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1 *Original Article*

## 2 **Cropping system diversification does not always beget weed diversity**

3

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15

### 16 **Abstract**

17 Cropping system (CS) diversification appears as a promising solution to increase CS sustainability.  
18 However, weed community response to different options of CS diversification remains poorly  
19 documented. Moreover, these effects are expected to be more pronounced in experimental than  
20 commercial farms because experimental farms explore more diverse combinations of farming  
21 practices. We hypothesized that (i) CS diversification would increase weed diversity at multiple  
22 spatio-temporal scales but that (ii) different options of CS diversification would select different weed  
23 communities and that (iii) responses could differ between experimental and commercial farms. Hence,  
24 weed density per species was measured over a 6-year time period in a CS experiment and in a farmers'  
25 network (both resorting to diverse CSs that were numerically summarized to allow their comparison,  
26 *i.e.* different positions along gradients of tillage intensity, herbicide use, crop rotation length etc.).  
27 Weed density measures were used to compute weed diversity indices (taxonomic and functional, at  
28 annual and plurennial scales) and community weighted means on key response traits for each CS. All  
29 experimented alternative CSs (diversified crop sequences with coherent but different combinations of  
30 weed management tools) showed that diverse combinations of agronomic tools are available to  
31 increase weed diversity, as highlighted by a 3 and 2-fold increase in species richness at the annual and

32 plurennial scales, respectively. In contrast, only one farmer CS (3-year rotation, low tillage intensity,  
33 intermediate herbicide reliance) showed significantly higher levels of weed diversity, possibly because  
34 the reduced tillage intensity was not compensated by other agronomic levers (*e.g.* increase of herbicide  
35 use and/or crop rotation diversity). Such outcomes were attributed to (i) reduced CS complexity in  
36 commercial compared to experimental farms and (ii) high herbicide reliance in commercial farms,  
37 irrespectively of CS complexity. Across both experimental and commercial farms, tillage, weed  
38 management and crop type appeared as the main factors structuring weed communities. Systems with  
39 reduced tillage were associated with a higher percentage of grasses and perennials. Systems with  
40 spring/summer crops and/or mechanical weeding were associated with a higher proportion of  
41 spring/summer and perennial species. These results suggest that solutions are readily available for  
42 farmers to implement sustainable weed management, but supports are required to address the factors  
43 hindering the adoption of these experimented CS in commercial conditions.

44 **Keywords:** functional diversity, taxonomic diversity, traits, composition, crop rotation, tillage,  
45 herbicides, long-term experiment

46

## 47 1. Introduction

48 The oversimplification of cropping systems (CSs) (low crop diversity coupled with intensive use of  
49 tillage, herbicides and nitrogen fertilisers) has led to a drastic decline in weed diversity (Stoate et al.,  
50 2001; Albrecht et al., 2016). This loss of within field weed diversity has generated an erosion of the  
51 natural capital on which sustainable crop production is founded (Marshall et al., 2003; Storkey and  
52 Neve, 2018). Indeed, weeds represent the base of food chains in agroecosystems, and therefore support  
53 all higher trophic levels (*e.g.* beneficial insects and birds), responsible for a wide set of agroecosystem  
54 services, such as pollination and biological control (Pocock et al., 2012; Blaix et al., 2018). On the  
55 other hand, weeds can generate severe yield losses at high levels of abundance, which has justified  
56 their management (Cousens, 1985; Milberg and Hallgren, 2004). Therefore, identifying CSs which  
57 maintain weed diversity while preventing important yield losses was cited as a top research priority in  
58 weed science (Neve et al., 2018).

59 CS diversification (*i.e.* crop rotation and farming operations associated with each crop) has been  
60 proposed as a key approach to increase the sustainability of weed management (Liebman et al., 2001;  
61 Wezel et al., 2014), *i.e.* to maintain weed diversity while alleviating weed:crop competition (see the  
62 review of Colbach et al. (2020)). CS diversification can be carried out at both the annual and  
63 plurennial scales (Wezel et al., 2014). For example, conventional winter wheat (*Triticum aestivum* L.),  
64 which involves summer bare soil before sowing and chemical weed control, can be diversified at the  
65 annual scale through the adoption of cover crops or false seedbed operations, cultivar or crop mixtures  
66 and a combination of mechanical and site-specific chemical weeding (Jabran et al., 2017). At the

67 plurennial scale, short winter-cereal based rotations can be diversified with crops of different botanical  
68 families (*e.g.* winter faba bean, *Vicia faba* L.), sowing periods (*e.g.* spring barley, *Hordeum vulgare*  
69 L.) or even life cycle duration (*e.g.* alfalfa, *Medicago sativa* L., or other perennial legumes such as  
70 common sainfoin, *Onobrychis viciifolia* Scop.) (Cirujeda et al., 2019; Weisberger et al., 2019). The  
71 integration of new crops in the crop sequence is usually associated with a diversification of selection  
72 pressure on weeds because crops largely determine tillage timing, sowing date, fertiliser rate, type of  
73 herbicides and/or mechanical weeding, etc. (Fried et al., 2008; Koocheki et al., 2009). Hence, focusing  
74 on coherent sets of agronomic practices, rather than apprehending them individually and  
75 independently, should provide a greater understanding of how weed communities are shaped in real  
76 farming conditions (Swanton and Weise, 1991).

77 Cropping system effects on weed diversity should be considered at different spatio-temporal scales.  
78 Studies which have focused on annual snapshots of weed flora in a given crop (*e.g.* Fried et al. (2008)  
79 and Schumacher et al. (2018)) may have identified farming practices that promote annual weed  
80 diversity (*e.g.* reduced fertilisation rate or herbicide dose) but have provided little information  
81 concerning how CSs may be designed to promote weed diversity at both the annual and plurennial  
82 scales while limiting yield losses. Different management practices may promote weed diversity at  
83 different spatial scales in a given year (*e.g.* quadrat, lowest hierarchical level of weed sampling or  
84 plot:year scale, pool of all quadrats for a given plot and year) and over time (*e.g.* plot scale, pool of all  
85 quadrats for a given plot over time). This is of considerable importance because weed diversity at the  
86 quadrat and plot:year scales do not necessarily provide the same type of agroecosystem services. Weed  
87 diversity at the quadrat scale could mitigate weed:crop competition through complementarity in  
88 resource use in space and time (Adeux et al., 2019b) whereas weed diversity at the plot:year scale  
89 could maintain a greater diversity of mobile organisms, such as pollinators and/or natural enemies  
90 (Nicholls and Altieri, 2013; Schuldt et al., 2019). Greater inter-annual variability of crop types and  
91 management practices is expected to increase the diversity of habitats favorable to different weed  
92 species (Weibull et al., 2003), which should be reflected through higher cumulated weed diversity at  
93 the plot scale. Finally, the growing recognition that ecosystem processes depend on species' traits  
94 rather than on species richness (Hooper et al., 2005) has led researchers to characterize diversity  
95 through the extent of trait dissimilarity within the community, *i.e.* functional diversity (Garnier and  
96 Navas, 2012). Therefore, an additional focus on functional diversity could shed light on whether more  
97 diversified CSs promote more functionally diverse weed communities (Mahaut et al., 2019), thereby  
98 potentially maximizing ecosystem multifunctionality (Gross et al., 2017).

99 Different combinations of agronomic practices may lead to similar levels of taxonomic or functional  
100 diversity through the selection of different sets of functional response traits (Légère et al., 2005).  
101 Indeed, assembly rules in weed community ecology state that each set of farming practices will act as  
102 a set of filters on weed species traits (Booth and Swanton, 2002). However, different combinations of

103 agronomic practices may reflect different farming objectives (*e.g.* maximizing economic profitability  
104 and/or enhancing soil health and/or minimizing reliance on external inputs). CSs tend to be designed  
105 to maximise profitability in commercial farming conditions (Colbach et al., 2020), whereas  
106 experimenters tend to explore more alternative strategies designed according to different and more  
107 diverse sets of objectives (Deytieux et al., 2012). Indeed, farmers tend to give more importance to the  
108 negative facet of weeds (*e.g.* yield loss) than experimenters (Vissoh et al., 2007; Wilson et al., 2008),  
109 usually resulting in higher management intensity in commercial farming conditions than in  
110 experimental farms. Combing such datasets could allow to investigate whether the volume of CS  
111 diversification space explored in commercial farms is sufficient to modify weed communities or if  
112 more complex changes (as explored in experimental farms) are required (Deytieux et al., 2016;  
113 Lechenet et al., 2017a). To our knowledge, no study has investigated the long-term effect of different  
114 options of CS diversification on weed communities (albeit different options across commercial and  
115 experimental farms), from both a taxonomic and functional perspective, and at different  
116 spatio-temporal scales.

117 The objectives of this study are (i) to identify if different options of CS diversification – that were  
118 previously confirmed as viable (*i.e.* low weed:crop competition), either in an experimental station  
119 (Adeux et al., 2019a) or on a farmers' network (Yvoz et al., 2020b) – could promote weed diversity at  
120 different spatial scales (*i.e.* quadrat, plot:year, plot) and (ii) to investigate the response traits of the  
121 corresponding weed communities in order to identify potential weed community assembly rules at the  
122 CS level. We hypothesized that (1) taxonomic and/or functional weed diversity could be promoted at  
123 different spatial scales through different options of CS diversification but (2) that each option would  
124 select weed communities with an adapted set of functional attributes. The study was based on weed  
125 surveys originating from two neighboring sites of the same production situation: an integrated weed  
126 management CS experiment aiming to reduce herbicide reliance through four alternative CSs (in  
127 comparison to a regional reference) and a network of farmers implementing various CSs to maximize  
128 economic profitability. Each dataset combined six years of weed samplings (weed density and biomass  
129 per species, after weeding, in all crops) and management practices over the same period.

130

## 131 **2. Materials and Methods**

132 Both sites are located in the same production situation (47° 14'11.2"N, 5° 05'56.1"E) in southern  
133 Burgundy, France (Figure 1), which is subject to a semi-continental climate, characterized by cold wet  
134 winters (average daily temperature of 4°C and average monthly precipitation of 43 mm) and warm  
135 summers (average daily temperature of 18°C and average monthly precipitation of 69 mm).

136 [Figure 1]

137 **2.1. Cropping system experiment**

138 The study focused on the last six years (harvest 2012 to harvest 2017) of a long-term CS experiment  
139 initiated in 2000 at the INRAE experimental farm in Bretenière, France (Adeux et al., 2019a). The  
140 experiment was set up as a randomized complete block design. For each of the five experimental CSs  
141 (ECSs), the set of decision rules was replicated on two blocks, separated by a distance of 1 km  
142 (Figure 1) and characterized by clay soils (40-50%) of medium depth (50-90 cm). The will to  
143 implement ECSs in farm scale conditions (plot size=1.7 ha) led to experimental limitations. Hence,  
144 only one term of the rotation was present for a given combination of block:year:ECS. Moreover, two  
145 different entry points (*i.e.* crop) were chosen for the two plots of a given CS to limit, to some extent,  
146 complete overlap between ECS:year and ECS:year:crop effects (Lechenet et al., 2017b).

147 Main characteristics of the five ECSs are presented in Table 1. The reference CS (ECS1), typical of  
148 the Burgundy region, was designed to maximize financial return. It was characterized by a triennial  
149 oilseed rape (*Brassica napus* subsp. *napus* L.) – winter wheat – winter barley rotation, near-systematic  
150 moldboard ploughing (in autumn due to high clay content), early sowing of winter cereals, herbicides  
151 as sole curative weed management tool, and high nitrogen fertilisation (Table 2). All alternative CSs  
152 (ECS2 to ECS5) were designed to mimic farmers aiming to reduce herbicide reliance through different  
153 agronomic options and resulted in more diversified 6-year rotations (Table 2), which included one  
154 autumn-sown oilseed rape crop, three winter crops (mainly cereals), one spring sown crop (mainly  
155 barley) and one summer sown crop (Table 2). In ECS5, alfalfa, a perennial forage crop, was included  
156 in order to manage Canada thistle (*Cirsium arvense* (L.) Scop.) through repeated mowing. The  
157 introduction of legume crops was the main driver of reduced nitrogen fertilisation (-29 to -49%) at the  
158 CS scale for all alternative ECSs (Table 2).

159 The alternative CSs (ESC2-5) also differed by their tillage type and weed management strategies,  
160 including a wide array of preventive and cultural weed management tools, such as false seedbed  
161 technique, delayed sowing of winter cereals, and increased crop density (Table 2). ECS2 was a  
162 transition from reduced tillage (*i.e.* no inversion tillage from 2001 to 2010) to permanent no-till (2010-  
163 2017 in conservation agriculture) whereas ECS3, ECS4 and ECS5 implemented moldboard ploughing  
164 about every two years (Table 2). ESC2 and ECS3 resorted exclusively to herbicides for curative weed  
165 control (50% corresponding to burndown applications of glyphosate in ECS2, Table 2) whereas ECS5  
166 resorted exclusively to mechanical weeding (Table 2). ECS4 aimed to be the typical integrated weed  
167 management system, resorting preferentially to mechanical weeding, post-emergence applications of  
168 specialized herbicides on target species remaining possible when weather conditions were not suitable  
169 for mechanical weeding or to control weeds with low sensibility to mechanical weeding (*e.g.* *Galium*  
170 *aparine* L.).

171 [Table 1] + [Table 2]

## 172 **2.2. Farmers' network**

173 The present study also focuses on six years of data (harvest 2008 to harvest 2013) originating from  
174 farmer's fields located within the Fény platform, near Dijon (north-eastern France), which borders the  
175 INRAE experimental station (Figure 1), and thus shares similar weather and soil conditions. The  
176 Fény platform represents a 950 ha zone of contiguous fields cultivated by 23 farmers, where weed  
177 communities and farming practices are recorded since 2004 by INRAE . The fields of the area were  
178 previously classified into eight crop management strategies (here denoted FCS for farmer CS), based  
179 on 14 indicators describing the diversity of crop sequences and the intensity of practices such as  
180 ploughing, tillage, nitrogen and pesticide use over the 2004-2016 period (Yvoz et al., 2020b). For this  
181 study, only the fields in which weeds were surveyed after all weeding operations every year over the  
182 2008-2013 period were retained (N=17). Therefore, the final layout (Figure 1) did not correspond to  
183 any experimental or sampling design (hence considered as completely randomized in following  
184 statistical section). This sub-dataset comprised 4 FCSs, whose main characteristics are summarized in  
185 Table 1. FCS2 (N=8 fields) and FCS3 (N=3 fields) were characterized by short rotations dominated by  
186 autumn-sown crops, but differed by the frequency of moldboard ploughing (highest in FCS2), the use  
187 of secondary tillage (lowest in FCS3) and their reliance on herbicides (highest in FCS3, particularly  
188 before sowing, Table 2). FCS4 (N=2 fields) was characterized by moderately diversified crop  
189 sequences based on systematic moldboard ploughing, but relatively low reliance on herbicides and  
190 secondary tillage operations. FCS7 (N=4 fields) was characterized by a diversified crop sequence, low  
191 reliance on moldboard ploughing and herbicides and was the unique FCS implementing mechanical  
192 weeding (Table 2).

