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# 1 **Better grazed than weeded: promising weeds digestibility in** 2 **perennial Mediterranean agroecosystems**

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## 13 **Abstract**

14 Biodiversity presence in perennial agroecosystems increases the provision of ecosystem  
15 services (ES). Weeds are known to deliver supporting or regulating services but their potential  
16 to provide provisioning services is less studied. Our study aims to quantify the potential of  
17 weeds to provide forage resources for livestock in two Mediterranean perennial  
18 agroecosystems: olive groves and vineyards., We used a trait-based approach to investigate the  
19 abiotic determinants of weed quality and quantity variations at both the species and community  
20 levels. We surveyed spontaneous vegetation in 16 vineyards and 16 olive groves in the French  
21 Mediterranean region with contrasting pedoclimatic conditions and agricultural practices,  
22 during spring and fall 2021. Four leaf traits were measured: Leaf Dry Matter Content (LDMC),  
23 Specific Leaf Area (SLA), Leaf Nitrogen Content (LNC) and leaf C/N ratio (Leaf C/N) and  
24 four forage potential indicators: dry matter digestibility (DMD), crude proteins (CP), fiber  
25 content (NDF) and aboveground biomass (AB). We found that DMD of perennial  
26 agroecosystems weeds is high ( $689 \pm 116 \text{ g kg}^{-1}$ ), and can be compared to those of forage  
27 species. Using linear mixed models and path analysis, we found that, at the community scale,  
28 LDMC is negatively linked to weed forage quality and that disturbing agricultural practices like

29 tillage, increase weed forage quality. However, at the scale of our study, we found no effect of  
30 agricultural practices or pedoclimate on weeds leaf traits or on weeds quantity. Our results  
31 revealed the potential of considering weeds as qualitative forage resources for livestock. The  
32 long-term aim is to promote the integration of livestock in perennial cropping systems in order  
33 to reduce the use of herbicides and/or tillage and to diversify agricultural production.

34 Keywords : forage resources ; leaf dry matter content ; soil management ; vineyards ; olive  
35 groves

## 36 **1. Introduction**

37 Weeds were seen as a burden for a long time, but nowadays their potential to provide supporting  
38 or regulating ecosystem services (ES) is increasingly recognized (Zhang et al., 2007; Milanovic  
39 et al., 2021). This potential is particularly relevant in perennial woody agroecosystems where  
40 the spontaneous vegetation provides resources and habitats for biodiversity (Simon et al., 2010).  
41 In these perennial agroecosystems, temporal soil management on both rows and inter-rows  
42 allows weeds presence at specific times without disturbing the agricultural production (Garcia  
43 et al., 2019). Vineyards and olive groves can potentially host diverse weeds communities to  
44 provide ES (Demestihis et al., 2017; Winter et al., 2018; Carpio et al., 2019; Paiola et al., 2020).  
45 Both crops are traditional and patrimonial agroecosystems in the Mediterranean region,  
46 representing almost 300 000 ha of vineyards and slightly more than 17 700 ha of olive groves  
47 in the cultivated areas in Mediterranean France (Agreste, 2021). Under the Mediterranean  
48 climate, it is crucial to manage weeds to limit competition for water during dry periods and  
49 preserve crop yields. During recent decades, inter-row weeds have been increasingly managed  
50 through tillage or mowing while herbicide application strongly decreases. However, these  
51 agricultural practices have an important impact on biodiversity and affect its ability to provide  
52 ES (Dale and Polasky, 2007; Syswerda and Robertson, 2014), partly because they modify the  
53 composition and structure of weed communities (Fried et al., 2012). Weeds are often associated  
54 with supporting or regulating ES, but in perennial agroecosystems, they can also be used for  
55 provisioning services; livestock fodder, for example. Moreover, sheep grazing in the inter-rows  
56 can be an alternative to herbicide, mowing (Niles et al., 2018), or tillage without affecting the  
57 yield (Lazcano et al., 2022).

58 Weed biomass quality and quantity define forage potential. Their nutritive value and  
59 palatability has rarely been evaluated in perennial woody agroecosystems and only at the  
60 species level (Marten and Andersen, 1975; Marten et al., 1987). Dry matter digestibility (DMD)  
61 is a key property to evaluate plant quality to feed ruminants because it estimates animal  
62 digestion (Bruinenberg et al., 2002). It is positively linked to the crude proteins (CP), the total  
63 amount of protein present and negatively to the fiber content (NDF) which is the total amount  
64 of fiber present. Dry matter digestibility is known to be related to different leaf traits. Studies  
65 about the relationships between traits, environment, and digestibility usually focused on  
66 spontaneous vegetation of the pastures or the hays (Abaye et al., 2009; Bunton et al., 2019), but  
67 never on weeds. The most documented relationship is the negative link between DMD, and/or  
68 its components (fiber content, crude proteins), and leaf dry matter content (LDMC). The  
69 dominance hypothesis (Grime, 1998), based on the idea that dominant species have a major  
70 impact on processes compared to other species, appears to apply in explaining the digestibility  
71 of the biomass of multi-species communities. This link between LDMC and forage quality was  
72 found both at the species (Khaled., 2006; Pontes et al., 2007; Bumb et al., 2016; Tasset et al.,  
73 2019) and community level (Andueza et al., 2010 ; Gardarin et al., 2014; Tasset et al., 2019).  
74 DMD is positively linked to leaf nitrogen content (LNC) (Pontes et al., 2007; Bumb et al., 2016)  
75 and specific leaf area (SLA) (Khaled., 2006; Pontes et al., 2007; Tasset et al., 2019). Leaf traits  
76 like LDMC or SLA are also significant determinants of biomass productivity of the vegetation  
77 (Pontes et al., 2007; Ansquer et al., 2009; Chollet et al., 2014).

78 Weeds represent a peculiar pool of species (Mahaut et al., 2020) that are favored in  
79 disturbed and fertilized environments, which are important ecological filters characterizing  
80 arable fields (Bourgeois et al., 2019). To cope with those filters, especially with high levels of  
81 disturbance in intensively-managed agroecosystems, weeds develop ruderal strategies (Grime  
82 et al., 1974) that are notably characterized by a fast life cycle (Wright et al., 2004). This strategy  
83 can be summarized by traits from the Leaf-Height-Seed (LHS) scheme. For instance, high SLA  
84 values suggest high biomass production, with fast growth, and early reproduction but smaller  
85 dispersing seeds (Westoby, 1998). Weeds were recently found to exhibit a homogeneous trait  
86 syndrome characterized by these ruderal strategies, especially with high SLA values (Bourgeois  
87 et al., 2019). This weed-trait syndrome identified by acquisitive and productive strategies could  
88 have an impact on forage quality because SLA is positively related to dry matter digestibility  
89 (Khaled, 2006; Pontes et al., 2007; Tasset et al., 2019) and productivity: the main determinants  
90 of forage potential of the vegetation. Similarly, SLA is strongly linked to LDMC and LNC,

91 which covariate with DMD (Khaled, 2006; Pontes et al., 2007; Andueza et al., 2010; Gardarin  
92 et al., 2014; Bumb et al., 2016; Tasset et al., 2019). These results suggest that weeds represent  
93 a promising potential to provide qualitative grazing resources according to the intensity of soil  
94 management.

