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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 Fénay 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 Fénay 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 m²
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 m² 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 m² area, <1, 1–2, 3–20, 21–50, and 51–
206 100 individuals m⁻²). 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⁻², 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 m²±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 m²
312 for ECS2 to ECS5 and nearly null (<1 g m²) 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 m²±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⁻²) 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. arvensis*, *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. arvensis/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

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948

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	F=47.67, P=0.001	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 ⁻¹	F=7.24, P=0.041	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	F=8.20, P=0.003	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	F=12.53, P=0.016	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 ⁻¹	F=32.31, P=0.003	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 ⁻¹	F=639.7, P<0.0001	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 ⁻¹	F=13.32, P=0.014	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 ⁻¹	F=23.77, P=0.005	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	F=6.88, P=0.005	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 ⁻¹	F=13.72, P=0.013	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 ⁻¹	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	F=9.02, P=0.002	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 ⁻¹	F=37.38, P=0.002	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 ⁻¹	F=29.14, P=0.003	154 \pm 8 a	94 \pm 6 b	96 \pm 5 b	109 \pm 2 b	79 \pm 12 b	F=4.06, P=0.03	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	F=0.00, P=0.00	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	Perfect fit*	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	F=13.20, P=0.0003	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	Perfect fit*	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	F=23.96, P<0.0001	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	F=8.60, P=0.03	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	F=5.51, P=0.01	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	Perfect fit*	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	Perfect fit*	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	F=3.60, P=0.04	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	F=31.0, P=0.003	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	F=5.96, P=0.009	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**	F=7.06, P=0.04	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	F=5.58, P=0.01	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.* $R^2=1$

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	$\chi^2=20.43$, P=0.0004	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	$\chi^2=21.41$, P=0.0003	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	$\chi^2=22.27$, P=0.0007	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	$\chi^2=10.20$, P=0.017	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	$\chi^2=14.53$, P=0.006	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	$\chi^2=22.83$, P=0.0001	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	$\chi^2=20.73$, P=0.0001	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	$\chi^2=11.86$, P=0.008	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	$\chi^2=20.59$, P=0.0004	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	$\chi^2=15.86$, P=0.003	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	$\chi^2=19.89$, P=0.0002	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	$\chi^2=7.37$, P=0.06	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

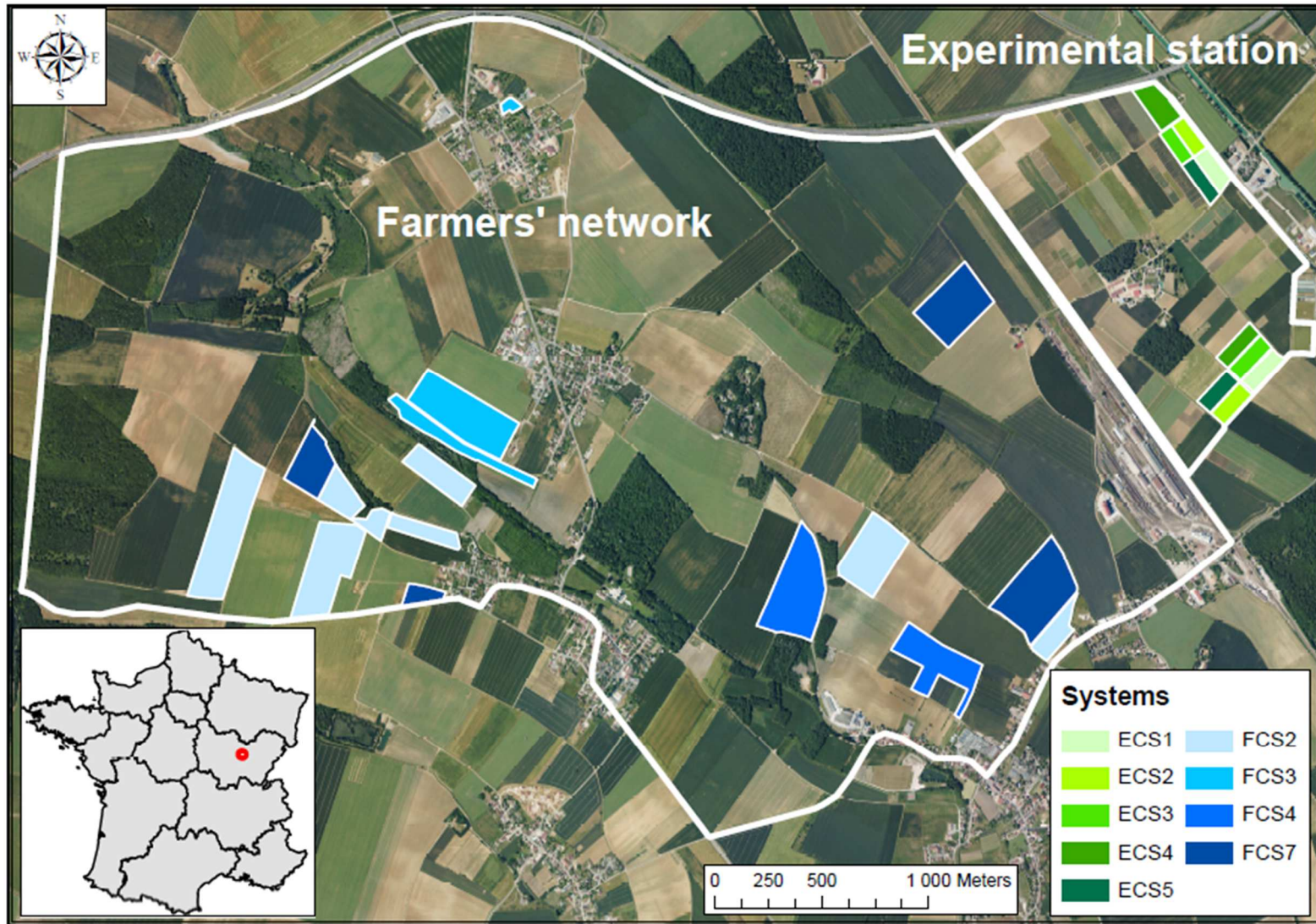
969 * No tests were performed at the plot scale due to lack of statistical power (N=10, d.f. cropping system effect=4)

