



HAL
open science

Taxonomic and functional characteristics of field edge weed communities along a gradient of crop management intensity

Séverin Yvoz, Sandrine Petit, Emilie Cadet, Fabrice Dessaint, Stéphane Cordeau

► To cite this version:

Séverin Yvoz, Sandrine Petit, Emilie Cadet, Fabrice Dessaint, Stéphane Cordeau. Taxonomic and functional characteristics of field edge weed communities along a gradient of crop management intensity. *Basic and Applied Ecology*, 2021, 57, pp.14-27. 10.1016/j.baae.2021.10.001 . hal-03483108

HAL Id: hal-03483108

<https://hal.inrae.fr/hal-03483108>

Submitted on 5 Jan 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

1 **Taxonomic and functional characteristics of field edge weed** 2 **communities along a gradient of crop management intensity**

3 Séverin Yvoz, Sandrine Petit, Emilie Cadet, Fabrice Dessaint, Stéphane Cordeau*

4 Agroécologie, AgroSup Dijon, INRAE, Univ. Bourgogne, Univ. Bourgogne Franche-Comté, F-21000
5 Dijon, France.

6 **Abstract**

7 The widespread loss of weed diversity and associated ecosystem functions is raising
8 important concerns. Field edges could play a major role in the maintenance of weed
9 functional diversity in arable landscapes as these habitats still harbour high weed diversity,
10 owing to either a reduced farming management intensity and/or to a spillover of species from
11 adjacent perennial field margins. Here, we investigated the taxonomic and functional
12 characteristics of weed species recorded in surveys of field edges and their associated field
13 cores over six consecutive years in 60 arable fields farmed with five crop management
14 strategies. We found that field edges were richer, with species more functionally diverse and
15 composition more stable over years than field core surveys. The distribution of individual
16 functional traits differed between field edges and field cores, with higher values for seed mass
17 and nitrophily (Ellenberg.N), and a wider distribution of specific leaf area values in field
18 edges. The bimodal distribution of plant height and germination period observed in field
19 edges became unimodal in field cores. Field edges harboured species with ecological
20 strategies associated with field cores (ruderal species) plus a conservative strategy which
21 could be explained by a spillover from the adjacent perennial field margins. Crop
22 management strategies impacted field edge flora, though to a lesser extent than the field core
23 flora whereas the functional differences between the field edge and the field core flora were
24 less marked when crop management intensity was lower. These results indicate that field
25 edges harbour a unique assemblage of species and highly contribute to the maintenance of
26 weed diversity in arable landscapes. Future studies should thus focus on the importance of
27 these specific functional traits to the agroecosystem functioning.

28 **Keywords:** biodiversity conservation, agroecology, functional ecology, ecological strategy,
29 species spillover, plant traits, field margin, disturbance.

*Corresponding author. Tel.: #+33 3 80 69 32 67

E-mail address: stephane.cordeau@inrae.fr

30 **Introduction**

31 Arable weeds are increasingly considered as key organisms supporting essential ecosystem
32 services in agroecosystems (Blaix et al. 2018). However, agricultural intensification,
33 including simplification of crop rotations and increased use of external inputs such as fertiliser
34 and herbicide, has led to their widespread decline in many fields in the world during the last
35 decades (Andreasen, Stryhn & Streibig 1996; Fried, Petit, Dessaint & Reboud 2009). The loss
36 of weed diversity in arable landscapes is raising important concerns as the drastic reduction of
37 these primary producers may trigger the decline of other taxa (Marshall et al. 2003), such as
38 farmland birds (Fuller et al. 1995; Holland, Hutchison, Smith & Aebischer 2006), bees
39 (Winfree et al. 2009) and invertebrates (Aebischer 1991; Van Swaay & Warren 1999) with
40 adverse consequences on agroecosystem functioning.

