Agricultural practices in olive groves modify weeds floral traits and resources throughout the year

Léa Genty, Aurélie Metay, Elena Kazakou, Mathilde Baude, Antoine Gardarin, Alice Michelot-Antalik, Karim Barkaoui

HAL Id: hal-04696500
https://hal.inrae.fr/hal-04696500v1

Agricultural practices in olive groves modify weeds floral traits and resources throughout the year

Léa Genty[1,9], Aurélie Metay[2], Elena Kazakou[3], Mathilde Baude[4,5], Antoine Gardarin[6], Alice Michelot-Antalik[7], Karim Barkaoui [1,8]

[1]CIRAD, UMR ABSys, F-34398 Montpellier, France
ABSys, Univ Montpellier, CIHEAM-IAMM, CIRAD, INRAE, Institut Agro, Montpellier, France

[2]ABSys, Univ Montpellier, CIHEAM-IAMM, CIRAD, INRAE, Institut Agro, Montpellier, France

[3]CEFE, Univ Montpellier, CNRS, EPHE, IRD, Institut Agro, Montpellier, France

[4]Université d'Orléans, Orléans, France

[5]Sorbonne Université, UPEC, Université Paris Cité, CNRS, IRD, INRAE, Institut d'Ecologie et des Sciences de l'Environnement (iEESParis), Paris, France

[6]Agronomie, Université Paris-Saclay, AgroParisTech, INRAE, 91120 Palaiseau, France

[7]Université de Lorraine, INRAE, LAE, F-54000 Nancy, France

[8]CIRAD, UMR AMAP, F-34398 Montpellier, France

AMAP, Univ Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France

[9]Anses, Laboratoire de la Santé des Végétaux, Unité Entomologie et Botanique, Montferrier-sur-Lez, France

Acknowledgements

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

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

76 are available in surrounding semi-natural environments and insects need food resources

77 (Rundlöf et al., 2014).

78   Few studies have evaluated the potential of weeds for providing floral resources to

79 insects in woody agroecosystems, by assessing their floral traits or their floral productivity, that

80 we defined as floral biomass produced by the weed community, and even fewer have monitored

81 weed floral resources diachronically over the year. Weeds are unstable communities mostly

82 composed of annual species, and change considerably within one year, both taxonomically and

83 functionally. Because floral traits vary significantly among weed species, floral resources in

84 agroecosystems are very diverse. Common weed species can be very attractive to insects, such

85 as *Picris hieracioides* L., *Taraxacum sp* or *Echium vulgare* L. (Balfour & Ratnieks, 2022;

86 Hernández-Villa et al., 2020; Kuppler et al., 2023), unlike others such as *Chenopodium album*

87 L*., Amaranthus spp.* or *Rumex spp.,* (Kuppler et al. 2023). In addition, the timing of flowering

88 is crucial for many insects, whose requirements peak at specific periods of the year depending

89 on their life cycle. Previous studies have shown that anthesis occurs earlier and lasts longer in

90 weeds (Bourgeois et al., 2019). However, the impacts of agricultural practices on the floral

91 traits and productivity of weeds are poorly known because weed studies have mostly focused

92 on resource-use ecological strategies and effects on crops.

93   Floral traits are mostly studied as determinants of insect presence as they drive insect

94 visitation and richness at the community scale (Fornoff et al., 2017; Rowe et al., 2020).

95 However, their community-scale responses to environmental factors are rarely investigated

96 (Vojtko et al., 2020), and only in grasslands or semi-natural environments., A previous study

97 showed that floral functional diversity responds to soil characteristics in French grasslands

98 (Goulnik et al. 2021). Another recent work investigates the effects of water deficit on floral

99 traits, which reduces flower size and number, and nectar volume (Kuppler & Kotowska, 2021).

100 Dry Mediterranean conditions select for mostly small or short-lived flowers (Teixido and

101 Valladares, 2014) so as to maintain a positive water balance at the flower scale (Roddy et al.,

102 2023). However, weed floral traits response to the environment, pedoclimatic conditions or

103 agricultural practices, are almost unknown. At the species level, weed floral traits are linked to

104 Grime's CSR strategies (Genty et al., 2023), suggesting that they could be sensitive to

105 management and disturbance. One recent study showed that organic farming increases

106 functional richness and the number of red and zygomorphic flowers in weed communities

107 (Rotchés-Ribalta et al., 2023), but how other floral traits linked to insects respond to agricultural

108 practices is not known.

109   Flower abundance, usually measured as the flower cover, is another factor of insect

110 visitation (Hegland and Boeke, 2006; Wray et al., 2014). However, which practices determine

111 floral resources abundance, composition, and above all, dynamics, in agroecosystems is

112 scarcely studied. We suppose that low-disturbance practices should allow greater weed flower

113 production than intensive practices (Kratschmer et al., 2019). In addition, species richness,

114 especially of flowering species, should increase flower abundance and productivity. The

115 relationships between plant traits (Pontes et al., 2007) and productivity of vegetative biomass,

116 as well as those between diversity and -productivity (Lehman and Tillman, 2000) are well

117 studied. They indicate that more diverse plant communities with specific values for vegetative

118 traits are also more productive, however, these relationships this remains largely unexplored

119 for floral productivity.

120   In this study, we explored how agricultural practices, weather and pedoclimatic

121 conditions affected weed communities and flowers over one agricultural year in extensive olive

122 groves in southern France, focusing on optimising weed floral resources for insects. Our

123 hypotheses were that species richness and functional structure of weed communities (1) are

124 affected both by agricultural and pedoclimatic variables, in particular that low-disturbance

125 inter-row management practices (e.g. mowing), water availability and soil fertility would

126 enhance species richness and floral trait diversity, and (2) have a positive effect on floral

127 productivity *via* their effects on traits and richness that could drive temporal niche partitioning.

128 Weeds flowering earlier can be visited by different insects than those flowering later, thus

129 decreasing competition to attract pollinators and improving flower production. Greater diversity

130 in morphological floral traits in the community could increase flower-visiting insect richness

131 because different floral morphologies attract different insects. More flowers per plant on

132 average and longer mean flowering duration should increase floral productivity over the entire

133 year by extending the period during which flowers are present.

