. Before model selection and evaluation, correlation of fixed effects was tested using variance inflation (VIF). VIF values of 5 or higher are interpreted as revealing multicollinearity issues (Hair, 2009). We performed model stepwise comparisons comparing full, reduced and 'null' models built by combining all fixed effects, several fixed effects or only random effects. We selected the model with the lowest second-order Akaike Information Criterion value (AICc) corrected for small sample sizes (Burnham & Anderson, 2004). Two models were considered different if Δ AICc > 2 (Burnham & Anderson, 2004). When more than one model had the lowest AICc we selected the most parsimonious, with the lowest number of fixed effects. We used likelihood ratio tests to evaluate the selected models, and calculated the marginal and conditional R^2 (Nakagawa & Schielzeth, 2013).

The relation between floral traits and indicators of floral productivity was tested with a PCA ('community structure' PCA) with the community weighted means of the seven floral traits and flowering species richness, followed by a hierarchical ascendant classification to create three clusters based on the first two components. To test whether the four indicators of floral productivity differed among clusters, we ran Kruskal-Wallis' and pairwise Wilcoxon's tests as *post hoc* analyses.

3. Results

3.1. Effects of pedoclimate, weather and agricultural practices on flowering species richness, floral productivity and floral traits

'Pedoclimatic' PCA explained 62% of the total variance of pedoclimatic variables (Table S5). The coordinates of each field on the first two components were used as composite explanatory variables. The first component ('pedoclim1') explained 38% of the total variance and was positively linked to soil clay content (0.79), cation-exchange capacity (0.79), mean annual temperature (0.78) and soil nitrogen content (0.66), and negatively to annual temperature range (-0.85), soil sand content (-0.73) and maximum temperature of the warmest month (-0.68). The second component ('pedoclim2') explained 24% of the total variance and was positively linked to rainfall in the driest month (0.88) and annual rainfall (0.85), and negatively to rainfall coefficient of variation (-0.76).

Flower cover (Figure 5A) and species richness of flowering weeds ('floral richness') (Figure 5B) were significantly higher in April and May than in the other months. The five most abundant species in terms of flower cover at the year scale were *Medicago minima* L., *Crepis sancta* L., *Arenaria serpyllifolia* L., *Sherardia arvensis* L. and *Medicago arabica* L. (Table S6).

At the month scale, flower cover was positively correlated with time since the last mowing and floral richness with rainfall (Table 1). At the year scale, floral richness was positively affected by pedoclim2 and by the mean number of mowing interventions per year, while max flower cover date was the only indicator of floral productivity impacted by abiotic variables: it was postponed by N fertliziation and advanced by pedoclim2.

At the year scale mowing, N fertilization, irrigation, Pedoclim1 and 2, and Temp Min_{year} affected community weighted means and variances of all floral traits (see detailed results in Table 2).