41 Farming practices such as crop type, tillage regime, herbicide and fertiliser use are the main
42 factors shaping weed community composition and structure (Andersson & Milberg 1998;
43 Cordeau et al. 2017b; Fried, Norton & Reboud 2008; Stevenson et al. 1997). It is often
44 suggested that the edge of arable fields, which corresponds to the small disturbed area
45 between the adjacent perennial field margin and the first row of the crop, could play a major
46 role in the maintenance of weed diversity at the field scale (Rotchés-Ribalta et al. 2015).
47 These edges have been shown to shelter up to twice as many weed species as the adjacent
48 field cores (Cordeau, Petit, Reboud & Chauvel 2012b) and although this differential can vary
49 greatly depending on the farming practices conducted in the field (de Snoo 1997; José-María,
50 Armengot, Chamorro & Xavier Sans 2013). Poggio, Chaneton and Ghersa (2013) thus
51 showed field edge a higher richness of geophyte and therophyte species than the interior of
52 the field. A current limitation in our understanding of the role of field edges in the
53 maintenance of functional weed diversity in arable landscapes stems from the fact that
54 comparisons between weed communities in field edges and their adjacent field cores have
55 only been documented for few crop types. Moreover, weed survey is usually conducted for
56 one year and for one crop type (Bourgeois, Gaba, Plumejeaud & Bretagnolle 2020; Metcalfe,
57 Hassall, Boinot & Storkey 2019; Pinke & Gunton 2014). This most likely underestimates
58 weed functional diversity as crop type is a strong environmental filter allowing a small
59 portion of the weed seedbank diversity to be observed as emerged plants in a particular year
60 (Fried, Norton & Reboud 2008). A field survey over a diversified crop succession would
61 provide a more reliable basis for comparing the weed flora in the core and in the edge of the
62 same field. A pooling of data collected in the same location over consecutive annual surveys
63 would give a more accurate picture of the differences in the diversity and composition of the

64 weed flora in the two habitats, closer to the composition of the soil seedbank (Sjursen 2001),
65 which is associated with the past farming practices applied in the field (Hawes et al. 2010;
66 Rotchés-Ribalta, Sans, Mayer & Mäder 2020).

67 The high field edge contribution to weed functional diversity could result from two main
68 processes. First, it is often argued that field edges are less subjected to fertiliser and herbicide
69 inputs than field cores, and as such, field edges could harbour weed species adapted to arable
70 conditions but unable to cope with the high level of disturbance in intensively managed field
71 cores, *i.e.* frequent tillage, and high herbicide and nitrogen inputs (Kovács-Hostyánszki,
72 Batáry, Báldi & Harnos 2011). Secondly, field edges could shelter the least competitive weed
73 species unable to withstand the increasing use of highly competitive crop varieties (Seifert,
74 Leuschner, Meyer & Culmsee 2014). Field edges would thus act as refugia for arable weeds,
75 an idea supported by long-term comparison studies showing that some species that were
76 widespread in field cores some decades ago are now only observed in field edges (Fried, Petit,
77 Dessaint & Reboud 2009). This would also explain why the differences in functional weed
78 diversity between the edge and the core are less marked when fields are under less intensive
79 or organic management (Romero, Chamorro & Sans 2008; Roschewitz, Gabriel, Tschardtke
80 & Thies 2005). Another hypothesis for the higher functional weed diversity found in field
81 edges is that they harbour species that have spilled over from neighbouring habitats, notably
82 adjacent perennial field margins (Dutoit, Gerbaud & Ourcival 1999; Metcalfe, Hassall, Boinot
83 & Storkey 2019; Poggio, Chaneton & Ghera 2013). This is supported by studies showing
84 that field edge weed communities are composed of species commonly observed in the
85 adjacent grass boundary or hedge (Cordeau, Petit, Reboud & Chauvel 2012a; Marshall &
86 Moonen 2002; Romero, Chamorro & Sans 2008; Wilson & Aebischer 1995). Each of these
87 two processes could explain the higher functional weed diversity observed in field edges
88 compared to field cores but their relative contribution remains unclear.

89 One way to assess the relative contribution of these two processes and the real contribution of
90 field edges in functional weed diversity is to compare the taxonomic and functional
91 composition of field edge weed flora to field core communities. Functional weed ecology
92 approaches have proven successful in investigating how different factors select for or against
93 different types of weeds, resulting in different levels of weed diversity (*e.g.* José-María et al.
94 (2011); Ryan et al. (2010); Storkey et al. (2010); Cordeau et al. (2017a)). Comparisons of the
95 distribution of key weed response traits in field edges and field cores could help deciphering
96 the relative role of the ecological processes at play. For example, the spillover of species from
97 the grass margin to the field edge would be reflected by a high proportion of perennials such
98 as geophytes and hemicryptophytes (*e.g.* Grime's competitive and competitive/ruderal

99 strategies). Field edges could also shelter species expressing a shade avoidance syndrome
100 (high height and low specific leaf area) not observed in field cores (Perronne, Gaba, Cadet &
101 Le Corre 2014).