95 Yet, disturbing agricultural practices like mowing, and fertilization are known to  
96 increase the forage quality of plants (Duru et al., 1997; Gardarin et al., 2014; Bumb et al., 2016)  
97 and traits directly linked to forage quality in grasslands (Garnier et al., 2016). These  
98 relationships need to be investigated in perennial agroecosystems, where agricultural practices  
99 often represent types of disturbance (like tillage or frequent mowing) that differ from those  
100 usually found in grasslands. By cutting aboveground biomass, mowing keeps plants at the  
101 vegetative stage, where they are the most digestible (Pontes et al., 2007; Gardarin et al., 2014).  
102 Soil tillage is supposed to represent a higher disturbance for weeds than mowing (Gaba et al.,  
103 2014; Kazakou et al., 2016) because it destroys both above and belowground biomass. Tillage  
104 is known to select species with ruderal strategy (low LDMC and high LNC and SLA, according  
105 to Kazakou et al., 2016) and may therefore also increase forage quality (Gaba et al., 2014).  
106 However, the direct effect of tillage on digestibility has not been investigated yet. Interestingly,  
107 olive groves and vineyards are not managed similarly: in France, vineyard inter-rows are  
108 frequently tilled, especially in Mediterranean region (Fernandez-Mena et al., 2021), whereas  
109 olive groves are usually mown. Consequently, plant species composition and diversity differ  
110 between these agroecosystems, with usually lower taxonomic and functional diversity in  
111 vineyards than in olive groves. In vineyards, there are usually more generalist species associated  
112 with ruderal characteristics and disturbed environments (Cohen et al., 2015). These  
113 disturbances can modify weed leaf traits and positively influence their digestibility.

114 Lastly, pedoclimatic conditions and season are also known to have an impact on both  
115 leaf traits, quality and quantity of forage resources. Indeed, the digestibility of grassland species  
116 is known to be higher in wetter conditions than in dryer ones (Gardarin et al., 2014) and higher  
117 early in the season (Bumb et al., 2016). The biomass of grassland species decreases when water  
118 soil content decreases (Chollet et al., 2014), but these relationships remain unknown for weed  
119 species. Leaf traits related to digestibility are also affected by climate (Garnier et al., 2019), and  
120 soil conditions (Jager et al., 2015). Based on these findings, we can hypothesize that  
121 pedoclimatic conditions and the season will modify the forage potential of weeds in perennial  
122 agroecosystems.

123 Our study aims at quantifying the potential of weeds to provide forage resources in  
124 perennial agroecosystems across seasons under different soil management practices and  
125 pedoclimatic conditions. Using a trait-based approach, we investigated the determinants of  
126 weed quality and quantity variations in olive groves and vineyards at both the species and  
127 community levels. We hypothesized that (1) forage quality would be high (high dry matter  
128 digestibility and crude proteins and low fiber content) and related to leaf traits (high SLA and  
129 LNC, low LDMC) ; (2) forage quality and associated traits would vary both between and within  
130 agroecosystems. Due to different agricultural practices between agroecosystems, we expected  
131 higher forage quality but lower biomass production in vineyards than in olive groves.  
132 Specifically, we expected that disturbing practices like tillage would promote more digestible  
133 species with higher LNC and SLA and lower LDMC compared to mowing; (3) forage quality,  
134 associated traits, and biomass production would be all affected by pedoclimatic conditions. We  
135 expected that low rainfall and low soil fertility would decrease forage quality by selecting less  
136 digestible species with lower SLA and LNC and higher LDMC. To test these hypotheses, we  
137 assessed weed composition and diversity and evaluated their forage quality and biomass  
138 production in 16 vineyards and 16 olive groves with contrasting agricultural practices along a  
139 pedoclimatic gradient in the French Mediterranean region during the spring and fall of 2021.  
140 We measured leaf traits related to forage quality and digestibility and evaluated the forage  
141 potential of the monitored communities both at the species and the community levels.

## 142 **2. Material and methods**

### 143 **2.1. Study sites**

144 We selected 32 fields corresponding to two agroecosystems (16 olive groves and 16 vineyards)  
145 located in the French Mediterranean region, in an area of 60 km around Montpellier (Occitanie).  
146 We chose the fields according to three criteria: (i) no herbicide use on the inter-row, (ii)  
147 contrasting pedoclimatic conditions, and (iii) different soil management practices (tillage or  
148 mowing).

149 To characterize agricultural practices in each field, we interviewed the farmers twice a  
150 year in 2020 and 2021, focusing on inter-row management where most weed plants grow. The  
151 questionnaire (composed of 61 questions for wine-growers and 45 questions for olive growers)  
152 was divided into two principal sections: (1) general information about the farmland and the  
153 studied fields, and (2) agricultural practices and soil management. We collected six variables

154 related to agricultural practices: the average number of tillages per year, the average depth of  
155 tillage, the average number of mowing per year, the average return interval between two weed  
156 destructions, the average applied nitrogen quantity, and the average quantity of irrigation per  
157 year (mm) (Table S1).

158

## 159 **2.2. Climatic conditions**

160 Climatic conditions in each field were described using data from the nearest weather station to  
161 each field. In total, for the 32 fields, we used 12 weather stations. The mean distance between  
162 a field and a station was  $8.65 \pm 4.2$  km. The nearest station was located 0.5 km from the nearest  
163 field, and the farthest station was located 19.7 km. We collected monthly rainfall, maximum  
164 and minimum temperatures from 1980 to 2021. We used the function *biovars* from the *dismo*  
165 (Hijmans 2017) package in the R software version 4.1.1 to calculate 6 climatic variables  
166 representing the local seasonal trends: mean annual temperature, annual rainfall, rainfall of the  
167 driest month, maximum temperature of the warmest month, annual temperature range and  
168 precipitation seasonality (Table S2).