## 193 **2.3. Weed sampling**

194 In the CS experiment, weed density was counted per species in 8 randomly positioned 0.36 m<sup>2</sup>  
195 quadrats in each plot each year at crop flowering (*i.e.* few weeks after final weeding operations).  
196 Sampling quadrats were placed anew each year in a given plot. Crop volunteers were not included in  
197 the counts so as to focus on natural vegetation. Aboveground weed biomass was sampled per weed  
198 species concurrently. Biomass samples were then oven dried for 48 h at 80°C and weighed. Weed  
199 biomass and density of each species was pooled at the quadrat level to obtain total weed biomass and  
200 density per quadrat. In the farmers' network, weed density was visually estimated per species within  
201 one 2000 m<sup>2</sup> area (50 m\*40 m, located 20 m away from the field margin and fixed in time) each year  
202 in each field before crop elongation stage and after weeding (*i.e.* early spring for winter cereals, late  
203 spring for spring crops and mid-summer for summer crops). Weed density was visually estimated  
204 using a slightly modified version of the scale of abundance developed by Barralis (1976), which  
205 proposes 6 classes of abundance (one individual in the 2000 m<sup>2</sup> area, <1, 1–2, 3–20, 21–50, and 51–  
206 100 individuals m<sup>-2</sup>). Total weed abundance was then computed using the center of each density class

207 (*i.e.* 0.0005, 0.5, 1.5, 11.5, 35.5, and 75.5 individuals m<sup>-2</sup>, respectively) following the methodology of  
208 previous studies (Fried et al., 2009; Trichard et al., 2013; Chamorro et al., 2016).

## 209 **2.4. Numerical and statistical analyses**

210 The two datasets were analysed separately so as to account for their differences in structure and  
211 sampling methodology. All the results presented in the main text are based on density as the measure  
212 was common to both datasets but additional results based on biomass are also provided as  
213 Supplementary Materials for the CS experiment.

### 214 *2.4.1. Weed community descriptors*

215 All diversity indices were computed at three different scales: the quadrat scale, the plot:year scale (the  
216 8 quadrats for a given combination of plot:year were summed, *i.e.* 60 plot:year observations in total  
217 for the CS experiment) and the plot scale (the 48 quadrats for a given plot were summed across years,  
218 *i.e.* 10 plot observations in total for the CS experiment; the 6 annual surveys for a given plot were  
219 summed across years, *i.e.* 17 plot observations in total for the farmers' network). Quadrat and  
220 plot:year scale are referred to as the annual scale whereas the plot scale is referred to as the plurennial  
221 scale.

222 Weed diversity was characterized through two taxonomic indices (species richness and Shannon  
223 diversity index) and one index of functional dispersion (Rao's quadratic entropy). Species richness  
224 was computed as the number of species and Shannon diversity index was computed as  $H' =$   
225  $-\sum_{i=1}^S p_i \times \ln(p_i)$  where  $p_i$  represents the relative abundance of species  $i$  and  $S$  represents species  
226 richness (Scheiner, 2012). Rao's quadratic entropy (Botta-Dukát, 2005) was computed with the  
227 functional diversity function (FD) of the R FD package (Laliberté and Legendre, 2010) on eight  
228 attributes reflecting plant strategies: 1) life cycle duration (annual vs. perennial), 2) number of  
229 cotyledons (grasses vs. broadleaves), 3) growth form (rosette, hemirosette or erosulate (*i.e.* no rosette  
230 during the whole plant cycle)), 4) germination period (non-seasonal, strict spring, strict summer,  
231 staggered germination from spring to summer, autumn and spring with no preference, autumn and  
232 spring with a preference for autumn), 5) specific leaf area, 6) flowering period (indifferent,  
233 spring/summer, summer, summer/autumn), 7) average height and 8) seed mass. Rao's quadratic  
234 entropy was weighted by density so as to account for the potential dominance of species with specific  
235 functional attributes (otherwise the indicator is simply based on absence/presence and a species  
236 representing 75% of abundance has as much weight on the analysis as a species representing 5%).  
237 Average height and seed mass were ln-transformed prior to the computation of Rao's quadratic  
238 entropy to reduce skewness. All attributes were either extracted from the LEDA (Kleyer et al., 2008),  
239 BioFlor (Kühn et al., 2004) or Kew Gardens databases (Kew, 2020). Monospecific or empty surveys  
240 were attributed the lowest possible value of both Shannon diversity index (*i.e.* 0) and Rao's quadratic



241 entropy (*i.e.* 0). These surveys were maintained because their removal would have inflated the average  
242 level of weed diversity, and hence, would have lacked to reflect the real level of weed diversity,  
243 particularly at the quadrat scale.

244 Community weighted means (CWM, average value of a given attribute weighted by the relative  
245 abundance of each species) were also computed on five attributes (life cycle duration, number of  
246 cotyledons, average height, seed mass, germination period) reflecting weed community response to  
247 agricultural practices (Lavorel et al., 2008; Ricotta and Moretti, 2011). CWM of life cycle duration,  
248 number of cotyledons, height and seed mass were computed at the plot:year scale to account for the  
249 patchy distribution of certain weed species with key response traits. CWM of germination periods was  
250 computed at the plot scale in order to encompass the whole crop sequence.

#### 251 2.4.2. Data analysis

252 All statistical analyses were carried out with the R software version 3.6.2 (R Core Team, 2016).  
253 Generalized linear mixed effect models were fitted with the R glmmTMB package (Brooks et al.,  
254 2017) in order to account for the nature of certain response variables (*e.g.* Poisson distribution for  
255 species richness), the hierarchical design of the data (*e.g.* repeated sampling in a given field in time  
256 and space) and/or zero inflation to account for the excess zeroes (with respect to Tweedie distribution)  
257 in Shannon diversity index at the quadrat scale for the CS experiment (where ECS1 showed a high  
258 proportion of empty quadrats). The list of all the fitted models can be found in Supplementary Table 1.  
259 All response variables (weed biomass, weed density, diversity indicators, CWMs) were modelled as a  
260 function of block (for the CS experiment only) and CSs (ECS or FCS) in order to highlight potential  
261 differences between CSs. Statistical models were fitted at the quadrat, plot:year and plot scale (except  
262 the plot scale for the CS experiment due to lack of statistical power (N=10, d.f. CS effect=4)).  
263 Temporal coverage was identical for all three scales for a given dataset (2012-2017 for the CS  
264 experiment and 2008-2013 for the farmers' network) and no data was missing. Year (as factor), plot,  
265 block:year (CS experiment only), and CS:year were considered as random effects at both the quadrat  
266 and plot:year scales. A unique plot:year identifier was added as a random effect for analyses carried  
267 out at the quadrat scale in order to account for pseudoreplication (CS experiment only). Significance  
268 of CS effects (*i.e.* ECS or FCS) were determined through likelihood ratio tests. Model diagnostics (*i.e.*  
269 QQ plot residuals, quantile regression of residual vs. fitted, overdispersion, zero-inflation) were  
270 visualized using the DHARMA package (Hartig, 2020). Contrasts were adjusted using the emmeans  
271 package (Lenth, 2019). Magnitude and significance of correlations between diversity variables at  
272 different scales were assessed through the Spearman correlation coefficient and test, respectively.

273 Partial canonical correspondence analysis (pCCA) was performed at the plot:year scale to determine  
274 the percentage of variance in weed community data which could be explained by ECS or FCS, after  
275 accounting for the covariates year (both datasets) and block (CS experiment dataset, pCCA #1,

276 covariates are shown in parenthesis). The response matrix consisted of 60 or 102 rows (the plot:years)  
277 by 38 and 40 columns (one for each species observed in more than one plot:year), respectively for the  
278 CS experiment and farmers' network. In the CCA analysis, weed densities were  $\ln(X+1)$ -transformed  
279 to reduce the influence of dominants. The following CCA analyses were conducted:

280 pCCA #1: weed communities~ECS or FCS+(block)+(year)

281 The proportion of partial variance explained by crop type was determined by replacing ECS or FCS in  
282 pCCA #1 by crop type (pCCA #2):

283 pCCA #2: weed communities~crop type+(block)+(year)

284 To determine whether ECS or FCS effects were simply due to the integration of new crop types  
285 (combination of botanical family and sowing period), the percentage of partial variation explained by  
286 pCCA #1 was compared to the percentage of partial variation explained by the joint effect of ECS or  
287 FCS and crop type (pCCA #3):

288 pCCA #3: weed communities ~ECS or FCS +crop type+(block)+(year)

289 The difference in explained variance between pCCA #3 and #2 can be interpreted as ECS or FCS  
290 effects which cannot simply be explained by crop type, whereas the difference between pCCA #3 and  
291 #1 can be interpreted as the net effect of crop type which cannot be explained by associated  
292 agricultural operations. To identify whether ECS or FCS effects were identical across all crops, the  
293 percentage of variance explained by the joint effect of ECS or FCS and crop type (pCCA #3) was  
294 compared to the percentage of variance explained by the interaction between ECS or FCS and crop  
295 type (*i.e.* pCCA #4, where "\*" denotes all simple effects and the first order interaction).

296 pCCA #4: weed communities~ECS or FCS\*crop type+(block)+(year)

297 Due to the lack of a complete experimental design (*e.g.* all phases of the crop rotation of a given CS  
298 were not present every year in each block), meaningful (*i.e.* restricted) permutations were not feasible  
299 and hence, only percentages of explained variance were retained. The ordination diagrams were  
300 produced with the CANOCO software (Šmilauer and Lepš, 2014).

### 301 3. Results

302 In the CS experiment, 46 taxa were observed over the 2012-2017 period. The dominant weed species  
303 were *Alopecurus myosuroides* Huds., *Viola arvensis* Murray, *Fallopia convolvulus* (L.) A.Löve,  
304 *Galium aparine*, *Lysimachia* spp. (*arvensis* (L.) U.Manns & Anderb. and *foemina* (Mill.) U.Manns &  
305 Anderb.) and *Polygonum aviculare* L., representing 15, 14, 12, 8, 7 and 6% of total weed density after  
306 weeding, respectively (Figure 2A). Over half (*i.e.* 53%) of the quadrats sampled in ECS1 did not  
307 contain any weed species at crop flowering, *i.e.* after weeding (vs. 2-12% in ECS2-ECS5). Average  
308 weed density after weeding (plant m<sup>2</sup>±SE) at the quadrat scale was greater in ECS2 (39.0±11.0),  
309 ECS3 (51.2±14.3), ECS4 (34.7±9.8) and ECS5 (53.4±14.9) than in ECS1 (7.3±2.3). Equivalent  
310 information based on biomass for the ECS can be found in Supplementary materials (Supplementary  
311 Tables 2, 3, 4, Supplementary Figures 1, 2, 3). Weed biomass was comprised between 8 and 23 g m<sup>2</sup>  
312 for ECS2 to ECS5 and nearly null (<1 g m<sup>2</sup>) for ECS1.

313 In the farmers' network, 61 taxa were observed over the 2008-2013 period. The dominant weed  
314 species were *V. arvensis*, *F. convolvulus*, *Solanum nigrum* L., *Veronica hederifolia* L., *A.*  
315 *myosuroides*, *Geranium dissectum* L., *Aethusa cynapium* L. and *Scandix pecten-veneris* L.,  
316 representing 29, 14, 10, 8, 5, 4, 4 and 3% of the total weed density after weeding, respectively  
317 (Figure 2B). Average weed density after weeding (plant m<sup>2</sup>±SE) at the plot:year scale was generally  
318 low and not significantly different between FCS (FCS2=3.8±1.2, FCS3=5.5±1.9, FCS4=6.1±2.3 and  
319 FCS7=4.7±1.7).

320 [Figure 2]

#### 321 3.1. Taxonomic and functional diversity at different scales

322 In the CS experiment, CS had a significant effect on weed species richness, Shannon diversity index  
323 and Rao's quadratic entropy at both the quadrat and the plot:year scales (Table 3). All alternative CSs  
324 (ECS2-ECS5) generated greater diversity values than the reference system (ECS1) at all three scales.  
325 Even though less pronounced, differences tended to persist at the plot scale for species richness,  
326 Shannon diversity index and Rao's quadratic entropy (no statistical test performed, Table 3).  
327 Correlations between weed diversity indicators were all significant between each other at both the  
328 quadrat and plot:year scales but not at the plot scale (Supplementary Table 3). For a given  
329 combination of plot and year, average weed diversity at the quadrat scale showed to be highly  
330 correlated with weed diversity computed across all quadrats (Supplementary Table 3). However, only  
331 average species richness at the plot:year scale was significantly correlated with its reciprocal at the  
332 plot scale (Supplementary Table 3).

333 [Table 3]

334 In the farmers' network, CS had a significant effect on weed species richness, Shannon diversity index  
335 and Rao's quadratic entropy at both the plot:year and the plot scale, excepted for Rao's quadratic  
336 entropy at the plot scale (Table 3). FCS3 expressed higher weed diversity values than the 3 other CSs  
337 at the plot:year scale, although less pronounced at the plot scale (Table 3). Weed diversity indicators  
338 were significantly correlated between each other, except species richness and the Rao's quadratic  
339 entropy at the plot scale (Supplementary Table 3).

### 340 **3.2. Associations between cropping systems, weed species and functional traits**

341 In the CS experiment, ECS alone explained 25.7% of partial variation (after the removal of year and  
342 block effect, which explained 14.5% of total variation, pCCA #1) whereas crop type alone explained  
343 30.6% of partial variation (pCCA #2, Figure 3). ECS and crop type (pCCA #3) jointly explained 50%  
344 of partial variation, indicating that ECS had a unique effect on weed community composition on top of  
345 crop type (*i.e.*  $50-30.6=19.4\%$  of partial variation). The interaction between ECS and crop type  
346 (pCCA #4) explained 64.9% of partial variation, highlighting important variations in weed community  
347 composition across ECS for a given crop type.

348 When the analysis was solely constrained by ECS (after the removal of year and block effects,  
349 pCCA #1), the first and second axis explained 9.4 and 9% of partial variation, respectively (Figure  
350 4A). The first axis clearly discriminated ECS2 (no-till) from the other ploughing-based systems and  
351 could therefore be associated with the presence or absence of ploughing (Table 2). Weed species  
352 associated with no-till (ECS2) were *Echinochloa crus-galli* (L.) P.Beauv., *Convolvulus arvensis* L.,  
353 *Lapsana communis* L., *Plantago lanceolata* L., *Senecio vulgaris* L., *Sonchus* spp. (*asper* L. and  
354 *oleraceus* L.), *Myosotis arvensis* (L.) Hill, *C. arvensis*, *Taraxacum officinale* F.H.Wigg., and *Lolium*  
355 *perenne* L.. Weed species associated with tillage (ECS1, ECS3, ECS4, ECS5) were *P. aviculare*,  
356 *Euphorbia exigua* L., *Fumaria officinalis* L., *Chaenorhinum minus* (L.) Lange, and *Thlaspi arvense*  
357 L.. The second axis clearly discriminated ECS5 (mechanical weeding) from ECS3 (chemical  
358 weeding), and was associated with weed management type in spring/summer crops (Table 2). Weed  
359 species associated with mechanical weeding in spring/summer crops (ECS5) were *Polygonum* spp.  
360 (*persicaria* L., *lapathifolium* L., and *aviculare* L.), *Rumex* spp. (*obtusifolius* L. and *crispus* L.), *S.*  
361 *nigrum*, *Chenopodium album* L., *C. arvensis*, and *Lipandra polysperma* (L.) S.Fuentes, Uotila &  
362 Borsch.. Weed species associated with chemical weed control (ECS3) were *T. arvensis*, *C. minus*,  
363 *Capsella bursa-bastoris* (L.) Medik., *V. arvensis* and *Veronica hederifolia* L..