2. Material and methods

2.1. Sampled fields

136
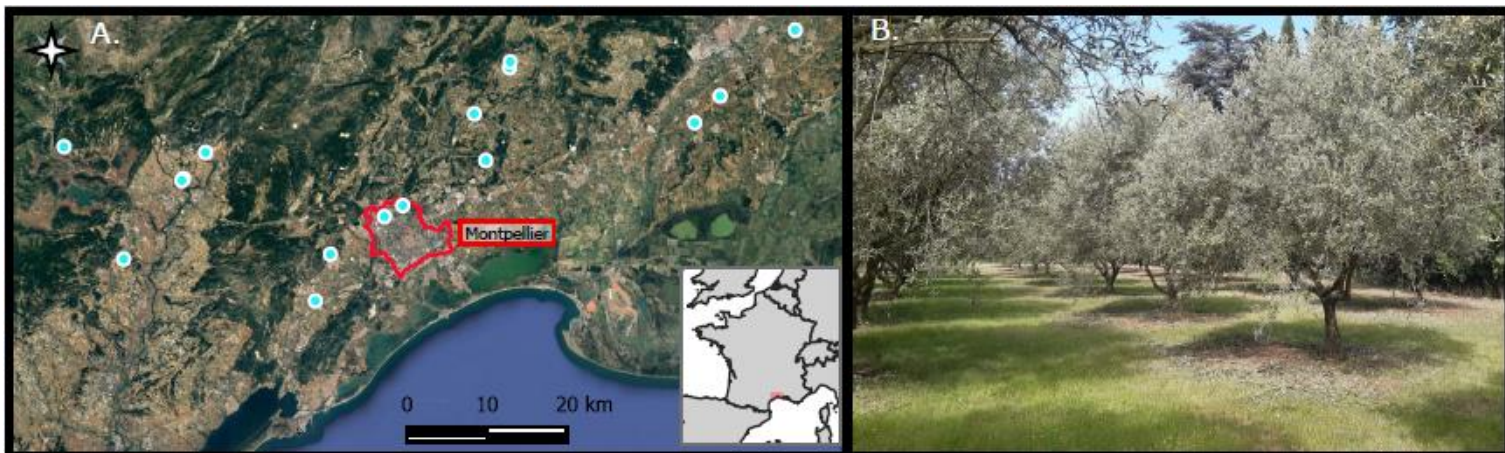
137 *Figure 1. A. Locations of the sampled olive groves (Google©, 2022) in the Mediterranean*

138 *part of the Occitanie region, France. B. One example of surveyed grove in Spring 2022.*

139

140 We surveyed 16 olive groves in the hinterland of Montpellier, southern France, in a

141 Mediterranean climatic area (Figure 1). Agricultural practices were assessed by interviewing

142 farmers in 2021 and 2022, focusing on inter-row management (Genty et al., 2023). Mowing

143 was the only management practice used to control weeds and was described using the mean

144 number of mowing interventions per year (1-5)(('mowing'). We also recorded the yearly

145 amount of water used for irrigation ('irrig')(0-190 mm) and inorganic and organic nitrogen (N)

146 applied for fertilisation and amendments (0-641 kg of N/ha) ('N fertilization"),.

2.2. Pedoclimatic conditions

148 We used the data from six weather stations of the national meteorological network (Météo

149 France), located 0.5-19.7 km from the 16 surveyed olive groves, to describe the long-term

150 climatic trends (1980-2021). We calculated six climatic variables describing seasonal trends

151 using the 'biovars' function from the R package *dismo* (Hijmans et al., 2017): mean annual

152 temperature (15.3±0.33°C, mean±SD), annual rainfall (704±124mm), rainfall in the driest

153 month (6.06±1.84mm), maximum temperature of the warmest month (36.8±1.1°C), annual

154 temperature range (41.8±15.8°C) and rainfall coefficient of variation (89.6±2.25mm). In

155 addition, we recorded rainfalls ('Rainfalls$_{sampl}$') and mean temperature ('Mean Temp$_{sampl}$')

156 between successive sampling dates to assess short-term weather effects at the monthly scale.

157 We also calculated the rainfall over the agricultural year ('Rainfalls$_{year}$') and the annual

158 minimum temperature ('Temp min$_{year}$') to describe weather effects at the yearly scale (Table

159 S5). Soil pH (NF ISO10390), nitrogen content, total organic matter content (NF ISO 14235),

160 cation-exchange capacity (CEC) and texture (NF X 31-107 method) were determined for each

161 olive grove on a 20-cm-deep composite soil sample. More informations on the soil analyses can

162 be found in Genty et al. (2022).

## 2.3. Botanical survey of flower cover

164 Five permanent quadrats of 0.25 m^2 were randomly placed in the inter-rows of each olive grove

165 (n = 80 quadrats), keeping a minimum distance of two metres from the field edge. We sampled

166 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.
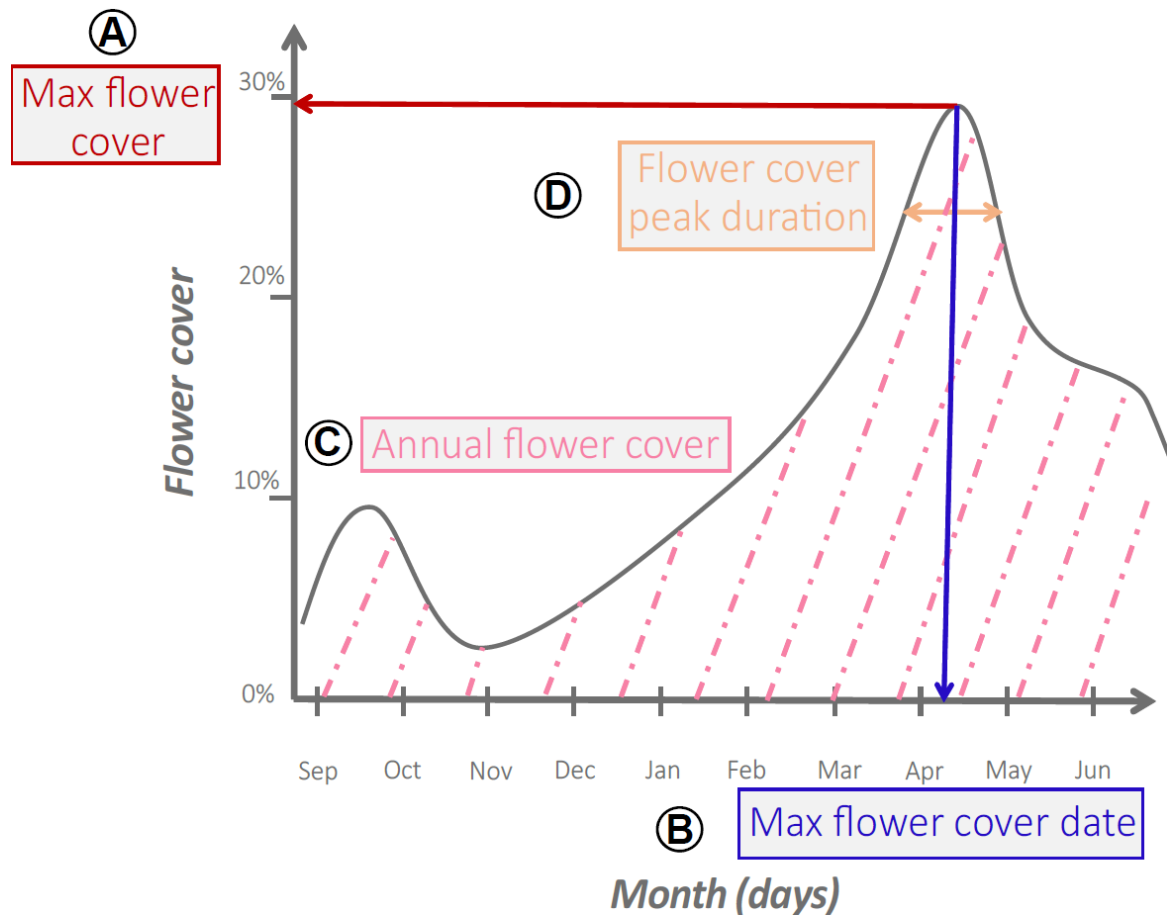
Figure 2. Dynamics of flower cover throughout the year, presenting the four floral productivity indicators: A. Max flower cover (flower cover maximum value in %), B. Max flower cover date (number of days since the start of the sampling, on 17-09-2021), C. Annual flower cover (% calculated as the normalised integral of the regression curve), and D. Flower cover peak duration (number of days with flower cover ≥ 80% of flower cover maximum).

