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► To cite this version:

Léa Genty, Aurélie Metay, Elena Kazakou, Mathilde Baude, Antoine Gardarin, et al.. Agricultural practices in olive groves modify weeds floral traits and resources throughout the year. *Agriculture, Ecosystems & Environment*, 2025, 377, pp.109280. 10.1016/j.agee.2024.109280 . hal-04696500

HAL Id: hal-04696500

<https://hal.inrae.fr/hal-04696500v1>

Submitted on 18 Sep 2024

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1 **Agricultural practices in olive groves modify weeds**

2 **floral traits and resources throughout the year**

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20

21

22 **Acknowledgements**

23 This work was supported by the Occitanie Region (ALDOCT-001073), the French National
24 Agency for Research (ANR-19-P026-0008-01) and LabEx AGRO 2011-LABX-002,
25 coordinated by the Agropolis Fondation (ID 2101-052).

26 **Authors' contributions**

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

30 **Data availability statement**

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

32 (temporary link:

33 [https://dataverse.cirad.fr/dataset.xhtml?jsessionid=d1fe6f791a3566c0ca444ff52930?persistentId=doi%
34 3A10.18167%2FDVN1%2FB9HXLE&version=DRAFT \)](https://dataverse.cirad.fr/dataset.xhtml?jsessionid=d1fe6f791a3566c0ca444ff52930?persistentId=doi%3A10.18167%2FDVN1%2FB9HXLE&version=DRAFT)

35 **Declaration of competing interest**

36 The authors declare no conflict of interest.

37

38 **Abstract**

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

50 **Keywords**

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

52

53 1. Introduction

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

70 In woody agroecosystems, weeds are a biodiversity component contributing to inter-
71 row ground cover and can be managed in a biodiversity-friendly way by cover cropping or
72 mowing, which maintain higher plant and insect richness and abundance than tillage or
73 herbicide spraying (Carpio et al., 2019 ; Kratschmer et al., 2019 ; Kazakou et al., 2016). Low-
74 intensity management such as moderate mowing (once or twice a year) maintain soil cover and
75 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.

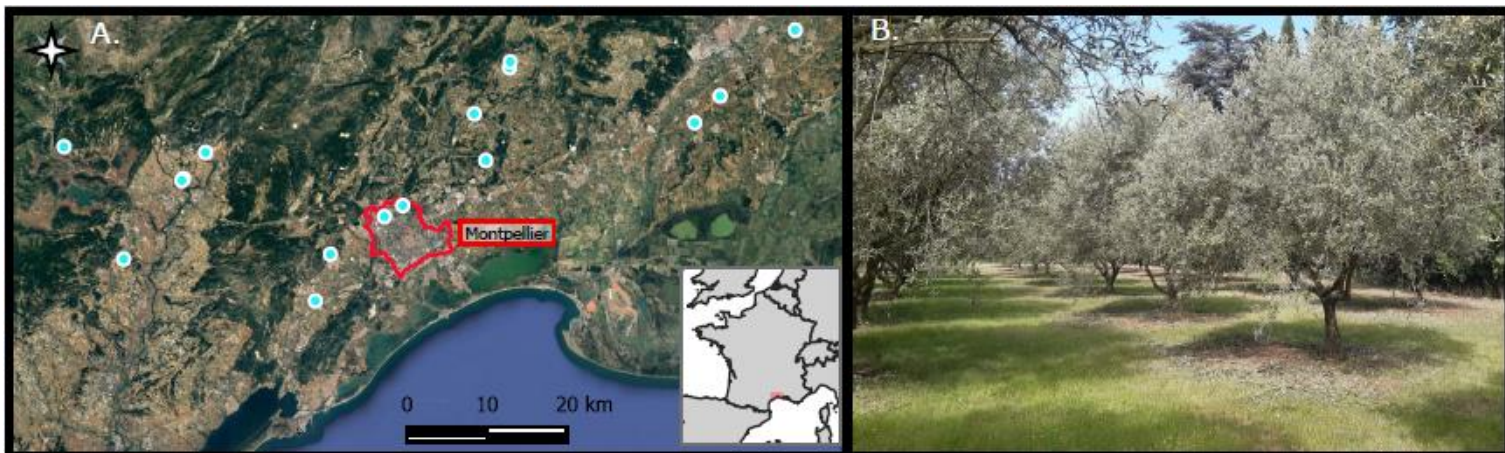
120 In this study, we explored how agricultural practices, weather and pedoclimatic
121 conditions affected weed communities and flowers over one agricultural year in extensive olive
122 groves in southern France, focusing on optimising weed floral resources for insects. Our
123 hypotheses were that 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.