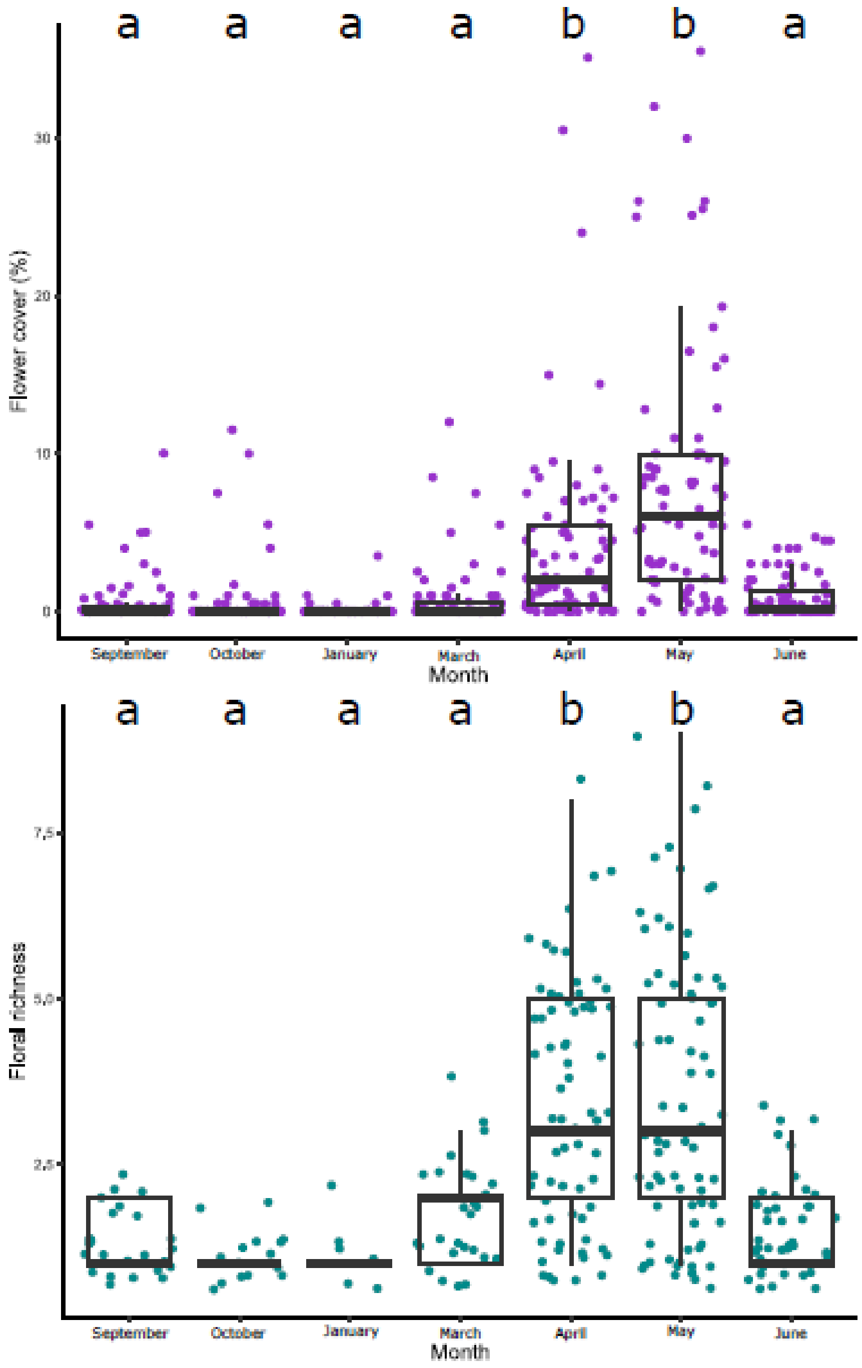

Figure 5. Flower cover (A), and number of flowering species (B) in each quadrat on each visit (%). Letters represent the results of pairwise Wilcoxon's tests.

Table 1. Individual effect of pedoclimatic characteristics and agricultural practices on floral richness, indicators of flower productivity and flower cover at a monthly and yearly scale. Field and month are random effects for the models at the month scale. Field is a random effect for models at the year scale. Marginal R2 (R2m) represents the proportion of variance explained by fixed effects in the model. Conditional R2 (R2c) includes random effects. Significance stars are from the type II ANOVA's Chi^2.

Temporal scale	Response variable	Explanatory variable	Estimate	R2m	R2c
Month	Flower cover	last mowing	0.005*	0.01	0.37
	Floral richness	$\text{Rainfalls}_{\text{sampl}}$	-0.005*	0.04	0.49
Year	Floral richness	pedoclim2 mowing	0.730* 1.021*	0.23	0.56
	Annual flower cover	ns	-	-	-
	Max flower cover	ns	-	-	-
	Max flower cover date	pedoclim2 N fertilization	-3.754* 0.009-	0.13	0.20
	Flower cover peak duration	ns	-	-	-

*Notes: ns, not significant; - p <0.1, * p <0.05; ** p <0.01; *** p <0.001.*

Last mowing : number of days since the last mowing event, Rainfalls$_{sampl}$: quantity of rainfalls between two samplings, pedoclim2 : second axis of 'pedoclimatic' PCA, mowing : mean number of mowing events per year, N fertilization : mean N dose applied per year, irrig : mean quantity of irrigation per year, Temp min$_{year}$: mean minimal temperature during the sampling period, Rainfalls $_{year}$: total quantity of rainfalls during the sampling period

Table 2. Individual effect of pedoclimatic characteristics and agricultural practices on community weighted means (CWM) and variances (CWV) of floral traits at the year scale with field as random effect.