102 In this study, we analysed the taxonomic and functional differences of field edge and field
103 core weed surveys recorded for six consecutive years in 60 fields under different crop
104 management strategies. Firstly, we hypothesised that (i) the distribution of key plant response
105 traits, namely height, specific leaf area (SLA), seed mass, Ellenberg N and L indicator values,
106 germination onset, germination duration, flowering onset, flowering duration, plant class and
107 Raunkiaer's life forms will differ between field edges and field cores. We expected the range
108 of trait values to be wider in field edges in comparison to field cores due to the presence in
109 field edges of species adapted to field core conditions (*i.e.* role of refuge habitat), species
110 excluded from field cores due to higher disturbances and competition and species adapted to
111 the perennial grass margin. Secondly, considering all the traits together, we hypothesised that
112 (ii) the relative proportion of identified functional groups differs between the two habitats, the
113 differences becoming less marked when the farming intensity in the field decreases (*e.g.*
114 ploughing, tillage or herbicide frequency). Finally, we hypothesised that (iii) field edge
115 surveys are more stable between successive years than field cores due to the presence of
116 perennial species generally associated with field margins and a lower intensity of farming
117 practices compared to field cores.

118 **Materials and methods**

119 ***Study system***

120 The study was carried out on the Fénay study site (950 ha) located near Dijon in eastern
121 France (47°13'N, 5°03'E). We assume homogeneous continental climate conditions across
122 the area with an average temperature of 10.7 °C and an average precipitation of 744 mm per
123 year, mainly in winter. Between 2008 and 2013, crop successions were mainly composed of a
124 three-year rotation based on a *Brassicaceae* crop and two winter cereals. More rarely, some
125 rotations included spring (*e.g.* barley, peas) and/or summer crops (*e.g.* sunflower, soybean).
126 Since 2004, annual interviews with farmers of the studied area have documented their
127 practices in each field and enabled us to classify fields into eight crop management strategies
128 (Yvoz, Petit, Biju-Duval & Cordeau 2020). The eight crop management strategies reflected
129 different combinations of farming practices intensity (*i.e.* intensity of tillage, herbicide and
130 fertiliser use, crop diversity).

131 The 60 fields selected in this study belong to five of the eight strategies, described in
132 Appendix A: Table 1. All strategies were conventional (*i.e.* no organic strategies) and crop
133 rotation were composed of annual grain crops (*i.e.* no leys due to the absence of livestock in
134 the area). Strategy 2 (17 fields) is characterised by short rotations with mainly winter crops,
135 based on mouldboard ploughing and chemical crop protection. Strategy 3 (14 fields) gathers
136 short rotations with mainly winter crops, based on tillage practices, chemical crop protection
137 and herbicide split applications. Strategy 5 (8 fields) combines moderately diversified
138 rotations based on low use of mouldboard ploughing and fertilisation, but high herbicide and
139 other tillage operations. Strategy 7 (15 fields) is characterised by diversified successions with
140 spring and summer crops and intermediate use of mouldboard ploughing and tillage and a low
141 use of herbicide and chemical crop protection. Strategy 8 (6 fields) gathers diversified
142 rotations including a high proportion of summer crops, reduced tillage and fertilisation,
143 intermediate levels of mouldboard ploughing and chemical crop protection but exhibits a
144 heavy reliance on herbicide.

145 ***Weed surveys***

146 Weed surveys were carried out annually between 2008 and 2013 in the 60 fields. The timing
147 of the survey was adapted to the crop type and conducted after most of the weeding
148 operations (*i.e.* March for winter crops, April for spring crops and June for summer crops). In
149 each field and year, weed communities were surveyed the same day in the core and the edge
150 of the field, leading to a dataset of 720 annual weed surveys (60 fields x 2 locations x 6
151 years). As described by Yvoz, Petit, Biju-Duval & Cordeau (2020), weeds were recorded in
152 the field core following a “W” pattern within a 2000 m² area (50 m by 40 m, real prospected
153 area 130 m by 1.5 m) located 20 m away from the adjacent perennial field margin (Fig. 1).
154 Weeds were recorded in the field edge in a 50 m linear transect alongside the adjacent
155 perennial field margin, in front of the field core sampled area. The width of this sampled area
156 corresponded to the space between the first row of the crop and the grass margin, *i.e.*
157 averaging 30 cm width. The prospected areas differed between both locations because i) our
158 sampling design required both sampled areas to be in front of each other to ensure a
159 meaningful comparison of weed flora and ii) because field edge harboured higher weed
160 richness and abundance than the field core in the study area, thus allowing a smaller
161 prospected area to assess the composition of weed flora (*e.g.* 80% of the weed diversity) (He
162 & Legendre 2002). In both areas, weeds were identified to the species level except for 16 taxa
163 of the 147 identified, and named according to Jauzein (1995). Their abundance was estimated
164 visually using the scale developed by Barralis (1976) with six classes of density (one