134 **2. Material and methods**

135 **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’),.

147 **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 ($15.3 \pm 0.33^\circ\text{C}$, mean \pm SD), annual rainfall ($704 \pm 124\text{mm}$), rainfall in the driest
153 month ($6.06 \pm 1.84\text{mm}$), maximum temperature of the warmest month ($36.8 \pm 1.1^\circ\text{C}$), annual
154 temperature range ($41.8 \pm 15.8^\circ\text{C}$) and rainfall coefficient of variation ($89.6 \pm 2.25\text{mm}$). In
155 addition, we recorded rainfalls (‘Rainfalls_{sample}’) and mean temperature (‘Mean Temp_{sample}’)
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).

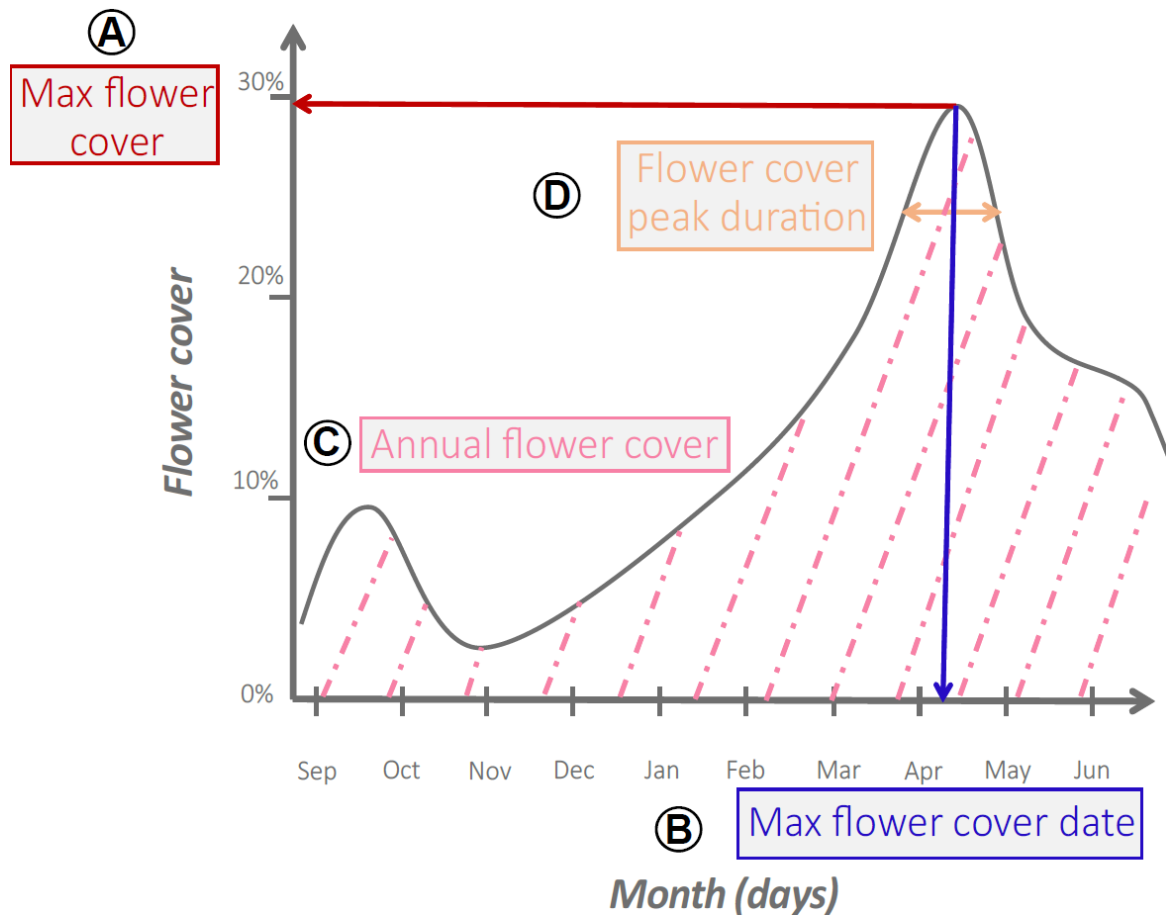
163 **2.3. Botanical survey of flower cover**