195
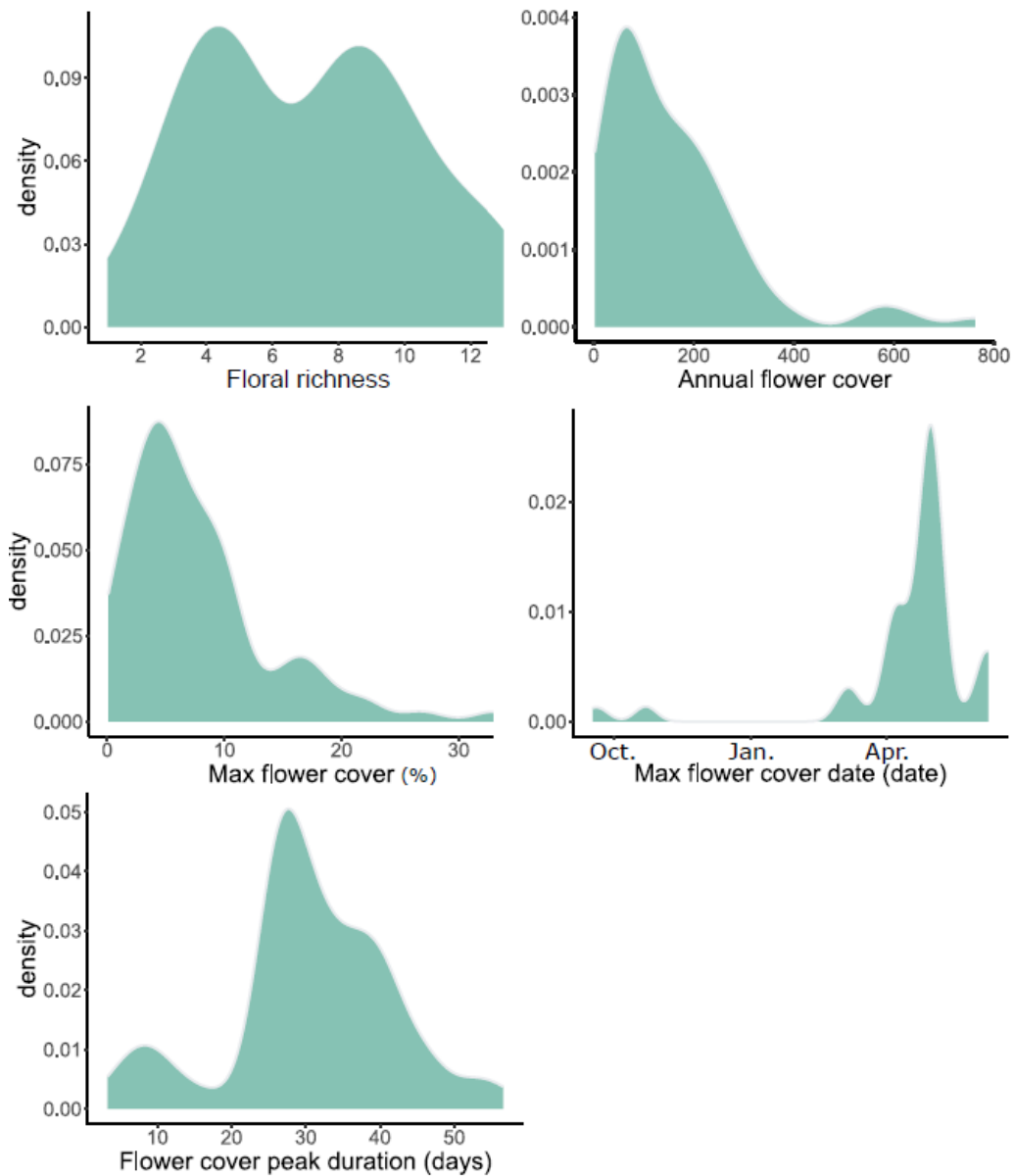
Figure 3. Distribution of floral richness, annual flower cover, max flower cover, max flower cover date and flower cover peak duration among weed communities (n=80).

199

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

204   floral units per plant ('floral unit number'), reproductive height ('height'), flower area ('area'),

205   flowering duration ('duration') and flowering onset ('onset').
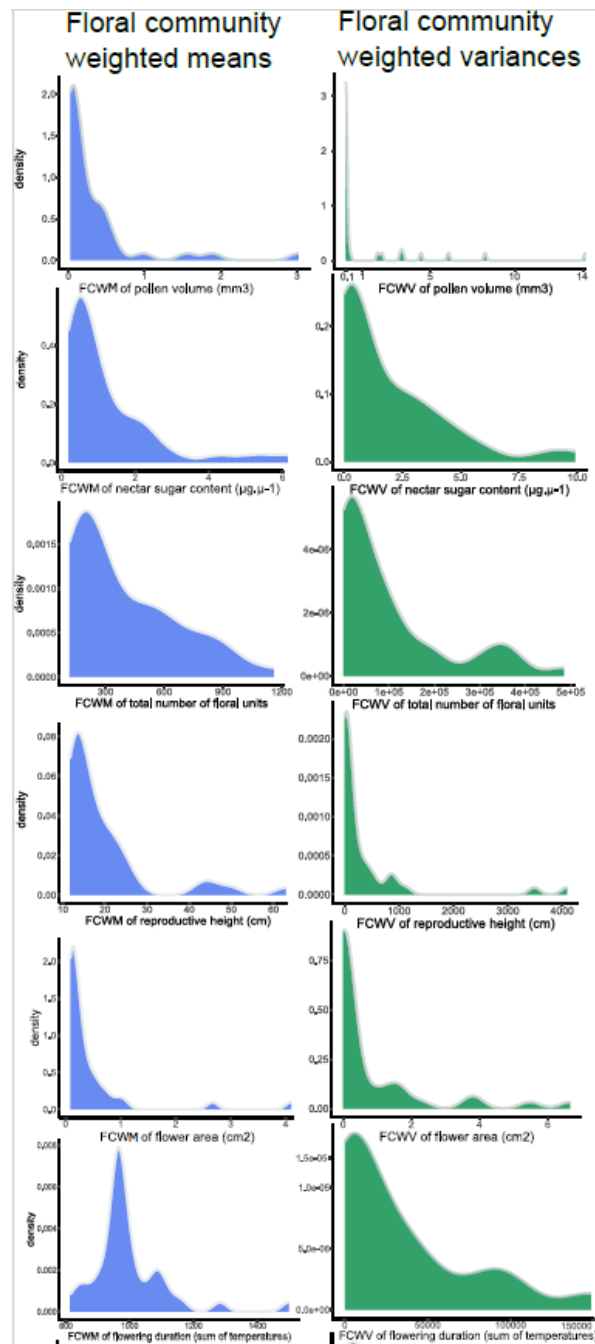
206

207   *Figure 4. Distribution of community weighted means and variances of floral traits: pollen*

208   *volume, nectar sugar content, total number of floral units, reproductive height, flower area,*

209   *flowering duration and onset among weed communities (n=40).*

210

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).