364 The proportion of monocotyledonous species was greater in ECS2 than in ECS1 (Table 4), which is  
365 coherent with ECS2's association with *Echinochloa crus-galli* and *Lolium perenne* (Figure 4A), and  
366 the dominance of *P. convolvulus* in ECS1 (74% of total abundance, Figure 2A). The proportion of  
367 perennials was greater in ECS2 and ECS5 than in ECS1 (Table 4), which is coherent with ECS2  
368 association with *L. perenne*, *C. arvensis*, *P. lanceolata*, *T. officinale*, and ECS5's association with

369 *Rumex* spp. and *C. arvensis* (Figure 4A). Community weighted mean of height was greater in ECS1  
370 and ECS5 than in ECS3 (Table 4), which is coherent with ECS5's association with *Rumex* spp., *C.*  
371 *arvensis*, *C. album*, *S. nigrum*, and *L. polysperma* and ECS3's association with *V. arvensis* or *V.*  
372 *hederifolia* (Figure 4A). Community weighted mean of seed mass was greater in ECS1 than in all  
373 other ECS (Table 4), mostly as a result of *P. convolvulus*.

374 ECS could be classified into three main categories according to weed germination period profiles  
375 (Figure 5A): 1) those with a high proportion of autumn and/or spring germinating species (ECS1,  
376 ECS3, and ECS4), 2) those with a high proportion of indifferent or summer (mainly due to  
377 *Echinochloa crus-galli*) germinating species (ECS2) and 3) those with a high proportion of spring  
378 and/or summer germinating species (ECS5).

379 [Table 4 + Figure 4 + Figure 5]

380 In the farmers' network, FCS alone explained 10.8% of partial variation (after the removal of year  
381 effect, which explained 6.6% of total variation, pCCA #1) whereas crop type alone (pCCA #2)  
382 explained 14.6% of partial variation. FCS and crop type (pCCA #3) jointly explained 21.5% of partial  
383 variation, indicating that FCS had a unique effect on weed community composition on top of crop type  
384 (*i.e.* 21.5-14.6=6.9% of partial variation). The interaction between FCS and crop type (pCCA #4)  
385 explained 31% of partial variation, highlighting slight variations in weed community composition  
386 across FCS for a given crop type.

387 When the analysis was solely constrained by FCS (after the removal of year effect, pCCA #1), the first  
388 and second axis explained 5.1 and 3.6% of partial variation, respectively (Figure 4B). The first axis  
389 clearly discriminated FCS4 (high frequency of spring-sown crops, Table 2) from the other FCS and  
390 could therefore be associated with crop diversification through the introduction of spring-sown crops.  
391 Weed species associated with the introduction of spring-sown crops (FCS4) were *Euphorbia*  
392 *helioscopia* L., *S. asper*, *Bidens tripartita* L., *Mercurialis annua* L., and *S. nigrum*. The second axis  
393 clearly discriminated FCS3 from FCS2 and FCS7, and could therefore be associated with a  
394 combination of weed management type and tillage intensity (*i.e.* minimum tillage, pre-sowing  
395 herbicide and in-crop herbicide applications at low dose in FCS3 vs. ploughing and few herbicide  
396 applications at high dose in FCS2/FCS7, Table 2). Weed species associated with low tillage intensity,  
397 pre-sowing herbicides and in-crop herbicide applications at low dose (FCS3) were *L. communis*,  
398 *Elymus repens* (L.) Gould, *Legousia hybrida* (L.) Delarbre, *Equisetum arvense* L., *Cyanus segetum*  
399 Hill, *Geranium columbinum* L., *S. pecten-veneris*, and *Medicago* spp.. Weed species associated with  
400 ploughing and few herbicide applications at high dose (FCS2, FCS7) were *V. hederifolia*, *V. arvensis*,  
401 *C. album*, *Aphanes arvensis* L., *E. exigua*, *M. arvensis*, and *A. cynapium*.

402 The proportion of monocotyledonous species was not significantly different across FCS (Table 4). The  
403 proportion of perennials was greater in FCS3 than in FCS2 (Table 4), which is coherent with FCS3's

404 association with *E. repens*, *E. arvense* and *Medicago* spp. (Figure 4B). Community weighted mean of  
405 height tended to be lower in FCS2 but was not significantly different across FCS (Table 4).  
406 Community weighted mean of seed mass was greater in FCS3 than in FCS2, which showed the lowest  
407 (Table 4).

408 FCS could be classified into two main categories according to weed germination period profiles  
409 (Figure 5B): 1) those with a high proportion of autumn and/or spring germinating species (FCS2,  
410 FCS3, and FCS7), and 2) those with a high proportion of summer germinating species (FCS4).

411

## 412 **4. Discussion**

### 413 **4.1. Various options of cropping diversification promote taxonomic and functional weed** 414 **diversity**

#### 415 *4.1.1. Diversity at the annual (quadrat and plot:year) scale*

416 All alternative ECSs (ECS2 to ECS5) and one FCS (FCS3), which were previously shown to limit  
417 crop yield losses to low levels (Albrecht et al., 2016; Adeux et al., 2019a; Yvoz et al., 2020b),  
418 illustrated that multiple agronomic options were possible to promote high weed diversity at the annual  
419 scale (*i.e.* quadrat and plot:year scales). Higher weed density in all alternative experimented cropping  
420 systems (ECS2-5) did not transcribe into levels of weed biomass susceptible of generating significant  
421 crop yield losses (Adeux et al., 2019a) because weed management tactics targeted the most  
422 competitive weed species (e.g. *Galium aparine*, *Alopecurus myosuroides*, *Cirsium arvense*) and  
423 because a high proportion of total weed density was represented by late germinating weeds (possibly  
424 promoted by mechanical weeding and/or late sampling). Weed densities in the farmers' network were  
425 too low (<7 plants m<sup>-2</sup>) to generate any significant yield loss (Quinio et al., 2017; Yvoz et al., 2020b).  
426 Competitive species were observed well below their 5% yield loss threshold (Wilson and Wright,  
427 1990).

428 The regional reference (ECS1) and three of the four FCS (FCS2, FCS4 and FCS7) were illustrative of  
429 the dramatically low level of weed diversity present in intensively managed agricultural fields in the  
430 study region, but also in accordance with other central and northern European countries (Andreasen et  
431 al., 1996; Sutcliffe and Kay, 2000; Baessler and Klotz, 2006; Fried et al., 2009; Albrecht et al., 2016).  
432 Fields managed under ECS1 principles showed less than one species per quadrat on average and fields  
433 managed under FCS2, FCS4 and FCS7 principles harbored only three to four species per field on  
434 average each year. These results could be attributed to the oversimplified and intensive practices  
435 implemented in ECS1 and FCS2, namely low crop diversity, near systematic ploughing, repeated use  
436 of pre- and post-emergence broad spectrum herbicides, and high nitrogen fertilisation (Gressel and  
437 LeBaron, 1982; Haas, 1982; Nikolich et al., 2012). However, low weed diversity could not be

438 attributed to the same reasons for FCS4 and FCS7, which resorted to a more diversified crop sequence.  
439 The detailed characterization of farming practices highlighted that FCS remained intensive on a yearly  
440 basis, with nitrogen and herbicide use being as important as in ECS1 (mechanical weeding being  
441 insignificant). In contrast, all alternative ECS (ECS2 to ECS5) showed three species per quadrat and  
442 FCS3 averaged 7.9 species per field each year. Such results are of considerable importance because  
443 they stress that diverse strategies are available to promote weed diversity while preventing yield loss  
444 (Adeux et al., 2019a). Moreover, higher weed diversity at the local scale (*i.e.* quadrat) could mitigate  
445 crop yield losses (for a given level of weed biomass) through more complementary use of resources in  
446 space and time (Adeux et al., 2019b) and promote other organisms sustaining ecosystem services  
447 (Marshall et al., 2003; Blaix et al., 2018).

448 The adopted CS approach did not allow to disentangle the relative effects of crop sequence, tillage,  
449 and weed control on weed diversity. Nevertheless, greater weed diversity at the annual scale in the  
450 different agronomic options cited above most likely resulted either from less intensive in-crop weed  
451 control in the CS experiment (Doucet et al., 1999; Légère et al., 2005), or from inefficient long-term  
452 weed management in FCS3 (Colbach et al., 2020; Yvoz et al., 2020b). Increased weed diversity in  
453 ECS3 (chemical weeding only) highlights that a well-balanced rotation including a diverse suite of  
454 weed management tactics (targeted use of post-emergence herbicide included) can reduce total  
455 herbicide use (-40% compared to ECS1), increase weed diversity and limit yield losses due to  
456 competitive dominants, as shown in (Adeux et al., 2019b) on the same CSs. To reach similar levels of  
457 performance in terms of weed diversity while limiting yield losses, ECS5 (mechanical weeding only)  
458 had to resort to more than twice as many weeding operations. Indeed, weed management strategies in  
459 alternative CSs relied on a combination of non-chemical weed management tools with partial effect  
460 rather than broadcast use of broad spectrum herbicides (Swanton and Weise, 1991), as it was the case  
461 for the farmers' network. Higher weed diversity in all alternative ECSs may also have resulted from  
462 reduced nitrogen fertilisation (which was not the case in the farmers' network) and crop productivity  
463 (Albrecht et al., 2016; Adeux et al., 2019a). Indeed, higher nitrogen fertilisation in ECS1 and all FCS  
464 may have exerted a strong competitive effect on weed species susceptible to shading (Kleijn and van  
465 der Voort, 1997), thereby reflecting potential antagonisms between weed diversity and crop  
466 productivity in highly productive agricultural contexts (Albrecht et al., 2016).

467 Surprisingly, ECS2 (no-till) promoted higher weed diversity at the annual scale even though total  
468 herbicide use was 47% greater than in ECS1. The same trends were observed in the farmers' network:  
469 FCS3 (reduced-tillage) showed the highest weed diversity at the annual scale even through total  
470 herbicide use was 8 to 15% greater than in the other FCS. Three complementary hypotheses could be  
471 formulated to explain this result. First, ECS2 and FCS3 showed the greatest proportion of glyphosate  
472 in total herbicide use, a systemic non-residual herbicide used for burn-down weed control prior to crop  
473 sowing, which had no direct effect on weed seedlings emerging after sowing (due to the timing of

474 application and mode of action). This hypothesis is in line with Plaza et al. (2011), Dorado and Lopez-  
475 Fando (2006), Murphy et al. (2006), Villora et al. (2019) and numerous other authors whom reported  
476 no difference in weed diversity between tillage systems, or greater weed diversity in no-till, although  
477 no-till resorted to glyphosate applications for burn-down control in addition to the other in-crop  
478 herbicides used in the other systems. Second, in-crop herbicide use was actually 30% lower in ECS2  
479 than ECS1. No pre-emergence herbicides were applied in ECS2, due to their low efficacy in no-till  
480 systems, where organic matter is concentrated on top of the soil surface (Peter and Weber, 1985;  
481 Blumhorst et al., 1990). Such weeding constraints could have allowed a greater diversity to establish  
482 in the crop. This second hypothesis cannot be applied to FCS3, which presented similar herbicide use  
483 after sowing than the three other FCS. Third, no-till (ECS2) or superficial tillage (FCS3) generate a  
484 concentration of the weed seedbank in the top soil layers (Mohler et al., 2006), thereby increasing the  
485 probability of weed seed recruitment, except for species exhibiting decreased germination on the soil  
486 surface (Cordeau et al., 2015).

#### 487 4.1.2. *Diversity at the plurennial scale*

488 Differences in annual weed diversity across CSs clearly persisted at the plurennial scale (*i.e.* plot  
489 scale) when considering species richness. Increasing crop diversity while reducing herbicide use  
490 increased species diversity in all alternative ECSs, which harbored twice as many species as ECS1  
491 over the course of the experiment. Such results could be attributed to a greater diversity of sowing  
492 periods which allowed the development of weed species with different germination requirements  
493 (Gunton et al., 2011). Indeed, Mahaut et al. (2019) showed across a large-scale French weed  
494 monitoring network encompassing 1045 crop sequences that greater variability of sowing dates was  
495 associated to greater weed species richness at the plurennial scale. Murphy et al. (2006) and Sosnoskie  
496 et al. (2006) also reported a more diverse weed seedbank after a 3-year rotation integrating summer  
497 and winter-sown crops than after a 2-year rotation integrating only summer crops or a monoculture.  
498 Furthermore, a diverse set of studies spanning different continents report clear associations between  
499 crops (and hence sowing dates) and weed species (Hyvönen and Salonen, 2002; Poggio et al., 2004;  
500 Ryan et al., 2010; Andrade et al., 2017), suggesting that a greater turnover in crops species (and hence  
501 sowing dates) can favor weed species turnover in time. In the farmers' network, herbicide use  
502 remained high, irrespectively of crop diversity, thereby generating little differences in weed diversity  
503 across FCS (exception made of FCS3). Higher weed diversity in FCS3 could rather be attributed to the  
504 combination of low crop diversity, low tillage intensity and moderate use of in-crop herbicides. Little  
505 variation could be observed across ECSs or FCSs in terms of Shannon diversity and of Rao's quadratic  
506 entropy at the plurennial scale. Such outcomes could arise from the fact that (i) a species with high  
507 abundance a given year can lead to dominance at the CS scale if total abundance is low the other  
508 years, even if species relative abundance is evenly distributed within the other years, and that (ii) the  
509 most abundant and frequent weed species were able to maximize weed functional trait space in the CS



510 experiment (based on the selected traits extracted from databases). Ecosystem services associated with  
511 weeds also depend on species abundance (Tarjuelo et al., 2019), thereby questioning the capacity of  
512 ECS1 and all FCS to provide ecosystem services with extremely low levels of weed abundance.