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-

167 2021; 14-10-2021; 27-01-2022; 01-03-2022; 04-04-2022; 04-05-2022; 06-06-2022). On each
168 date and for each quadrat we recorded the latest mowing date ('last mowing') and visually
169 recorded the phenological stage and flower cover per species as the total percentage of the
170 ground covered by open flowers and flower buds in each quadrat. We also recorded the number
171 of species at the flowering stage ('floral richness') in each quadrat, and the total species richness
172 of each field based on sampling from Genty et al., 2023. Recorded data concerned insect-
173 pollinated species exclusively.

174 **2.4. Indicators of floral productivity at the year scale**

175 We used a loess regression to model flower cover dynamics over the year (Cleveland & Devlin,
176 1988) for each quadrat based on the seven samplings. We extracted four indicators of floral
177 productivity (Figures 2 and 3): (1) annual flower cover, calculated as the normalised integral of
178 the regression curve ('annual flower cover'); (2) flower cover maximum value in % of surface
179 ('max flower cover'); (3) date of the flower cover maximum ('max flower cover date'),
180 expressed as the number of days since the beginning of the sampling (17th of September 2021);
181 and (4) number of days during which the flower cover reached or exceeded 80% of its flower
182 cover maximum, representing the period of abundant flower presence in the field ('flower cover
183 peak duration'). For flower cover peak duration, we excluded nine quadrats in which 80% of
184 the max flower cover was under 1% (Table S1). The four indicators were measured at the year
185 scale (n = 80) by pooling the data of the seven surveys, considering each quadrat survey as one
186 community composed of all the sampled species proportionally. We recorded the species
187 richness of flowering weeds in each community over the full season.



