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# Relative importance of region, seasonality and weed management practice effects on the functional structure of weed communities in French vineyards

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1 **Title:** Relative Importance of Region, Seasonality and Weed Management Practice Effects on the  
2 Functional Structure of Weed Communities in French Vineyards

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15

16 **Abstract**

17 Winegrowers have diversified their weed management practices over the last two decades  
18 changing the structure and the composition of weed communities. Complementary to taxonomic  
19 studies, trait-based approaches are promising ways for a better understanding of weed community  
20 responses to environmental and agronomic filters. In the present study, the impacts of climate, soil  
21 characteristics, seasons and weed management practices (chemical weeding, tillage and mowing)  
22 were assessed on weed communities from 46 plots in three French wine-growing regions  
23 (Champagne, Languedoc and Rhône valley). These agro-environmental gradients structuring weed  
24 communities according to their combinations of traits were highlighted using multivariate analysis  
25 (RLQ). The impacts of these filters on Community Weighted Means (CWM) and Community Weighted  
26 Variance (CWV) of weed communities were analysed using mixed and null modelling. Our results  
27 showed that spatio-temporal and weed management practice variables explained from 13% to 48%  
28 of the total variance of CWM (specific leaf area, maximum height, seed mass, flowering onset and  
29 duration and lateral spread). Region, seasonality and management practices explained 53%, 28% and  
30 19% of CWM marginal variance, respectively. Weed management impacted CWM and CWV through  
31 two main gradients: (i) a soil disturbance gradient with high mechanical disturbance of soil in tilled  
32 plots and low mechanical disturbance in chemically weeded plots and (ii) a vegetation cover gradient  
33 with high vegetation abundance in mowed plots compared to barer soils in tilled and chemically  
34 weeded plots. In Languedoc, chemical weeding filtered weed communities with ruderal strategy trait  
35 values (low seed mass, small-stature) while mowed communities were more competitive (higher  
36 seed mass, higher stature and lower SLA). In Languedoc and Champagne, tillage favoured  
37 communities with high seed mass that increases the viability of buried seeds and high lateral spread  
38 values associated to the ability to resprout after tillage. This study demonstrated that trait-based  
39 approaches can be successfully applied to perennial cropping systems such as vineyards, in order to  
40 understand community assembly to better guide weed management practices.

41 **Keywords:** trait-based approach, French wine-growing regions, weed communities, seasonality,  
42 tillage, chemical weeding, mowing

43

## 44        **1. Introduction**

45            Weed communities have an important role in maintaining biodiversity in agroecosystems,  
46 potentially delivering multiple ecosystem services as long as their negative impact on crops are  
47 limited (Gaba et al., 2015; Paiola et al., 2020; Storkey and Westbury, 2007; Winter et al., 2018).  
48 Understanding how weed communities respond to abiotic, biotic and anthropogenic factors is  
49 essential to better guide weed management practices and thus to increase their ecosystem services  
50 (e.g. climate regulation through carbon stockage, nitrogen supply) and decrease their ecosystem  
51 disservices (e.g. competition for soil water) (Mahaut et al., 2020).

52            In vineyards, winegrowers have diversified their weed management practices over the last  
53 two decades (Fernández-Mena et al., 2021; Novara et al., 2018; Simonovici, 2019). Chemical  
54 weeding, especially in inter-rows, is less applied seeing a change in favour of superficial tillage and  
55 mowing. These alternative practices have impacted the structure of weed communities (Fried et al.,  
56 2019; Gago et al., 2007; Steenwerth et al., 2016). For instance, the combination of tillage and  
57 mowing of inter-rows has been significantly associated with higher richness and abundance unlike  
58 tillage or chemical weeding (Fried et al., 2019).

59            In addition to the taxonomic characterization of weed communities, trait-based approaches  
60 can be used to explain the response of weed communities to environmental filters and weed  
61 management practices (Kazakou et al., 2016). Traits are any morphological, physiological or  
62 phenological features that are measurable at the individual level, from the cell to the whole-  
63 organism level (Violle et al., 2007). As with other environmental drivers (e.g. climate, soil  
64 characteristics, seasonality), weed management practices filter weed species within communities  
65 according to their trait values, or 'response trait' (Damour et al., 2018; Kazakou et al., 2016; Lavorel  
66 and Garnier, 2002). Filtering processes can shape functional structure of weed communities in two  
67 major dimensions. Firstly, the mean trait value of communities reflects the major weed strategy to  
68 adapt to local conditions (e.g. early flowering onset to avoid disturbance). Secondly, the range of

69 possible trait values expresses the dissimilarity of weed strategies within a community (e.g. a wide  
70 range of flowering onset within a community might increase the probability that some species flower  
71 in a disturbed environment). Reduced or wide range of possible trait values, driven by agro-  
72 environmental filters, lead respectively to convergent or divergent distributions (Bernard-Verdier et  
73 al., 2012; Perronne et al., 2017).

74         So far, trait-weed management practices relationships have been mostly explored in annual  
75 cropping systems (Alarcón Vllora et al., 2019; Armengot et al., 2016; Fried et al., 2012; Hernández  
76 Plaza et al., 2015; Smith, 2006; Storkey et al., 2010; Trichard et al., 2013) while few studies have  
77 investigated these relationships in perennial crop systems such as the grapevine (Fiera et al., 2020;  
78 Hall et al., 2020; MacLaren et al., 2019; Mainardis et al., 2020). In vineyards, tillage, chemical  
79 weeding and mowing are the most frequent weed management practices applied in France  
80 (Simonovici, 2019). Tillage and chemical weeding can be considered to be high disturbances as they  
81 destroy pre-existing living plant biomass (Gaba et al., 2014; Grime, 1979). Highly disturbed soils can  
82 result in convergent trait values distributions within the communities and favour trait values  
83 associated to ruderal weed communities (species with short stature, small seeds and high specific  
84 leaf area) (Grime, 2006; Kazakou et al., 2016). In contrast, mowing only partially destroys weed  
85 biomass. This intermediate disturbance (Grime, 2006), leads to a more divergent trait distribution  
86 (i.e. increased range of possible trait values) and to more competitive weed communities as  
87 vegetation cover is expected to be higher (species with large stature, high seed mass and high  
88 specific leaf area) (Kazakou et al., 2016; Mainardis et al., 2020).

89         Moreover, other abiotic filters such as climate, soil characteristics or seasonality can impact  
90 the functional structure of weed communities strongly (Keddy, 1992). Firstly, climate (e.g.  
91 temperature, precipitation) affects functional metrics at the community level (Alarcón Vllora et al.,  
92 2019; Hall et al., 2020). For instance, Alarcón Vllora et al. (2019) found that climatic inter-annual  
93 fluctuations drove the functional structure of weed communities more than management practices

94 in cereal-legume rotation. Secondly, seasonality was one of the main factors explaining weed  
95 community composition in annual crop fields (Fried et al., 2008; Hallgren et al., 1999; Lososová et al.,  
96 2004). However, few studies have explored the relative importance of those abiotic filters compared  
97 to weed management practices on functional structure of weeds in vineyards. Indeed, most studies  
98 have been made at the experimental level (except (Hall et al., 2020)) in fixed abiotic conditions  
99 without considering the effect of pedoclimatic variations.

100 In vineyards, some recent trait-based studies have considered functional diversity using  
101 various metrics (e.g. richness, evenness, divergence, dispersion) (Fiera et al., 2020; Hall et al., 2020;  
102 Mainardis et al., 2020). However, to the best of our knowledge, none of these studies have tested  
103 the filtering effect of weed management practices on variations in trait values of weed communities  
104 by using null models. These randomization procedures make it possible to distinguish the effect of  
105 the specific richness from the effect of the functional richness (Mason et al., 2013) that can be mixed  
106 up. Indeed, functional diversity metrics (functional richness, functional divergence, functional  
107 evenness...) depend partly on the number of species occurring within a community (i.e. the more  
108 species in a community, the higher the probability that they might have different trait values)  
109 (Mouchet et al., 2010). Null model approaches are largely used in community ecology to detect  
110 signatures of niche-based mechanisms (Perronne et al., 2017) and could be applied to managed  
111 weed communities in vineyards.