#### 513 **4.2. Different options of cropping system diversification generate different combinations of** 514 **weed traits**

515 Different options of CS diversification reached similar levels of weed diversity through the selection  
516 of weed communities with different functional attributes. In accordance with previous studies, tillage,  
517 crop and weed control methods appeared as major filters on the functional composition of weed  
518 communities (Légère et al., 2005; Ryan et al., 2010; Gunton et al., 2011; Fried et al., 2012; Trichard et  
519 al., 2013). The first and second axis of the ordination of the CS experiment and the farmers' network,  
520 respectively, clearly illustrated the role of ploughing (*i.e.* inversion tillage) in structuring weed  
521 communities. The lack of soil disturbance in ECS2 and reduced tillage in FCS3 was reflected by their  
522 association with perennials and wind-disseminated *Asteraceae* species (confounded with non-seasonal  
523 species), and the association of ECS2 with grasses, as previously reported by *e.g.* Froud-Williams et  
524 al. (1988), Thomas et al. (2004) or Mirsky et al. (2013) in other reduced or no-till systems. In  
525 accordance with previous studies (Dorado and Lopez-Fando, 2006; Giambalvo et al., 2012; Hernández  
526 Plaza et al., 2015; Pardo et al., 2019), weed communities in ECS1 (near systematic ploughing) were  
527 characterized by species with more important seed mass than all other ECS (which ranged from a  
528 ploughing frequency of 0.5 for ECS3-5 to 0 for ECS2). Under systematic conventional tillage, high  
529 seed mass could confer species an advantage in terms of germination depth and competitive ability  
530 (Turnbull et al., 1999; Gardarin et al., 2009) whereas under permanent no-till, greater seed mass could  
531 limit seed:soil contact and hence weed seed imbibition and recruitment (Chauhan et al., 2012). The  
532 lack of differences between ECS2 (systematic no-till) and ECS3-5 (ploughing once every two years)  
533 or the opposite trends observed in farmers' network (the community with the highest seed mass was  
534 found in the FCS with the lowest ploughing frequency) could point out to intense filtering of seed  
535 mass in absence of soil disturbance (systematic ploughing vs. no-till) but a more diverse set of  
536 winning strategies at higher levels (Hernández Plaza et al., 2015). Indeed, Fried et al. (2012)  
537 highlighted that low seed mass (and hence high seed production) could also confer species an  
538 advantage to cope with frequent soil disturbances. Such discrepancies could arise from the data type  
539 that was used to compute CWM: density (as in Fried et al. (2012)) could give more weight to ruderal  
540 species with low seed mass and high seed production, whereas biomass (as in Barberi et al. (2018))  
541 could give more weight to competitive species with high seed mass (*e.g.* *A. myosuroides* and *G.*  
542 *aparine*). Finally, it is important to stress that CSs act on multiple species traits at once (some of which  
543 may be correlated) and that higher seed mass in ECS1 may simply be confounded with other traits  
544 which conferred *G. aparine* or *F. convolvulus* an advantage (*e.g.* herbicide tolerance).

545 The second and first axis of the ordination of the CS experiment and farmers' network, respectively,  
546 revealed an association between spring/summer and strict spring weed species (*e.g.* *C. arvense*, *C.*  
547 *album*, *P. aviculare*, *S. nigrum*, *Persicaria* spp.) and high proportion of spring crops in the rotation for  
548 ECS4/ECS5 and FCS4. Such effects could not only be attributed to crop diversification as ECS4 (6-  
549 year rotation) was closely associated with ECS1 (3-year rotation) in the ordination. Rather, we  
550 hypothesize that (i) mechanical weeding (main and unique technique for direct weed control in ECS4  
551 and ECS5) was not as efficient as chemical weeding on species in spring/summer crops, possibly due  
552 to staggered germinations or quick growth rate, (ii) late mechanical weeding operations in cereal crops  
553 stimulated new germinations (Mohler, 1993; Benvenuti et al., 2021), and (iii) that high herbicide use  
554 in ECS1 (3-year rotation with winter crops) selected against autumn/winter germinating species and  
555 for species capable of germinating after herbicide applications (*i.e.* strict spring weed species).

556 The high proportion of perennials in ECS5 and FCS3 could not be attributed to the same reasons.  
557 First, herbicides in ECS1/ECS3/ECS4 and FCS2/FCS4/FCS7 allowed an efficient management of  
558 *C. arvense/Rumex* spp. and *P. lanceolata/C. vulgare*, the two dominant couples of perennials in the CS  
559 experiment and farmers' network, respectively. Second, technical difficulties in one of the two ECS5  
560 plot did not allow a successful establishment of alfalfa, which has previously been shown to be an  
561 efficient weed management tool (*i.e.* through repeated mowing operations) against perennials in  
562 herbicide-free CSs (Lukashyk et al., 2008; Lacroix et al., 2021). Finally, the proportion of perennials  
563 was high in FCS3 because reduced tillage intensity was not coherently compensated by other efficient  
564 agronomic levers such as a diversified crop sequence including cover cropping, as farmers do when  
565 transitioning to conservation agriculture (Chauhan et al., 2012; Derrouch et al., 2020).

#### 566 **4.3. Insights on how and when to assess weed diversity**

567 One of the originalities of our study was to assess weed diversity from a taxonomic and functional  
568 point of view, based on density or biomass, and at the quadrat, plot:year and plurennial scales. The  
569 results provide insights for future works to guide weed sampling and computation of diversity indices.

##### 570 *4.3.1. Gain to move from a taxonomic to a functional point of view*

571 Our results showed that functional diversity provided little additional insight compared to taxonomy-  
572 based diversity indicators (*i.e.* species richness and Shannon diversity index). The ranking between  
573 ECS or FCS was highly consistent across all taxonomic and functional diversity indicators. In the CS  
574 experiment, Rao's quadratic entropy and taxonomy-based indicators showed highly significant  
575 correlations (see Supplementary Table 3). This can be explained by the relatively small species pool of  
576 our study sites and the fact that the five most abundant species of the experiment were functionally  
577 unique. Therefore, an increase in species richness was necessarily associated with an increase in  
578 functional diversity. However, it is important to note that intraspecific trait variability was not  
579 considered (Kazakou et al., 2014; Yvoz et al., 2020a).

580       4.3.2.   *Describing weeds by their density or biomass*

581   All the alternative ECSs showed greater weed diversity values than ECS1, whether indices were based  
582   on density or on biomass. Nevertheless, diversity indices based on density tended to magnify these  
583   differences. The species producing the most biomass within a CS were not necessarily the species  
584   found at greatest density (*e.g.* in ECS3, *A. myosuroides* was dominant in terms of biomass whereas *V.*  
585   *arvensis* was dominant in terms of density). Sampling weed biomass per species is often considered  
586   time consuming and is therefore substituted by weed density (Fried et al., 2008; Santín-Montanyá et  
587   al., 2013; Trichard et al., 2013; Mahaut et al., 2019) or weed cover (Hiltbrunner et al., 2008; Ulber et  
588   al., 2009), even though some authors have argued biomass as more relevant to compute diversity  
589   indices (Guo and Rundel, 1997). However, such considerations could have important implications.  
590   Density-based indicators do not reflect species' competitive ability, whereas biomass-based indicators  
591   gave more weight to competitive species. Therefore, density indicators appear relevant for species  
592   centered analysis (*i.e.* the diversity of successful reproductive strategies) whereas biomass indicators  
593   appear more suitable for agroecosystem centered analysis (*i.e.* the diversity of species which  
594   contributed to agroecosystem functioning, weed-crop competitive relationships).

595       4.3.3.   *Relation between diversity at different spatio-temporal scales*

596   The assessment of weed diversity at different scales allowed us to appreciate weed diversity turnover  
597   between quadrats at the plot:year scale and between years at the plot scale. Species richness increased  
598   by roughly a 3-fold from the quadrat to the plot:year scale for all ECSs and by a 3- and 2-fold from the  
599   plot:year scale to the plot scale for ECS1/all FCS and all other ECS, respectively. Such low species  
600   turnover at the plot scale could be associated with generalist species which can tolerate a wide range of  
601   agronomic practices (Fried et al., 2010) or to weed samplings positioned late in the crop cycle causing  
602   an overlap between two crop seasons, (Hanzlik and Gerowitt, 2016). This multi-scale approach also  
603   allows to conclude that all alternative ECSs (ECS2 to ECS5) harbored as many weed species a given  
604   year as ECS1 harbored over the whole length of the crop sequence. This was also the case in the  
605   farmers' network, in which FCS3 harbored as many weed species a given year as FCS2/FCS4/FCS7  
606   harbored over the whole length of the crop sequence.

607       **4.4. Differences between experimented and farmer cropping systems**

608   All alternative ECS harbored higher weed diversity than the reference system, and were previously  
609   shown to limit yield losses due to weeds (Adeux et al., 2019a). All these alternative ECS expressed  
610   similar levels of weed diversity but weed functional response was dependent on the combination of the  
611   adopted farming practices. Conversely, weed diversity did not increase with crop diversification in the  
612   farmer's network. All FCSs expressed levels of weed diversity similar to ECS1, except FCS3. This  
613   could be explained by the short length of the CS diversification gradient explored in the farmers'  
614   network, in comparison with the CS experiment which resorted to highly differentiated agronomic

615 options. Moreover, all FCS relied on high herbicide use, similar to that of ECS1. Nevertheless,  
616 previous studies have reported contradictory results concerning the effect of herbicide use on species  
617 richness: certain authors report little effect (Mahn and Helmecke, 1979; Derksen et al., 1995), while  
618 others highlight a negative effect (José-María et al., 2013).

619 The CS experiment highlighted that different options of CS diversification are available to increase  
620 weed diversity without deteriorating weed management. However, farmers remain reluctant to  
621 implement such innovative systems. Results collected in experimental stations can differ from those  
622 collected in farms because experimenters tend to explore extreme alternative strategies without having  
623 to assume the economic consequences (Deytieux et al., 2012). Reducing herbicide reliance requires  
624 long-term strategic weed management, which aims to prevent rather than to control weed infestations  
625 (Mace et al., 2007), while the current mainstream practices focus on control rather than on prevention  
626 (Wilson et al., 2008). Risk aversion also influences weed management strategies: farmers tend to  
627 minimize the risk of failure, even at the cost of reducing their economic performance (Doohan et al.,  
628 2010), while experimenters accept failure as a response of the agronomic practices tested. This is  
629 coherent with previous studies reporting higher herbicide use and lower weed diversity in commercial  
630 farming conditions than in experimental stations (Colbach and Cordeau, 2018).

## 631 **5. Conclusion**

632 Through an in-depth analysis of weed communities across a complete rotation cycle, we highlighted  
633 that diverse options of CS diversification could promote weed diversity at both the annual and  
634 plurennial scales. Reduction of herbicide use through CS diversification appeared as the main driver of  
635 increased weed diversity and efficient long-term weed management. Tillage, weed management and  
636 crop type appeared as the main drivers of weed community functional structure. Due to the limited  
637 species pool, the functional diversity approach provided little additional insight compared to  
638 taxonomy-based diversity approach. However, CS effects on weed diversity were clearer at the  
639 plot:year (*i.e.* annual) than plot (*i.e.* plurennial) scale. CS diversification did not have the same effect  
640 in the farmers' network as in the CS experiment, possibly because all FCSs relied on high levels of  
641 herbicide use. These results suggest that diverse opportunities are available to promote weed diversity  
642 in commercial farming conditions or that further research is required to identify the factors limiting the  
643 transposability of these alternative ECSs in commercial farming conditions.

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657

## 658 **Conflict of Interest**

659 The authors declare that they have no conflict of interest.

660

## 661 **References**

- 662 Adeux, G., Munier-Jolain, N., Meunier, D., Farcy, P., Carlesi, S., Barberi, P., Cordeau, S., 2019a.  
663 Diversified grain-based cropping systems provide long-term weed control while limiting  
664 herbicide use and yield losses. *Agron. Sustainable Dev.* 39, 42.
- 665 Adeux, G., Vieren, E., Carlesi, S., Bàrberi, P., Munier-Jolain, N., Cordeau, S., 2019b. Mitigating crop  
666 yield losses through weed diversity. *Nature Sustainability* 2, 1018-1026.
- 667 Albrecht, H., Cambecèdes, J., Lang, M., Wagner, M., 2016. Management options for the conservation  
668 of rare arable plants in Europe. *Botany Letters* 163, 389-415.
- 669 Andrade, J.F., Satorre, E.H., Ermàcora, C., Poggio, S.L., 2017. Weed communities respond to changes  
670 in the diversity of crop sequence composition and double cropping. *Weed Res* 57, 148-158.
- 671 Andreasen, C., Stryhn, H., Streibig, J., 1996. Decline of the flora in Danish arable fields. *J. Appl. Ecol.*,  
672 619-626.
- 673 Baessler, C., Klotz, S., 2006. Effects of changes in agricultural land-use on landscape structure and  
674 arable weed vegetation over the last 50 years. *Agr Ecosyst Environ* 115, 43-50.
- 675 Bàrberi, P., Bocci, G., Carlesi, S., Armengot, L., Blanco-Moreno, J.M., Sans, F.X., 2018. Linking species  
676 traits to agroecosystem services: a functional analysis of weed communities. *Weed Res* 58,  
677 76-88.
- 678 Barralis, G., 1976. Méthode d'étude des groupements adventices des cultures annuelles. Ve Colloque  
679 International sur l'Écologie et la Biologie des Mauvaises herbes. COLUMA, Paris (France), pp.  
680 59-68.
- 681 Benvenuti, S., Selvi, M., Mercati, S., Cardinali, G., Mercati, V., Mazzoncini, M., 2021. Stale seedbed  
682 preparation for sustainable weed seed bank management in organic cropping systems.  
683 *Scientia Horticulturae* 289, 110453.
- 684 Blaix, C., Moonen, A.C., Dostatny, D., Izquierdo, J., Le Corff, J., Morrison, J., Von Redwitz, C.,  
685 Schumacher, M., Westerman, P., 2018. Quantification of regulating ecosystem services  
686 provided by weeds in annual cropping systems using a systematic map approach. *Weed Res*  
687 58, 151-164.
- 688 Blumhorst, M.R., Weber, J.B., Swain, L.R., 1990. Efficacy of selected herbicides as influenced by soil  
689 properties. *Weed Technology* 4, 279-283.
- 690 Booth, B.D., Swanton, C.J., 2002. Assembly theory applied to weed communities. *Weed Sci* 50, 2-13.
- 691 Botta-Dukát, Z., 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple  
692 traits. *Journal of Vegetation Science* 16, 533-540.

693 Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J.,  
694 Machler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages  
695 for zero-inflated generalized linear mixed modeling. *The R journal* 9, 378-400.

696 Chamorro, L., Masalles, R., Sans, F., 2016. Arable weed decline in Northeast Spain: does organic  
697 farming recover functional biodiversity? *Agriculture, Ecosystems & Environment* 223, 1-9.

698 Chauhan, B.S., Singh, R.G., Mahajan, G., 2012. Ecology and management of weeds under  
699 conservation agriculture: A review. *Crop Protection* 38, 57-65.

700 Cirujeda, A., Marí, A.I., Murillo, S., Aibar, J., Pardo, G., Solé-Senan, X.-O., 2019. May the Inclusion of a  
701 Legume Crop Change Weed Composition in Cereal Fields? Example of Sainfoin in Aragon  
702 (Spain). *Agronomy* 9, 134.

703 Colbach, N., Cordeau, S., 2018. Reduced herbicide use does not increase crop yield loss if it is  
704 compensated by alternative preventive and curative measures. *European Journal of*  
705 *Agronomy* 94, 67-78.

706 Colbach, N., Petit, S., Chauvel, B., Deytieux, V., Lechenet, M., Munier-Jolain, N., Cordeau, S., 2020.  
707 The pitfalls of relating weeds, herbicide use and crop yield: don't fall into the trap! A critical  
708 review. *Frontiers in Agronomy* 2,  
709 <https://www.frontiersin.org/articles/10.3389/fagro.2020.615470/>.

710 Cordeau, S., Guillemin, J.P., Reibel, C., Chauvel, B., 2015. Weed species differ in their ability to  
711 emerge in no-till systems that include cover crops. *Ann Appl Biol* 166, 444-455.

712 Cousens, R., 1985. A simple model relating yield loss to weed density. *Ann Appl Biol* 107, 239-252.

713 Derksen, D., Thomas, A., Lafond, G., Loepky, H., Swanton, C., 1995. Impact of post-emergence  
714 herbicides on weed community diversity within conservation-tillage systems. *Weed Res* 35,  
715 311-320.