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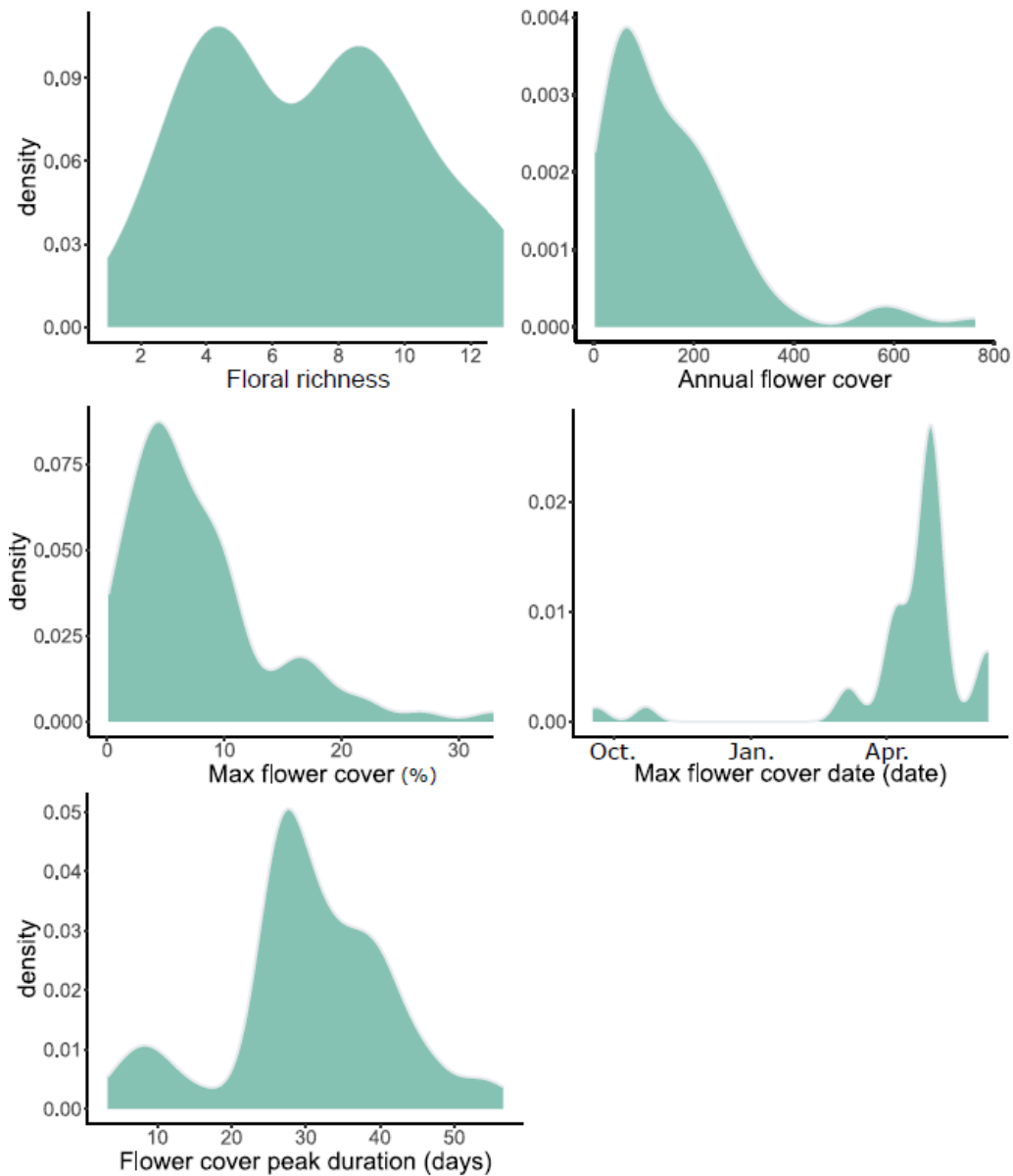
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Figure 2. Dynamics of flower cover throughout the year, presenting the four floral productivity indicators: A. Max flower cover (flower cover maximum value in %), B. Max flower cover date (number of days since the start of the sampling, on 17-09-2021), 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 $\geq 80\%$ of flower cover maximum).