112 In this study, the relative importance of the filtering effects of wine-growing regions covering a  
113 wide range of climate and soil characteristics, seasonality and weed management practices on the  
114 functional structure of weed communities was assessed using Fried et al. (2019) large data set of 46  
115 vineyards (the Biovigilance network) from three wine-growing French regions (Champagne,  
116 Languedoc and Rhône valley). The general objective of our study was to test whether changes in  
117 weed species composition in vineyards caused by environmental and anthropogenic filters shown in  
118 Fried et al. (2019) would also lead to changes in functional structure. First, we highlighted the main

119 agro-environmental gradients structuring weed communities according to their combination of traits,  
120 using multivariate analysis (RLQ). Then, two different aspects of the functional structure of the weed  
121 communities were assessed using trait values from databases: Community Weighted Means (CWM)  
122 which is the mean value of traits of weed communities, and Community Weighted Variance (CWV)  
123 which is the variability of these trait values within the community. We used mixed linear models to  
124 test the effects of the explanatory variables on the CWM of weed communities. Secondly, we  
125 evaluated the seasonality and weed management practices effects on CWM within each wine-  
126 growing region. Thirdly, we tested if CWV were significantly impacted by weed management  
127 practices and seasonality using a null model approach to disentangle the effect of functional variance  
128 from the effect only due to species richness (Perronne et al., 2017). We expected that seasonality  
129 and region would explain more CWM variability than weed management practices. We hypothesized  
130 that tillage and chemical weeding would restrict the range of possible trait values within weed  
131 communities leading to a convergent distribution of trait values and favour more ruderal strategies  
132 (Kazakou et al., 2016). On the contrary, we hypothesized that mowing would increase functional  
133 diversity within communities (divergent distribution) and favour more competitive strategies.  
134 Moreover, we hypothesized that intraspecific variation was lower than interspecific variation  
135 (species robustness assumption) (Garnier et al., 2001; Kazakou et al., 2014).

136

## 137 2. Materials and Methods

### 138 2.1. Climate, soil characteristics and weed management practices

139 Weed surveys were performed in 46 vineyards from 2006 to 2012 in three main wine production  
140 regions in France (the 'Biovigilance network'): i) Champagne, northeast France (10 plots) ii) Beaujolais  
141 and the northern Rhône valley, central east of France (18 plots), and iii) Languedoc, central south of  
142 France (18 plots) (for more details on the timing of plots survey, see Table A.1). The climate of  
143 Champagne is continental with oceanic influences (Table A.2). The mean annual temperature of  
144 Champagne is 10.1°C with 657 mm annual rainfall in the surveyed plots (Table A.2). The climate of  
145 Rhône valley is semi-continental with a mean annual temperature of 11.4°C and 776 mm annual  
146 rainfall in the surveyed plots. The climate of Languedoc is Mediterranean with a mean annual  
147 temperature of 14.1 °C and 686 mm annual rainfall in the surveyed plots.

148 The soils of the Champagne vineyard plots are silty (45.7 %) with a neutral pH (pH of 7.1) with  
149 low bulk density (fine earth) mean value (1387.3 kg/m<sup>3</sup>) (Table A.2). Rhône vineyard soils are  
150 characterized by the highest soil organic carbon content (19.7 %) with a slightly acidic pH (6.7).  
151 Languedoc plots soils are alkaline (pH of 7.5), have a high bulk density (1528 kg/m<sup>3</sup>) and have 27% of  
152 clay. A PCA using all the soil-climate variables was performed (Fig. A.1) and showed that plots were  
153 well discriminated according to their regions of origin (based on Kruskal-Wallis tests comparing the  
154 distribution of plot coordinates on PCA Axes 1 and 2, Fig. A.2). Because of this strong correlation  
155 between regions and pedoclimate variables, we have chosen to keep only the "region" variable,  
156 assuming that this largely represents the soil-climate differences.

157 Three different weed management practices were applied on rows and inter-rows in these  
158 vineyards: chemical weeding, tillage and mowing. As mowing on rows was only exceptionally applied  
159 in our dataset (applied in two plots in Rhône, representing 7 floristic surveys), we decided not to  
160 consider this variable. At the global dataset scale, chemical weeding concerned one third of the inter-  
161 rows and 90% of the rows. Farmers of the vineyard network used pre-emergence and post-

162 emergence herbicides. Active ingredients of post-emergence herbicide were mostly glyphosate. Pre-  
163 emergence herbicide was mostly constituted of oryzalin. Tillage was applied on one third of the inter-  
164 rows and 17% of rows. Tillage was mostly superficial (mean of 12 cm and ranging from 5 cm to more  
165 than 20 cm). Mowing concerned one third of inter-rows.

166 Weed management practices differed according to wine-growing regions. In Languedoc,  
167 tillage was more common (70% of inter-row practices and 27% of row practices) and more frequent  
168 (1.5 tillage of inter-rows and 0.9 cultivations of rows per year) than in the other regions (Table 1). In  
169 contrast, inter-rows of plots in Champagne and Rhône were mostly chemically weeded and mowed.  
170 Rows were mainly chemically weeded in Champagne (84% of rows, 1.7 chemical weeding per year)  
171 and Rhône (95% of rows, 2.7 chemical weeding per year). The timing of weed management was quite  
172 similar between regions. On average, chemical weeding and tillage management were applied earlier  
173 (April-May-June) than mowing (June-July) by farmers.

174 **Table 1** Characteristics of weed management practices of rows and inter-rows in Champagne, Languedoc and Rhône. Combination of different management  
 175 practices can be applied on rows or inter-rows so total percentage per region are not equal to 100%. Abbr., abbreviations ; % plots, proportion of plots ;  
 176 freq, the number of weeding per year ; Jan., January ; Feb., February ; Mar., March ; Apr., April ; Aug., August ; Sept., September ; Oct., October ; Nov.,  
 177 November.

Location	Weed management practices	Abbr.	Champagne			Languedoc			Rhône		
			% plots	Freq	Timing	% plots	Freq	Timing	% plots	Freq	Timing
<b>Inter-rows</b>	Chemical weeding	Chem.IR	48%	0.6	May (Mar.- (0-3) Aug.)	26%	0.5	May (Mar.- (0-3) Oct.)	45%	0.7	May (Mar.- (0-3) Aug.)
	Mowing	Mow.IR	63%	1.7	June (Mar.- (0-5) Sept.)	13%	0.3	June (Apr.- (0-3) Aug.)	52%	1.8	July (Mar.- (0-5) Sept.)
	Tillage	Till.IR	28%	0.5	June (Mar.- (0-4) Sept.)	70%	1.5	June (Jan.- (0-5) Nov.)	7%	0.4	May (Feb.- (0-4) Sept.)
<b>Rows</b>	Chemical weeding	Chem.R	84%	1.7	May (0-5) (Feb.-Aug.)	85%	1.3	April (Mar.- (0-3) Oct.)	95%	2.3	May (Mar.- (0-4) Oct.)
	Tillage	Till.R	17%	0.6	June (Mar.-	27%	0.9	May (Feb.-	9%	0.2	May (Mar.-

---

(0-5) Aug.)

(0-4) Oct.)

(0-2) Aug/)

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178 *3.2. Floristic surveys*

179 From 2006 to 2012, floristic surveys were performed in late winter to early spring (January to  
180 April), summer (May to July) and late summer to early autumn (August to October) (see Table A.1 for  
181 more details). Two temporal variables were considered in this study: the year of floristic survey and  
182 the number of days between the 1<sup>st</sup> January of the same year and the day of the floristic survey,  
183 which is considered as an indicator of the seasonality. In each vineyard plot, plant species were  
184 surveyed over an area of 2000m<sup>2</sup> (in a rectangle 50 m long and 40 m wide). To estimate species  
185 abundance, we used five abundance classes developed in Barralis (1976): '1', less than 1  
186 individual/m<sup>2</sup> ; '2', 1–2 individuals/m<sup>2</sup> ; '3', 3–20 individuals/m<sup>2</sup> ; '4', 21–50 individuals/m<sup>2</sup> ; '5', more  
187 than 50 individuals/m<sup>2</sup>. We transformed these scores into a quantitative scaling using the median of  
188 the range of each density class as followed: '1', 0.5 individual/m<sup>2</sup> ; '2', 1.5 individuals/m<sup>2</sup> ; '3', 11.5  
189 individuals/m<sup>2</sup> ; '4', 35.5 individuals/m<sup>2</sup> ; '5', 75 individuals/m<sup>2</sup>. A list of species and distinct  
190 abundance scores were noted for rows and inter-rows. However, in this study, we focused on the  
191 plot-scale flora resulting from the combination of row and inter-row practices (following MacLaren et  
192 al. (2019)). Therefore, plant community composition was estimated from the whole 2000 m<sup>2</sup>  
193 surveyed including both the row and the inter-row (hereafter vineyard plot scale) taking the  
194 maximum abundance score for species occurring in both areas. In total, 270 surveys were recorded  
195 at the vineyard plot scale (46 in Champagne, 102 in Languedoc and 122 in Rhône, Table A.1).