234   To test whether agricultural practices and weather affected monthly flowering species

235   richness and flower cover, we ran linear mixed models with 'last mowing', 'Rainfalls$_{sampl}$' and

236   'Mean Temp$_{sampl}$' as fixed effects and 'month' and 'field' as random effects. To test whether

237   they influenced annual flowering species richness, floral productivity indicators, floral

238   community weighted means and variances, we ran linear mixed models with 'pedoclim1',

239   'pedoclim2', 'mowing', 'irrig', 'N fertilization', 'Rainfalls$_{year}$' and 'Temp min$_{year}$' as fixed

240   effects, and 'field' as random effect. Before model selection and evaluation, correlation of fixed

241   effects was tested using variance inflation (VIF). VIF values of 5 or higher are interpreted as

242   revealing multicollinearity issues (Hair, 2009). We performed model stepwise comparisons

243   comparing full, reduced and 'null' models built by combining all fixed effects, several fixed

244   effects or only random effects. We selected the model with the lowest second-order Akaike

245   Information Criterion value (AICc) corrected for small sample sizes (Burnham & Anderson,

246   2004). Two models were considered different if Δ AICc > 2 (Burnham & Anderson, 2004).

247   When more than one model had the lowest AICc we selected the most parsimonious, with the

248   lowest number of fixed effects. We used likelihood ratio tests to evaluate the selected models,

249   and calculated the marginal and conditional R^2 (Nakagawa & Schielzeth, 2013).

250   The relation between floral traits and indicators of floral productivity was tested with a

251   PCA ('community structure' PCA) with the community weighted means of the seven floral

252   traits and flowering species richness, followed by a hierarchical ascendant classification to

253   create three clusters based on the first two components. To test whether the four indicators of

254   floral productivity differed among clusters, we ran Kruskal-Wallis' and pairwise Wilcoxon's

255   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.

277   At the year scale mowing, N fertilization, irrigation, Pedoclim1 and 2, and Temp Min_{year}

278   affected community weighted means and variances of all floral traits (see detailed results in

279   Table 2).
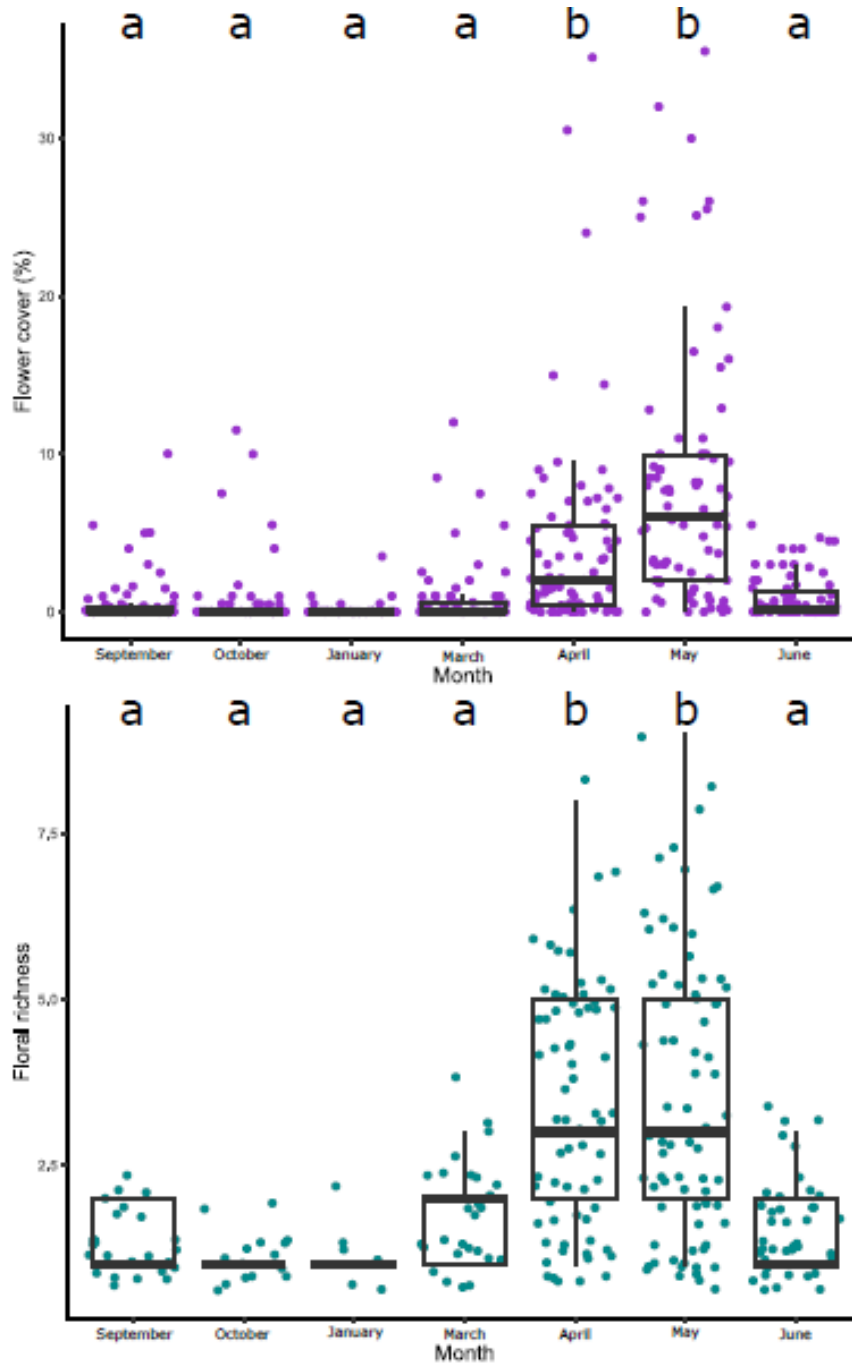
280   *Figure 5. Flower cover (A), and number of flowering species (B) in each quadrat on each*

281   *visit (%). Letters represent the results of pairwise Wilcoxon's tests.*

282

283 *Table 1. Individual effect of pedoclimatic characteristics and agricultural practices on floral*

284 *richness, indicators of flower productivity and flower cover at a monthly and yearly scale.*

285 *Field and month are random effects for the models at the month scale. Field is a random*

286 *effect for models at the year scale. Marginal R2 (R2m) represents the proportion of variance*

287 *explained by fixed effects in the model. Conditional R2 (R2c) includes random effects.*

288 *Significance stars are from the type II ANOVA's Chi^2.*

289

Temporal scale	Response variable	Explanatory variable	Estimate	R2m	R2c
Month	Flower cover	last mowing	0.005*	0.01	0.37
	Floral richness	Rainfalls$_{sampl}$	-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	-	-	-

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

290

291 *Table 2. Individual effect of pedoclimatic characteristics and agricultural practices on*

292 *community weighted means (CWM) and variances (CWV) of floral traits at the year scale*

293 *with field as random effect.*

Functional indicator	Trait (response variable)	Explanatory variable	Estimate	R2m	R2c
CWM	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
	Floral units number	N fertilization	0.884***	0.6	0.6
		irrig	2.064**		
		Temp min$_{year}$	91.063**		
	Duration	N fertilization	-0.284**	0.27	0.27
		irrig	0.794*		
	Onset	N fertilization	-0.648***	0.66	0.68
		irrig	1.483***		
		Temp	-49.732**		

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

*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

294

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).