196

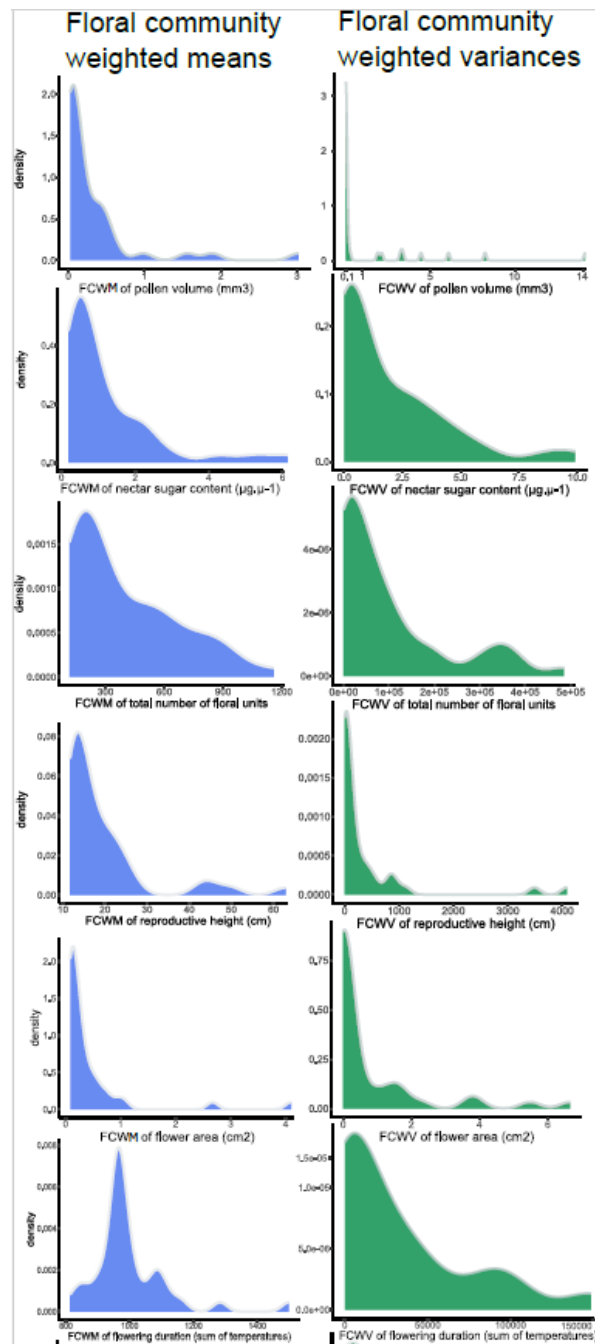
197 *Figure 3. Distribution of floral richness, annual flower cover, max flower*
 198 *cover date and flower cover peak duration among weed communities (n=80).*

199

200 **2.5. Trait measurements and functional indices at the community level**

201 Seven floral traits linked to insect attraction (Table S2) were measured for 17 common weed
 202 species in olive grove (Table S3) in a greenhouse experiment during the spring and summer of
 203 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

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

223 **2.6. Data analysis**

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

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

231 To summarise soil and climatic characteristics of the study sites we ran a PCA with all
232 the pedoclimatic variables. The coordinates of each individual on the first two components were
233 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 $\Delta AICc > 2$ (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.