## 169 **2.3. Soil analysis**

170 To characterize the soil texture and properties, we sampled five soil cores in five randomly-  
171 chosen inter-rows per field down to a depth of 20 cm. By pooling the five samples, we obtain  
172 one composite soil sample per field. The pH (NF ISO 10390), soil texture (NF X 31-107  
173 method), nitrogen content, cation-exchange capacity (CEC), and total organic matter content  
174 (NF ISO 14235) were determined for each field sample ( $n = 32$ ) following standard protocols  
175 by a soil analysis laboratory (Table S3).

## 176 **2.4. Botanical surveys**

177 We conducted two seasonal botanical surveys in the inter-rows of each field, avoiding field  
178 margins, during spring (March-April) and fall (November-December) 2021. We used five  
179 randomly located  $0.25 \text{ m}^2$  quadrats per field. We assessed the weeds by identifying each taxon  
180 to the species, or genus level when species identification was not possible. We estimated species  
181 abundance by visual assessment of cover percentage in each quadrat. We determined the  
182 species' phenological stage using the method of Yvoz and al. (2021). We also recorded the  
183 bare-soil cover for each quadrat.

## 184 **2.5. Leaf functional traits at the species level**

185 Based on the botanical surveys, we selected 74 species in vineyards and 64 in olive groves,  
186 representing 80 % of the plant abundance represented by the plant cover in each quadrat. Some  
187 species (n= 34) were found in both types of agroecosystem but were collected separately in  
188 vineyards and olive groves as they represent different populations. Five functional leaf traits  
189 were measured on 8 individuals per species in each type of agroecosystem according to the  
190 standard protocols described in Pérez-Harguindeguy et al. (2013): (1) leaf dry matter content  
191 (LDMC,  $\text{mg g}^{-1}$ ) which is the oven-dry mass of a leaf, divided by its water-saturated fresh mass;  
192 (2) specific leaf area (SLA,  $\text{m}^2 \text{kg}^{-1}$ ) which is the one-sided area of a fresh water-saturated leaf  
193 divided by its oven-dry mass, (3) leaf nitrogen content (LNC,  $\text{mg g}^{-1}$ ), (4) leaf carbon content  
194 (LCC,  $\text{mg g}^{-1}$ ) and (5) leaf C/N ratio (C/N ratio,  $\text{mg g}^{-1}$ ) were measured pooling the 8 individuals  
195 leaves at the species level with elemental combustion analysis (NF ISO 10694) (Table S4) with  
196 three repeated measures.

## 197 **2.6. Plant biomass production and quality indicators at the species and** 198 **community level**

199 We collected, oven-dried ( $60^\circ\text{C}$ , 48 h), weighed, and ground (knife mill with 1mm sieve) the  
200 plant aboveground biomass (AB) present in each quadrat separately. Dry matter *in vitro*  
201 digestibility (DMD,  $\text{g kg}^{-1}$ ) and two chemical components, neutral detergent fiber (NDF,  $\text{g kg}^{-1}$ )  
202 and crude protein (CP,  $\text{g kg}^{-1}$ , Table 1), were determined at the community (n = 305) and at  
203 the species (n = 86) levels.

204 Analysis was performed using near-infrared reflectance spectroscopy (NIRS). NIRS is a non-  
205 destructive physical method to estimate chemical plant biomass composition.

206 Reflectance spectra were collected using a FOSS NIRSystem 6500 spectrometer (FOSS  
207 NIRSystems, Silver Spring, MD, USA) operating at 400–2500nm with a 2 nm step (i.e., 1050  
208 data points). Spectra were taken on ground samples in ring cells equipped with quartz glass.  
209 Duplicate spectra measurements were performed (two different cup fillings) and averaged.

210 To perform prediction, calibrations already existing at CIRAD (French International Centre of  
211 Agricultural Research for Development, Montpellier, France) were used after being adapted to  
212 our samples. To do this, a subset of our samples was analysed with reference methods in the  
213 laboratory. NDF content was measured using the Van Soest method (Van Soest et al., , 1991)  
214 and CP content was measured with Kjeldahl method. DMD was measured by an *in vitro*



215 enzymatic method with pepsin and cellulase (Aufrère et al., 2007). Calibration was performed  
216 using modified partial least square regression with the WINISI software (Version 4, Infrasoft  
217 185 International, Port Matilda, PA, USA).

## 218 **2.7. Community structure indices**

219 Community Weighted Means (CWM) were calculated at the quadrat level for the five leaf traits  
220 cited above (**Table 1**). CWM is the average value of a given trait in a community and is  
221 calculated as the average trait value  $trait_i$  of each species  $i$  weighted by its abundance  $p_i$  (Garnier  
222 et al., 2004) according to equation 1.

$$223 \quad CWM_{trait} = \sum_{i=1}^n p_i \times trait_i \quad \text{Equation 1}$$

## 224 **2.8. Data analysis**

225 All statistical analyses were performed using the R software version 4.1.1 (R Core Team, 2021)  
226 and the R packages *Tidyverse* (Wickham., 2009), *lme4* (Bates et al., 2015), *FactoMineR* (Josse  
227 and Husson., 2008), *MuMIn* (Barton., 2020), *car* (Fox and Weisberg., 2019) and *piecewiseSEM*  
228 (Lefcheck et al., 2020).

229 First, we conducted a Principal Component Analysis (PCA) with the six climatic  
230 variables and the six soil variables to analyze the co-variations between pedoclimatic variables.  
231 Similarly, we conducted a second PCA with the six variables related to agricultural practices.  
232 The coordinates of the fields on the first two axes of both PCAs were used as composite  
233 variables indicating the position of each field along two ‘pedoclimatic gradients’ (PC1<sub>pedoclim</sub>,  
234 PC2<sub>pedoclim</sub>) and two ‘agricultural gradients’ (PC1<sub>agri</sub>, PC2<sub>agri</sub>) as explanatory environmental and  
235 agronomic variables in the further analyses. We tested the effects of agroecosystem type  
236 (vineyards vs. olive groves) on the explanatory variables from both PCAs using Student’s T-  
237 tests. We tested the relationship between pedoclimatic conditions and agricultural practices  
238 using Pearson’s correlation.

239 We tested the relationships between field-averaged AB, DMD, NDF and CP using  
240 Pearson’s correlations. We tested the effects of agroecosystem type (vineyards vs. olive groves)  
241 and season (spring vs. autumn) on the variables using Student’s T-tests at the field level.

242 We tested the effects of agroecosystem type (vineyards vs. olive groves) and season  
243 (spring vs. autumn) on the CWM of the five leaf traits.