307   The 'community structure' PCA explained 64.2% of the variability (Figure 6A). The

308   first component (35.1% of explained variability) was positively correlated with the community

309   weighted means of floral height (0.91), area (0.73), duration (0.71), pollen (0.67) and floral

310   richness (0.62) ; high values on this component indicate that the species invest in more costly

311   flowers while lower values indicate cheaper flowers (Roddy et al., 2021). The second

312   component (29.1% of explained variability) was positively correlated with the community

313   weighted mean of floral units number (0.84) and floral specific richness (0.56), and negatively

314   with the community weighted means of flowering onset (-0.70) and duration (-0.57). The

315   ascending hierarchical classification (Figure 6B) identified three clusters: cluster 1 'cheap, few

316   and late-flowering flowers', composed of 23 communities and linked to low scores on both

317   components, cluster 2 'cheap, numerous and early-flowering flowers' (13 communities) linked

318   to low scores on the first component and high scores on the second, and cluster 3 'costly

319   flowers' (4 communities) linked to high scores on the first component. 'Few and late-flowering

320   flowers' communities were more often mown (1,5 *vs* 2,5) and irrigated than 'numerous and

321   early-flowering flowers' communities (Figure 7A), and their flower cover peak duration was 6

322   days longer (Figure 7B).

323

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	5*	0.26	0.34
		Nectar	-3.481**		
Flower cover peak duration	CWM	Onset	-0.022**	0.32	0.67
		Nectar	2.784**		
Annual flower cover	CWV	-	ns	ns	ns
Max flower cover	CWV	Nectar	1.025*	0.16	0.52
		Duration	-0.535**		
Max flower cover date	CWV	-	ns	ns	ns
Flower cover peak duration	CWV	Height	1.657**	0.20	0.63
		Area	-6.283*		

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

328
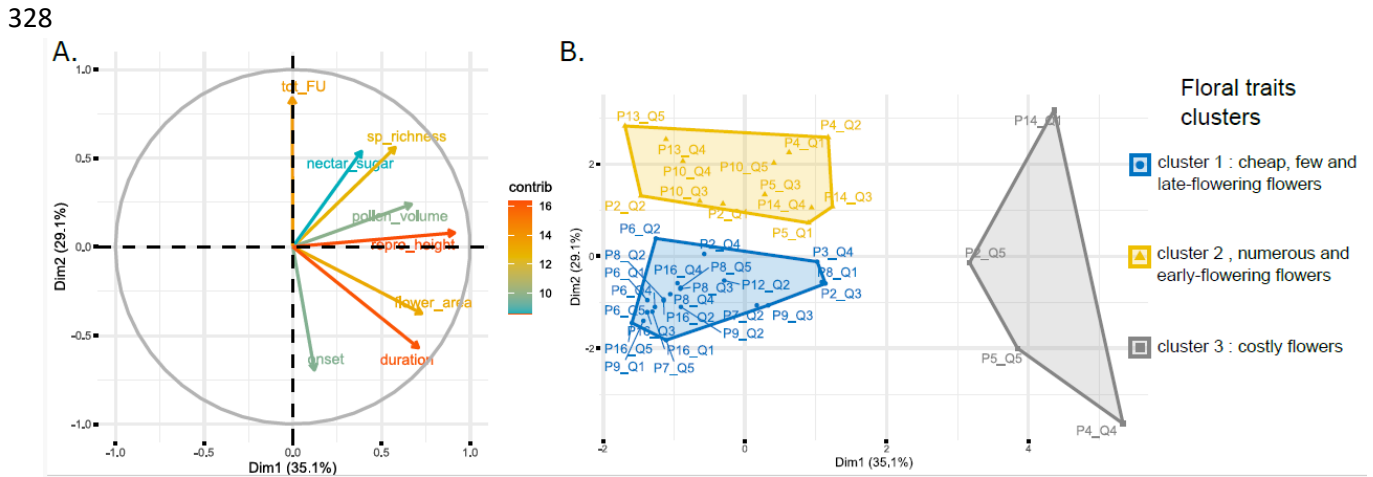
333

334

335

338
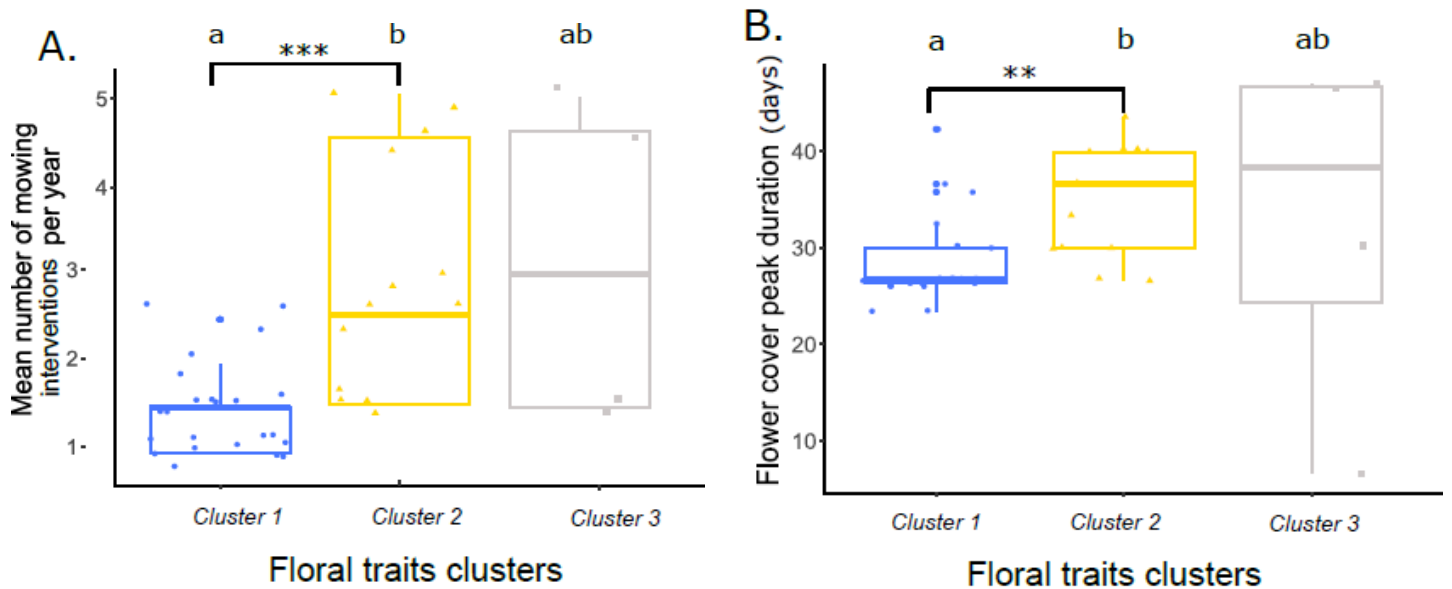
4. Discussion

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

362   efficient to regulate phenology so as to provide more diversified and abundant floral resources

363   for flower-visiting insects (Yvoz et al., 2021).