256 **3. Results**

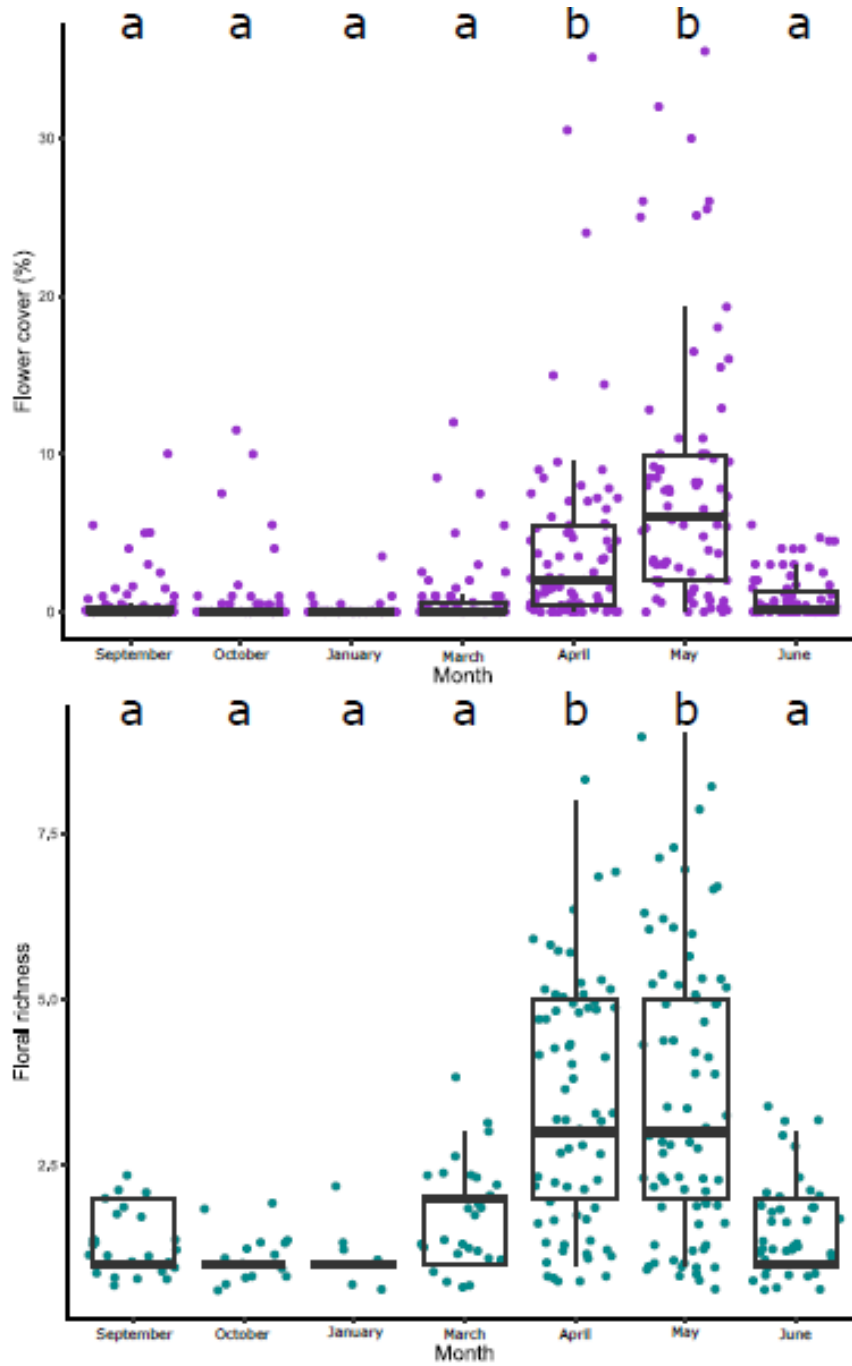
257 **3.1. Effects of pedoclimate, weather and agricultural practices on flowering** 258 **species richness, floral productivity and floral traits**

259 ‘Pedoclimatic’ PCA explained 62% of the total variance of pedoclimatic variables (Table S5).
260 The coordinates of each field on the first two components were used as composite explanatory
261 variables. The first component (‘pedoclim1’) explained 38% of the total variance and was
262 positively linked to soil clay content (0.79), cation-exchange capacity (0.79), mean annual
263 temperature (0.78) and soil nitrogen content (0.66), and negatively to annual temperature range
264 (-0.85), soil sand content (-0.73) and maximum temperature of the warmest month (-0.68). The
265 second component (‘pedoclim2’) explained 24% of the total variance and was positively linked
266 to rainfall in the driest month (0.88) and annual rainfall (0.85), and negatively to rainfall
267 coefficient of variation (-0.76).

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

272 At the month scale, flower cover was positively correlated with time since the last
273 mowing and floral richness with rainfall (Table 1). At the year scale, floral richness was
274 positively affected by pedoclim2 and by the mean number of mowing interventions per year,
275 while max flower cover date was the only indicator of floral productivity impacted by abiotic
276 variables: it was postponed by N fertilization 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 Chi².*
 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	-	-	-

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

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***		
			irrig	2.064**	0.6	0.6
	Duration		Temp min _{year}	91.063**		
			N fertilization	-0.284**	0.27	0.27
	Onset		irrig	0.794*		
			N fertilization	-0.648***	0.66	0.68
			irrig	1.483***		
			Temp	-49.732**		

		min _{year} mowing	-44.292**		
CWV	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
	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

295 **3.2. Relationships between floral productivity, richness and traits**

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

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

301

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; - $p < 0.1$, * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.*