Functional indicator	Trait (response variable)	Explanatory variable	Estimate	R2m	R2c
	Area	mowing	0.306***	0.27	0.27
	Pollen	pedoclim2	0.106*	0.12	0.14
	Nectar	irrig	0.014**	0.32	0.64
	Height	mowing	3.117*	0.12	0.17
CWM	Floral units number	N fertilization irrig Temp min$_{year}$	0.884*** 2.064** 91.063**	0.6	0.6
	Duration	N fertilization irrig	-0.284** 0.794*	0.27	0.27
	Onset	N fertilization irrig Temp	-0.648*** 1.483*** -49.732**	0.66	0.68

		min_{year} mowing	-44.292**		
	Area	mowing N fertilization	72.360*** -0.280*	0.39	0.39
	Pollen	$Rainfalls_{year}$	1.628***	0.26	0.26
	Nectar	mowing	75.102*	0.14	0.30
	Height	-	ns	ns	ns
CWV					
	Floral units number	pedoclim2	3 490 184**	0.28	0.43
	Duration	-	ns	ns	ns
	Onset	pedoclim1 irrig mowing Temp min_{year}	-736 813*** -29 414** 1 374 079*** 2 894 065***	0.44	0.44

*Notes: ns, not significant; - p <0.1, * p <0.05; ** p <0.01; *** p <0.001.*

Last mowing : number of days since the last mowing event, $Rainfalls_{sampl}$: quantity of rainfalls between two samplings, pedoclim2 : second axis of 'pedoclimatic' PCA, mowing : mean number of mowing events per year, N fertilization : mean N dose applied per year, irrig : mean quantity of irrigation per year, Temp min_{year} : mean minimal temperature during the sampling period, $Rainfalls_{year}$: total quantity of rainfalls during the sampling period

3.2. Relationships between floral productivity, richness and traits

Annual flower cover, max flower cover and flower cover peak duration positively correlated with floral richness, but not with total species richness. Only max flower cover date was uncorrelated with floral richness (Table 3).

Table 3. Individual effects of floral richness on indicators of flower productivity with field as random effect.

Indicator (response variable)	Explanatory variable	Estimate	R2m	R2c
Annual flower cover	Floral richness	22.56***	0.26	0.53
Max flower cover	Floral richness	0.751***	0.15	0.53
Max flower cover date	ns	-	-	-
Flower cover peak duration	Floral richness	1.158**	0.10	0.27

*Notes: ns, not significant; - p <0.1, * p <0.05; ** p <0.01; *** p <0.001.*

Mean and variances of floral traits were related to max flower cover, max flower cover date and flower cover peak duration: the composition of communities, affected both functional structure and flower productivity indicators, demonstrating that quality, quantity and temporality of floral resources are strongly linked (see details in Table 4).

The ‘community structure’ PCA explained 64.2% of the variability (Figure 6A). The first component (35.1% of explained variability) was positively correlated with the community weighted means of floral height (0.91), area (0.73), duration (0.71), pollen (0.67) and floral richness (0.62) ; high values on this component indicate that the species invest in more costly flowers while lower values indicate cheaper flowers (Roddy et al., 2021). The second component (29.1% of explained variability) was positively correlated with the community weighted mean of floral units number (0.84) and floral specific richness (0.56), and negatively with the community weighted means of flowering onset (-0.70) and duration (-0.57). The ascending hierarchical classification (Figure 6B) identified three clusters: cluster 1 ‘cheap, few and late-flowering flowers’, composed of 23 communities and linked to low scores on both components, cluster 2 ‘cheap, numerous and early-flowering flowers’ (13 communities) linked to low scores on the first component and high scores on the second, and cluster 3 ‘costly flowers’ (4 communities) linked to high scores on the first component. ‘Few and late-flowering flowers’ communities were more often mown (1,5 *vs* 2,5) and irrigated than ‘numerous and early-flowering flowers’ communities (Figure 7A), and their flower cover peak duration was 6 days longer (Figure 7B).