364   Even though agricultural practices are considered the main driver of trait variability in

365   weed communities at the regional scale (Bourgeois et al., 2021), pedoclimatic and weather

366   variables also matter, especially for trait variance (Poinas et al., 2023). In our study, the

367   homogenising effect of greater soil fertility, e.g. higher levels of organic matter and clay

368   contents (pedoclim1), may be due to selection of the most competitive species (Fried et al.,

369   2022) that develop earlier and exclude later species by pre-empting light resources (Grime,

370   1974). Higher temperatures allowed some cold-tolerant and sensitive species to survive, thus

371   diversifying functional structure, but also decreased community weighted mean of flowering

372   onset, advantaging competitive species that flower early. Rainfall also had a diversifying effect

373   leading to greater FCWVs of total floral unit number and pollen: water deficit may force weeds

374   to allocate less resources to flowers or pollen production (Kuppler & Kotowska, 2021). As

375   found by Bourgeois et al. (2021) for weeds in annual agroecosystems, pedoclimate affected the

376   variance more than the mean of floral traits.

377   **4.2. Floral productivity is linked to community floral richness and traits**

378   Not all floral traits were linked to floral productivity, indicating that communities with any

379   floral strategy could potentially provide floral resources. However four floral traits were found

380   to be positively correlated with floral productivity: mean nectar sugar content (Table 4), number

381   of flowers, onset of flowering (Figures 5 and 6) and floral richness (Table 3), the last increasing

382   all the indicators of floral productivity.

383   Weed richness enhanced floral productivity and thereby provided a diversity of food

384   resources for insects (Balfour & Ratnieks, 2022). The most abundant species, e.g. *M. minima*

385   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).

References

Aedo, C., Garmendia, F. M., & Pando, F. (1998). World checklist of *Geranium* L. (*Geraniaceae*). *Anales Del Jardín Botánico de Madrid*, *56*(2), Article 2. https://doi.org/10.3989/ajbm.1998.v56.i2.230

Andreasen, C., Stryhn, H., & Streibig, J. C. (1996). Decline of the Flora in Danish Arable Fields. *Journal of Applied Ecology*, *33*(3), 619-626. https://doi.org/10.2307/2404990

Aviron, S., Berry, T., Leroy, D., Savary, G., & Alignier, A. (2023). Wild plants in hedgerows and weeds in crop fields are important floral resources for wild flower-visiting insects, independently of the presence of intercrops. *Agriculture, Ecosystems & Environment*, *348*, 108410. https://doi.org/10.1016/j.agee.2023.108410

Baessler, C., & Klotz, S. (2006). Effects of changes in agricultural land-use on landscape structure and arable weed vegetation over the last 50 years. *Agriculture, Ecosystems & Environment*, *115*(1), 43-50. https://doi.org/10.1016/j.agee.2005.12.007

Balfour, N. J., & Ratnieks, F. L. W. (2022). The disproportionate value of 'weeds' to pollinators and biodiversity. *Journal of Applied Ecology*, *59*(5), 1209-1218. https://doi.org/10.1111/1365-2664.14132

Barton, K. (2009). MuMIn : Multi-model inference. *http://r-forge. r-project. org/projects/mumin/*.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using **lme4**. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Bopp, M.-C., Kazakou, E., Metay, A., & Fried, G. (2022). Relative importance of region, seasonality and weed management practice effects on the functional structure of weed communities in

435   French vineyards. *Agriculture, Ecosystems & Environment*, *330*, 107892.

436   https://doi.org/10.1016/j.agee.2022.107892

437   Bopp, M.-C., Fried, G., Metay, A., Bastianelli, D., Bonnal, L., & Kazakou, E. (2022). Linkages between

438   traits and decomposition of weed communities along a soil management and pedoclimate gradient in

439   Mediterranean vineyards. *Annals of Botany*, *130*(4), 547-560. https://doi.org/10.1093/aob/mcac099

440   Bourgeois, B., Munoz, F., Gaba, S., Denelle, P., Fried, G., Storkey, J., & Violle, C. (2021). Functional

441   biogeography of weeds reveals how anthropogenic management blurs trait–climate relationships.

442   *Journal of Vegetation Science*, *32*(2). https://doi.org/10.1111/jvs.12999

443   Bretagnolle, V., & Gaba, S. (2015). Weeds for bees? A review. *Agronomy for Sustainable Development*,

444   *35*(3), 891-909. https://doi.org/10.1007/s13593-015-0302-5

445   Burnham, K. P., & Anderson, D. R. (2004). Multimodel Inference : Understanding AIC and BIC in

446   Model Selection. *Sociological Methods & Research*, *33*(2), 261-304.

447   https://doi.org/10.1177/0049124104268644

448   Carpio, A. J., Castro, J., & Tortosa, F. S. (2019). Arthropod biodiversity in olive groves under two soil

449   management systems : Presence versus absence of herbaceous cover crop: Arthropod diversity

450   in olive with two managements. *Agricultural and Forest Entomology*, *21*(1), 58-68.

451   https://doi.org/10.1111/afe.12303

452   Cleveland, W. S., & Devlin, S. J. (1988). Locally weighted regression : An approach to regression

453   analysis by local fitting. *Journal of the American statistical association*, *83*(403), 596-610.

454   Cohen, M., Bilodeau, C., Alexandre, F., Godron, M., Andrieu, J., Grésillon, E., Garlatti, F., & Morganti,

455   A. (2015). What is the plant biodiversity in a cultural landscape? A comparative, multi-scale

456   and interdisciplinary study in olive groves and vineyards (Mediterranean France). *Agriculture,*

457   *Ecosystems & Environment*, *212*, 175-186. https://doi.org/10.1016/j.agee.2015.06.023

458 E-Vojtkó, A., Bello, F., Durka, W., Kühn, I., & Götzenberger, L. (2020). The neglected importance of

459 floral traits in trait-based plant community assembly. *Journal of Vegetation Science*, *31*(4), 529-539.

460 https://doi.org/10.1111/jvs.12877

461 Fornoff, F., Klein, A.-M., Hartig, F., Benadi, G., Venjakob, C., Schaefer, H. M., & Ebeling, A. (2017).

462 Functional flower traits and their diversity drive pollinator visitation. *Oikos*, *126*(7), 1020-1030.

463 https://doi.org/10.1111/oik.03869

464 Fox, J., Weisberg, S., Adler, D., Bates, D., Baud-Bovy, G., Ellison, S., Firth, D., Friendly, M., Gorjanc,

465 G., & Graves, S. (2012). Package 'car'. *Vienna: R Foundation for Statistical Computing*, *16*.

466 Fried, G., Kazakou, E., & Gaba, S. (2012). Trajectories of weed communities explained by

467 traits associated with species' response to management practices. Agriculture,

468 Ecosystems & Environment, 158, 147-155.

469 Fried, G., Blanchet, C., Cazenave, L., Bopp, M.-C., Kazakou, E., Metay, A., Christen, M., Alard, D., &

470 Cordeau, S. (2022). Consistent response of weeds according to Grime's CSR strategies along

471 disturbance and resource gradients in Bordeaux vineyards. *Weed Research*, *62*(5), 347-359.