165 individual in the prospected area, <1, 1-2, 3-20, 21-50, and 51-100 individuals.m⁻²). The total
166 weed abundance was computed using the centre of each density class (0.0005, 0.5, 1.5, 11.5,
167 35.5, and 75.5 individuals.m⁻², respectively) to be able to sum species densities. To study the
168 global effect of the within-field location (field core or field edge) and the crop management
169 strategy on the weed functional traits, independently of the effects of the crop and the year,
170 we focussed on the cumulated weed surveys over the six-year period. Thus, for the core and
171 the edge of the 60 fields, we averaged the abundance of the six annual surveys for each
172 species (null abundance when the species was not observed). Subsequent analyses were
173 applied on these 120 weed assemblages over six years (60 fields x 2 locations), called
174 hereafter cumulated weed surveys.

175 *Weed species traits and ecological descriptors*

176 Weed species were described with seven functional response traits: maximum height
177 (Height), seed mass (Seed.mass), specific leaf area (SLA), germination onset (Germ.onset)
178 and duration (Germ.dur) and flowering onset (Flow.onset) and duration (Flow.dur), two
179 functional descriptors: Plant class (Class) and Raunkiaer's life form (Raunkiaer) and two
180 ecological indicators, Ellenberg indicator values for Nitrogen (Ellenberg.N) and for Light
181 (Ellenberg.L), all hereinafter called traits, known to respond to the intensity of disturbances
182 (tillage or herbicide use), the competition for resources (light and nutrient) and the species
183 spillover (Table 1, detailed description and references in Appendix A: Table 2). We selected
184 nine of the ten traits defined by Fried et al. (2012) as traits responding to the major farming
185 management practices in the French context. We added the Ellenberg indicators for nitrogen
186 and light preferences since they were useful in previous studies (Bourgeois, Gaba,
187 Plumejeaud & Bretagnolle 2020) to detect potential differences of competition levels under
188 various resources availability between the edge and the core of the field (Fried, Petit, Dessaint
189 & Reboud 2009). Data for these 11 traits were collected from the literature, using various
190 databases (Table 1). For SLA, the median value was kept for each species. For taxa not
191 identified to the species level, we used data from the most frequently observed species of the
192 same genus in the studied area.

193 *Statistical analyses*

194 All statistical analyses were implemented with the R software version 4.0.2 (R Core Team
195 2020). The 120 cumulated weed surveys were first described by five metrics: species richness
196 (Sp_Richness), total abundance (Abundance), Pielou's equitability index (Evenness), Rao's
197 functional diversity (Rao_FD) and inter-annual species turnover (Turnover) (See correlations

198 between metrics in Appendix A: Fig. 1). The functional diversity was calculated as the Rao's
199 quadratic entropy (Botta-Dukát 2005) computed from the species-species distance matrix
200 based on the eleven functional traits (Table 1) using the dbFD function from the [FD]
201 package. The turnover was calculated as $(b + c)/(a + b + c)$, where b and c are the number of
202 species gained and lost between two successive years, respectively, and a the number of
203 species observed in both years, (*i.e.* 2008/2009, 2009/2010, 2010/2011, 2011/2012,
204 2012/2013). The turnover was computed using the function turnover from the package
205 [codyn], then averaged for each weed survey over the six-year period. Turnover ranges from 0
206 to 1 and is high when the proportion of species shared between two successive years is low.

207 *Weed survey composition*

208 We tested the effect of the Within-field location (edge vs. core of the field), the Crop
209 management strategy (five strategies) and their interaction on the five metrics (see
210 Appendix A: Table 3 for details on statistical models and functions and R packages used).
211 Linear mixed models were used for abundance (Abundance), Generalised linear mixed model
212 was used for species richness (Sp_Richness) and beta-regression models for Evenness,
213 Rao_FD and Turnover (Appendix A: Table 3). In the five models, Within-field location and
214 Crop management strategy were considered as fixed effects and the field was added as a
215 random effect to consider that edge and core surveys are paired within fields (Appendix A:
216 Table 3). Significance of main fixed effects was tested by a type II ANOVA and estimated
217 marginal means of Strategies and Within-field locations compared by pair. We checked for
218 spatial autocorrelation and normal distribution in residuals of the five models.