196 *2.2. Traits data*

197 Six plant traits were selected to capture plant responses to environmental variations and weed  
198 management practices. Three traits of the Leaf-Height-Seed (LHS) strategy scheme were selected  
199 (Westoby, 1998) : (a) specific leaf area (SLA) which is the light-catching area deployed per unit of  
200 previously photosynthesized dry mass, is related to the speed of resources acquisition (Wright et al.,  
201 2004), (b) maximum height which expresses the possible amount of growth in an undisturbed  
202 environment and which is related to light and nutrient acquisition (Westoby et al., 2002), (c) seed

203 mass which represents the ‘colonisation-competition’ trade-off (Moles and Westoby, 2006)  
204 illustrating two strategies : ‘producing a large number of small seeds, each with low establishment  
205 ability and high colonizing capacity’ and ‘producing fewer, larger seeds, each with a higher chance of  
206 successful establishment’ (Westoby et al., 2002). Three other traits related to persistence and  
207 regeneration in disturbed habitats were selected: (d) flowering onset, (e) flowering duration and (f)  
208 lateral spread ability. Lateral spread is a qualitative trait which represents species abilities to develop  
209 horizontally (species with rhizomes or forming tussocks); it is rated as followed: ‘1’, therophytes ; ‘2’,  
210 perennials with compact unbranched rhizomes or forming small tussocks (less than 100 mm in  
211 diameter) ; ‘3’, perennials with rhizomatous system or tussocks reaching from 100 to 250 mm ; ‘4’,  
212 perennials reaching diameter of 251 to 1000 mm.

213 The trait values were extracted from different databases: the LEDA Traitbase for SLA (Kleyer  
214 et al., 2008), Flora Gallica for maximum height (Tison and De Foucault, 2014), the Seed Information  
215 Database (SID) for seed mass (Royal Botanic Gardens Kew, 2021), Baseflor for flowering onset and  
216 duration (Julve, 1998) and lateral spread from Hodgson et al. (1995) supplemented by expert opinion  
217 (G. Fried, pers. com.).

218 We calculated the community weighted means (CWM) (Garnier et al., 2004) and the  
219 Community Weighted Variances (CWV) (Sonnier et al., 2010) of each trait at the vineyard plot scale  
220 using the following equations:

221 
$$CWM = \sum_{i=0}^n p_i \times trait_i \text{ (Eq. 1)}$$

222 
$$CWV = \sum_{i=0}^n p_i \times (trait_i - CWM)^2 \text{ (Eq. 2)}$$

223 Where  $p_i$  is the proportion of abundance of the species  $i$  within a community,  $trait_i$  is the value of  
224 trait of the species  $i$  and  $n$  is the total number of species within the community. CWM as the  
225 weighted average trait values of the community, expresses the most probable trait value of an

226 individual randomly picked up within a community (Garnier et al., 2004). CWV expresses the  
227 variability of the trait values around the average value within the community (Sonnier et al., 2010).

### 228 3.3. Data analyses

#### 229 3.3.1. RLQ and fourth-corner analysis

230 To characterize the covariation of the functional structure of weed communities with  
231 management practices and spatio-temporal variables (i.e. region, seasonality and the year of floristic  
232 survey), we combined an RLQ analysis and a fourth-corner approach using Dray et al. (2014)  
233 framework. RLQ analysis investigates co-inertia between 3 types of data: i) region, year and season of  
234 floristic surveys (i.e. the number of days since the beginning of the year) and soil management  
235 variables (R table), ii) floristic composition (L table), iii) species trait attributes (Q table). Species  
236 density were square-root transformed. Firstly, correspondence analysis (CA) was applied to the table  
237 L. Then, we performed a Hill and Smith analysis on the R and Q tables using respectively the row and  
238 the column scores of the CA. Finally, the RLQ performed two co-inertia analyses on the R-L and L-Q  
239 tables. A Monte Carlo permutation (n=999) test was used to test the global significance of the  
240 relationship between the agro-environmental table R and the trait table Q. Based on the results of  
241 the RLQ analysis, a fourth-corner analysis was performed to test the significance of the relationship  
242 between traits and agro-environmental variables. At this step, we tested the associations between  
243 individual traits and environmental gradients obtained from RLQ scores, and between individual  
244 environmental variables and trait syndromes obtained from RLQ scores. We used a permutation  
245 model (n=49 999) to test the null hypothesis that species are distributed independently of their trait  
246 values and their preferences for agro-environmental conditions in the vineyard plots (Dray and  
247 Legendre, 2008). Adjusted p-values were used rather than p-values to limit the overall error rate of  
248 multiple testing. Multivariate analyses such as RLQ give a good idea of the main agro-environmental  
249 gradients. To further understand the effect of each agro-environmental variable on each trait, we  
250 analysed the variations in CWM and CWV.

251 *3.3.2. Mixed linear models of CWM*

252 To evaluate the relative importance of region, temporal variables and weed management  
253 practices effects on CWM, we constructed mixed linear models for each CWM ('lmer' function of  
254 lme4 package (Bates et al., 2015)). We defined two random effects in each model: the vineyard plot  
255 identity and the year of floristic survey. Seed mass, lateral spread and flowering duration were  
256 logarithmised to validate hypotheses of linear models. Prior to model construction, the collinearity of  
257 explanatory variables was investigated using the variance inflation factor (VIF <5). Model selection  
258 was performed using a backward step selection procedure based on AIC (Burnham and Anderson,  
259 2004). We calculated the explained variance of each covariate as the percentage of variance  
260 additionally explained when each variable was added one by one to the model. As region had a major  
261 effect on CWM, we investigated the weed management practice variables, the seasonality and the  
262 year of survey effects on CWM within each region.

263 *3.3.3. Covariations between CWM and weed management practices and temporal variable*  
264 *gradients*

265 To characterize the gradient of weed management practices and temporal variation of floristic  
266 surveys, we performed a Principal Component Analysis (PCA). Then, we tested the correlations  
267 between CWM and the PCA scores of the sites on the first two axes representing gradients of  
268 management practices (Spearman's rank correlation). We corrected p-values from multivariate  
269 testing using Bonferroni corrections.

270 *3.3.4. Null modelling and covariations between effect sizes of CWV and weed management*  
271 *practices and temporal variable gradients*

272 To test whether CWV values were randomly distributed along the weed management practices  
273 gradient, we first used a null model approach. We constructed a 'population-based fixed-zero per  
274 sites' null model to test the following null hypothesis: abundance is randomly distributed within plots  
275 with respect to trait values. We shuffled species x site matrix for the observed species, while keeping

276 species x trait matrix unchanged, breaking the link between abundance and trait values (Bernard-  
277 Verdier et al., 2012; Perronne et al., 2017). Thus, the richness, the list of the observed species and  
278 the abundance distribution within a plot remained unchanged. This randomization type allows to  
279 disentangle the effects of environmental and agronomic drivers on functional diversity from effects  
280 simply related to the richness of communities. For each plot, we calculated an effect size (ES) that  
281 quantifies the probability for each weed community that the observed CWV is higher or lower than  
282 999 CWV randomly generated by null models (Bernard-Verdier et al., 2012; Kelt et al., 1995) (Eq. 3).

$$283 \quad ES = \text{number}(\text{null} < \text{obs}) / 999 - 0.5 \text{ (Eq. 3)}$$

284 Where  $\text{number}(\text{null} < \text{obs})/999$ , is the proportion of simulated CWV generated by null models  
285 that are lower than the observed CWV for each community on 999 simulations. ES measures the  
286 strength of convergence and divergence (Botta-Dukát, 2018). ES values close to zero indicate that  
287 observed CWV values are not different from random CWV values. In contrast, high and low ES values  
288 quantify respectively strong divergent ( $0 < ES \leq 0.5$ ) and convergent ( $-0.5 \leq ES < 0$ ) functional  
289 structure of weed communities. In order to detect a general pattern of community structure  
290 regardless of the spatio-temporal and agronomic characteristics, we tested if ES was overall different  
291 from 0 using a two-tailed Wilcoxon signed-ranks test (Bernard-Verdier et al., 2012; Jung et al., 2010).  
292 To investigate the impact of the weed management practices gradient on CWV, we used the same  
293 procedure as for CWM. Within each wine-growing region, we tested the significance of correlations  
294 between effect sizes of CWV and the coordinates of the plots on the first two axes of the PCA, using  
295 Spearman's rank correlation. All the statistical analyses were performed with R (3.6.2 version). All  
296 multivariate analyses (RLQ, PCA) were conducted using ade4 package (Chessel et al., 2004).