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).

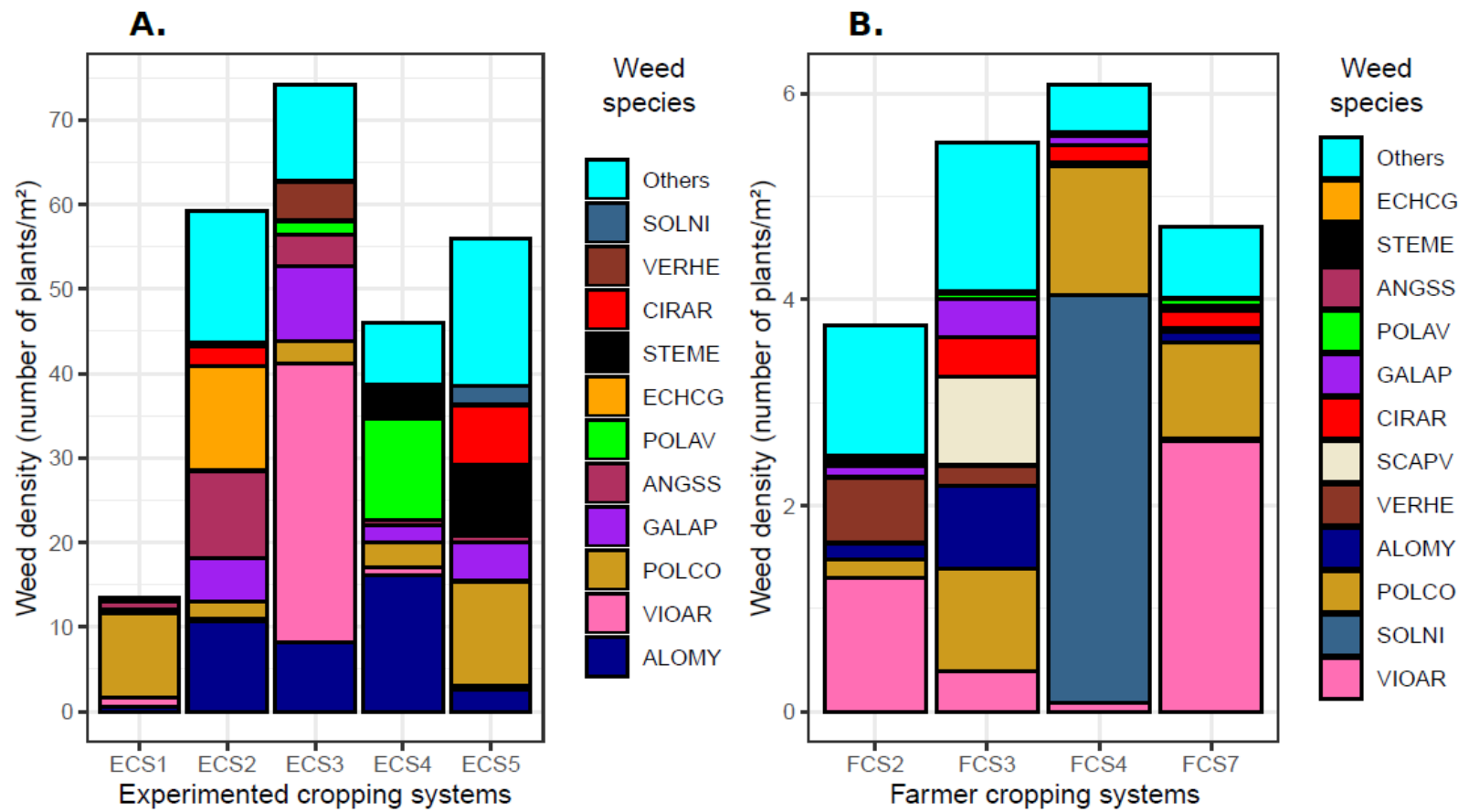
Response variable	Cropping system experiment								Farmers' network						
	Scale	Experimented cropping system effect (df=4)	N	ECS1	ECS2	ECS3	ECS4	ECS5	Scale	Farmer cropping system effect (df=3)	N	FCS2	FCS3	FCS4	FCS7
Proportion of monocotyledonous species	Plot:year	$\chi^2=9.34$, P=0.05	60	0.12 \pm 0.04 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
Proportion of perennial species	Plot:year	$\chi^2=11.73$, P=0.02	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	$\chi^2=10.01$, P=0.02	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
CWM height	Plot:year	$\chi^2=11.81$, P=0.02	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	$\chi^2=9.22$, P=0.03	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
CWM seed mass	Plot:year	$\chi^2=13.77$, P=0.008	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	$\chi^2=8.23$, P=0.05	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