Table 4. Individual effects of community weighted means (CWM) and variances (CWV) of floral traits on indicators of flower productivity with field as random effect.

Indicator (response variable)	Functional indicator	Trait	Estimate	R2m	R2c
Annual flower cover	CWM	Nectar	50.992**	0.29	0.68
Max flower cover	CWM	Nectar	2.599***	0.27	0.76
Max flower cover date	CWM	Area Nectar	5* -3.481**	0.26	0.34
Flower cover peak duration	CWM	Onset Nectar	-0.022** 2.784**	0.32	0.67
Annual flower cover	CWV	-	ns	ns	ns
Max flower cover	CWV	Nectar Duration	1.025* -0.535**	0.16	0.52
Max flower cover date	CWV	-	ns	ns	ns
Flower cover peak duration	CWV	Height Area	1.657** -6.283*	0.20	0.63

*Notes: ns, not significant; - p <0.1, * p <0.05; ** p <0.01; *** p <0.001.*

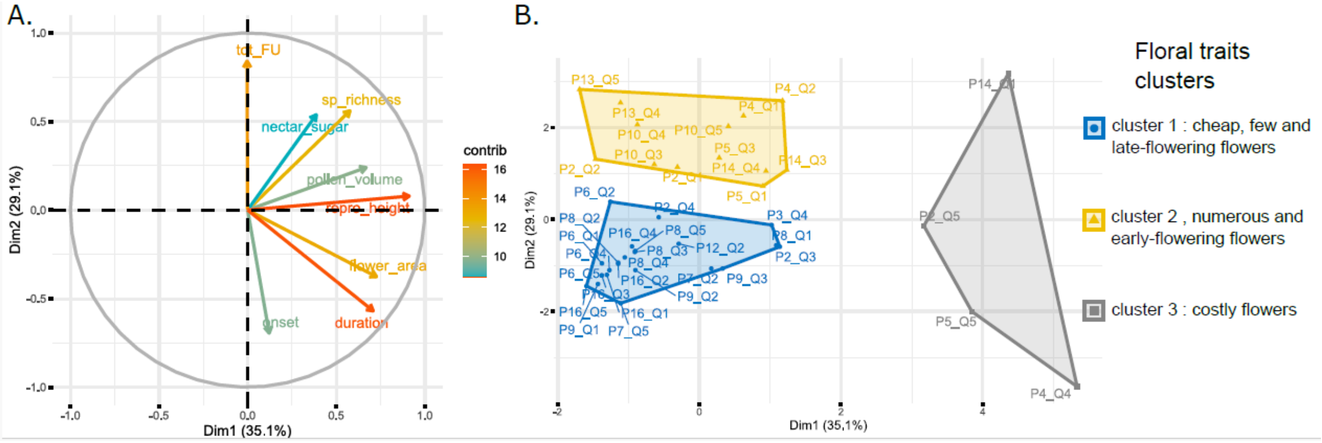

Figure 6. A. First two components of the 'community structure' PCA. The individuals are the 40 quadrats at the year scale in which at least 60% of the community was composed of species with documented floral traits. B. The three clusters created with the hierarchical ascending classification.