297

298        **3. Results**

299        *3.1. Covariation of the functional structure of weed communities across management practices*  
300                *and spatio-temporal variables*

301                The first two axes of the RLQ explained 95% of inertia (81 % explained by the first axis and  
302        14% explained by the second axis) (Fig. 1). The co-structure between R and Q was significant (Monte-  
303        Carlo test,  $P < 0.001$ ) demonstrating the global significance of the relationships between species  
304        traits and agro-environmental variables (region, seasonality, year of floristic survey and weed  
305        management practices as specified in Table 1). According to the fourth-corner analysis combined  
306        with the RLQ analysis, all the spatio-temporal and agronomic variables except Rhône region were  
307        correlated to the first axis of the RLQ, which described most of the variability (Fig. A.3a). The first RLQ  
308        axis opposed spring surveys to autumn surveys, earlier surveys to later surveys, chemically weeded  
309        rows and inter-rows to tilled rows and inter-rows, Champagne region to Languedoc region (Fig. 1a,  
310        A.3a).

311                Weed species located in Champagne had high SLA and long flowering duration (e.g. *Stellaria*  
312        *media*) while those located in Languedoc had low SLA and short flowering duration (e.g. *Cirsium*  
313        *arvense*) (Fig. 1, 2). Autumn species had larger stature and later flowering onset (e.g. *Cirsium*  
314        *arvense*) compared to spring species (e.g. *Crepis sancta*). Species identified during the last years of  
315        floristic surveys (e.g. 2011, 2012) had long flowering duration (e.g. *Taraxacum officinale*) (Fig. 1, 2).  
316        Chemical weeding of rows and inter-rows were associated with low stature species, low seed mass  
317        and low lateral spread abilities (e.g. *Cardamine hirsuta*). Species in mowed plots had long flowering  
318        duration (e.g. *Veronica persica*) while species located in tilled inter-rows had short flowering duration  
319        (e.g. *Lolium multiflorum*) (Fig. 1, 2). Species located in tilled rows had high seed mass and high lateral  
320        spread abilities (e.g. *Rubia peregrina*).

321 *3.2. Relative importance of the weed management practices and spatio-temporal variables*  
322 *explaining weed community's functional response*

323 Spatio-temporal and weed management practice variables explained from 13% to 48% of the  
324 total variance of CWM of the different traits (Fig. 3, Supplementary 4). Overall, 'region' explained  
325 most of CWM marginal variance (53%), followed by seasonality (28%) and some weed management  
326 practice variables (19%).

327 The region of floristic surveys explained a large part of variance in maximum height (60%, Fig.  
328 3a1), SLA (99%, Fig. 3b1), flowering onset (59%, Fig. 3e1) and duration of flowering (100%, Fig. 3f1).  
329 Weed communities from Champagne region had high SLA, early flowering onset and long flowering  
330 duration (Fig. 3b2, e2, f2 respectively). The estimate of flowering duration in Rhône was almost null (-  
331 0.02) but the effect was significant showing that duration of flowering was average in that region and  
332 different from Champagne's short duration of flowering and the long duration of flowering in  
333 Languedoc (Fig. 3f2).

334 'Seasonality' was the most frequently selected effect in CWM models. This explained significant  
335 proportions of variance of CWM of maximum height (35%, Fig. 3a1), seed mass (38%, Fig. 3c1),  
336 lateral spread (54%, Fig. 3d1), flowering onset (41%, Fig. 3e1) but low variance of SLA (<1%, Fig. 3b1).  
337 The communities of autumn floristic surveys had high stature (Fig. 3a2), high seed mass (Fig. 3c2),  
338 high lateral spread abilities (Fig. 3d2) late flowering onset (Fig. 3e2) and low SLA (Fig. 3b2).

339 Chemical weeding and mowing explained large proportions of variance in seed mass (29% and  
340 33% respectively, Fig. 3c1) and lateral spread (24% and 22% respectively, Fig. 3d1). Chemically  
341 weeded communities on inter-rows had low stature (Fig. 3a2), low seed mass (Fig. 3c2) and low  
342 lateral spread abilities (Fig. 3d2). Mowed weed communities in inter-rows showed low seed mass  
343 (Fig. 3c2) and low lateral spread tendency (Fig. 3d2). Tillage of rows and inter-rows had no direct  
344 effects on CWM of weed species and in general, the management of the rows did not impact  
345 significantly CWM of weed communities.

346 The plot random effect described significant proportions of total variance (35% of lateral spread  
347 abilities, 20% of seed mass, 13% of flowering duration, 10% of SLA, 9% of maximum height, 8% of  
348 flowering onset). The random effect of the year of the floristic survey was only selected in the  
349 flowering onset CWM model and represented 10% of the total variance of this CWM.

350

351 *3.3. Functional response of weed communities to weed management practices within each region*

352 *3.3.1. Community Weighted Means (CWM) response to weed management practices within*  
353 *each region*

354 In order to disentangle the effect of region from the effects of the other variables, we explored  
355 weed functional responses to weed management practices, seasonality and year of survey within  
356 each region. Fig. A.4 displays the gradients of these variables, excluding the regional effect. The first  
357 two axes represented 54% of total variance. They described mostly weed management practices  
358 gradients (Table A.3). Seasonality and year of survey variables contributed poorly to total inertia of  
359 these axes (7% of explained variance for the first two axes). The first axis explaining 31% of variance  
360 opposed tilled rows and inter-rows (positive coordinates) and chemically weeded rows (negative  
361 coordinates). It represented the soil disturbance gradient from tilled soils with high below-ground  
362 mechanical disturbances to chemically weeded soils with low below-ground mechanical disturbance.  
363 The second axis explaining 23% of variance opposed mostly mowed inter-rows (negative coordinates)  
364 to combinations of tilled and chemical weeded inter-rows (positive coordinates). It represented the  
365 vegetation cover gradient with high vegetation cover in mowed inter-rows and low vegetation cover  
366 in tilled and chemically weeded inter-rows.

367 The significance and the values of the coefficients of correlation between CWM within each  
368 region and the first two axes of the PCA performed on weed management practices, season and year  
369 of survey variables are reported in Table 2. The Fig. A.5, A.6, A.7, A.8, A.9 and A.10 display CWM  
370 variation along these first two PCA axes. The effect of management practice on CWM differed

371 according to the wine-growing regions (for means and standard deviations of CWM per region, see  
372 Table A.5).

373 In Languedoc, significantly higher CWM of seed mass and lateral spread abilities were found  
374 in tilled rows and inter-rows compared to chemically weeded rows (Table 2). Mowing was  
375 significantly associated with lower CWM for SLA and higher CWM for maximum height, seed mass,  
376 lateral spread abilities and flowering onset compared to chemically weeded inter-rows and to  
377 combined tillage and chemical weeding of inter-rows. In Champagne, tillage on rows and inter-rows  
378 was associated with higher lateral spread abilities as in the Languedoc region and higher maximum  
379 height compared to chemically weeded rows (Table 2). In the Rhône region, chemical weeding on  
380 rows was significantly associated with shorter flowering, higher stature and later flowering compared  
381 to tillage of rows and inter-rows (Table 2).

382

383

384 **Table 2** Coefficients of correlation between Community Weighted Means (CWM) and weed  
385 management gradients (two first PCA axes, see Fig. A.4) for each region. P-values were corrected  
386 from multiple comparisons testing using Bonferroni correction. The first PCA axis opposed chemical  
387 weeding of rows (Chem.R, negative coordinates) and tillage of rows and inter-rows (Till.IR, Till.R,  
388 positive coordinates). The second PCA axis opposed mowing of inter-rows (Mow.IR, negative  
389 coordinates) to combination of tillage and chemical weeding of inter-rows (Chem.IR + Till.IR, positive  
390 coordinates). \*  $p < 0.05$  ; \*\*  $p < 0.01$  ; \*\*\*  $p < 0.001$  ; no asterisks, non-significant ( $p > 0.05$ ). SLA,  
391 Specific Leaf Area ; PCA, Principal Component Analysis.