716 Derrouch, D., Chauvel, B., Felten, E., Dessaint, F., 2020. Weed Management in the Transition to  
717 Conservation Agriculture: Farmers' Response. *Agronomy* 10, 843.

718 Deytieux, V., Munier-Jolain, N., Caneill, J., 2016. Assessing the sustainability of cropping systems in  
719 single- and multi-site studies. A review of methods. *European Journal of Agronomy* 72, 107-  
720 126.

721 Deytieux, V., Nemecek, T., Freiermuth Knuchel, R., Gaillard, G., Munier-Jolain, N.M., 2012. Is  
722 Integrated Weed Management efficient for reducing environmental impacts of cropping  
723 systems? A case study based on life cycle assessment. *European Journal of Agronomy* 36, 55-  
724 65.

725 Doohan, D., Wilson, R., Canales, E., Parker, J., 2010. Investigating the human dimension of weed  
726 management: new tools of the trade. *Weed Sci* 58, 503-510.

727 Dorado, J., Lopez-Fando, C., 2006. The effect of tillage system and use of a paraplow on weed flora in  
728 a semiarid soil from central Spain. *Weed Res* 46, 424-431.

729 Doucet, C., Weaver, S.E., Hamill, A.S., Zhang, J., 1999. Separating the effects of crop rotation from  
730 weed management on weed density and diversity. *Weed Sci* 47, 729-735.

731 Fried, G., Kazakou, E., Gaba, S., 2012. Trajectories of weed communities explained by traits  
732 associated with species' response to management practices. *Agriculture, Ecosystems &*  
733 *Environment* 158, 147-155.

734 Fried, G., Norton, L.R., Reboud, X., 2008. Environmental and management factors determining weed  
735 species composition and diversity in France. *Agriculture, Ecosystems & Environment* 128, 68-  
736 76.

737 Fried, G., Petit, S., Dessaint, F., Reboud, X., 2009. Arable weed decline in Northern France: Crop edges  
738 as refugia for weed conservation? *Biological Conservation* 142, 238-243.

739 Fried, G., Petit, S., Reboud, X., 2010. A specialist-generalist classification of the arable flora and its  
740 response to changes in agricultural practices. *BMC Ecology* 10, 1-11.

741 Froud-Williams, R., 1988. Changes in weed flora with different tillage and agronomic management  
742 systems. *Weed Management in Agroecosystems: Ecological Approaches*. CRC Press, Boca  
743 Raton, FL, 213-236.

744 Gardarin, A., Dürr, C., Colbach, N., 2009. Which model species for weed seedbank and emergence  
745 studies? *Weed Res* 49, 117-130.

746 Garnier, E., Navas, M.-L., 2012. A trait-based approach to comparative functional plant ecology:  
747 concepts, methods and applications for agroecology. A review. *Agron. Sustainable Dev.* 32,  
748 365-399.

749 Giambalvo, D., Ruisi, P., Saia, S., Di Miceli, G., Frenda, A.S., Amato, G., 2012. Faba bean grain yield, N  
750 2 fixation, and weed infestation in a long-term tillage experiment under rainfed  
751 Mediterranean conditions. *Plant and Soil* 360, 215-227.

752 Gressel, J., LeBaron, H.M.E., 1982. *Herbicide resistance in plants*. Wiley.

753 Gross, N., Le Bagousse-Pinguet, Y., Liancourt, P., Berdugo, M., Gotelli, N.J., Maestre, F.T., 2017.  
754 Functional trait diversity maximizes ecosystem multifunctionality. *Nature ecology &  
755 evolution* 1, 1-9.

756 Gunton, R.M., Petit, S., Gaba, S., 2011. Functional traits relating arable weed communities to crop  
757 characteristics. *Journal of Vegetation Science* 22, 541-550.

758 Guo, Q., Rundel, P.W., 1997. Measuring dominance and diversity in ecological communities: choosing  
759 the right variables. *Journal of Vegetation Science* 8, 405-408.

760 Haas, H., 1982. Changing patterns of weed distribution as a result of herbicide use and other  
761 agronomic factors. *Herbicide resistance in plants*, 57-79.

762 Hanzlik, K., Gerowitt, B., 2016. Methods to conduct and analyse weed surveys in arable farming: a  
763 review. *Agron. Sustainable Dev.* 36, 11.

764 Hartig, F., 2020. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression  
765 Models. R package version 0.2.7.

766 Hernández Plaza, E., Navarrete, L., González-Andújar, J.L., 2015. Intensity of soil disturbance shapes  
767 response trait diversity of weed communities: The long-term effects of different tillage  
768 systems. *Agriculture, Ecosystems & Environment* 207, 101-108.

769 Hiltbrunner, J., Scherrer, C., Streit, B., Jeanneret, P., Zihlmann, U., Tschachtli, R., 2008. Long-term  
770 weed community dynamics in Swiss organic and integrated farming systems. *Weed Res* 48,  
771 360-369.

772 Hooper, D.U., Chapin, F.S., Ewel, J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.,  
773 Loreau, M., Naeem, S., 2005. Effects of biodiversity on ecosystem functioning: a consensus of  
774 current knowledge. *Ecol. Monogr.* 75, 3-35.

775 Hyvönen, T., Salonen, J., 2002. Weed species diversity and community composition in cropping  
776 practices at two intensity levels—a six-year experiment. *Plant Ecology* 159, 73-81.

777 Jabran, K., Mahmood, K., Melander, B., Bajwa, A.A., Kudsk, P., 2017. Chapter three - Weed dynamics  
778 and management in wheat. In: Sparks, D.L. (Ed.), *Advances in Agronomy*. Academic Press, pp.  
779 97-166.

780 José-María, L., Armengot, L., Chamorro, L., Xavier Sans, F., 2013. The conservation of arable weeds at  
781 crop edges of barley fields in northeast Spain: Arable plants at crop edges. *Ann Appl Biol* 163,  
782 47-55.

783 Kazakou, E., Violle, C., Roumet, C., Navas, M.L., Vile, D., Kattge, J., Garnier, E., 2014. Are trait-based  
784 species rankings consistent across data sets and spatial scales? *Journal of Vegetation Science*  
785 25, 235-247.

786 Kew, R.B.G., 2020. *Seed Information Database (SID)*. Version 7.1.

787 Kleijn, D., van der Voort, L.A., 1997. Conservation headlands for rare arable weeds: the effects of  
788 fertilizer application and light penetration on plant growth. *Biological Conservation* 81, 57-  
789 67.

790 Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., Van  
791 Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G.M., Hermy, M., Adriaens, D.,  
792 Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J.G., Jackel,  
793 A.-K., Kühn, I., Kunzmann, D., Ozinga, W.A., Römermann, C., Stadler, M., Schlegelmilch, J.,  
794 Steendam, H.J., Tackenberg, O., Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E.,

795 Peco, B., 2008. The LEDA Traitbase: a database of life-history traits of the Northwest  
796 European flora. *Journal of Ecology* 96, 1266-1274.

797 Koocheki, A., Nassiri, M., Alimoradi, L., Ghorbani, R., 2009. Effect of cropping systems and crop  
798 rotations on weeds. *Agron. Sustainable Dev.* 29, 401-408.

799 Kühn, I., Durka, W., Klotz, S., 2004. BioFlor: A New Plant-Trait Database as a Tool for Plant Invasion  
800 Ecology. *Divers. Distrib.* 10, 363-365.

801 Lacroix, O., Aubertot, J.-N., Bohanec, M., Cordeau, S., Corrales, D.C., Robin, M.H., 2021. IPSIM-  
802 *Cirsium*, a qualitative expert-based model to predict infestations of *Cirsium arvense* *Frontiers*  
803 *in Agronomy* 3, 1-16.

804 Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from  
805 multiple traits. *Ecology* 91, 299-305.

806 Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S., Garden, D., Dorrough, J., Berman, S., Quétier, F.,  
807 Thébault, A., Bonis, A., 2008. Assessing functional diversity in the field—methodology  
808 matters! *Functional Ecology* 22, 134-147.

809 Lechenet, M., Dessaint, F., Py, G., Makowski, D., Munier-Jolain, N., 2017a. Reducing pesticide use  
810 while preserving crop productivity and profitability on arable farms. *Nature Plants* 3, 17008.

811 Lechenet, M., Deytieux, V., Antichi, D., Aubertot, J.-N., Bàrberi, P., Bertrand, M., Cellier, V., Charles,  
812 R., Colnenne-David, C., Dachbrodt-Saaydeh, S., Debaeke, P., Doré, T., Farcy, P., Fernandez-  
813 Quintanilla, C., Grandeau, G., Hawes, C., Jouy, L., Justes, E., Kierzek, R., Kudsk, P.,  
814 Lamichhane, J.R., Lescourret, F., Mazzoncini, M., Melander, B., Messéan, A., Moonen, A.-C.,  
815 Newton, A.C., Nolot, J.-M., Panozzo, S., Retaureau, P., Sattin, M., Schwarz, J., Toqué, C.,  
816 Vasileiadis, V.P., Munier-Jolain, N., 2017b. Diversity of methodologies to experiment  
817 Integrated Pest Management in arable cropping systems: Analysis and reflections based on a  
818 European network. *European Journal of Agronomy* 83, 86-99.

819 Légère, A., Stevenson, F.C., Benoit, D.L., 2005. Diversity and assembly of weed communities:  
820 contrasting responses across cropping systems. *Weed Res* 45, 303-315.

821 Lenth, R., 2019. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version  
822 1.3.5.

823 Liebman, M., Mohler, C.L., Staver, C.P., 2001. *Ecological management of agricultural weeds.*  
824 Cambridge University Press.

825 Lukashyk, P., Berg, M., Köpke, U., 2008. Strategies to control Canada thistle (*Cirsium arvense*) under  
826 organic farming conditions. *Renew Agric Food Syst* 23, 13-18.

827 Mace, K., Morlon, P., Munier-Jolain, N., Quere, L., 2007. Time scales as a factor in decision-making by  
828 French farmers on weed management in annual crops. *Agricultural Systems* 93, 115-142.

829 Mahaut, L., Gaba, S., Fried, G., 2019. A functional diversity approach of crop sequences reveals that  
830 weed diversity and abundance show different responses to environmental variability. *J. Appl.*  
831 *Ecol.* 56, 1400-1409.

832 Mahn, E.G., Helmecke, K., 1979. Effects of herbicide treatment on the structure and functioning of  
833 agro-ecosystems II. Structural changes in the plant community after the application of  
834 herbicides over several years. *Agro-Ecosystems* 5, 159-179.

835 Marshall, E.J.P., Brown, V.K., Boatman, N.D., Lutman, P.J.W., Squire, G.R., Ward, L.K., 2003. The role  
836 of weeds in supporting biological diversity within crop fields. *Weed Res* 43, 77-89.

837 Milberg, P., Hallgren, E., 2004. Yield loss due to weeds in cereals and its large-scale variability in  
838 Sweden. *Field Crops Research* 86, 199-209.

839 Mirsky, S.B., Ryan, M.R., Teasdale, J.R., Curran, W.S., Reberg-Horton, C.S., Spargo, J.T., Wells, M.S.,  
840 Keene, C.L., Moyer, J.W., 2013. Overcoming Weed Management Challenges in Cover Crop-  
841 Based Organic Rotational No-Till Soybean Production in the Eastern United States. *Weed*  
842 *Technol* 27, 193-203.

843 Mohler, C.L., 1993. A model of the effects of tillage on emergence of weed seedlings. *Ecol Appl* 3, 53-  
844 73.

845 Mohler, C.L., Frisch, J.C., McCulloch, C.E., 2006. Vertical movement of weed seed surrogates by tillage  
846 implements and natural processes. *Soil and Tillage Research* 86, 110-122.



847 Murphy, S.D., Clements, D.R., Belaoussoff, S., Kevan, P.G., Swanton, C.J., 2006. Promotion of weed  
848 species diversity and reduction of weed seedbanks with conservation tillage and crop  
849 rotation. *Weed Sci* 54, 69-77.

850 Neve, P., Barney, J.N., Buckley, Y., Cousens, R.D., Graham, S., Jordan, N.R., Lawton-Rauh, A., Liebman,  
851 M., Mesgaran, M.B., Schut, M., Shaw, J., Storkey, J., Baraibar, B., Baucom, R.S., Chalak, M.,  
852 Childs, D.Z., Christensen, S., Eizenberg, H., Fernández-Quintanilla, C., French, K., Harsch, M.,  
853 Heijting, S., Harrison, L., Loddo, D., Macel, M., Maczey, N., Merotto, A., Mortensen, D.,  
854 Necajeva, J., Peltzer, D.A., Recasens, J., Renton, M., Riemens, M., Sønderskov, M., Williams,  
855 M., 2018. Reviewing research priorities in weed ecology, evolution and management: a  
856 horizon scan. *Weed Res* 58, 250-258.

857 Nicholls, C.I., Altieri, M.A., 2013. Plant biodiversity enhances bees and other insect pollinators in  
858 agroecosystems. A review. *Agron. Sustainable Dev.* 33, 257-274.

859 Nikolich, L., Milošević, D., Seremesich, S., Dalovich, I., Vuga-Janjatov, V., 2012. Diversity of weed flora  
860 in wheat depending on crop rotation and fertilisation. *Bulgarian Journal of Agricultural  
861 Science*.

862 Pardo, G., Cirujeda, A., Perea, F., Verdú, A., Mas, M., Urbano, J., 2019. Effects of reduced and  
863 conventional tillage on weed communities: results of a long-term experiment in  
864 southwestern Spain. *Planta Daninha* 37.

865 Peter, C.J., Weber, J.B., 1985. Adsorption, mobility, and efficacy of alachlor and metolachlor as  
866 influenced by soil properties. *Weed Sci* 33, 874-881.

867 Plaza, E.H., Kozak, M., Navarrete, L., González-Andújar, J.L., 2011. Tillage system did not affect weed  
868 diversity in a 23-year experiment in Mediterranean dryland. *Agriculture, Ecosystems &  
869 Environment* 140, 102-105.

870 Pocock, M.J., Evans, D.M., Memmott, J., 2012. The robustness and restoration of a network of  
871 ecological networks. *Science* 335, 973-977.

872 Poggio, S.L., Satorre, E.H., de la Fuente, E.B., 2004. Structure of weed communities occurring in pea  
873 and wheat crops in the Rolling Pampa (Argentina). *Agriculture, Ecosystems & Environment*  
874 103, 225-235.

875 Quinio, M., De Waele, M., Dessaint, F., Biju-Duval, L., Buthiot, M., Cadet, E., Bybee-Finley, A.K.,  
876 Guillemain, J.-P., Cordeau, S., 2017. Separating the confounding effects of farming practices on  
877 weeds and winter wheat production using path modelling. *European Journal of Agronomy*  
878 82, 134-143.

879 R Core Team, 2016. *R: A Language and Environment for Statistical Computing*. R Foundation for  
880 Statistical Computing, Vienna, Austria.

881 Ricotta, C., Moretti, M., 2011. CWM and Rao's quadratic diversity: a unified framework for functional  
882 ecology. *Oecologia* 167, 181-188.