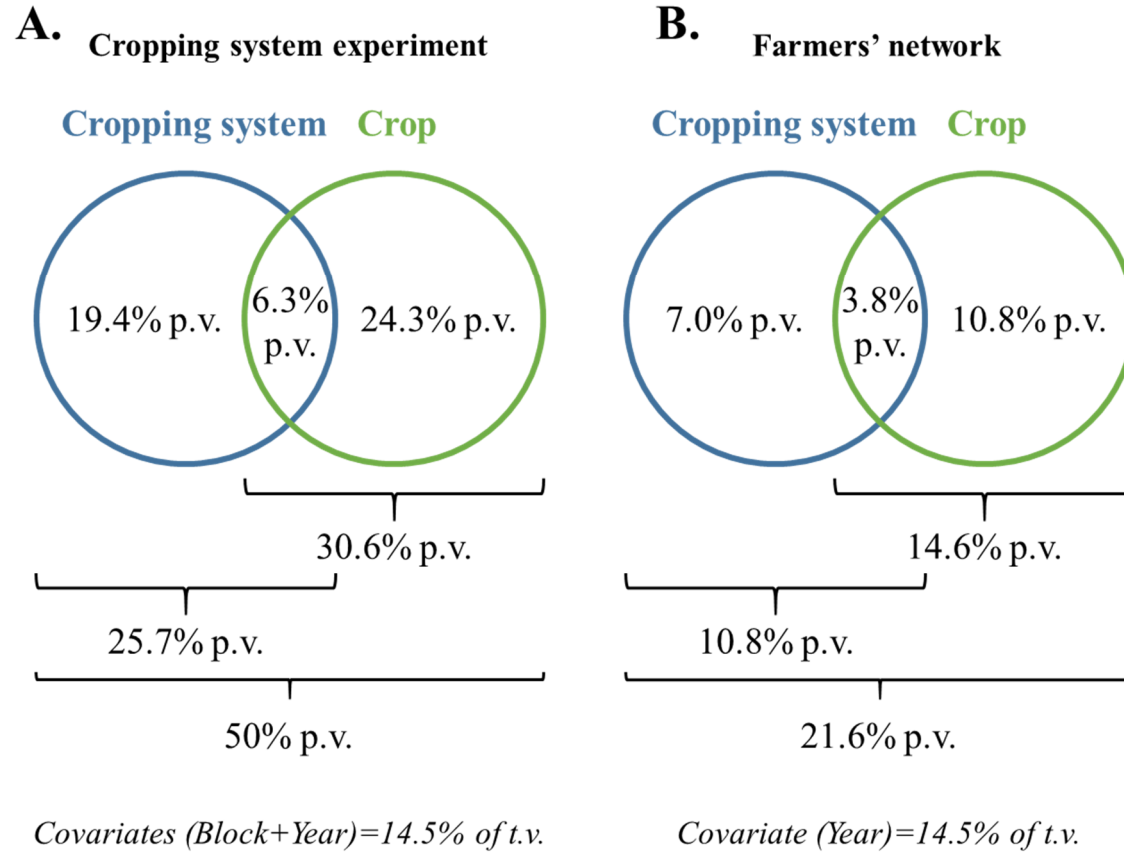
975

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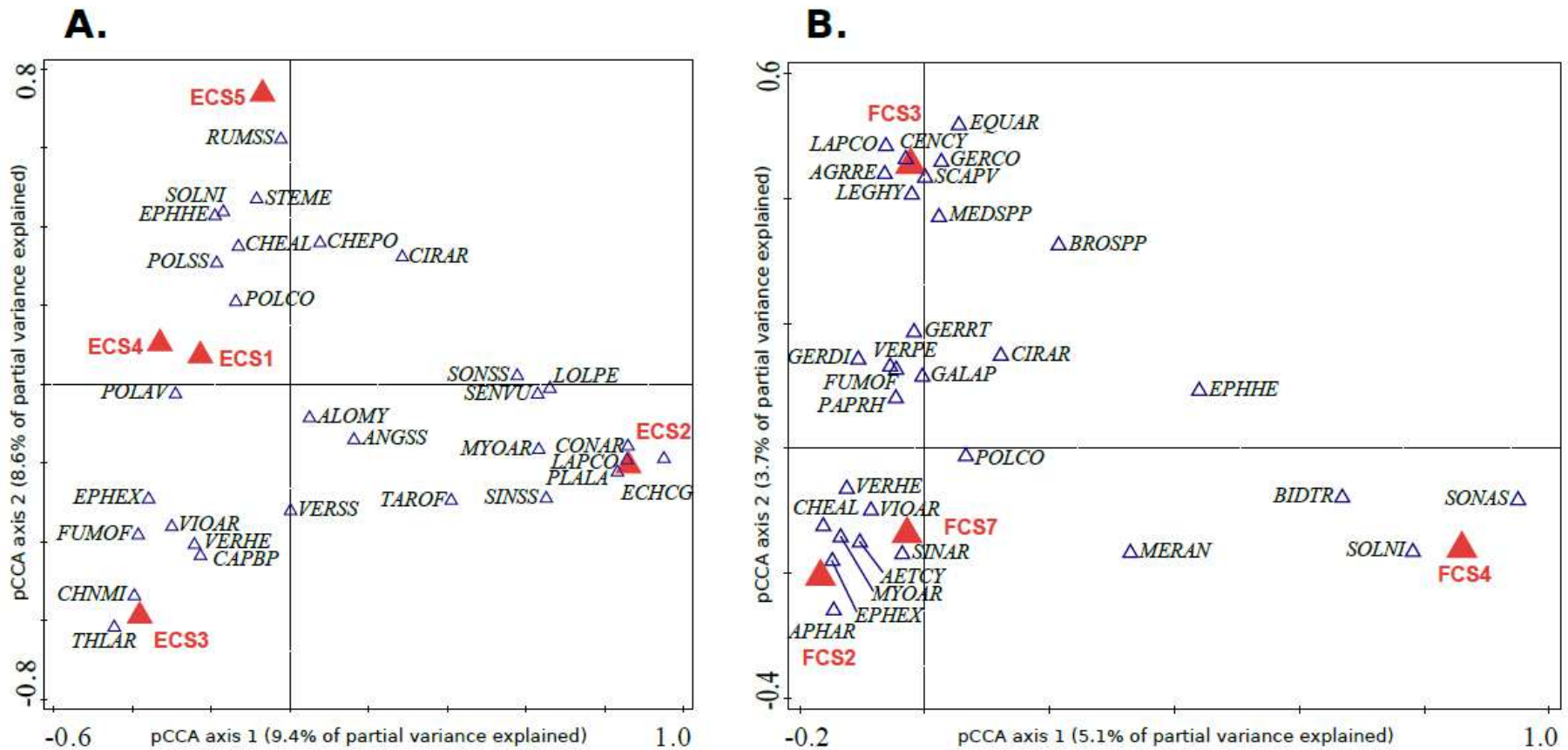
981 **Figure 3:** Gross and net effects of cropping system and crop on weed community composition for A) the cropping system experiment and for B) the farmers'
 982 network. T.v.: total variation; p.v.: partial variation