244 We ran a series of linear mixed-effects models to test the influence of the four abiotic  
245 descriptors ( $PC1_{pedoclim}$ ,  $PC2_{pedoclim}$ ,  $PC1_{agri}$ ,  $PC2_{agri}$ ) on (1) the forage quality (DMD, NDF, CP,  
246 AB), (2) the CWM of LDMC, SLA, LNC, LCC and C/N ratio, and (3) the influence of the  
247 CWM of LDMC, SLA, LNC, LCC and C/N ratio on the forage quality. The field was added to  
248 all models as a random effect. Before model selection and evaluation, we tested the collinearity  
249 of the fixed effects in the model using the variance inflation factors with the *vif* function. VIF  
250 values of 10 or higher are usually interpreted as revealing severe multicollinearity issues (Hair  
251 et al., 2006) and were removed. For the pedoclimate and agricultural practices variables VIF of  
252  $PC1_{pedoclim}$ ,  $PC2_{pedoclim}$ ,  $PC1_{agri}$ ,  $PC2_{agri}$  were  $< 2$ , so we kept all the explanatory variables in the  
253 tested models. For the CWM of the five leaf traits, the VIF of the CWM of LCN, LCC and C/N  
254 ratio were  $>10$  so we removed the CWM of LCC. When we removed LCC all VIFs were  $< 2$ .  
255 We kept the CWM of LDMC, SLA, LCN, and C/N ratio in the tested models. We then used the  
256 function ‘dredge’, which performs a stepwise comparison between full, reduced and ‘null’  
257 models built from the combination of all, several, or only one fixed effect. We selected the  
258 model with the lowest second-order Akaike Information Criterion value (AICc values)  
259 corrected for small sample sizes (Burnham et al., 2002). The cut-off to select a model was set  
260 at  $\Delta AICc < 2$  (Burnham et al., 2002). When possible, we kept the most parsimonious model,  
261 i.e. the simplest one. Finally, we evaluated the best-selected models using likelihood ratio tests  
262 and calculated the marginal and conditional  $R^2$  following Nakagawa & Schielzeth 2012.

263 Path analysis was used to understand the relationships between leaf traits, agricultural  
264 practices, pedoclimate, and season on digestibility and its structural components. A  
265 combination of linear models is used to quantify the relative effect of different variables on  
266 digestibility and biomass with the field added as a random effect. The tested variables were  
267 those selected by the linear mixed models performed before. Covariations were tested between  
268 the pedoclimate and agricultural practice variables, between the CWM of leaf traits and between  
269 digestibility and biomass. We tested the significance of estimated regression path coefficients  
270 associated with each causal relationship between variables. Standardized regression path  
271 coefficients are conventionally considered to strongly influence the variable when they are  
272 above 0.8, moderately between 0.2 and 0.8, and little below 0.2 (Shipley et al., 2009).

273

## 274 **3. Results**

### 275 **3.1. Pedoclimatic and agricultural practice gradients**

276 The first two axes of the ‘pedoclimatic gradient’ PCA explained 59.9 % of the total variance  
277 among the 32 study fields. The first axis ( $PC1_{pedoclim}$ , 36.4 %) discriminated between the fields  
278 with high annual temperature ranges, high maximal temperatures and heavy rainfall from the  
279 fields with high annual mean temperatures and lower rainfalls.  $PC1_{pedoclim}$  opposed the  
280 ‘continental’ fields with positive values to ‘coastal’ fields with negative values. The second axis  
281 ( $PC2_{pedoclim}$ , 23.9 %) discriminated the fields with high soil organic nitrogen content, soil  
282 organic matter, cation-exchange capacity, and presence of clay from the fields with high sand  
283 content (**Table 2**).  $PC2_{pedoclim}$  opposed the ‘fertile’ fields with positive values to ‘low-resource’  
284 fields with negative values (**Table 2**). The coordinates of the fields on the first two axes of the  
285 pedoclimatic PCA were extracted to create environmental explanatory variables found in **Table**  
286 **2**.  $PC1_{pedoclim}$  ( $P < 0.0001$ ) and  $PC2_{pedoclim}$  ( $P < 0.0001$ ) significantly differed between  
287 agroecosystems, they were higher in olive groves than in vineyards.

288 The first two axes of the ‘agricultural practices gradient’ PCA explained 67.6 % of the  
289 total variance among the 32 study fields. The first axis ( $PC1_{agri}$ , 43.1 %) discriminated between  
290 the fields with high tillage and the mown ones.  $PC1_{agri}$  opposed the ‘tilled’ fields with positive  
291 values, mostly vineyards, to the ‘mown’ fields with negative values, mostly olive groves. The  
292 second axis ( $PC2_{agri}$ , 24.5 %) was negatively correlated with the duration between two weed  
293 destruction dates (-0.67) and positively correlated with irrigation amount and mowing  
294 frequency.  $PC2_{agri}$  mainly reflected the heterogeneity of agricultural practices within the olive  
295 groves: opposing ‘irrigated and regularly mown’ fields with positive values to ‘rarely mown’  
296 fields with negative values. The coordinates of the fields on the first two axes of the agricultural  
297 practices PCA were extracted to create agricultural practice explanatory variables (**Table 2**).  
298  $PC1_{agri}$  ( $P < 0.0001$ ) significantly differed between agroecosystems: it was higher in vineyards  
299 than in olive groves.  $PC2_{agri}$  did not differ between agroecosystems.

300  $PC2_{pedoclim}$  and  $PC1_{agri}$  were negatively correlated ( $R : -0.55, P = 0.0008$ ): fields located  
301 on more fertile soils were managed by mowing more than by tillage. There were no other  
302 correlations between  $PC1_{pedoclim}$ ,  $PC2_{pedoclim}$ ,  $PC1_{agri}$  and  $PC2_{agri}$ .

### 303 **3.2. Weed communities: species composition and their digestibility**

304 During the two sessions (Spring 2021, Fall 2021) we identified 178 weed species overall  
305 (vineyards and olive groves), and the five most abundant were *Medicago minima* (Fabaceae),  
306 *Plantago lanceolata* (Plantaginaceae), *Bromus madritensis* (Poaceae), *Diplotaxis erucoides*  
307 (Brassicaceae) and *Geranium mole* (Geraniaceae)(Table S5). In vineyards, the five most  
308 abundant species were *Diplotaxis erucoides* (Brassicaceae), *Helminthotheca echioides*  
309 (Asteraceae), *Veronica persica* (Plantaginaceae), *Erodium cicutarium* (Geraniaceae) and *Malva*  
310 *sylvestris* (Malvaceae). In olive groves, the five most abundant species were *Medicago minima*  
311 (Fabaceae), *Plantago lanceolata* (Plantaginaceae), *Bromus spp* (including *B. madritensis*, *B.*  
312 *hordeaceus*, *B. sterilis*) (Poaceae), *Geranium molle* (Geraniaceae) and *Vulpia ciliata* (Poaceae).  
313 30 species were only found in vineyards and 60 species only in olive groves so there were 88  
314 species found both in olive groves and vineyards. 51 species were only found in spring and 35  
315 only in fall so there were 92 species found both in spring and fall.