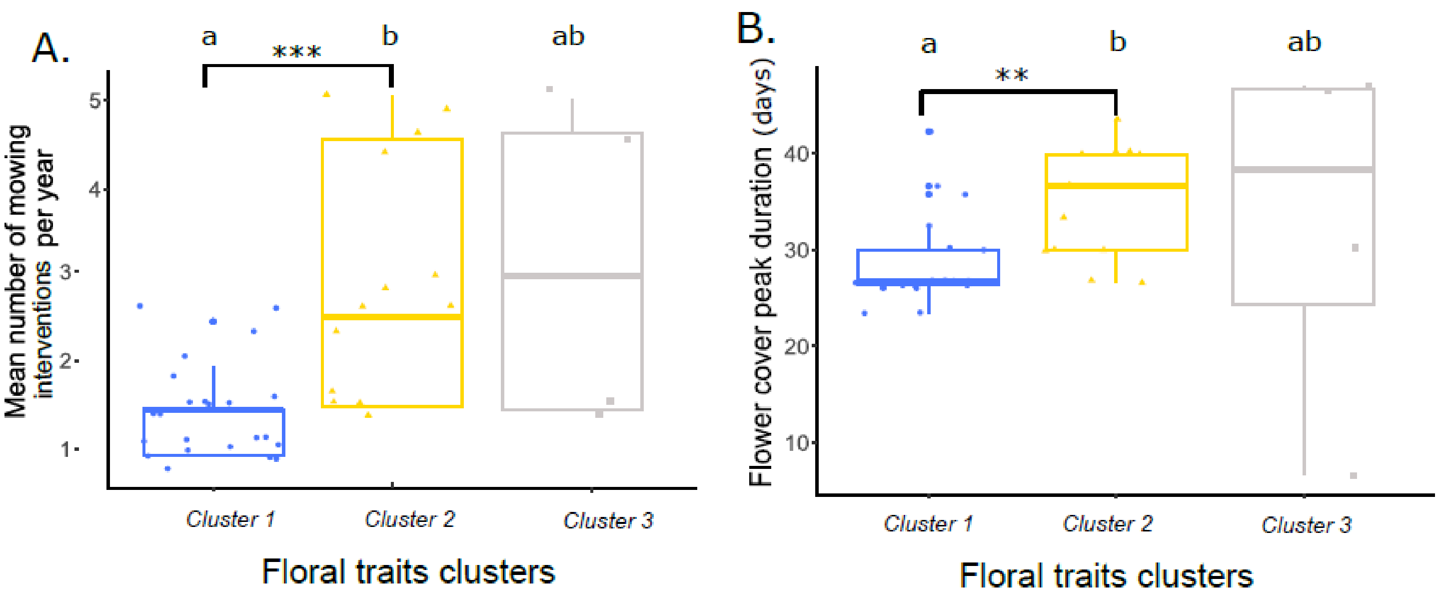

Figure 7. A. Mean yearly number of mowing interventions. B. Flower cover peak duration, according to the floral traits clusters. Letters reflect the results of pairwise Wilcoxon's tests.

4. Discussion

4.1. Weed floral traits and richness are affected by pedoclimate and agricultural practices

Our results indicate that agricultural practices affect the floral functional structure of weed communities in Mediterranean olive groves. More mowing interventions (min : 0, max : 5 in the network) increased floral richness (Table 1), functional heterogeneity (i.e. wider community weighted variances) of floral area, nectar sugar content and flowering onset, postponed mean flowering onset, and resulted in communities with larger and taller flowers (Table 2), supposedly more attractive to insects (Lundin et al., 2019; Rowe et al., 2020). The diversifying effect can be explained by the positive effect of low-to-intermediate disturbance of mowing on species diversity and trait variance in the community, as predicted by the intermediate disturbance hypothesis (Wilkinson et al., 1999). The number of mowing interventions ranged from 1 to 5 per year, with a mean of 2.19, which is considered fairly low but disturbing enough to curb the dominance of the most competitive species. However, this relationship may not hold when mowing is more frequent.