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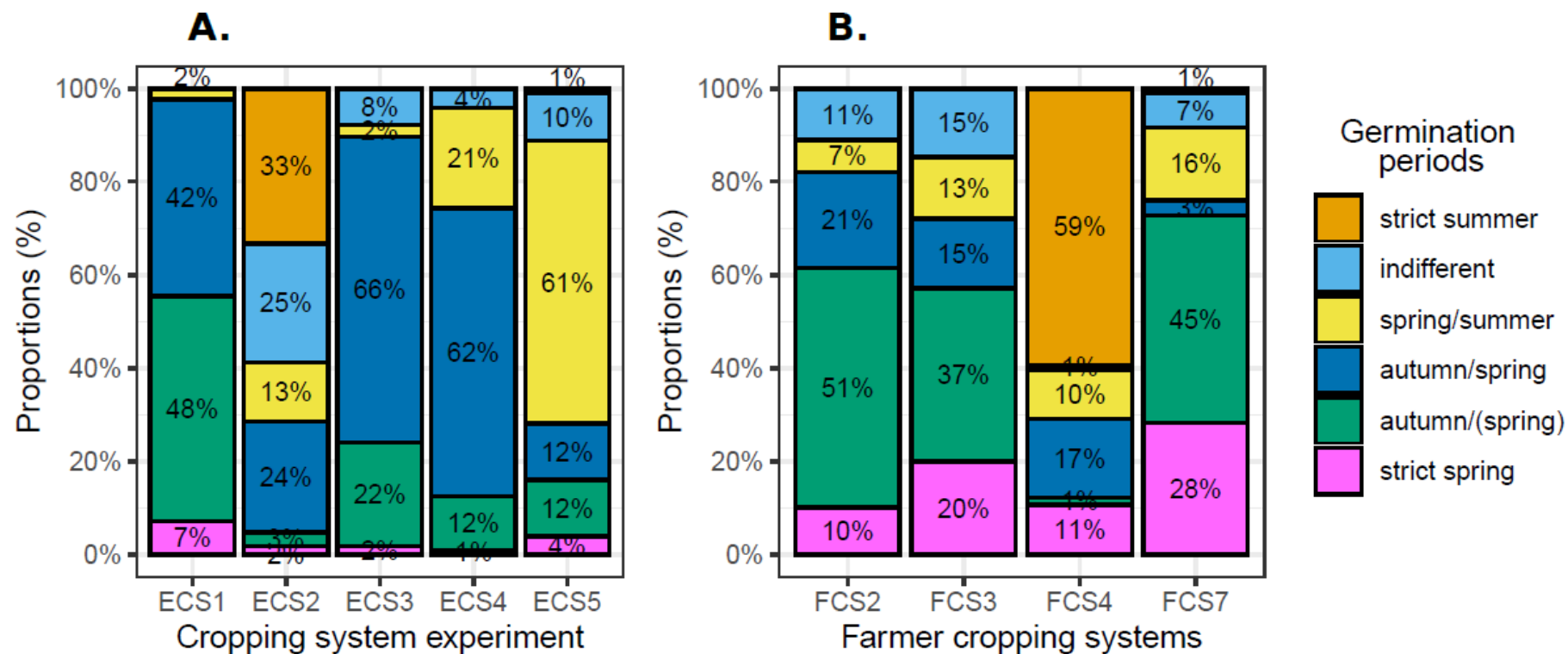
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985 **Figure 4:** Partial canonical correspondence analyses highlighting the relationship between (A) experimented cropping systems or (B) farmer cropping systems
 986 (red triangles) and weed species (empty blue triangles, named by to their EPPO codes, <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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