CWM	Languedoc		Champagne		Rhône	
	1 <sup>st</sup> PCA axis	2 <sup>nd</sup> PCA axis	1 <sup>st</sup> PCA axis	2 <sup>nd</sup> PCA axis	1 <sup>st</sup> PCA axis	2 <sup>nd</sup> PCA axis
	Chem.R →	Mow.IR →	Chem.R →	Mow.IR →	Chem.R →	Mow.IR →
	Till.IR, Till.R	Chem.IR + Till.IR	Till.IR, Till.R	Chem.IR + Till.IR	Till.IR, Till.R	Chem.IR + Till.IR
<b>Maximum height</b>	0.06	-0.29 **	0.41*	-0.2	-0.25*	-0.05
<b>SLA</b>	-0.12	0.31**	-0.17	0.26	0.09	0.06
<b>Seed mass</b>	0.26*	-0.4***	0.001	0.04	-0.01	-0.16
<b>Lateral spread</b>	0.53***	-0.32**	0.36*	-0.21	-0.09	-0.21
<b>Flowering onset</b>	0.01	-0.24*	0.07	-0.34	-0.33***	0.01
<b>Flowering duration</b>	0.05	0.16	-0.01	0.23	0.24*	-0.22

392

393 3.3.2. *Community Weighted Variance (CWV) response to weed management practices within*  
394 *each region*

395 Half of the CWV were significantly different from random expectations of null models (Fig. A.11,  
396 A.12, A.13, A.14, A.15, A.16). More precisely, most of the CWV were lower than expectations  
397 demonstrating a convergent distribution and a restricted variance of trait values within weed  
398 communities (for means and standard deviations of CWV per region, see Table A.5).

399 In the Champagne region, lateral spread CWV were convergent while flowering onset and  
400 duration had divergent distributions (Fig. A.14). In Languedoc, SLA, lateral spread, flowering onset  
401 and seed mass had convergent distributions (Fig. A.11, A.12). In the Rhône, seed mass and lateral  
402 spread were convergent (Fig. A.15, A.16). Four effect sizes out of 36 were significantly correlated to  
403 one axis of the PCA (Table 3) demonstrating different functional responses to the filtering effect of  
404 weed management practices. In Languedoc, the effect size of lateral spread CWV was positively  
405 correlated with the first axis, showing that species located in chemically weeded row communities  
406 had similar lateral spread abilities while species within tilled communities had dissimilar lateral  
407 spreading strategies (Table 3). In Champagne, the effect sizes of SLA CWV, flowering onset CWV and  
408 flowering duration CWV were positively correlated with the second axis (Table 3) demonstrating that  
409 combination of chemical weeding and tillage of inter-rows was associated with high variations of SLA,  
410 flowering onset and duration within weed communities.

411

412

413

414

415 **Table 3** Coefficients of correlation between effect sizes of Community Weighted Variance (CWV) and  
 416 weed management gradients (two first PCA axes, see Fig. A.4) for each region. P-values were  
 417 corrected from multiple comparisons testing using the Bonferroni correction. The first PCA axis  
 418 opposed chemical weeding of rows (Chem.R, negative coordinates) and tillage of rows and inter-rows  
 419 (Till.IR, Till.R, positive coordinates). The second PCA axis opposed mowing of inter-rows (Mow.IR,  
 420 negative coordinates) to combination of tillage and chemical weeding of inter-rows (Chem.IR + Till.IR,  
 421 positive coordinates. \*  $p < 0.05$  ; \*\*  $p < 0.01$  ; \*\*\*  $p < 0.001$  ; no asterisks, non-significant ( $p > 0.05$ ).  
 422 SLA, Specific Leaf Area ; PCA, Principal Component Analysis.

Effect sizes of CWV	Languedoc		Champagne		Rhône	
	1 <sup>st</sup> PCA axis	2 <sup>nd</sup> PCA axis	1 <sup>st</sup> PCA axis	2 <sup>nd</sup> PCA axis	1 <sup>st</sup> PCA axis	2 <sup>nd</sup> PCA axis
	Chem.R →	Mow.IR →	Chem.R →	Mow.IR →	Chem.R →	Mow.IR →
	Till.IR, Till.R	Chem.IR + Till.IR	Till.IR, Till.R	Chem.IR + Till.IR	Till.IR, Till.R	Chem.IR + Till.IR
<b>Maximum height</b>	0.02	-0.01	0.03	0.08	-0.1	0.07
<b>SLA</b>	0.09	0.11	-0.26	0.4 *	-0.08	0.09
<b>Seed mass</b>	-0.06	-0.06	-0.07	0.02	-0.01	0.03
<b>Lateral spread</b>	0.45***	-0.19	0.17	0.08	-0.11	-0.03
<b>Flowering onset</b>	0.1	0.01	-0.12	0.38*	-0.19	0.03
<b>Flowering duration</b>	0.03	-0.11	-0.08	0.41*	-0.07	-0.09

#### 423 **4. Discussion**

424 Our study highlighted that the functional structure of vineyard weed communities responded  
425 strongly to agro-environmental factors with high variation of trait values across regions, seasons and  
426 management practices. In addition to CMW, we explored the filtering effect of weed management  
427 practices through the analysis of CWV. To our knowledge, this is the first study to investigate weed  
428 management practice effects on the functional structure of weeds through null modelling of  
429 community weighted variances in vineyards. Null modelling has allowed us to test if CWV were  
430 restricted or increased by weed management, independently of the effect of weed management  
431 community richness shown in Fried et al. (2019). This method, widely applied on natural ecosystems,  
432 are still sparsely applied in agricultural contexts, especially in vineyards. We hypothesized that  
433 chemical weeding and tillage would act as stronger filters compared to mowing, and we expected  
434 that communities under chemical weeding and tillage would have convergent values of trait values  
435 with low variation. Half of the CWV had a significantly different distribution than random distribution  
436 and most of the CWV had convergent distribution. This demonstrates that regions, seasonality, year  
437 of survey and weed management practices impacted traits variabilities, mostly restricting the  
438 possible range of values of average trait values of weed communities. Moreover, it is likely that the  
439 assembly of species into communities in vineyards, which remains a disturbed environment, is also  
440 the result of neutral processes related to spatial colonization–extinction dynamics as shown in  
441 annual crop fields (Perronne et al., 2015). However, the separated analysis by region limited our  
442 statistical power and the results of our analysis should be interpreted with care.

#### 443 *4.1. Region and seasonality are the main drivers of the variation of community weighted means*

444 Region was the main driver of traits related to resource acquisition (maximum height, SLA)  
445 and phenology (flowering onset and flowering duration) while season explained most of the variation  
446 of the regenerative traits (seed mass and lateral spread). According to our hypotheses, region and  
447 seasonality affected the functional structure of a community more than management practices.

448 Regional effects encompass different environmental effects, mostly differences in climate  
449 and soil characteristics. In the literature, the pedoclimatic effects on weed functional structures  
450 depend on the scale of studies. For instance, within the same wine-growing region in South Africa,  
451 MacLaren et al. (2019) found no significant effects of soil characteristics and climate on communities  
452 weighed means. In contrast, in several European countries, Hall et al. (2020) showed that the country  
453 effect was the main factor affecting traits. Within the same country, our study showed that divergent  
454 edaphoclimatic conditions between wine-growing regions had major impacts on traits.

455 More precisely, regional effects encompass the differences in climate between Languedoc,  
456 Rhône and Champagne and had contrasted effects on CWM of communities in Champagne (drier and  
457 colder climate) and communities in Languedoc (hotter climate). In Champagne, weed communities  
458 presented higher SLA values compared to Languedoc. This result is consistent with other studies at  
459 the individual scale showing that SLA was negatively correlated with mean annual temperature  
460 (Garnier et al., 2019; Moles et al., 2014; Wright et al., 2005, 2004) and positively with precipitation  
461 (Garnier et al., 2019). Indeed, plants with low SLA invest in the leaf structure to adapt to dry  
462 conditions (e.g. thick leaf blade to limit evapotranspiration; small and thick-walled cells) (Wright et  
463 al., 2005). On average, flowering onset was later in Languedoc compared to Champagne where most  
464 of the weed species flowered in spring. This could be explained by the bi-modality of the flowering  
465 period (Thompson, 2007) in Languedoc region. Two favourable periods are possible to flower: (i)  
466 early spring before the summer drought and (ii) early autumn after the first rainfalls (Kummerow,  
467 1983; Thuiller et al., 2004). Due to higher temperatures in autumn, more thermophile species can  
468 flower and produce seeds during this season in the Mediterranean region (e.g. *Dittrichia viscosa*,  
469 *Heliotropium europaeum*, *Sorghum halepense*, *Tribulus terrestris*). Thus, on average, this could  
470 explain the later flowering communities of the Languedoc.