316 The five species with the lowest DMD were three Poaceae (*Bothriochloa barbinodis*:  
317 537 g kg<sup>-1</sup>, *Vulpia ciliata*: 615 g kg<sup>-1</sup>, *Cynodon dactylon*: 628 g kg<sup>-1</sup>) and two Cyperaceae  
318 (*Cyperus rotundus*: 538 g kg<sup>-1</sup>, *Carex ornithopoda*: 609 g kg<sup>-1</sup>) (Fig. 2). The five species with  
319 the highest DMD were *Chenopodium album* (953 g kg<sup>-1</sup>, Amaranthaceae), *Calendula arvensis*  
320 (936 g kg<sup>-1</sup>, Asteraceae), *Urtica urens* (919 g kg<sup>-1</sup>, Urticaceae), *Diplotaxis erucoides* (886 g kg<sup>-1</sup>,  
321 Brassicaceae) and *Galium aparine* (870 g kg<sup>-1</sup>, Rubiaceae, Fig. 2).

322 We created four groups according to the DMD of each species by following the  
323 thresholds indicated by Bosworth et al. (1986). This study indicated that under 500 g kg<sup>-1</sup> the  
324 DMD value was too low to fulfill all ruminant needs, but none of our species were below this  
325 threshold, so we did not retain that group. According to Bosworth et al., (1986), a digestibility  
326 above 600 g kg<sup>-1</sup> was high, so we assumed that between 500 and 600 g kg<sup>-1</sup> the digestibility is  
327 low, and we created our group 1 “low digestibility” with this threshold. Group 1 contained only  
328 two species whose total cover was 1.64 %. The group 2 “high digestibility” contained species  
329 between 600 and 800 g kg<sup>-1</sup> and contained 49 species whose total cover was 51.9 %. Finally,  
330 we extrapolated and placed species whose DMD was above 800 g kg<sup>-1</sup> in a third group: “very  
331 high digestibility” with 41 species whose total cover was 37.69 %. There were 8.77 % of the  
332 species cover for which the DMD was not measured at the species level.

333 **3.3. Digestibility, fiber content, crude protein and aboveground biomass at**  
334 **the community level and their covariations across the agroecosystem and the**  
335 **season**

336 At the community level, DMD (mean:  $689 \pm 116 \text{ g kg}^{-1}$ ), NDF (mean:  $394 \pm 101 \text{ g kg}^{-1}$ ) and  
337 CP (mean:  $156 \pm 50 \text{ g kg}^{-1}$ ) were significantly affected by both the agroecosystem and the  
338 season, except for AB (mean:  $60.2 \pm 46.7 \text{ g m}^2$ ) which did not differ between olive groves and  
339 vineyards (**Table 3**). Communities found in olive groves had significantly higher NDF and  
340 lower DMD and CP compared to vineyards, which is consistent with the results of the green  
341 cover of each quality group. Communities collected during fall had significantly higher NDF  
342 and CP and lower DMD and AB than those collected in spring (**Table 3**).

343 We found that DMD was negatively related to NDF ( $R = -0.85$ ,  $P < 0.0001$ , Fig. 3A)  
344 and positively to CP ( $R = 0.59$ ,  $P < 0.0001$ ) (Fig. 3B). NDF was negatively related to CP ( $-0.42$ ,  
345  $P = 0.0006$ , Fig. 3C). AB and CP were negatively related ( $-0.33$ ,  $P = 0.008$ , Fig. 3D). No  
346 significant relationship was found between AB and DMD ( $P = 0.94$ ) nor with NDF ( $P = 0.79$ ).

347 **3.4. Variability of traits according to season and agroecosystem at the**  
348 **community level**

349 The CWM of LDMC was the leaf trait with the highest range ( $84$  to  $463 \text{ mg g}^{-1}$ ), and the CWM  
350 of LCC was the leaf trait with the smallest range ( $224$  to  $444 \text{ mg g}^{-1}$ , **Table 1**). We found  
351 inconsistent effects of the season and the agroecosystem on CWM of leaf traits: the only leaf  
352 trait that was significantly affected by both the agroecosystem and the season was CWM LCC:  
353 it was significantly higher in olive groves ( $P = 0.03$ ) than in vineyards and in spring ( $P = 0.002$ )  
354 than during fall. CWM LNC ( $P = 0.0002$ ) was not affected by the agroecosystem but was  
355 significantly higher in fall than during spring. CWM SLA was not affected by the season but  
356 was significantly higher in olive groves ( $P < 0.0001$ ) than in vineyards. No effect of the  
357 agroecosystem or season was found on the CWM LDMC and the CWM C/N ratio.

358 The CWM SLA was negatively correlated with the  $PC1_{\text{agri}}$  (estimate =  $-1.52$ ,  $P = 0.007$ )  
359 : tilled communities had higher CWM SLA than mown communities. The CWM C/N ratio was  
360 negatively correlated with the  $PC2_{\text{agri}}$  (estimate =  $-5.59$ ,  $P = 0.03$ ): communities that were less  
361 regularly mown and irrigated had a higher CWM C/N ratio than those more regularly mown  
362 and irrigated. None of the other axes affected CWM SLA or CWM C/N ratio. None of the  
363 agricultural practices nor pedoclimatic axes were correlated with CWM of the three other leaf

364 traits (LDMC, LNC, LCC). The best models selected to explain the CWM of the three other  
365 leaf traits were always the null models, keeping only the random effect of the field.