In contrast, irrigation and fertilisation had a homogenising effect, reducing community weighted variances of floral area and flowering onset (Table 2), perhaps because high levels of resources benefited the most competitive species. For example, flowering onset was earlier in more frequently mown, fertilised but unirrigated olive groves, which is logical because more disturbed communities are traditionally composed of species flowering earlier (Fried et al., 2012).Higher levels of resources (N fertilization, irrigation) also selected for species producing more floral units that flower for a longer period, which is allowed by the available resources, as showed in vinetards by Guerra et al. (2021). Managing the regularity of mowing seems efficient to regulate phenology so as to provide more diversified and abundant floral resources for flower-visiting insects (Yvoz et al., 2021).

Even though agricultural practices are considered the main driver of trait variability in weed communities at the regional scale (Bourgeois et al., 2021), pedoclimatic and weather variables also matter, especially for trait variance (Poinas et al., 2023). In our study, the homogenising effect of greater soil fertility, e.g. higher levels of organic matter and clay contents (pedoclim1), may be due to selection of the most competitive species (Fried et al., 2022) that develop earlier and exclude later species by pre-empting light resources (Grime, 1974). Higher temperatures allowed some cold-tolerant and sensitive species to survive, thus diversifying functional structure, but also decreased community weighted mean of flowering onset, advantaging competitive species that flower early. Rainfall also had a diversifying effect leading to greater FCWVs of total floral unit number and pollen: water deficit may force weeds to allocate less resources to flowers or pollen production (Kuppler & Kotowska, 2021). As found by Bourgeois et al. (2021) for weeds in annual agroecosystems, pedoclimate affected the variance more than the mean of floral traits.

4.2. Floral productivity is linked to community floral richness and traits

Not all floral traits were linked to floral productivity, indicating that communities with any floral strategy could potentially provide floral resources. However four floral traits were found to be positively correlated with floral productivity: mean nectar sugar content (Table 4), number of flowers, onset of flowering (Figures 5 and 6) and floral richness (Table 3), the last increasing all the indicators of floral productivity.

Weed richness enhanced floral productivity and thereby provided a diversity of food resources for insects (Balfour & Ratnieks, 2022). The most abundant species, e.g. *M. minima* and *S. arvensis*, had ruderal floral strategies and produced many small flowers (Genty et al., 2023b) excluded by wild bees (Kuppler et al., 2023) but preferentially visited by other important pollinators such as Diptera and Coleoptera (Lanuza et al., 2023). However, the great floral richness found in the olive groves (99 flowering species) enhanced their potential for hosting plants visited by all types of pollinator, among which *E. vulgare* and *P. hieracioides,* favoured by wild bees (Kuppler et al., 2023). Regarding year-round flower presence, which is important for flower-visiting insects, we found that floral resources in olive groves peaked in mid-April overall, with local variations from March to June. This means that flowers were present early in the season, supplying food at a critical time for insects (Pelletier and MacNeil, 2003), however very few resources were available late in the season, which is another critical period for foraging.

4.3. Mowing is a promising practice for enhancing floral productivity

Since floral richness, mean traits and trait variances were directly affected by agricultural practices (Tables 1 and 2), and were linked to floral resources productivity, we conclude that agricultural practices affect floral productivity in olive groves. Indeed, the most regularly mown communities were composed of species flowering earlier and with more flowers per individual produced flowers for a longer period (Fig. 6, 7). The intermediate level of disturbance caused by two or three mowing interventions per year increased weed floral richness and trait diversity, as in grasslands (Piseddu et al., 2021). This finding suggests that the impact of agricultural practices on floral richness can rival that of environmental drivers (Pittarello et al., 2020). This may be due to the greater instability of weed communities compared with grasslands: because weeds are mostly annual species, they are more responsive to intra-annual events like management practices than communities of perennial species.

Mowing two to three times a year appears to be a beneficial practice for weed species richness and related ecosystem services in woody agroecosystems (Winter et al., 2020). In our work, we found that regular mowing frequency favors higher floral productivity over the year in olive groves. We conclude as other studies for different services (Bopp et al., 2022b; Kavvadias and Koubouris, 2019), that mowing is a biodiversity-friendly weed management practice able to both deliverecosystem services and ensure satisfactory yield in Mediterranean woody agroecosystems (Guerra et al., 2022).

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