471 Moreover, soil characteristics are also encompassed in the regional effect. In our dataset,  
472 vineyard plots located in the Rhône had more fertile soils (high soil organic content) compared to

473 vineyard plots of the other regions (Table A.1). Fertile soils are usually associated with weed  
474 communities with high photosynthetic assimilation rates, high SLA, high height at maturity and low  
475 seed mass (Garnier et al., 2016). However, only flowering duration was significantly different in the  
476 Rhône region while the other traits were not significantly different from the other regions.

477 In addition to different soils and climates, the regional effect might also include some  
478 management practices and technical characteristics that vary according to wine-growing regions: the  
479 amount of applied nutrients through fertilization and amendments, the density of vine stocks (higher  
480 density in Rhône than in Languedoc) or grape variety (Gamay and Syrah in Rhône, Cabernet  
481 Sauvignon and Grenache in Languedoc).

482 In addition to the regional effect, seasonality was the most frequently selected effect in the  
483 reduced models explaining CWM. Interestingly, Fried et al. (2019) found that season was the main  
484 driver of the taxonomic composition of weed community in vineyards. Surveyed autumn weed  
485 communities had higher maximum height, lower SLA, heavier seeds, high lateral spread abilities and  
486 later flowering onset than at other survey dates. This can be explained by the changes in  
487 environmental conditions throughout the growing seasons (Wolkovich and Cleland, 2014): in late  
488 winter, disturbance is high in the vineyards (first weeding passages) with non-limiting weather  
489 conditions (regular rainfall, increasing temperatures) selecting early-flowering species with rapid-  
490 growth and acquisitive strategies (high SLA, low stature, low seed mass) while in summer, disturbing  
491 events such as weeding are less frequent and weather conditions can lead to water stress or heat  
492 stress. Consequently, more stress-tolerant communities might develop during the summer drought  
493 with slow-growth and more conservative strategies (low SLA, high stature, high weight seeds).

#### 494 *4.2. Soil disturbance gradient: soil tillage versus chemical weeding*

495 The first PCA axis of weed management practices and temporal variables (seasonality and year of  
496 floristic surveys) represented the soil disturbance gradient from tilled soils with high below-ground  
497 mechanical disturbances to chemically weeded soils with no below-ground mechanical disturbance.

498 According to our hypotheses, chemical weeding on rows was associated to most of the trait  
499 values characterizing ruderal communities (low seed mass, short stature in Champagne, low lateral  
500 spread, early flowering). However, SLA was not significantly higher in chemically weeded  
501 communities than in tilled communities. Moreover, communities from chemically weeded plots in  
502 the Rhône had high stature which is not an expected trait value of ruderal strategy communities. In  
503 contrast to our hypotheses, tillage seemed to favour weed communities with high seed mass which is  
504 inconsistent with the trait values of ruderal communities. Different mechanisms could explain these  
505 contrasted trait values between these two types of weed management. One possible explanation  
506 relates to the changes of seed positions in the soil which depend on the different weed management  
507 practices. Indeed, chemical weeding associated to no-till practices favours superficial position of  
508 seeds, whereas tillage commonly buries the seeds deeper into the soil. Unburied seeds are more  
509 likely to be eliminated by predation or impaired by desiccation. Therefore, under chemical weeding,  
510 producing a large number of low weight seeds might increase the probability that some of them  
511 survive. On the contrary, large and high weight seeds have a greater probability to germinate when  
512 they are buried (Benvenuti et al., 2001; Hernández Plaza et al., 2015; MacLaren et al., 2019). Under  
513 superficial tillage practices (as here in vineyards), large-seeded community have been found in  
514 several studies in line with our results (Armengot et al., 2016; Hernández Plaza et al., 2015a;  
515 MacLaren et al., 2019).

516 Moreover, tillage is a soil disturbance (Gaba et al., 2014) that selects annual species with a  
517 seedbank but also species that can regenerate from fragments such as rhizome species (e.g.  
518 *Convolvulus arvensis* or *Cirsium arvense*) with high lateral spread abilities as highlighted here in two  
519 regions (Languedoc and Champagne). Tillage was also associated to high variability of lateral spread  
520 values within communities. Thus, tillage seemed to favour two different strategies (Fig. A.17): the  
521 main strategy would be the ability to re-sprout using vegetative multiplication after tillage (high

522 lateral spread communities). The second minor strategy would be similar to chemically weeded  
523 communities: short life cycle communities with low lateral spread abilities.

#### 524 4.3. Vegetation cover gradient: mowing versus tillage and chemical weeding

525 In contrast to Fried et al. (2019) findings on taxonomic composition, mowing has here been  
526 found to be a major driver of functional structure of weed communities in the Languedoc. Vegetation  
527 abundance (i.e. the sum of the abundance of each species per plot) in mowed inter-rows were much  
528 higher than in chemically weeded and/or tilled inter-rows (Fried et al., 2019). The weeding practice  
529 gradient from chemical weeding and tillage to mowing can therefore be interpreted as vegetation  
530 cover gradient from bare soils (tillage and chemical weeding) to high vegetation cover (mowing) (Hall  
531 et al., 2020).

532 Interestingly, the combination of chemical weeding and tillage on inter-rows seemed to favour  
533 ruderal communities in Languedoc (short-stature, high SLA, low seed mass, low lateral spread  
534 abilities and early flowering) and were opposed to more competitive communities on mowed inter-  
535 rows. In Languedoc, mowing was associated to rosette plants like *Lactuca serriola*, *Crepis vesicaria*  
536 and *Torilis arvensis* which can reach 67 cm to more than 1.5 m height. The sequential application of a  
537 belowground (soil tillage) and an aboveground (herbicides) action thus act as a severe disturbance  
538 for vegetation. It may select species with a rapid life-cycle that flower early to escape disturbances,  
539 have a high acquisitive strategy (high SLA), a low investment in vegetative parts (low maximum  
540 height) and a massive production of low weight seeds to increase the probability that some survive  
541 (Grime, 1977; White and Pickett, 1985).

542 In contrast, mowing was associated with late flowering species communities compared to  
543 chemical weeding and tillage in the Rhône. This could be explained by the timing of weed  
544 management practices. Indeed, mowing is generally carried out later than the other weed  
545 management practices: early July on average for mowing, May for chemical weeding and for tillage in  
546 the Rhône (Table 1).

547 We expected that highly disturbed rows and inter-rows such as tilled and chemically weeded  
548 rows would lead to a reduction in the range of trait values (convergent distributions) compared to  
549 mowed rows and inter-rows (divergent distributions) (Kazakou et al., 2016). In contrast with our  
550 expectations, combined tillage and chemical weeding were associated with high CWV of SLA,  
551 flowering onset and duration while mowing was associated to more convergent distributions in  
552 Champagne. A possible explanation is that chemical weeding and tillage select contrasted strategies  
553 (e.g., geophytes with high lateral spread and therophytes) leading to higher variability of trait values  
554 when combining them (Fig. A.17).

#### 555 *4.4. Limits and perspectives*

556 Trait-based approaches are promising a better understanding of the functional shaping of weed  
557 communities by weed management practices. In our study, the lateral spread ability of communities  
558 was certainly one of the major response traits. Other traits, absent from the databases, such as the  
559 presence of epicuticular wax on leaves or seed coat thickness, might be response traits of interest to  
560 include in such studies where herbicide pressure is an important filter (Gaba et al., 2014). However,  
561 these specific traits are still lacking in trait databases.