### 366 **3.5. Environmental variables and CWM of leaf traits modified digestibility** 367 **and structural components**

368 Concerning environmental variables, we found that DMD was positively linked to PC1<sub>agri</sub>  
369 opposing tilled vs. no-tilled/mown fields (estimate = 23.1, P = 0.01): plant communities in tilled  
370 fields had higher DMD than mown ones (**Table 4**). DMD was also negatively linked to PC2<sub>pedo</sub>  
371 opposing fertile vs. low resource soils (estimate = -23.6, P = 0.003): communities from more  
372 fertile fields had significantly lower DMD than communities from low-resource soils (**Table**  
373 **4**). Similarly, NDF was negatively linked to PC1<sub>agri</sub> (estimate = -36.5, P < 0.0001): mown  
374 communities had higher NDF than tilled ones. NDF was also negatively linked to the  
375 PC1<sub>pedoclim</sub> opposing “continental” to “coastal” fields (estimate = -11.8, P = 0.01): coastal fields  
376 had higher NDF than continental ones (**Table 4**). In contrast, CP was positively linked to PC1<sub>agri</sub>  
377 (estimate = 9.75, P = 0.009): tilled communities had higher CP than mown ones (**Table 4**).  
378 PC2<sub>agri</sub> was never linked to DMD or any of its structural components. DMD and CP were not  
379 linked to PC1<sub>pedoclim</sub> and the digestibility structural components (NDF and CP) were not linked  
380 to PC2<sub>pedoclim</sub>. Finally, none of the agricultural practices nor pedoclimatic PCs affected AB. The  
381 best model selected to explain AB was always the null model, keeping only the random effect  
382 of the field.

383 Concerning leaf traits, we found that DMD was negatively related with CWM LDMC  
384 (estimate = -0.51, P = 0.002, Fig. 4A) and CWM C/N ratio (estimate = -0.67, P = 0.009, Fig.  
385 4B) and positively with CWM LNC (estimate = 2.13, P = 0.04, Fig. 4C, Table 5). NDF was  
386 positively related with CWM LDMC (estimate = 0.85, P < 0.0001, Table 5). A positive  
387 relationship was also established between CP and CWM LNC (estimate = 3.15, P < 0.0001)  
388 and negatively with CWM C/N ratio (estimate = -0.45, P < 0.0001, Table 5). CWM LNC was  
389 also negatively related to AB (estimate = -1.42, P = 0.006, Table 5). Finally, CWM SLA was  
390 not related to digestibility, any of its structural components nor to AB.

391 Path analysis confirmed our previous results and showed that agricultural practices and  
392 pedoclimatic conditions did not modify the CWM of LCC, C/N ratio, and LDMC but directly  
393 had an impact on DMD (Fig. 5): PC1<sub>agri</sub> increased DMD (P = 0.007), and PC2<sub>pedoclim</sub> decreased  
394 DMD (P = 0.007). It also showed that CWM LDMC (P = 0.002) and CWM C/N ratio (P = 0.02)  
395 decreased DMD whereas LNC increased DMD (P = 0.002, Fig. 5). Only the season had an

396 impact on both DMD ( $P < 0.0001$ ) and AB ( $P < 0.0001$ ): they were both higher in spring than  
397 in fall. We found no effect of CWM of leaf traits or agricultural practices and pedoclimate  
398 variables on AB: only the season affected AB, which was higher in spring ( $P < 0.0001$ , Fig. 5).  
399 Season also modified CWM LDMC ( $P = 0.01$ ) and CWM LNC ( $P < 0.0001$ ) which were both  
400 higher in fall than in spring. Finally, we found strong covariations between CWM C/N ratio  
401 and CWM LDMC ( $P < 0.0001$ ) and between CWM C/N ratio and CWM LNC ( $P < 0.0001$ )  
402 and between  $PC1_{agri}$  and  $PC2_{pedoclim}$  ( $P < 0.0001$ , Fig. 5). We found no covariation between  
403 DMD and AB. To summarize, we found low but significant effects of CWM LNC and CWM  
404 C/N ratio on DMD and only a seasonal effect on CWM LNC, CWM LDMC, and DMD. We  
405 also found moderate but significant effects of  $PC1_{agri}$ ,  $PC2_{pedoclim}$ , and CWM LDMC on DMD.  
406 Finally, the strongest effect observed, considered moderate according to Shipley et al., 2009, is  
407 the effect of the season on the AB, which is higher in spring than in fall (Fig. 5).

## 408 4. Discussion

### 409 4.1. Olive grove and vineyard weeds had a potential to provide forage 410 resources for livestock.

411 This study evaluates whether weeds have a potential to provide quality forage for livestock.  
412 Our results indicate a promising potential for forage resources for sheep (Figure 2, Table 3).  
413 Studied species and communities have a high *in vitro* digestibility ( $> 600 \text{ g kg}^{-1}$ ) with a mean  
414 digestibility of around  $769 \text{ g kg}^{-1}$  at the leaf species level and  $689 \text{ g kg}^{-1} (\pm 116)$  at the  
415 community level. These DMD values are suitable for ruminants (Bosworth et al., 1986, Fig. 2).  
416 According to the indicator of Cruz et al. (2010), which proposes four categories of plant forage  
417 quality based on their leaf traits values (LDMC), the majority of species (71.6%, Table 4) and  
418 communities (87 %, Table 1) of our study fitted in the most digestible category (group A).

419 When compared to natural or sown grassland species, the studied weed species had  
420 either equal (Bumb et al., 2016) or lower ranges of digestibility (Khaled et al., 2007). However,  
421 the studied weed communities had a lower forage quality overall than sown grasslands  
422 composed of selected forage species. Only four of the studied species had higher or similar  
423 DMD than two of the most widespread sown forages species: *Lolium multiflorum* (mean DMD  
424 :  $892 \text{ g kg}^{-1}$ ) and *Medicago sativa* (mean DMD :  $880 \text{ g kg}^{-1}$ , Tables INRA, 2010) which cover  
425 respectively 600 000 ha and 300 000 ha of grasslands in France (Agreste, 2006). Although some  
426 of the most digestible species in our study: *Chenopodium album* ( $953 \text{ g kg}^{-1}$ ), *Diplotaxis*

427 *erucoides* (886 g kg<sup>-1</sup>), and *Galium aparine* (870 g kg<sup>-1</sup>) (Fig.2, Table S6), respectively the first,  
428 the fourth and the fifth most digestible, are usually of important concern as they are considered  
429 to be harmful weeds in annual cropping systems (herbicide-resistant, competitive, allelopathic)  
430 and are therefore suppressed by weed management instead of being used as forage (Defelice,  
431 2002; Qasem et al., 2007; Konstantinovic et al., 2015).

432 Contrary to quality, weed biomass production was low. Weeds in olive groves and  
433 vineyards produced 0.6 t ha<sup>-1</sup> on average (Table 1) which was considerably lower than the 3.5  
434 to 5 t ha<sup>-1</sup> of biomass produced in the permanent grasslands in the South of France (Agreste,  
435 2016). However, these low values should be interpreted with caution since when the sampling  
436 was realized, the peak of biomass was not reached for each weed community due to  
437 management constraints of the agroecosystems. In particular, some plots (n = 60/305) had  
438 already been mown or tilled before the vegetation sampling. Most of these plots were located  
439 in vineyards (n = 40/60) where management was more disturbing and weeds more often  
440 destroyed than in olive groves. Consequently, the potential biomass production may have been  
441 under-estimated. This low biomass is also due to the fact that in early spring most of the annual  
442 weeds are still young, which implies that their DMD is higher than when they reach their  
443 biomass peak (Klein et al., 2013). This temporality is a major explanation of the high DMD of  
444 the spring weed communities.