472 https://doi.org/10.1111/wre.12549

473 Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard,

474 A., Aubry, D., Bellmann, A., Neill, C., & Toussaint, J.-P. (2004). PLANT FUNCTIONAL

475 MARKERS CAPTURE ECOSYSTEM PROPERTIES DURING SECONDARY

476 SUCCESSION. *Ecology*, *85*(9), 2630-2637. https://doi.org/10.1890/03-0799

477 Genty, L., Kazakou, E., Metay, A., Bastianelli, D., Bopp, M.-C., & Barkaoui, K. (2023). Promising

478 weeds forage potential in perennial Mediterranean agroecosystems. *Agriculture, Ecosystems &*

479 *Environment*, *347*, 108388. https://doi.org/10.1016/j.agee.2023.108388

480 Genty, L., Kazakou, E., Metay, A., Baude, M., Gardarin, A., Michelot-Antalik, A., Leroy, A.,

481 Sotillo, A., Crouzet, J., & Barkaoui, K. (2023b). Flowers of ruderal species are

482 numerous but small, short and low-rewarding. *Oikos*, e10219.

483 Goulnik, J., Plantureux, S., Théry, M., Baude, M., Delattre, M., van Reeth, C., Villerd, J., & Michelot-
484   Antalik, A. (2020). Floral trait functional diversity is related to soil characteristics and positively
485   influences pollination function in semi-natural grasslands. *Agriculture, Ecosystems &*
486   *Environment*, *301*, 107033. https://doi.org/10.1016/j.agee.2020.107033

487 Goulson, D., Nicholls, E., Botías, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress
488 from parasites, pesticides, and lack of flowers. *Science*, *347*(6229), 1255957.

489 Grime, J. P. (1974). Vegetation classification by reference to strategies. *Nature*, *250*(5461), 26-31.

490 Guerra, J. G., Cabello, F., Fernández-Quintanilla, C., & Dorado, J. (2021). A trait-based
491 approach in a Mediterranean vineyard: Effects of agricultural management on the functional
492 structure of plant communities. *Agriculture, Ecosystems & Environment*, *316*, 107465.

493 Guerra, J. G., Cabello, F., Fernández-Quintanilla, C., Peña, J. M., & Dorado, J. (2022). How weed
494 management influence plant community composition, taxonomic diversity and crop yield : A long-term
495 study in a Mediterranean vineyard. Agriculture, Ecosystems & Environment, 326, 107816.
496 https://doi.org/10.1016/j.agee.2021.107816

497 Hatt, S., Uytenbroeck, R., Lopes, T., Mouchon, P., Osawa, N., Piqueray, J., Monty, A., & Francis, F.
498   (2019). Identification of flower functional traits affecting abundance of generalist predators in
499   perennial multiple species wildflower strips. *Arthropod-Plant Interactions*, *13*(1), 127-137.
500   https://doi.org/10.1007/s11829-018-9652-7

501 Hegland, S. J., & Boeke, L. (2006). Relationships between the density and diversity of floral resources
502 and flower visitor activity in a temperate grassland community. *Ecological Entomology*, *31*(5), 532-538.
503 https://doi.org/10.1111/j.1365-2311.2006.00812.x

504 Hegland, S. J., & Totland, Ø. (2005). Relationships between species' floral traits and pollinator visitation
505   in a temperate grassland. *Oecologia*, *145*(4), 586-594. https://doi.org/10.1007/s00442-005-
506   0165-6

507 Hernández-Villa, V., Vibrans, H., Uscanga-Mortera, E., & Aguirre-Jaimes, A. (2020). Floral visitors
508   and pollinator dependence are related to floral display size and plant height in native weeds of
509   central Mexico. *Flora*, *262*, 151505. https://doi.org/10.1016/j.flora.2019.151505

510 Hijmans, R. J., Phillips, S., Leathwick, J., Elith, J., & Hijmans, M. R. J. (2017). Package 'dismo'.
511   *Circles*, *9*(1), 1-68.

512 Kazakou, E., Fried, G., Richarte, J., Gimenez, O., Violle, C., & Metay, A. (2016). A plant trait-based
513   response-and-effect framework to assess vineyard inter-row soil management. *Botany Letters*,
514   *163*(4), 373-388. https://doi.org/10.1080/23818107.2016.1232205

515 Kavvadias, V., & Koubouris, G. (2019). Sustainable Soil Management Practices in Olive Groves. In D.
516 G. Panpatte & Y. K. Jhala (Éds.), *Soil Fertility Management for Sustainable Development* (p. 167-188).
517 Springer Singapore. https://doi.org/10.1007/978-981-13-5904-0_8

518 Kratschmer, S., Pachinger, B., Schwantzer, M., Paredes, D., Guzmán, G., Goméz, J. A., Entrenas, J. A.,
519   Guernion, M., Burel, F., Nicolai, A., Fertil, A., Popescu, D., Macavei, L., Hoble, A., Bunea, C.,
520   Kriechbaum, M., Zaller, J. G., & Winter, S. (2019). Response of wild bee diversity, abundance,
521   and functional traits to vineyard inter-row management intensity and landscape diversity across
522   Europe. *Ecology and Evolution*, *9*(7), 4103-4115. https://doi.org/10.1002/ece3.5039

523 Kuppler, J., & Kotowska, M. M. (2021). A meta-analysis of responses in floral traits and flower–visitor
524 interactions to water deficit. *Global Change Biology*, *27*(13), 3095-3108.
525 https://doi.org/10.1111/gcb.15621

526 Kuppler, J., Neumüller, U., Mayr, A. V., Hopfenmüller, S., Weiss, K., Prosi, R., Schanowski, A.,
527   Schwenninger, H.-R., Ayasse, M., & Burger, H. (2023). Favourite plants of wild bees.
528   *Agriculture, Ecosystems & Environment*, *342*, 108266.

529 Lanuza, B. J., Rader, R., Stavert, J., Kendall, L. K., Saunders, M. E., & Bartomeus, I. (2023). Covariation
530 among reproductive traits in flowering plants shapes their interactions with pollinators. *Functional*
531 *Ecology*, 1365-2435.14340. https://doi.org/10.1111/1365-2435.14340

532 Lê, S., Josse, J., & Husson, F. (2008). **FactoMineR** : An *R* Package for Multivariate Analysis. *Journal*

533   *of Statistical Software*, *25*(1). https://doi.org/10.18637/jss.v025.i01

534 Lefcheck, J. S., Byrnes, J. E., Isbell, F., Gamfeldt, L., Griffin, J. N., Eisenhauer, N., ... & Duffy, J. E.

535   (2015). Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats.

536   *Nature communications*, *6*(1), 1-7

537 Lefcheck, J. S. (2016). PIECEWISESEM : Piecewise structural equation modelling in R for ecology,

538   evolution, and systematics. *Methods in Ecology and Evolution*, *7*(5), 573-579.

539   https://doi.org/10.1111/2041-210X.12512

540 Lehman, C. L., & Tilman, D. (2000). Biodiversity, stability, and productivity in competitive

541 communities. *The American Naturalist*, *156*(5), 534-552.