302

303 Mean and variances of floral traits were related to max flower cover, max flower cover
 304 date and flower cover peak duration: the composition of communities, affected both functional
 305 structure and flower productivity indicators, demonstrating that quality, quantity and
 306 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

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

326

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; - $p < 0.1$, * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.*

327

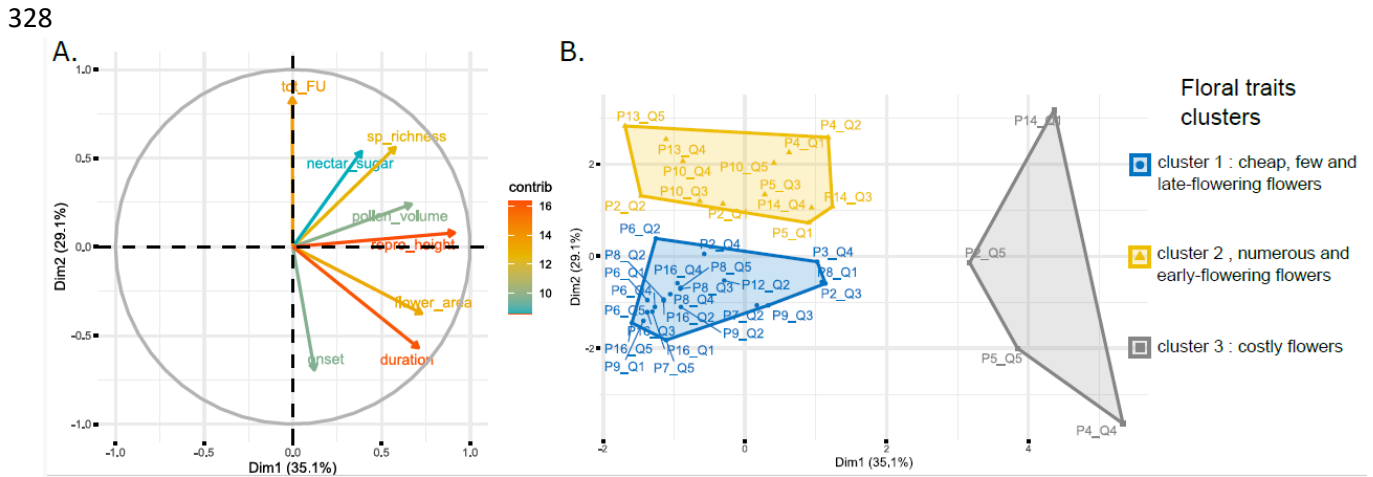


Figure 6. A. First two components of the ‘community structure’ PCA. The individuals are the 40 quadrats at the year scale in which at least 60% of the community was composed of species with documented floral traits. B. The three clusters created with the hierarchical ascending classification.