562 The use of pluriannual database of floristic surveys such as the Biovigilance network is an asset  
563 when considering the variations between years due to changing climatic conditions for instance.  
564 Moreover, the wide geographic range of our study allowed us to analyse the different weed  
565 management practices within regions and different pedoclimatic contexts. At this large-scale of  
566 analysis, one drawback is that we had to fragment the dataset to control the weed management and  
567 pedoclimatic contexts interactions therefore limiting the statistical power of our dataset. Another  
568 disadvantage is that it is difficult to use measured trait values. We therefore used database trait  
569 values based on the assumption that the ranking of species according to their trait values is stable  
570 across environments ('stable species hierarchy', Kazakou et al., 2014) as interspecific variability is

571 higher than intraspecific variability. A recent study has shown that this hypothesis was largely valid in  
572 vineyards (Garcia et al., 2020).

573 Another point is that our results demonstrated that weed management practices explained 19 %  
574 of variations of functional structure of weed communities. More detailed variables describing  
575 management practices could help better understand plant responses, for instance considering  
576 disturbance types such as frequency (e.g. number of applied management practices within a year)  
577 and intensity (e.g. herbicide dose or depth of tillage) (Gaba et al., 2014). For instance, the timing of  
578 weed management practices has been shown to be relevant to explain functional responses of weed  
579 communities (Cordeau et al., 2017; Smith, 2006).

580

581        **5. Conclusion**

582        In this paper, we have shown that the changes in composition of weed species caused by  
583 environmental and anthropogenic filters in vineyards also lead to changes in functional structure.  
584 Region, seasonality and weed management practices act as strong drivers of functional structure of  
585 weed communities. Weed management practices impacted both the mean trait values and their  
586 variance within weed communities. Chemically weeded communities shared most of the trait values  
587 of ruderal strategies (low seed mass, small-stature, early flowering, short lateral spread abilities).  
588 Weed communities from mowed plots were associated with more competitive strategies (higher  
589 seed mass, higher stature and lower SLA). Tillage favoured communities with high seed mass which  
590 increases the viability of buried seeds and high lateral spread abilities values related to the capacity  
591 to resprout after tillage. Nowadays, mowing and tillage are more and more applied in vineyards  
592 (Simonovici, 2019). Our results showed that this soil management shift might favour more  
593 competitive communities. These weed communities might also have different impacts on agrosystem  
594 processes such as nitrogen cycling or carbon sequestration through changes in soil microbial  
595 composition (Karimi et al., 2020). Understanding the effect of weed communities on such processes  
596 is needed to adapt weed management practices and better drive ecosystem services and disservices  
597 (Damour et al., 2018; Garcia et al., 2018; Petit et al., 2018; Storkey et al., 2015).

598

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615

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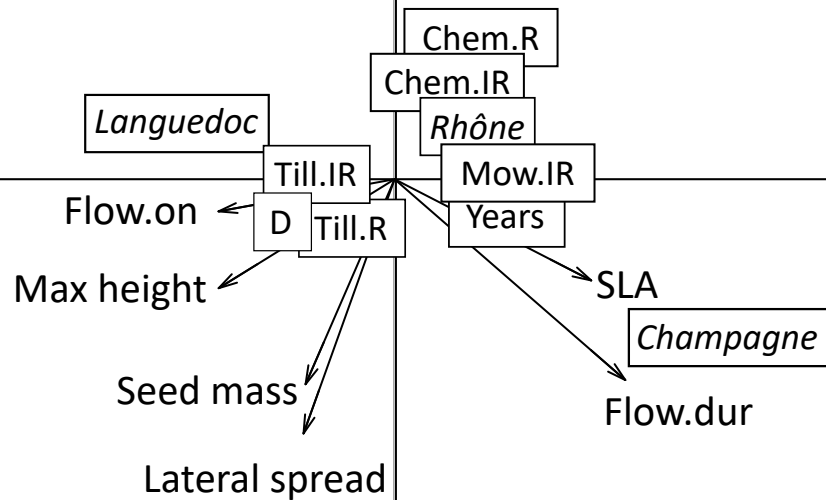
**Fig. 1** RLQ results carried out on three matrices: R (270 floristic surveys x 10 agro-environmental variables), L (270 floristic surveys x 227 weed species) and Q (227 weed species x 6 traits). The agro-environmental variables and weed traits (a) and weed species (b) are displayed along the first two RLQ axes. Abbreviations used in (a) are: D, seasonality (number of days since the beginning of the year of floristic survey) ; Year, year of floristic survey ; Flow.on, flowering onset ; Max height, maximum height, Flow.dur, flowering duration ; SLA, specific leaf area. The identities of the twenty most frequent species across all floristic surveys are specified in (b). CARHI, *Cardamine hirsuta* ; CIRAR, *Cirsium arvense* ; CONAR, *Convolvulus arvensis* ; CHEAL, *Chenopodium album* ; CVPSA, *Crepis sancta* ; DIPER, *Diploaxis eruroides* ; ERICA, *Erigeron canadensis* ; EROCI, *Erodium cicutarium* ; GERRT, *Geranium rotundifolium* ; LACSE, *Lactuca serriola* ; LOLMU, *Lolium multiflorum* ; LOLPE, *Lolium perenne* ; PLALA, *Plantago lanceolata* ; POAAN, *Poa annua* ; POLAV, *Polygonum aviculare* ; SENVU, *Senecio vulgaris* ; SONOL, *Sonchus oleraceus* ; STEME, *Stellaria media* ; TAROF, *Taraxacum officinale* ; VERPE, *Veronica persica*.

**Fig. 2** Significant associations of the fourth-corner tests between the agro-environmental variables and the species traits. Red boxes show positive correlations, blue boxes negative correlations and grey boxes non-significant relations. Years, year of floristic survey ; SLA, specific leaf area. Significance of associations are referred as following: \*  $p < 0.05$  ; \*\*  $p < 0.01$ .  $p$  are adjusted p-values.

**Fig. 3** Effects of region, seasonality and management practice variables on CWM of weed communities: (a) Maximum height CWM, (b) Specific Leaf Area (SLA) CWM, (c) logarithmised seed mass CWM, (d) logarithmised lateral spread CWM, (e) flowering onset CWM and (f) logarithmised flowering duration CWM. For each CWM, Figures (a1), (b1), (c1), (d1), (e1) and (f1) display the explained variance for each fixed effect selected in CWM models and the marginal variance (i.e. the total variance explained by all the fixed effect ( $R_{margin}$ )). Figures (a2), (b2), (c2), (d2), (e2) and (f2) report the standardized estimates of fixed effects selected in CWM models. Blue, green and red bars and texts represent respectively region, seasonality and weed management practices effects. Significance of estimated are referred as following: \*  $p < 0.05$  ; \*\*  $p < 0.01$  ; \*\*\*  $p < 0.001$ . CWM, Community Weighted Means.

(a)

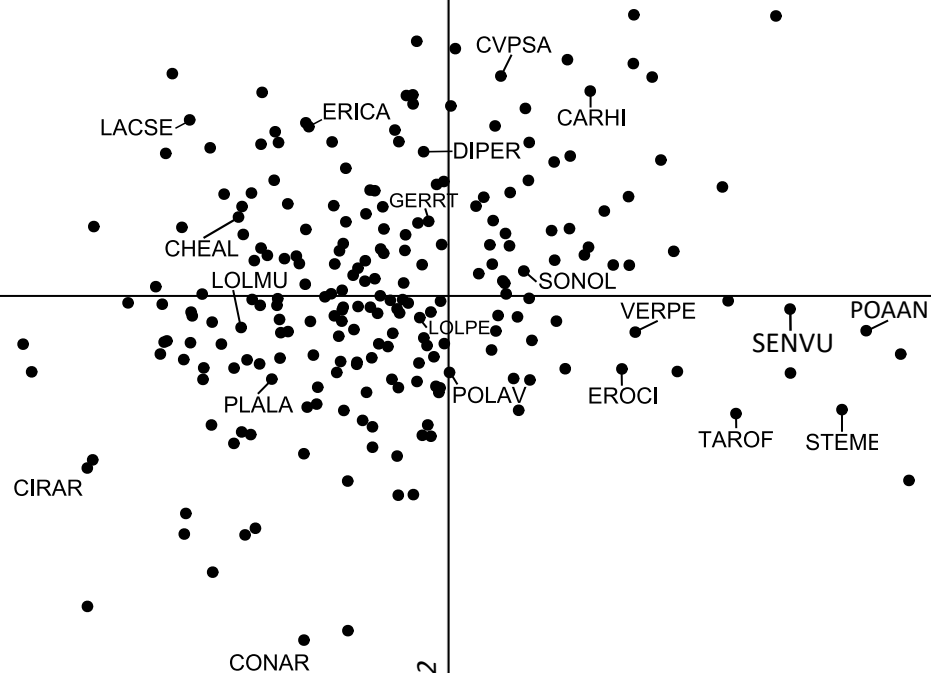
RLQ Axis 2 (14%)