542 Lundin, O., Ward, K. L., & Williams, N. M. (2019). Identifying native plants for coordinated habitat

543   management of arthropod pollinators, herbivores and natural enemies. *Journal of Applied*

544   *Ecology*, *56*(3), 665-676. https://doi.org/10.1111/1365-2664.13304

545 MacLaren, C., Storkey, J., Menegat, A., Metcalfe, H., & Dehnen-Schmutz, K. (2020). An ecological

546   future for weed science to sustain crop production and the environment. A review. *Agronomy*

547   *for Sustainable Development*, *40*(4), 24. https://doi.org/10.1007/s13593-020-00631-6

548 Meyer, S., Wesche, K., Krause, B., & Leuschner, C. (2013). Dramatic losses of specialist arable plants

549   in Central Germany since the 1950s/60s – a cross-regional analysis. *Diversity and Distributions*,

550   *19*(9), 1175-1187. https://doi.org/10.1111/ddi.12102

551 Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized

552   linear mixed-effects models. *Methods in ecology and evolution*, *4*(2), 133-142.

553 Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M. H. H., Oksanen, M. J., & Suggests, M.

554   (2007). The vegan package. *Community ecology package*, *10*(631-637), 719.

555 Pelletier, L., & McNeil, J. N. (2003). The Effect of Food Supplementation on Reproductive Success in

556 Bumblebee Field Colonies. *Oikos*, *103*(3), 688-694.

557   Piseddu, F., Bellocchi, G., & Picon-Cochard, C. (2021). Mowing and warming effects on grassland

558   species richness and harvested biomass : Meta-analyses. *Agronomy for Sustainable Development*, *41*(6),

559   74. https://doi.org/10.1007/s13593-021-00722-y

560   Pittarello, M., Lonati, M., Ravetto Enri, S., & Lombardi, G. (2020). Environmental factors and

561   management intensity affect in different ways plant diversity and pastoral value of alpine pastures.

562   *Ecological Indicators*, *115*, 106429. https://doi.org/10.1016/j.ecolind.2020.106429

563   Poinas, I., Fried, G., Henckel, L., & Meynard, C. N. (2023). *Spatial scale dependence in agricultural*

564   *drivers of field margin plant communities* (p. 2023.03.02.530797). bioRxiv.

565   https://doi.org/10.1101/2023.03.02.530797

566   Pontes, L. D. S., Soussana, J.-F., Louault, F., Andueza, D., & Carrère, P. (2007). Leaf traits affect the

567   above-ground productivity and quality of pasture grasses. *Functional Ecology*, *21*(5), 844-853.

568   https://doi.org/10.1111/j.1365-2435.2007.01316.x

569   Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global

570   pollinator declines Trends, impacts and drivers. *Trends in Ecology & Evolution*, *25*(6), 345-

571   353. https://doi.org/10.1016/j.tree.2010.01.007

572   Richner, N., Holderegger, R., Linder, H. P., & Walter, T. (2015). Reviewing change in the arable flora

573   of Europe : A meta-analysis. *Weed Research*, *55*(1), 1-13. https://doi.org/10.1111/wre.12123

574   Roddy, A., Guilliams, M., Fine, P., Mambelli, S., Dawson, T., & Simonin, K. (2023). Flowers are leakier

575   than leaves but cheaper to build. *bioRxiv*, 2023-04.

576   Rotchés-Ribalta, R., Marull, J., & Pino, J. (2023). Organic farming increases functional diversity and

577   ecosystem service provision of spontaneous vegetation in Mediterranean vineyards. *Ecological*

578   *Indicators*, *147*, 110023.

579 Roulston, T., & Goodell, K. (2011). The Role of Resources and Risks in Regulating Wild Bee

580 Populations. *Annual review of entomology*, *56*, 293-312. https://doi.org/10.1146/annurev-ento-120709-

581 144802

582 Rowe, L., Gibson, D., Bahlai, C. A., Gibbs, J., Landis, D. A., & Isaacs, R. (2020). Flower traits

583 associated with the visitation patterns of bees. *Oecologia*, *193*(2), 511-522.

584 https://doi.org/10.1007/s00442-020-04674-0

585 Rundlöf, M., Persson, A. S., Smith, H. G., & Bommarco, R. (2014). Late-season mass-flowering red

586 clover increases bumble bee queen and male densities. *Biological Conservation*, *172*, 138-145.

587 https://doi.org/10.1016/j.biocon.2014.02.027

588 Scheper, J., Reemer, M., van Kats, R., Ozinga, W. A., van der Linden, G. T. J., Schaminée, J. H. J.,

589 Siepel, H., & Kleijn, D. (2014). Museum specimens reveal loss of pollen host plants as key

590 factor driving wild bee decline in The Netherlands. *Proceedings of the National Academy of*

591 *Sciences*, *111*(49), 17552-17557. https://doi.org/10.1073/pnas.1412973111

592 Sonnier, G., Shipley, B., & Navas, M.-L. (2010). Quantifying relationships between traits and explicitly

593 measured gradients of stress and disturbance in early successional plant communities : Trait-

594 environment linkages in early successional communities. *Journal of Vegetation Science*, *21*(6), 1014-

595 1024. https://doi.org/10.1111/j.1654-1103.2010.01210.x

596 Steele, K. P., Ickert-Bond, S. M., Zarre, S., & Wojciechowski, M. F. (2010). Phylogeny and character

597 evolution in Medicago (Leguminosae) : Evidence from analyses of plastid trnK/matK and nuclear

598 GA3ox1 sequences. *American Journal of Botany*, *97*(7), 1142-1155.

599 Teixido, A. L., & Valladares, F. (2014). Disproportionate carbon and water maintenance costs of large

600 corollas in hot Mediterranean ecosystems. *Perspectives in Plant Ecology, Evolution and Systematics.*

601 16(2), 83-92. https://doi.org/10.1016/j.ppees.2014.02.002

602 Villéger, S., Mason, N. W. H., & Mouillot, D. (2008). NEW MULTIDIMENSIONAL FUNCTIONAL

603   DIVERSITY INDICES FOR A MULTIFACETED FRAMEWORK IN FUNCTIONAL

604   ECOLOGY. *Ecology*, *89*(8), 2290-2301. https://doi.org/10.1890/07-1206.1

605 Winter, S., Bauer, T., Strauss, P., Kratschmer, S., Paredes, D., Popescu, D., Landa, B., Guzmán, G.,

606   Gómez, J. A., Guernion, M., Zaller, J. G., & Batáry, P. (2018). Effects of vegetation

607   management intensity on biodiversity and ecosystem services in vineyards : A meta-analysis.

608   *Journal of Applied Ecology*, *55*(5), 2484-2495. https://doi.org/10.1111/1365-2664.13124

609 Wray, J. C., Neame, L. A., & Elle, E. (2014). Floral resources, body size, and surrounding landscape

610 influence bee community assemblages in oak-savannah fragments. *Ecological Entomology*, *39*(1), 83-

611 93. https://doi.org/10.1111/een.12070

612 Yvoz, S., Petit, S., Cadet, E., Dessaint, F., & Cordeau, S. (2021). Taxonomic and functional

613 characteristics of field edge weed communities along a gradient of crop management intensity. *Basic*

614 *and Applied Ecology*, *57*, 14-27. https://doi.org/10.1016/j.baae.2021.10.001