883 Ryan, M.R., Smith, R.G., Mirsky, S.B., Mortensen, D.A., Seidel, R., 2010. Management filters and  
884 species traits: weed community assembly in long-term organic and conventional systems.  
885 *Weed Sci* 58, 265-277.

886 Santín-Montanyá, M.I., Martín-Lammerding, D., Walter, I., Zambrana, E., Tenorio, J.L., 2013. Effects  
887 of tillage, crop systems and fertilization on weed abundance and diversity in 4-year dry land  
888 winter wheat. *European Journal of Agronomy* 48, 43-49.

889 Scheiner, S.M., 2012. *Biological Diversity: Frontiers in Measurement and Assessment* edited by Anne  
890 E. Magurran and Brian J. McGill. *The Quarterly Review of Biology* 87, 254-254.

891 Schuldt, A., Ebeling, A., Kunz, M., Staab, M., Guimarães-Steinicke, C., Bachmann, D., Buchmann, N.,  
892 Durka, W., Fichtner, A., Fornoff, F., Härdtle, W., Hertzog, L.R., Klein, A.-M., Roscher, C.,  
893 Schaller, J., von Oheimb, G., Weigelt, A., Weisser, W., Wirth, C., Zhang, J., Bruelheide, H.,  
894 Eisenhauer, N., 2019. Multiple plant diversity components drive consumer communities  
895 across ecosystems. *Nat Commun* 10, 1460.

896 Schumacher, M., Ohnmacht, S., Rosenstein, R., Gerhards, R., 2018. How Management Factors  
897 Influence Weed Communities of Cereals, Their Diversity and Endangered Weed Species in  
898 Central Europe. *Agriculture* 8, 172.

899 Šmilauer, P., Lepš, J., 2014. *Multivariate Analysis of Ecological Data using CANOCO 5*. Cambridge  
900 University Press, Cambridge.

901 Sosnoskie, L.M., Herms, N.P., Cardina, J., 2006. Weed seedbank community composition in a 35-yr-  
902 old tillage and rotation experiment. *Weed Sci* 54, 263-273.

903 Stoate, C., Boatman, N.D., Borralho, R.J., Carvalho, C.R., Snoo, G.R.d., Eden, P., 2001. Ecological  
904 impacts of arable intensification in Europe. *Journal of Environmental Management* 63, 337-  
905 365.

906 Storkey, J., Neve, P., 2018. What good is weed diversity? *Weed Res* 58, 239-243.

907 Sutcliffe, O.L., Kay, Q.O., 2000. Changes in the arable flora of central southern England since the  
908 1960s. *Biological Conservation* 93, 1-8.

909 Swanton, C.J., Weise, S.F., 1991. Integrated weed management: the rationale and approach. *Weed*  
910 *Technol* 5, 657-663.

911 Tarjuelo, R., Morales, M.B., Arribas, L., Traba, J., 2019. Abundance of weeds and seeds but not of  
912 arthropods differs between arable habitats in an extensive Mediterranean farming system.  
913 *Ecol. Res.* 34, 624-636.

914 Thomas, A.G., Derksen, D.A., Blackshaw, R.E., Van Acker, R.C., Légère, A., Watson, P.R., Turnbull, G.C.,  
915 2004. A multistudy approach to understanding weed population shifts in medium- to long-  
916 term tillage systems. *Weed Sci* 52, 874-880.

917 Trichard, A., Alignier, A., Chauvel, B., Petit, S., 2013. Identification of weed community traits response  
918 to conservation agriculture. *Agriculture, Ecosystems & Environment* 179, 179-186.

919 Turnbull, L.A., Rees, M., Crawley, M.J., 1999. Seed mass and the competition/colonization trade-off: a  
920 sowing experiment. *Journal of Ecology* 87, 899-912.

921 Ulber, L., Steinmann, H.-H., Klimek, S., Isselstein, J., 2009. An on-farm approach to investigate the  
922 impact of diversified crop rotations on weed species richness and composition in winter  
923 wheat. *Weed Res* 49, 534-543.

924 Villora, R.A., Plaza, E.H., Navarrete, L., Sánchez, M., Sánchez, A., 2019. Climate and tillage system  
925 drive weed communities' functional diversity in a Mediterranean cereal-legume rotation.  
926 *Agriculture, Ecosystems & Environment* 283, 106574.

927 Vissoh, P., Mongbo, R., Gbèhounou, G., Hounkonnou, D., Ahanchédé, A., Röling, N., Kuyper, T., 2007.  
928 The social construction of weeds: different reactions to an emergent problem by farmers,  
929 officials and researchers. *International Journal of Agricultural Sustainability* 5, 161-175.

930 Weibull, A.-C., Östman, Ö., Granqvist, Å., 2003. Species richness in agroecosystems: the effect of  
931 landscape, habitat and farm management. *Biodiversity & Conservation* 12, 1335-1355.

932 Weisberger, D., Nichols, V., Liebman, M., 2019. Does diversifying crop rotations suppress weeds? A  
933 meta-analysis. *PLOS ONE* 14, e0219847.

934 Wezel, A., Casagrande, M., Celette, F., Vian, J.-F., Ferrer, A., Peigné, J., 2014. Agroecological practices  
935 for sustainable agriculture. A review. *Agron. Sustainable Dev.* 34, 1-20.

936 Wilson, B., Wright, K., 1990. Predicting the growth and competitive effects of annual weeds in wheat.  
937 *Weed Res* 30, 201-211.

938 Wilson, R.S., Tucker, M.A., Hooker, N.H., LeJeune, J.T., Doohan, D., 2008. Perceptions and beliefs  
939 about weed management: perspectives of Ohio grain and produce farmers. *Weed Technol*  
940 22, 339-350.

941 Yvoz, S., Cordeau, S., Zuccolo, C., Petit, S., 2020a. Crop type and within-field location as sources of  
942 intraspecific variations in the phenology and the production of floral and fruit resources by  
943 weeds. *Agric. Ecosyst. Environ.* 302, 107082.

944 Yvoz, S., Petit, S., Biju-Duval, L., Cordeau, S., 2020b. A framework to type crop management  
945 strategies within a production situation to improve the comprehension of weed  
946 communities. *European Journal of Agronomy* 115, 10.

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949 **Figures and Tables**

950

951 **Table 1:** Overview of the main characteristics (black cells) of the different experimented (ECS) or  
 952 farmer (FCS) cropping systems present in this study.

	Cropping system experiment					Farmers' network			
	ECS1	ECS2	ECS3	ECS4	ECS5	FCS2	FCS3	FCS4	FCS7
Crop diversification									
No-till									
Reduced tillage									
Ploughing									
Chemical weeding									
Mechanical weeding									
False seed bed practices									
Increased sowing density									
Reduced N fertilization									
Delayed sowing of winter cereals									

953

954 **Table 2:** Differences in terms of farming practices between experimented cropping systems (over the 2012-2017 period) and farmer cropping systems (over the 2008-2013  
955 period). Effects were determined through F-tests on linear models. Values (observed means  $\pm$  standard deviation) were computed over the crop sequence and standardized at  
956 the annual scale. Cropping systems sharing identical letters are not significantly different at  $P < 0.05$  (p-values in bold). HTFI: Herbicide Treatment Frequency Index (average  
957 number of herbicide applications at the recommended dose).

	Cropping system experiment						Farmers' network				
	Experimented cropping system effect (df=4)	ECS1	ECS2	ECS3	ECS4	ECS5	Farmer cropping system effect (df=3)	FCS2	FCS3	FCS4	FCS7
Ploughing frequency	<b>F=47.67, P=0.001</b>	0.83 $\pm$ 0.00 a	0.00 $\pm$ 0.00 c	0.42 $\pm$ 0.12 b	0.42 $\pm$ 0.12 b	0.67 $\pm$ 0.00 ab	F=2.19, P=0.14	0.66 $\pm$ 0.33 a	0.34 $\pm$ 0.33 a	1.00 $\pm$ 0.00 a	0.50 $\pm$ 0.24 a
Average number of false seedbed operations year <sup>-1</sup>	<b>F=7.24, P=0.041</b>	1.75 $\pm$ 0.12 ab	0.00 $\pm$ 0.00 b	2.58 $\pm$ 0.59 a	2.67 $\pm$ 0.24 a	2.08 $\pm$ 1.30 ab	<b>F=8.20, P=0.003</b>	2.39 $\pm$ 0.36 c	1.78 $\pm$ 0.10 ab	2.50 $\pm$ 0.00 bc	1.67 $\pm$ 0.24 a
Frequency of delayed sowing of winter cereals	<b>F=12.53, P=0.016</b>	0.00 $\pm$ 0.00 b	0.75 $\pm$ 0.35 a	0.83 $\pm$ 0.24 a	1.00 $\pm$ 0.00 a	0.58 $\pm$ 0.12 ab	F=0.33, P=0.81	0.02 $\pm$ 0.06 a	0.00 $\pm$ 0.00 a	0.00 $\pm$ 0.00 a	0.00 $\pm$ 0.00 a
Average HTFI year <sup>-1</sup>	<b>F=32.31, P=0.003</b>	1.34 $\pm$ 0.18 ab	1.97 $\pm$ 0.18 a	0.82 $\pm$ 0.26 bc	0.50 $\pm$ 0.16 c	0.00 $\pm$ 0.00 c	F=0.66, P=0.59	1.51 $\pm$ 0.21 a	1.63 $\pm$ 0.25 a	1.42 $\pm$ 0.03 a	1.41 $\pm$ 0.27 a
Average HTFI before sowing year <sup>-1</sup>	<b>F=639.7, P&lt;0.0001</b>	0.02 $\pm$ 0.02 b	1.05 $\pm$ 0.06 a	0.02 $\pm$ 0.03 b	0.01 $\pm$ 0.01 b	0.00 $\pm$ 0.00 b	F=1.73, P=0.21	0.01 $\pm$ 0.04 a	0.15 $\pm$ 0.18 a	0.06 $\pm$ 0.09 a	0.05 $\pm$ 0.09 a
Average HTFI after sowing year <sup>-1</sup>	<b>F=13.32, P=0.014</b>	1.32 $\pm$ 0.16 a	0.92 $\pm$ 0.12 a	0.80 $\pm$ 0.29 ab	0.49 $\pm$ 0.17 ab	0.00 $\pm$ 0.00 b	F=0.67, P=0.58	1.49 $\pm$ 0.22 a	1.48 $\pm$ 0.36 a	1.36 $\pm$ 0.06 a	1.32 $\pm$ 0.10 a
Average number of herbicide applications year <sup>-1</sup>	<b>F=23.77, P=0.005</b>	1.25 $\pm$ 0.12 b	2.42 $\pm$ 0.35 a	1.42 $\pm$ 0.35 ab	0.83 $\pm$ 0.00 bc	0.00 $\pm$ 0.00 c	<b>F=6.88, P=0.005</b>	1.08 $\pm$ 0.13 b	1.61 $\pm$ 0.10 a	1.50 $\pm$ 0.47 ab	1.38 $\pm$ 0.21 ab
Average number of herbicide applications before sowing year <sup>-1</sup>	<b>F=13.72, P=0.013</b>	0.08 $\pm$ 0.12 b	1.17 $\pm$ 0.23 a	0.17 $\pm$ 0.23 b	0.08 $\pm$ 0.12 b	0.00 $\pm$ 0.00 b	F=0.72, P=0.56	0.02 $\pm$ 0.06 a	0.11 $\pm$ 0.10 a	0.08 $\pm$ 0.12 a	0.08 $\pm$ 0.17 a
Average number of herbicide applications after sowing year <sup>-1</sup>	F=3.26, P=0.14	1.17 $\pm$ 0.00 a	1.25 $\pm$ 0.59 a	1.25 $\pm$ 0.59 a	0.83 $\pm$ 0.00 a	0.00 $\pm$ 0.00 a	<b>F=9.02, P=0.002</b>	1.06 $\pm$ 0.09 b	1.5 $\pm$ 0.17 a	1.42 $\pm$ 0.35 a	1.29 $\pm$ 0.08 ab
Average number of mechanical weeding operations year <sup>-1</sup>	<b>F=37.38, P=0.002</b>	0.00 $\pm$ 0.00 b	0.00 $\pm$ 0.00 b	0.17 $\pm$ 0.24 b	1.83 $\pm$ 0.00 a	2.92 $\pm$ 0.58 a	F=1.10, P=0.38	0.00 $\pm$ 0.00 a	0.00 $\pm$ 0.00 a	0.00 $\pm$ 0.00 a	0.04 $\pm$ 0.08 a
Average nitrogen fertilisation kg N year <sup>-1</sup>	<b>F=29.14, P=0.003</b>	154 $\pm$ 8 a	94 $\pm$ 6 b	96 $\pm$ 5 b	109 $\pm$ 2 b	79 $\pm$ 12 b	<b>F=4.06, P=0.03</b>	149 $\pm$ 16 ab	163 $\pm$ 1 a	145 $\pm$ 2.62 ab	130 $\pm$ 10 b
Proportion of non-fertilised crops	F=5.67, P=0.06	0.00 $\pm$ 0.05 a	0.25 $\pm$ 0.05 a	0.25 $\pm$ 0.05 a	0.17 $\pm$ 0.05 a	0.25 $\pm$ 0.05 a	<b>F=0.00, P=0.00</b>	0.00 $\pm$ 0.00 a	0.00 $\pm$ 0.00 a	0.00 $\pm$ 0.00 a	0.00 $\pm$ 0.00 a
Proportion of autumn-sown crops	F=6.00, P=0.055	0.67 $\pm$ 0.04 b	0.50 $\pm$ 0.04 ab	0.50 $\pm$ 0.04 ab	0.50 $\pm$ 0.04 ab	0.42 $\pm$ 0.04 a	F=1.42, P=0.28	0.60 $\pm$ 0.18 a	0.67 $\pm$ 0.00 a	0.42 $\pm$ 0.12 a	0.63 $\pm$ 0.08 a
Proportion of winter-sown crops	F=6.00, P=0.055	0.00 $\pm$ 0.04 b	0.17 $\pm$ 0.04 ab	0.17 $\pm$ 0.04 ab	0.17 $\pm$ 0.04 ab	0.25 $\pm$ 0.04 a	F=3.00, P=0.07	0.10 $\pm$ 0.20 a	0.00 $\pm$ 0.00 a	0.25 $\pm$ 0.12 a	0.33 $\pm$ 0.14 a
Proportion of spring-sown crops	<b>Perfect fit*</b>	0.00 $\pm$ 0.00 b	0.17 $\pm$ 0.00 a	0.17 $\pm$ 0.00 a	0.17 $\pm$ 0.00 a	0.17 $\pm$ 0.00 a	<b>F=13.20, P=0.0003</b>	0.00 $\pm$ 0.00 b	0.00 $\pm$ 0.00 b	0.25 $\pm$ 0.12 a	0.04 $\pm$ 0.08 b
Proportion of summer-sown crops	<b>Perfect fit*</b>	0.33 $\pm$ 0.00 a	0.17 $\pm$ 0.00 b	0.17 $\pm$ 0.00 b	0.17 $\pm$ 0.00 b	0.17 $\pm$ 0.00 b	<b>F=23.96, P&lt;0.0001</b>	0.29 $\pm$ 0.08 b	0.33 $\pm$ 0.00 b	0.08 $\pm$ 0.12 a	0.00 $\pm$ 0.00 a
Number of crops	<b>F=8.60, P=0.03</b>	3.00 $\pm$ 0.35 b	5.00 $\pm$ 0.35 ab	5.50 $\pm$ 0.35 a	5.00 $\pm$ 0.35 ab	5.50 $\pm$ 0.35 a	<b>F=5.51, P=0.01</b>	3.75 $\pm$ 0.46 b	3.33 $\pm$ 0.58 b	3.5 $\pm$ 0.71 ab	4.75 $\pm$ 0.5 a
Number of botanical families	<b>Perfect fit*</b>	2.00 $\pm$ 0.00 c	4.00 $\pm$ 0.00 a	3.00 $\pm$ 0.00 b	4.00 $\pm$ 0.00 a	3.00 $\pm$ 0.00 b	F=1.78, P=0.20	2.00 $\pm$ 0.00 a	2.00 $\pm$ 0.00 a	2.50 $\pm$ 0.71 a	2.25 $\pm$ 0.5 a
Number of sowing periods	<b>Perfect fit*</b>	2.00 $\pm$ 0.00 b	4.00 $\pm$ 0.00 a	4.00 $\pm$ 0.00 a	4.00 $\pm$ 0.00 a	4.00 $\pm$ 0.00 a	<b>F=3.60, P=0.04</b>	2.25 $\pm$ 0.46 a	2.00 $\pm$ 0.00 a	3.00 $\pm$ 0.00 a	2.75 $\pm$ 0.50 a
Number of crop types	<b>F=31.0, P=0.003</b>	2.00 $\pm$ 0.22 b	5.00 $\pm$ 0.22 a	4.50 $\pm$ 0.22 a	5.00 $\pm$ 0.22 a	4.00 $\pm$ 0.22 a	<b>F=5.96, P=0.009</b>	2.50 $\pm$ 0.76 b	2.00 $\pm$ 0.00 b	3.50 $\pm$ 0.71 ab	3.75 $\pm$ 0.50 a
Functional diversity of crop sequence**	<b>F=7.06, P=0.04</b>	0.05 $\pm$ 0.01 b	0.08 $\pm$ 0.01 ab	0.08 $\pm$ 0.01 ab	0.09 $\pm$ 0.01 a	0.08 $\pm$ 0.01 ab	<b>F=5.58, P=0.01</b>	0.08 $\pm$ 0.01 b	0.07 $\pm$ 0.00 ab	0.09 $\pm$ 0.01 b	0.06 $\pm$ 0.00 a