219 The effects of Within-field location, Strategy and their interaction on cumulated weed survey
220 composition were tested with a permutation-based ANOVA (Anderson 2001) with $N = 999$
221 permutations, applied on the Bray-Curtis dissimilarity matrix accounting for weed presence
222 and abundance using the *adonis* function from the [vegan] package. The field was added as a
223 random effect (*i.e.* strata argument) to account for the paired field edges and cores.
224 Differences in heterogeneity between Within-field location, Crop management and their
225 interaction were tested using PERMDISP, an analysis of multivariate homogeneity of group
226 dispersions (Anderson 2006).

227 *Trait distributions*

228 We compared the distribution of the eleven functional traits (Table 1) between field edge and
229 field core surveys for each crop management strategy. Within each of the five crop
230 management strategies we compared the distribution of the nine quantitative traits (Gaussian

231 kernel density estimation weighted by the relative abundance of each species calculated with
232 the *density* function in R) between the core and the edge of the field using the approach
233 described by Perronne et al. (2014) and Bourgeois et al. (2019). We computed the
234 dissimilarity of traits distribution by calculating the proportion of the distributions in common
235 between the two within-field locations (*overlapTrue* function from the [*overlap*] package). We
236 used a randomization method to test whether the overlap between within-field locations in
237 each crop management strategy was significantly lower than the null hypothesis (random
238 layout of the weed surveys between within-field locations). The randomization procedure was
239 implemented within each crop management strategy by random permutations of the
240 cumulated weed surveys between field edges and field cores. Thus, we generated 10 000
241 random distributions and implemented a one-tailed direct test of significance for the non-
242 random structure (p-values < 0.05). P-values were estimated as the proportion of random
243 distributions having an overlap value lower than the observed overlap. Adjustments based on
244 the calculation of the false discovery rate (Benjamini & Hochberg 1995) were applied per
245 functional trait to deal with multiple comparisons within the five crop management strategies.
246 For the two qualitative traits, we assessed the differences in category distributions between
247 the edge and the core of each crop management strategy by Monte-Carlo simulation tests
248 based on 10,000 replicates.

249 *Weed functional groups*

250 To integrate simultaneously all eleven traits, we classified the 147 observed weed species into
251 functional groups and compared their relative representation according to Within-field
252 locations and Crop management strategies. Firstly, we implemented a Hill and Smith
253 multivariate analysis (Hill & Smith 1976) on the eleven quantitative and qualitative functional
254 traits (Table 1) with the *dudi.hillsmith* function from the [*ade4*] package. Quantitative traits
255 were centred and standardised before implementing the multivariate analysis. Based on the
256 distance matrix from the Hill and Smith analysis, we then identified species functional groups
257 using a Hierarchical Clustering Analysis (HCA) with the *HCPC* function from the
258 [*FactoMineR*] package. Functional groups were identified by an agglomerative hierarchical
259 clustering following the Ward's method and clusters were not consolidated. The number of
260 clusters kept was decided after examination of the dendrogram and confirmed using the gain
261 of explained variance when increasing the number of clusters. Trait levels belonging to each
262 functional group were finely described using a one-way analysis of variance (*catdes* function
263 from the [*FactoMineR*] package). Secondly, we compared the relative distribution of the
264 functional groups between the field edge and the field core of the five crop management

265 strategies. The effects of Strategy, Within-field location and their interaction on the
266 distribution of the functional groups were carried out using a test of independence with the
267 *mosaic* function from the [vcd] package. Significance of the effects was tested using a
268 Pearson Chi-squared test with the *assocstats* function from the [vcd] package.

269 *Interannual stability of the weed functional groups*

270 For each of the 120 cumulated weed surveys, we calculated the coefficient of variation
271 (standard deviation/mean) of the proportion of the different functional groups over the six
272 years of survey. Then, we evaluated the effect of the Within-field location, the Crop
273 management strategy and their interactions on the coefficient of variation values. Thus, we
274 applied a linear mixed model (detailed in Appendix A: Table 3) based on a gaussian
275 regression using the *lmer* function ([lme4] package). Field was added as a random effect.
276 Main effects were tested by a type II ANOVA applied with the *Anova* function from the [car]
277 package. Differences between Strategies and Within-field locations were estimated by least
278 significant difference analyses using the function *emmeans* from the [emmeans] package and
279 the function *cld* from the [multcomp] package.