RLQ Axis 1 (81%)

(b)

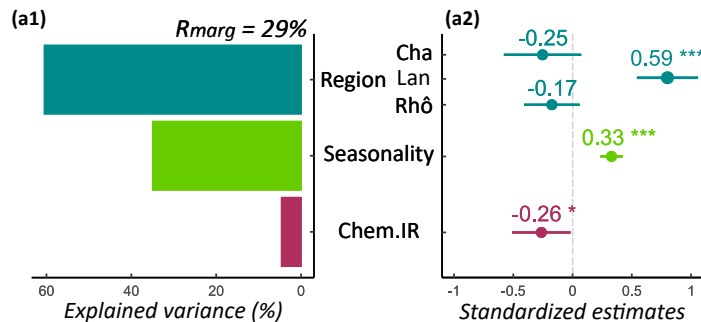
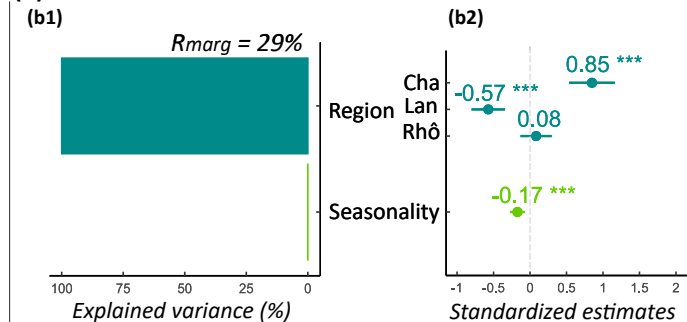
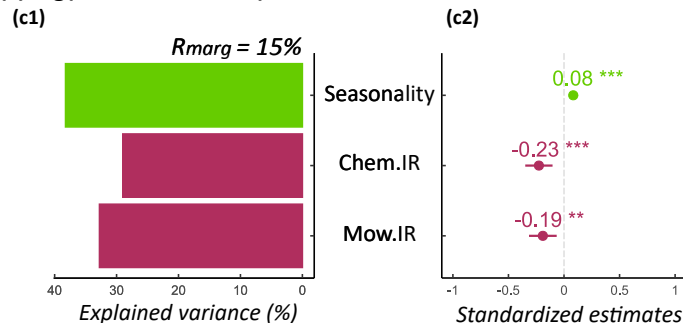
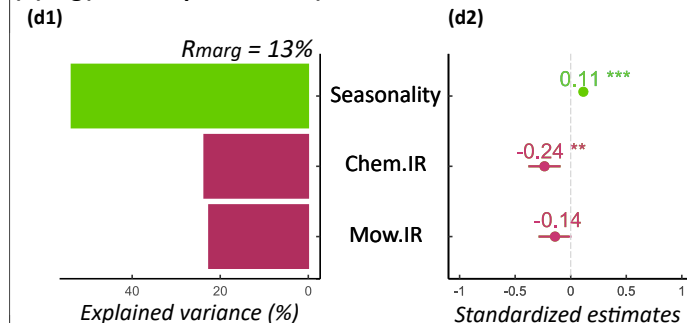
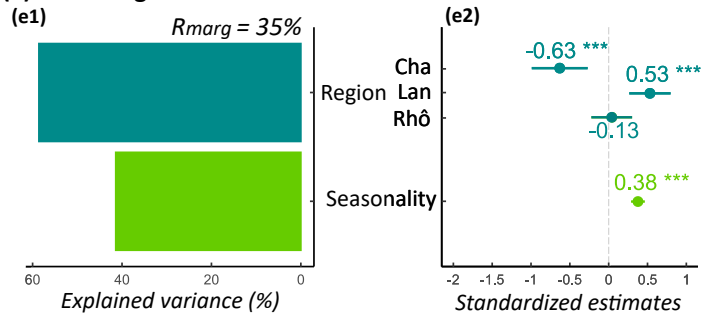
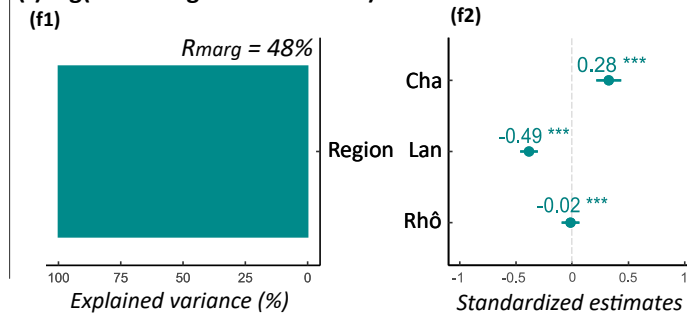
RLQ Axis 2 (14%)



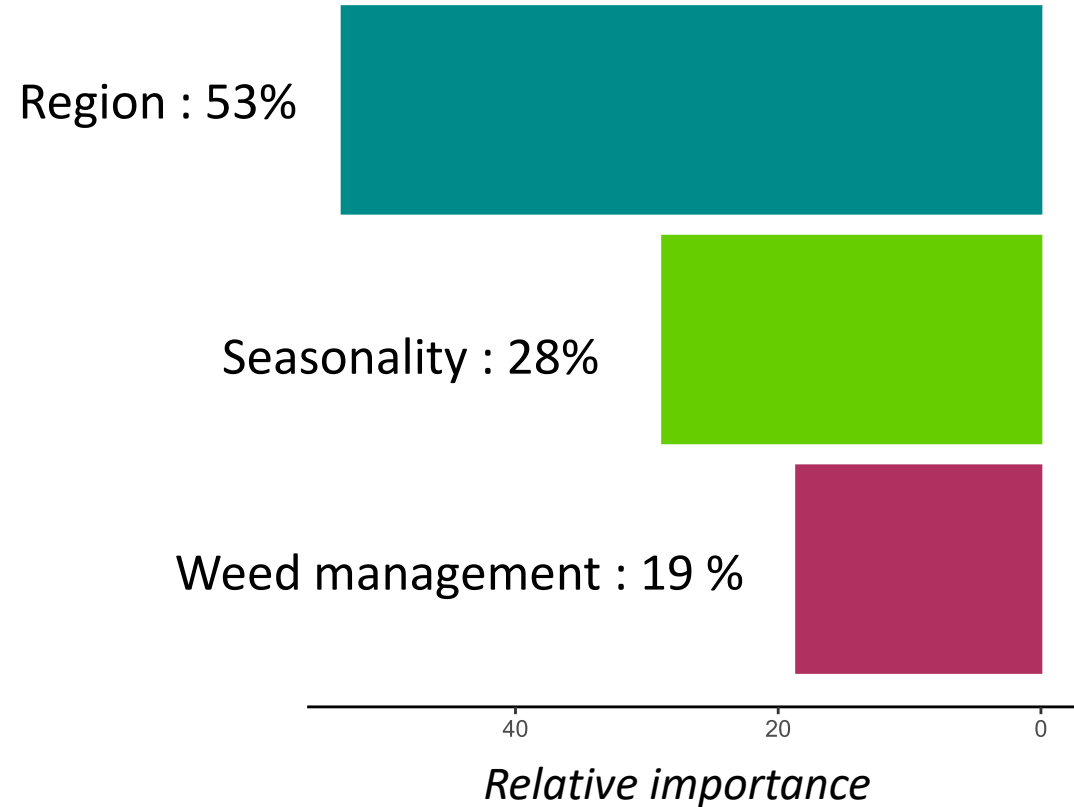
RLQ Axis 1 (81%)

*Region, temporal variables and  
weed management practices*

	Champagne	Languedoc	Rhône	Saisonnality	Years	Chem.IR	Mow.IR	Till.IR	Chem.R	Till.R
SLA	*	*								
Maximum height				*		*			*	
Seed mass						*			**	**
Flowering onset				**						
Flowering duration	**	**			*		**	*		
Lateral spread						*			**	*

**(a) Maximum height CWM****(b) SLA CWM****(c) log(Seed mass CWM)****(d) log(Lateral spread CWM)****(e) Flowering onset CWM****(f) log(Flowering duration CWM)**

# 1 Factors impacting functional structure of weed communities in vineyards



# 2 Community response to weed management

*E.g. in Languedoc :*