958 \*Perfect fit denotes a model where each level of the factor shows no variability, *i.e.* R<sup>2</sup>=1

959 \*\*Functional diversity of the crop sequence (1 value per plot over the period) was computed with Rao's quadratic entropy on 9 traits: life form (annual vs. perennial), sowing period (autumn, winter, spring,  
960 summer), number of cotyledons (monocotyledonous vs. dicotyledonous), nitrogen fixing ability (yes/no), seed mass, length of growing cycle, crop height at flowering, crop architecture (graminoid, multi-stem,  
961 rosette, single stem), and flowering onset. Rao's quadratic index was computed with the FD (functional diversity) function of the R FD package (Laliberté and Legendre, 2010) and weighted by frequency in the  
962 crop sequence (mixtures were partitioned according to the number of species). Seed mass, length of growing cycle and crop height at flowering were log transformed before the analysis.

963 **Table 3:** Effect of experimented or farmer cropping systems on weed diversity (species richness, Shannon diversity index, and Rao's quadratic entropy, the last two weighted  
 964 by density) at three different scales (quadrat for the cropping system experiment, plot:year and plot for the cropping system experiment and farmers' network) over the 2012-  
 965 2017 and 2008-2013 period, respectively. Values represent least square means ( $\pm$  standard error) whereas values for the cropping system experiment at the plot scale represent  
 966 observed means ( $\pm$  standard deviation). Effects were determined by likelihood ratio tests. Experimented or farmer cropping systems sharing identical letters are not  
 967 significantly different at  $P < 0.05$  (p-values in bold).

Diversity indicator	Scale	Cropping system experiment							Farmers' network					
		Experimented cropping system effect (df=4)	N	ECS1	ECS2	ECS3	ECS4	ECS5	Farmer cropping system effect (df=3)	N	FCS2	FCS3	FCS4	FCS7
Species richness	Quadrat	$\chi^2=20.43$ , <b>P=0.0004</b>	480	0.62 $\pm$ 0.13 b	2.49 $\pm$ 0.45 a	3.48 $\pm$ 0.62 a	2.65 $\pm$ 0.48 a	3.40 $\pm$ 0.61 a	NA	NA	NA	NA	NA	NA
	Plot:year	$\chi^2=21.41$ , <b>P=0.0003</b>	60	3.29 $\pm$ 0.56 b	9.54 $\pm$ 1.09 a	10.19 $\pm$ 1.14 a	8.53 $\pm$ 1.02 a	9.61 $\pm$ 1.10 a	$\chi^2=22.27$ , <b>P=0.0007</b>	102	3.6 $\pm$ 0.50 b	7.6 $\pm$ 1.32 a	3.1 $\pm$ 0.74 b	3.7 $\pm$ 0.64 b
	Plot	Not tested*	10	9.00 $\pm$ 5.66	21.50 $\pm$ 2.12	23.50 $\pm$ 6.37	19.00 $\pm$ 4.24	22.00 $\pm$ 0.00	$\chi^2=10.20$ , <b>P=0.017</b>	17	10.8 $\pm$ 1.16 b	18.0 $\pm$ 2.45 a	11.0 $\pm$ 2.35 ab	11.0 $\pm$ 1.66 ab
Shannon diversity index	Quadrat	$\chi^2=14.53$ , <b>P=0.006</b>	480	0.05 $\pm$ 0.04 c	0.61 $\pm$ 0.09 b	0.97 $\pm$ 0.07 a	0.77 $\pm$ 0.10 ab	0.93 $\pm$ 0.08 a	NA	NA	NA	NA	NA	NA
	Plot:year	$\chi^2=22.83$ , <b>P=0.0001</b>	60	0.59 $\pm$ 0.11 b	1.45 $\pm$ 0.17 a	1.62 $\pm$ 0.18 a	1.50 $\pm$ 0.17 a	1.41 $\pm$ 0.17 a	$\chi^2=20.73$ , <b>P=0.0001</b>	102	0.77 $\pm$ 0.09 b	1.62 $\pm$ 0.26 a	0.49 $\pm$ 0.13 b	0.90 $\pm$ 0.14 b
	Plot	Not tested*	10	1.14 $\pm$ 0.33	2.04 $\pm$ 0.24	2.02 $\pm$ 0.39	1.83 $\pm$ 0.02	2.04 $\pm$ 0.05	$\chi^2=11.86$ , <b>P=0.008</b>	17	1.39 $\pm$ 0.12 a	2.09 $\pm$ 0.25 a	1.16 $\pm$ 0.23 a	1.27 $\pm$ 0.17 a
Rao's quadratic entropy	Quadrat	$\chi^2=20.59$ , <b>P=0.0004</b>	480	0.00 $\pm$ 0.00 b	0.03 $\pm$ 0.01 a	0.04 $\pm$ 0.01 a	0.03 $\pm$ 0.01 a	0.04 $\pm$ 0.01 a	NA	NA	NA	NA	NA	NA
	Plot:year	$\chi^2=15.86$ , <b>P=0.003</b>	60	0.03 $\pm$ 0.00 b	0.08 $\pm$ 0.01 a	0.06 $\pm$ 0.01 a	0.06 $\pm$ 0.01 a	0.05 $\pm$ 0.01 a	$\chi^2=19.89$ , <b>P=0.0002</b>	102	0.03 $\pm$ 0.00 bc	0.07 $\pm$ 0.01 a	0.02 $\pm$ 0.01 c	0.04 $\pm$ 0.01 ab
	Plot	Not tested*	10	0.04 $\pm$ 0.01	0.08 $\pm$ 0.00	0.06 $\pm$ 0.00	0.07 $\pm$ 0.02	0.07 $\pm$ 0.00	$\chi^2=7.37$ , <b>P=0.06</b>	17	0.04 $\pm$ 0.01 a	0.07 $\pm$ 0.02 a	0.03 $\pm$ 0.01 a	0.04 $\pm$ 0.01 a

968 NA: not applicable, *i.e.* no data collected at this scale

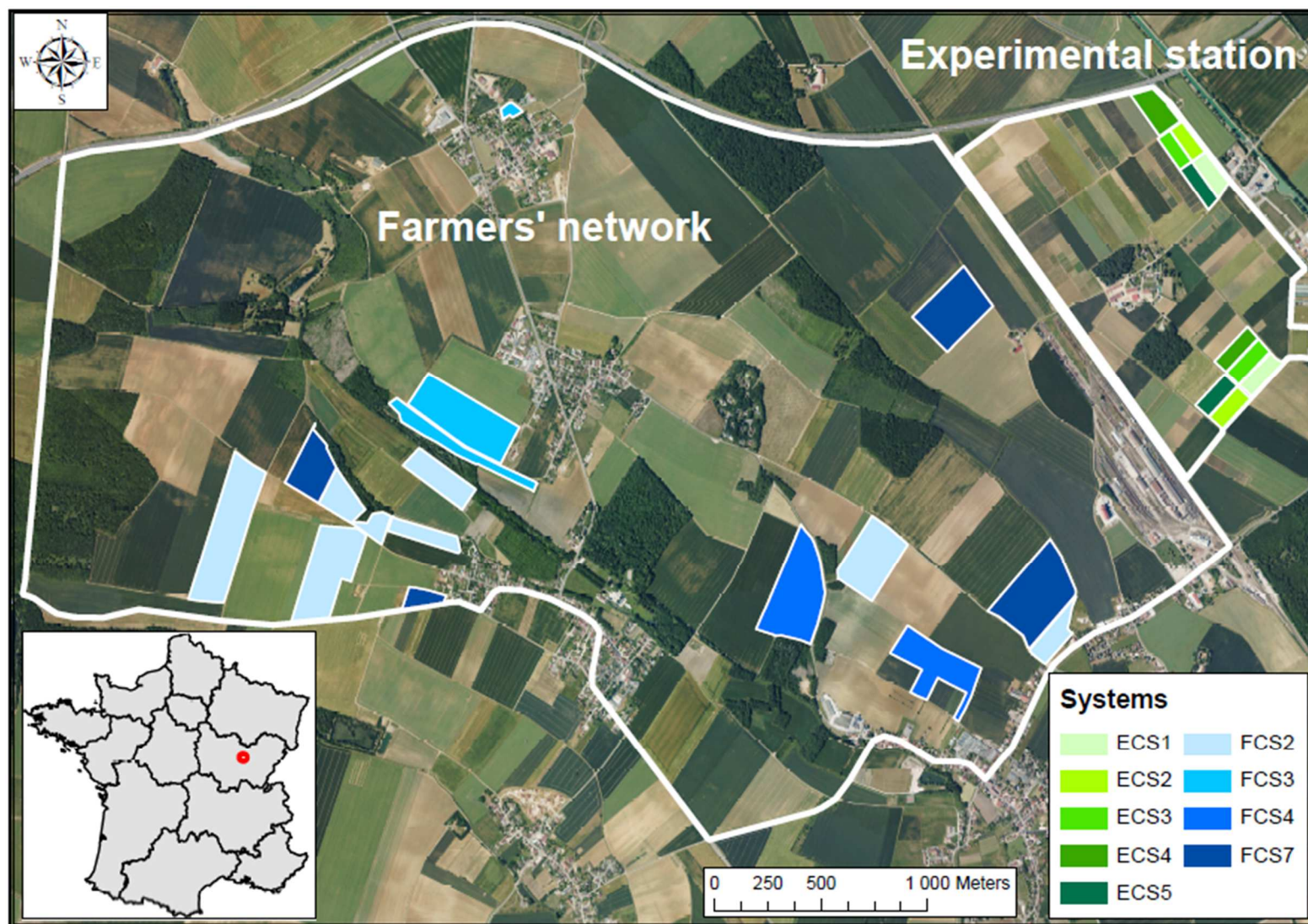
969 \* No tests were performed at the plot scale due to lack of statistical power (N=10, d.f. cropping system effect=4)

970

971 **Table 4:** Effect of cropping systems on community weighted means (CWM weighted by density) of different weed response traits. Values represent least square means ( $\pm$   
972 standard error). Effects were determined by likelihood ratio tests. Experimented or farmer cropping systems sharing identical letters for each response variable are not  
973 significantly different at  $P < 0.05$  (p-values in bold).