445 The forage potential was higher in spring than in fall, resulting from seasonal dynamics  
446 of both weed biomass quantity (AB) and quality (dry matter digestibility, crude proteins and  
447 fiber content) (**Table 3**). The lower forage potential in fall can be explained by a seasonal  
448 decrease in weed forage quality over the year (Abaye et al., 2009; Bumb et al., 2016) driven by  
449 plant trait responses to the drier climatic conditions during summer and before the fall rainfalls.  
450 Nevertheless, biomass production in fall can be an additional forage resource during a period  
451 of usually low vegetative productivity.

## 452 **4.2. Community scale weed forage potential was related to leaf traits**

453 Our second hypothesis was that the relationships between biomass quantity, quality and leaf  
454 traits would be consistent in perennial agroecosystems as demonstrated in grasslands (Bumb et  
455 al., 2016). Specifically, we found that forage quality increased with increasing LNC and more  
456 significantly with decreasing LDMC and C/N at both the species and community levels. Our  
457 results extend the genericity of trait-digestibility relationships previously demonstrated in



458 grasslands to weeds, despite their unique functional trait syndrome characterized by more  
459 ruderal strategies (Bourgeois et al. 2019, Table 5, Fig 4, Fig 5). Additionally, the dominance  
460 hypothesis was validated here as the CWM of different leaf traits calculated from the most  
461 abundant species, were significantly related to forage quality (dry matter digestibility, crude  
462 proteins and fiber content). Bumb et al. (2016) demonstrated that the increase of LDMC and  
463 C/N ratio decreases digestibility, whereas an increase in LNC promotes nutritional quality and  
464 increases digestibility. However, we did not find any relationship between SLA and forage  
465 quality, even if this relationship is well documented in the literature (Pontes et al., 2007; Tasset  
466 et al., 2019).

467 Unexpectedly, we found no relationship between weed leaf traits and biomass even if,  
468 in previous studies, LDMC was found to be negatively related to biomass production in  
469 grasslands (Pontes et al., 2007). Similarly, SLA has been repeatedly identified as a significant  
470 determinant of biomass production in grasslands (Garnier et al., 2016). We assume that the  
471 important presence of *Poaceae* with lower SLA than the other species could hide this  
472 relationship. The low variation in biomass between the studied fields may explain this result.  
473 Furthermore, the absence of significant relationships suggests that weed biomass may be driven  
474 by agricultural practices more than plant traits in these regularly tilled or mowed  
475 agroecosystems. However, to further understand trait-biomass relationships in such a particular  
476 context, it might be relevant to measure traits of the stems, in addition to leaves (Bumb et al.,  
477 2016), since they represent an important part of plant biomass and are usually part of the bite  
478 category of most of the studied species (Agreil and Meuret, 2004).

### 479 **4.3. Increased weed forage potential due to disturbance in specific** 480 **agroecosystems**

481 Reflecting differences in weed species composition, weed community forage quality differed  
482 between agroecosystems. The three forage quality indicators (dry matter digestibility, crude  
483 proteins and fiber content) revealed higher forage quality in vineyards than in olive groves  
484 (Table 3). This difference can be explained by differing species composition between the  
485 agroecosystems: contrary to olive groves, the frequent tillage of vineyards selected for more  
486 digestible species. Our results demonstrated a difference between the five more abundant  
487 species in each agroecosystem (Table S5). Two of the most abundant species of olive groves  
488 were *Poaceae*s with low digestibility values: *Vulpia ciliata* (mean DMD: 615 g kg<sup>-1</sup>) and  
489 *Bromus spp* (mean DMD: 655 g kg<sup>-1</sup>). More digestible species with higher DMD values were

490 more abundant in vineyards, : for example, the olive grove to vineyard comparison shows  
491 *Chenopodium album* one to three occurrences, *Diplotaxis erucoides* two to sixty-one  
492 occurrences and *Urtica urens* one to seventeen occurrences. Only *Calendula arvensis* was  
493 equally present in both systems with nine and seven occurrences in olive groves and vineyards  
494 respectively. *Diplotaxis erucoides* (mean DMD: 886 g kg<sup>-1</sup>), the most abundant (61  
495 occurrences) and dominant (10% of species cover) species in vineyards, was also one of the  
496 most digestible species found in the present study and compared to sown species.

497 Agricultural practices were the primary cause of weed forage quality differences between  
498 agroecosystems. As expected, in the more disturbed agroecosystems like vineyards, the forage  
499 quality was higher, but there was no effect of the agricultural practices nor of the agrosystem  
500 on biomass production. We found consistent positive effects of tillage on the forage quality  
501 (DMD, NDF, CP). These findings confirm those observed in grassland environments where  
502 higher levels of disturbance caused higher digestibility (Duru et al., 1997; Gardarin et al., 2014;  
503 Bumb et al., 2016). However, vineyards presented a significantly higher potential regarding the  
504 quality of the forage potential (mean DMD: 737 g kg<sup>-1</sup>) than olive groves (mean DMD: 644 g  
505 kg<sup>-1</sup>, **Table 3**), which was explained by differences in agricultural practices. The PC1<sub>agri</sub> showed  
506 that digestibility was higher when the soil was tilled rather than mown and increased with the  
507 frequency and depth of tillage (**Table 4, Fig 6**). In previous studies, the increase in digestibility  
508 with the number of mowings/grazing was explained by the effect of the defoliation that keeps  
509 the vegetation at the vegetative stage and stimulates fast regrowth with less investment in the  
510 structural tissue (Pontes et al., 2007; Gardarin et al., 2014) but also selects fast life-cycle  
511 species. We assumed that, even if mowing stimulated regrowth and thus higher digestibility  
512 (Pontes et al., 2007), tillage was selected for more ruderal and thus more digestible species at  
513 the community level. Because tillage uproots plants, it is associated to a higher level of  
514 disturbance than mowing, which likely selected for species with more ruderal strategies.  
515 However, in grassland studies, the type of disturbance was different (gradient of mowing and/or  
516 sheep grazing intensity and frequency) than in vineyards and none of the previous studies had  
517 studied the effect of tillage on digestibility. These disturbance-resistant species generally have  
518 acquisitive and fast-growing strategies (Grime., 1974; Wright et al., 2004) associated with traits  
519 that also promote high digestibility. Surprisingly our results did not show any direct effect of  
520 agricultural practices on the CWM of any leaf trait unlike previous studies where agricultural  
521 practices modified leaf traits like SLA or LDMC (Gaba et al., 2013; Kazakou et al., 2016; Bopp

522 et al., 2022). This could be due to the narrow range of variations of the CWMs of the leaf traits  
523 preventing detection of any covariation with the environmental variables.