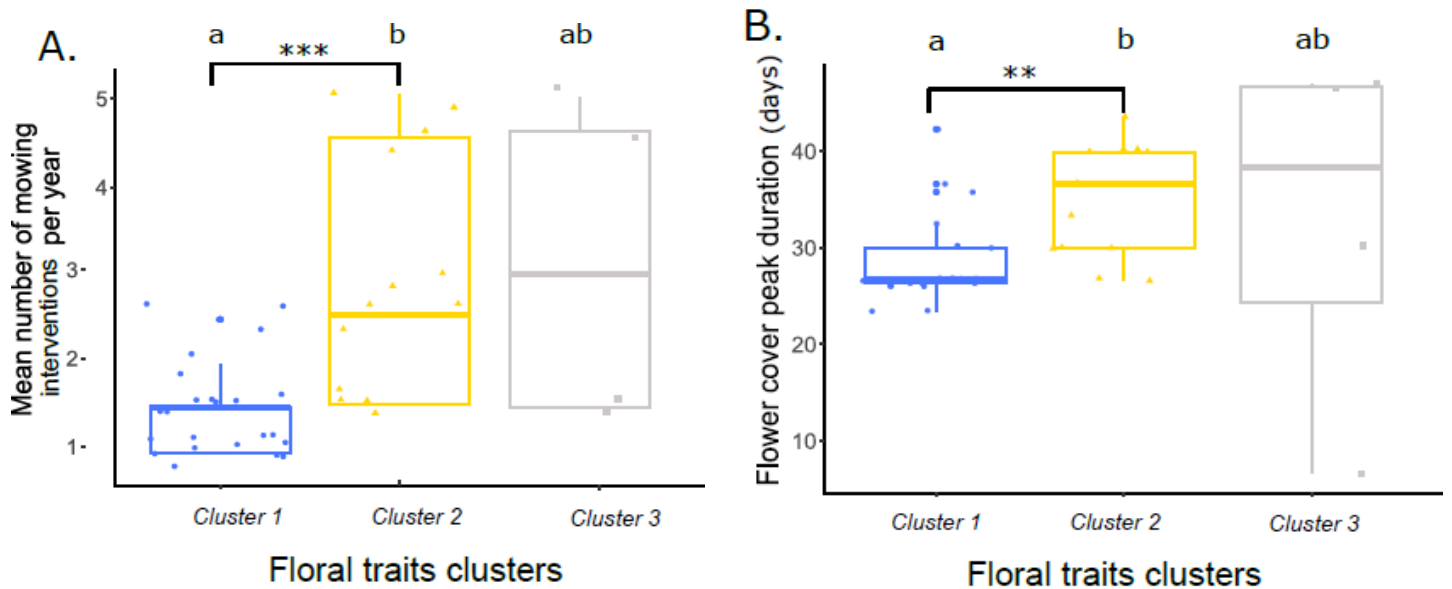


Figure 7. A. Mean yearly number of mowing interventions. B. Flower cover peak duration, according to the floral traits clusters. Letters reflect the results of pairwise Wilcoxon’s tests.

339 **4. Discussion**

340 **4.1. Weed floral traits and richness are affected by pedoclimate and** 341 **agricultural practices**

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

354 In contrast, irrigation and fertilisation had a homogenising effect, reducing community
355 weighted variances of floral area and flowering onset (Table 2), perhaps because high levels of
356 resources benefited the most competitive species. For example, flowering onset was earlier in
357 more frequently mown, fertilised but unirrigated olive groves, which is logical because more
358 disturbed communities are traditionally composed of species flowering earlier (Fried et al.,
359 2012). Higher levels of resources (N fertilization, irrigation) also selected for species producing
360 more floral units that flower for a longer period, which is allowed by the available resources,
361 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.,

386 2023b) excluded by wild bees (Kuppler et al., 2023) but preferentially visited by other important
387 pollinators such as Diptera and Coleoptera (Lanuza et al., 2023). However, the great floral
388 richness found in the olive groves (99 flowering species) enhanced their potential for hosting
389 plants visited by all types of pollinator, among which *E. vulgare* and *P. hieracioides*, favoured
390 by wild bees (Kuppler et al., 2023). Regarding year-round flower presence, which is important
391 for flower-visiting insects, we found that floral resources in olive groves peaked in mid-April
392 overall, with local variations from March to June. This means that flowers were present early
393 in the season, supplying food at a critical time for insects (Pelletier and MacNeil, 2003),
394 however very few resources were available late in the season, which is another critical period
395 for foraging.

396 **4.3. Mowing is a promising practice for enhancing floral productivity**

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

408 Mowing two to three times a year appears to be a beneficial practice for weed species
409 richness and related ecosystem services in woody agroecosystems (Winter et al., 2020). In our
410 work, we found that regular mowing frequency favors higher floral productivity over the year

411 in olive groves. We conclude as other studies for different services (Bopp et al., 2022b;
412 Kavvadias and Koubouris, 2019), that mowing is a biodiversity-friendly weed management
413 practice able to both deliver ecosystem services and ensure satisfactory yield in Mediterranean
414 woody agroecosystems (Guerra et al., 2022).

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