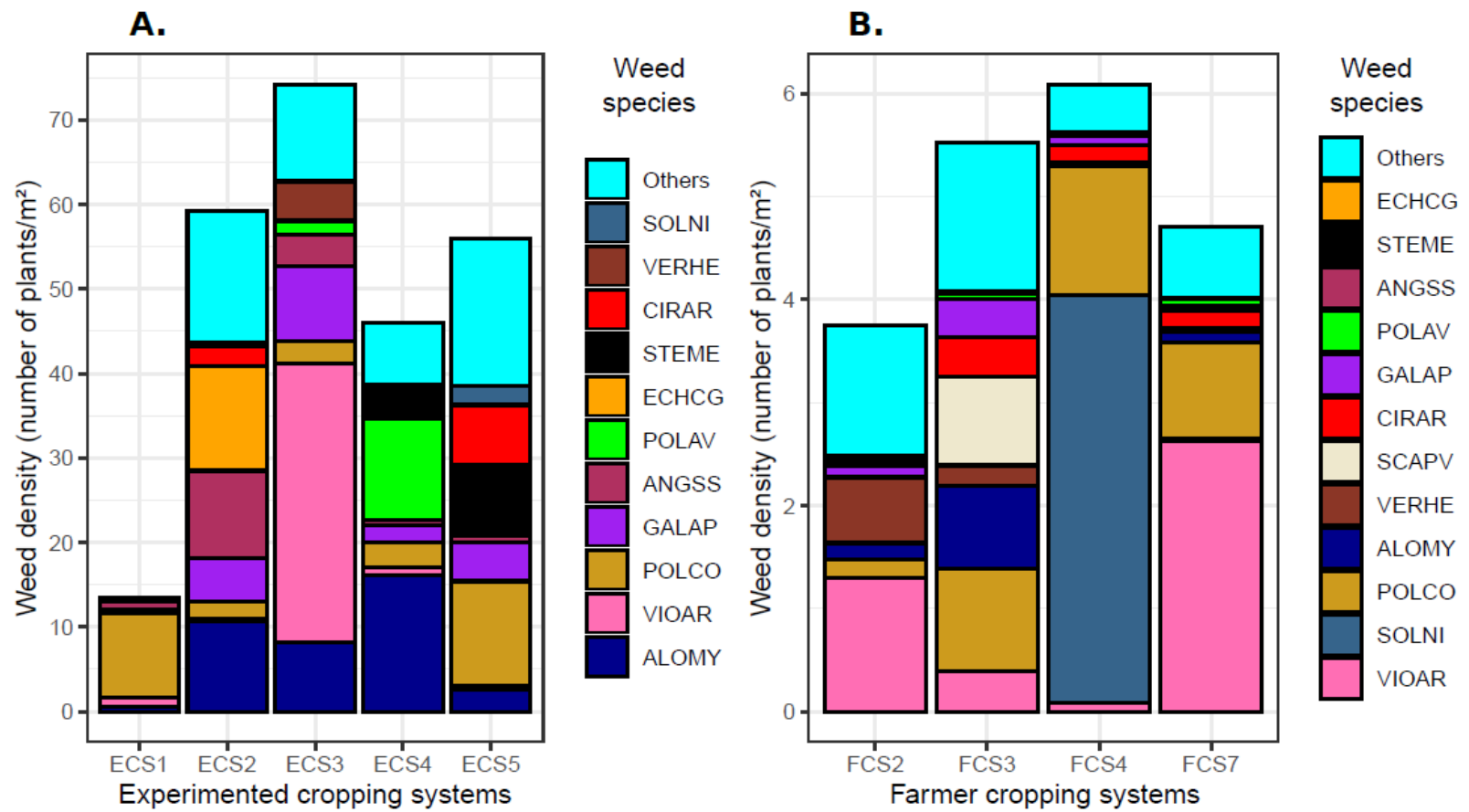
Response variable	Cropping system experiment								Farmers' network						
	Scale	Experimented cropping system effect (df=4)	N	ECS1	ECS2	ECS3	ECS4	ECS5	Scale	Farmer cropping system effect (df=3)	N	FCS2	FCS3	FCS4	FCS7
<b>Proportion of monocotyledonous species</b>	Plot:year	$\chi^2=9.34$ , <b>P=0.05</b>	60	0.12 $\pm$ 0.04 b	0.41 $\pm$ 0.08 a	0.22 $\pm$ 0.06 ab	0.24 $\pm$ 0.06 ab	0.17 $\pm$ 0.05 ab	Plot:year	$\chi^2=0.82$ , P=0.84	102	0.11 $\pm$ 0.04 a	0.09 $\pm$ 0.06 a	0.06 $\pm$ 0.05 a	0.07 $\pm$ 0.04 a
<b>Proportion of perennial species</b>	Plot:year	$\chi^2=11.73$ , <b>P=0.02</b>	60	0.04 $\pm$ 0.02 b	0.16 $\pm$ 0.05 a	0.04 $\pm$ 0.02 ab	0.04 $\pm$ 0.02 ab	0.17 $\pm$ 0.05 a	Plot:year	$\chi^2=10.01$ , <b>P=0.02</b>	102	0.05 $\pm$ 0.01 b	0.12 $\pm$ 0.03 a	0.08 $\pm$ 0.03 ab	0.08 $\pm$ 0.02 ab
<b>CWM height</b>	Plot:year	$\chi^2=11.81$ , <b>P=0.02</b>	60	49.1 $\pm$ 3.32 ab	44.6 $\pm$ 3.08 bc	36.8 $\pm$ 2.81 c	43.1 $\pm$ 3.03 bc	56.1 $\pm$ 3.53 a	Plot:year	$\chi^2=9.22$ , <b>P=0.03</b>	102	35.3 $\pm$ 2.4 b	45.1 $\pm$ 4.7 a	46.9 $\pm$ 6.0 a	46.4 $\pm$ 4.2 a
<b>CWM seed mass</b>	Plot:year	$\chi^2=13.77$ , <b>P=0.008</b>	60	5.33 $\pm$ 0.81 a	2.62 $\pm$ 0.39 b	2.27 $\pm$ 0.33 b	2.38 $\pm$ 0.35 b	2.84 $\pm$ 0.42 b	Plot:year	$\chi^2=8.23$ , <b>P=0.05</b>	102	2.12 $\pm$ 0.32 b	4.12 $\pm$ 0.87 a	2.78 $\pm$ 0.78 ab	3.38 $\pm$ 0.64 ab

974 **Figure 1:** Satellite image highlighting the vicinity of the experimental station with the farmer's network



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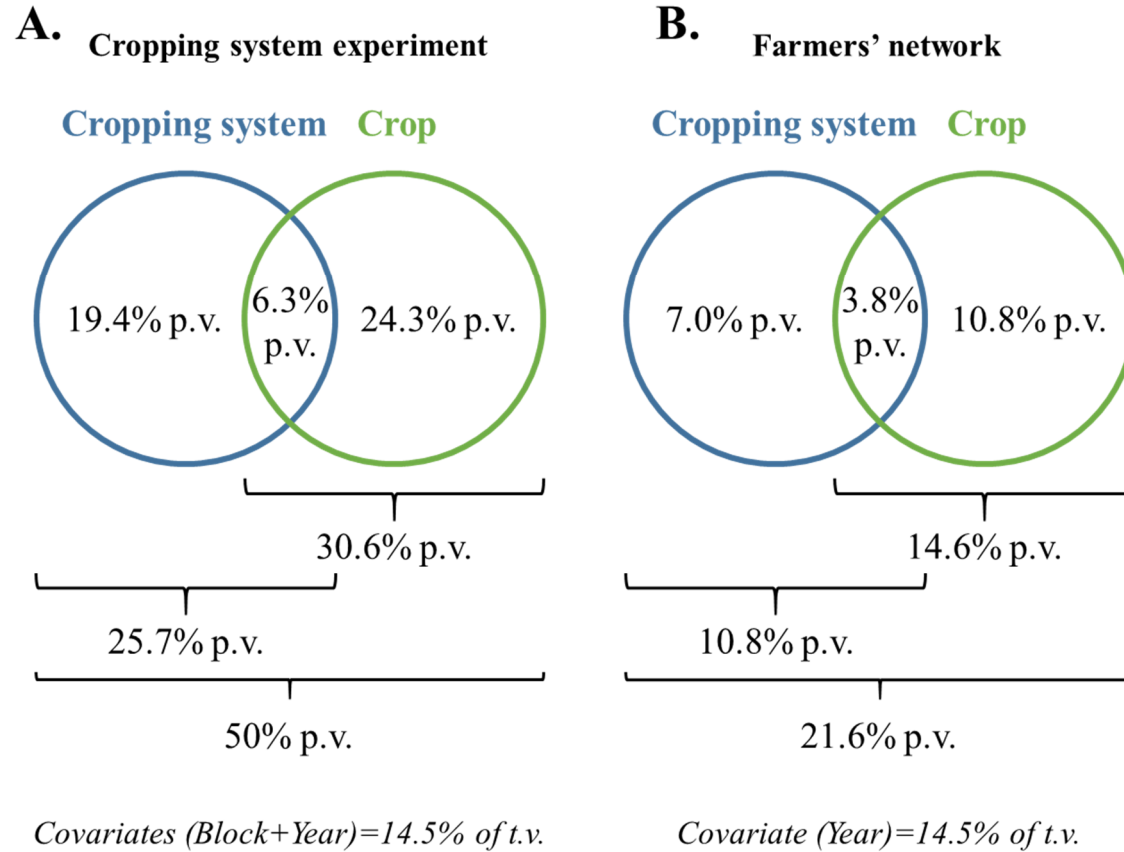
976 **Figure 2:** Observed mean weed density per species (named by to their EPPO code, <https://gd.eppo.int/>) after weeding (*i.e.* at crop flowering for A. and prior to crop  
 977 elongation for B.) between A) experimented cropping systems (ECS1 to ECS5) over the 2012-2017 period and between B) farmer cropping systems (FCS2 to FCS7) over the  
 978 2008-2013 period.



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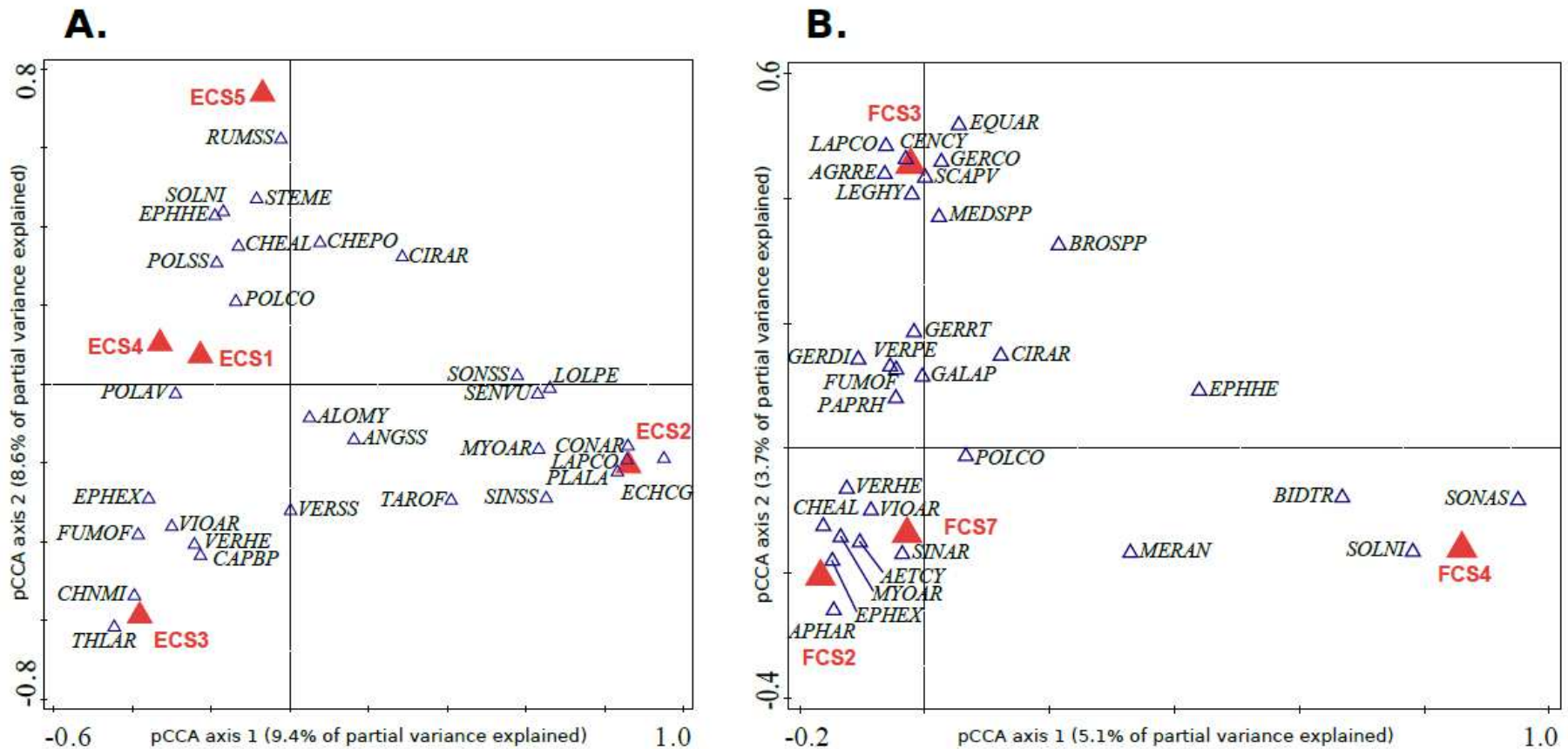
981 **Figure 3:** Gross and net effects of cropping system and crop on weed community composition for A) the cropping system experiment and for B) the farmers'  
 982 network. T.v.: total variation; p.v.: partial variation



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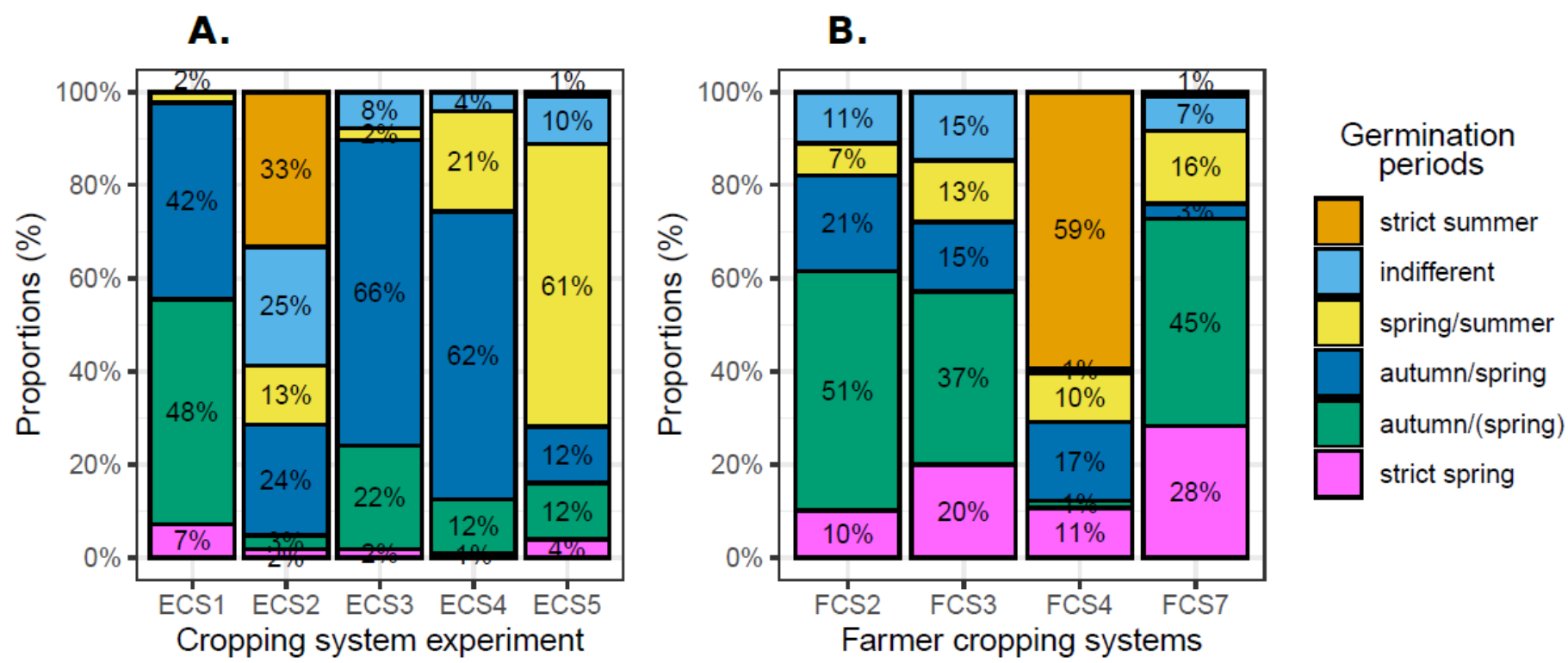
984

985 **Figure 4:** Partial canonical correspondence analyses highlighting the relationship between (A) experimented cropping systems or (B) farmer cropping systems  
 986 (red triangles) and weed species (empty blue triangles, named by to their EPPO codes, <https://gd.eppo.int/>) after the removal of block (A) and year (A and B)  
 987 effects. The response matrix consisted of 60 (A) and 102 (B) plot:years and weed density per species. Only the 30 best fitting species are represented for  
 988 graphical purposes.



989

990 **Figure 5:** Proportion of weed germination periods (weighted by density) between (A) experimented cropping systems and between (B) farmer cropping systems. Note:  
 991 autumn/(spring) refers to species which show a peak of germination during autumn that partially extends into the spring whereas autumn/springs refers to species which do  
 992 not show any preference between autumn and spring.



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