524 Contrary to our expectations, weed biomass was not explained by agricultural practices.  
525 We expected that agricultural practices would reduce weed biomass, especially tillage, because  
526 they specifically aim at reducing plant cover. This lack of effect of tillage on weed biomass  
527 production could be due to the frequent biomass destruction in all fields (mean number of  
528 mowings: 1.8, mean number of tillage: 3.6), which maintained a low level of weed biomass  
529 everywhere, not representative of species biomass production potential. Finally, maybe other  
530 variables could influence weed biomass production like temporal variations in the management  
531 at an annual scale or annual weather variables like the quantity of rainfall.

#### 532 **4.4. Weed forage potential was not affected by climatic conditions but varied** 533 **with soil fertility**

534 Despite a significant rainfall gradient among the surveyed fields, weed forage quality did not  
535 vary with climate. As suggested by Gardarin et al., 2014, we expected that forage quality would  
536 be lower under more arid conditions in response to more abundant stress-tolerant species with  
537 a high LDMC in weed communities. Soil fertility had a negative effect on DMD of weed  
538 communities (Table 4, Fig 6). This relationship was not verified for crude proteins and fiber  
539 content or aboveground biomass. This result contradicts previous studies, in grasslands, where  
540 fertile soils positively affected leaf traits like SLA or LNC or decreased LDMC, and increased  
541 digestibility (Duru et al., 2007; Ordoñez et al., 2009; Jager et al 2015). The negative relationship  
542 between fertility and digestibility found in our study can be due to the covariation between  
543 PC1<sub>agri</sub> (tillage VS mowing axis: Table 2) and PC2<sub>pedoclim</sub> (fertile vs not fertile soils: Table 2):  
544 tillage increases DMD but also decreases the organic matter in the soil. Consequently, the effect  
545 of tillage overrides the effect of soil fertility.

546 Finally, the absence of a relationship between pedoclimatic or agricultural practices and  
547 leaf traits made the role of leaf traits difficult to interpret in mediating the response of  
548 digestibility to environmental conditions (Garnier et al., 2019). However, the limited range of  
549 both gradients (pedoclimate, agricultural practices) can explain the weak response of  
550 digestibility traits across the field network (Fig 1, Table S2). A more detailed assessment of  
551 intraspecific trait variability could probably improve the detection of local effects of the  
552 environment.

#### 553 **4.5. Perspectives for perennial cropping systems management**

554 We demonstrated that weeds could represent a qualitative source of forage in vineyards and  
555 olive groves. Management practices with high disturbing effects like tillage increased forage  
556 quality but limited the biomass production below its peak by constantly removing the weeds.  
557 Moreover, previous studies demonstrated that tillage reduces biodiversity in perennial  
558 agroecosystems, especially of wild bees and arthropods (Kratschmer et al., 2018; Carpio et al.,  
559 2019), soil biodiversity (Sanchez-Moreno et al., 2015) or plant richness and abundance (Fried  
560 et al., 2019; Carpio et al., 2020). In contrast, cover crops or spontaneous vegetation often  
561 increase the biodiversity in the fields (Gomez et al., 2018; Cohen et al., 2015) and, consequently  
562 the provision of ES (Kavvadias et al., 2019; Daane et al., 2017). Even if tillage significantly  
563 increased weed digestibility, forage quality in non-tilled fields can already be considered high  
564 according to both *Bosworth et al.* (1986) and *Cruz et al.* (2010) : it is possible to achieve high  
565 forage quality and biodiversity-friendly farming practices simultaneously in highly disturbed  
566 ecosystems such as vineyards and olive groves.

567 In vineyards and olive groves weed quantity is low because of the disturbing agricultural  
568 practices. Unlike grasslands, biomass production is not the principal objective of the studied  
569 agroecosystems, and it would not be possible to produce a high quantity of weed biomass while  
570 preserving crop yields. However agricultural practices can be modified to avoid tillage or  
571 mowing before the sheep graze. It is also possible to manage the number of sheep or time spent  
572 grazing to adapt to the available biomass and to other targeted ES (Zhang et al., 2021).  
573 Additionally, weed biomass represents a complementary resource to grasslands and is not the  
574 principal sheep food source. Finally, even if the biomass is low at the field level, a lot of olive  
575 groves (17 700 ha) and overall vineyards (300 000 ha) are present in the French Mediterranean  
576 region (Agreste, 2021), representing a very important potential. Removing weeds by sheep  
577 grazing is also a biodiversity-friendly agricultural practice that does not affect the yield and  
578 helps to reduce time spent on mechanical or chemical weeding (Niles et al., 2018 ; Lazcano et  
579 al., 2022).

580 Our study suggest to change the temporality of management practices in olive groves  
581 and vineyards. Nowadays, most farmers destroy plant cover in spring to avoid competition for  
582 water with weeds (Fernandez-Mena et al., 2021; Kazakou et al., 2016; France Olive website,  
583 April 2022): this was the case of all of the wine-growers and 75% of olive growers in the study.  
584 Consequently, we suggest that the higher forage potential in spring is also interesting for sheep

585 farmers because it is early in the year, at a period where forage resources can still be rare in  
586 semi-natural or natural environments and where weed digestibility is high. It would be a win-  
587 win association to remove the weeds by sheep grazing in spring. Fall grazing can also be  
588 considered as an interesting option because it precedes (olive) or follows (grapevine) the  
589 harvest, and a lot of producers will also destroy the soil cover at this time of the year: 63% of  
590 the wine-growers and 33% of the olive growers destroy the weed biomass during fall. However,  
591 it might not be as interesting as in spring for sheep farmers because of the low weed quantity.

592 Finally, integrating sheep in vineyards and olive groves may represent economic  
593 benefits for producers by reducing herbicide costs or tillage and mowing time and fertilize the  
594 field (Niles et al., 2018 ; Schoof et al., 2021). It also increases ecological benefits by reducing  
595 agricultural practices that could negatively impact the biodiversity of agroecosystems. More  
596 broadly, this farming practice contributes to better integration of crop and livestock systems in  
597 Mediterranean agriculture. In this perspective, our study provides a sound basis for evaluating  
598 the forage potential of weeds found in vineyards and olive groves, two emblematic  
599 Mediterranean agroecosystems.

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