280 **Results**

281 *Weed survey structure and composition*

282 A total of 147 weed taxa, mostly at species level, and in some instances at genus level, were
283 recorded among which 46 and 6 were solely observed in the field edges and cores,
284 respectively. Sp_Richness, Rao_FD and Abundance were globally higher in field edges than
285 in field cores (Fig. 2). However, these differences varied according to Strategy for
286 Sp_Richness and Rao_FD, being lower in S7 and S8 than in S2, S3 and S5 (Fig. 2A and E),
287 however Rao_FD did not differ for S8. Evenness was not impacted by Within-field location
288 and Crop management strategy (Fig. 2D). Turnover was globally lower in field edges than in
289 field cores (Fig. 2F) but was not impacted by Crop management strategy.

290 Compositions of the 120 weed surveys differed between Within-field location and Strategy
291 (Appendix A: Fig. 2A, p-values < 0.001), but not by their interaction. Field edge surveys were
292 more associated with grass species (*e.g. Elytrigia repens, Alopecurus myosuroides, Bromus*
293 *sp., Lolium sp., Poa annua*) and perennials (*e.g. Daucus carota, Galium mollugo, Achillea*
294 *millefolium*) than field core surveys (Appendix A: Fig. 2B). Overall, all species were more
295 associated with field edges than field cores due to their higher abundance in field edges. Field
296 cores of S7 and S8, were characterised by summer-germinated species (*i.e. Aethusa*
297 *cynapium, Persicaria maculosa* and *Solanum nigrum*). The analysis of variance homogeneity

298 showed no significant differences between strategies nor between combinations of Within-
299 field location and Strategy (p-values > 0.05). However, the composition of weed surveys in
300 field cores was more variable than those of field edges (p-value < 0.001), as shown by the
301 wider ellipses for field cores (Appendix A: Fig. 2A).

302 ***Functional traits distribution***

303 The distributions of the nine quantitative trait values differed between field edge and field
304 core (Fig. 3) except for Ellenberg.L (overlap > 0.83), Germ.onset (overlap > 0.74) and SLA
305 (only significant in S5). The effect of Within-field location was dependent on Crop
306 management strategy, with no trait distribution differing between field edges and field cores
307 in S8 (Fig. 3). We detected three major differences in the distribution of traits between field
308 edges and field cores: (i) the mean trait value shifted, with higher values in edges (*e.g.*
309 Seed.mass, Ellenberg.N, Flow.onset), (ii) the unimodal distribution of some traits in field
310 cores became bimodal in field edges (*e.g.* Germ.dur, Height), and (iii) there was a wider
311 distribution of trait values in field edges, *i.e.* a higher standard deviation was observed (*e.g.*
312 SLA). Globally, field edges displayed a higher proportion of tall plants (> 100 cm), with
313 heavier seeds (> 3 mg) and higher nitrophily (Ellenberg.N > 7 in S2, S3 and S5). The most
314 conventional/intensive strategies (*i.e.* low crop diversification and/or high use of inputs) such
315 as S2, S3 and S5 showed the highest differences in trait distributions between field edges and
316 cores (with 6, 4 and 6 out of the 9 traits differing, respectively), compared with the least
317 intensive strategies (*e.g.* high crop diversification and/or low inputs use) such as S7 (2 traits
318 differing) and S8 where the distribution of traits was similar in field edges and field cores.
319 Except in S8, grasses and forbs were always over- and under-represented in field edges,
320 respectively (Fig. 3). Therophyte species were always over-represented in field cores. In S5
321 and S7, geophyte and hemicryptophyte species were over-represented in field edges (Fig. 3).

322 ***Weed functional groups***

323 The 147 weed species were grouped into five functional groups (Appendix A: Fig. 3). All
324 traits, except Ellenberg.N and Ellenberg.L significantly contributed to the grouping (p-values
325 < 0.001). The functional group FG1 included 14 weed species (Appendix A: Fig. 3C) with
326 low SLA and Flow.dur values, but high Height and Seed.mass values (Fig. 4). Geophyte
327 species were over-represented in this group. The group FG2 was composed of 48 weed species
328 (Appendix A: Fig. 3C) with low SLA, Germ.dur and Flow.dur values, but high Height,
329 Germ.onset and Flow.onset values (Fig. 4). Forb and hemicryptophyte species were over-
330 represented in this group. The group FG3 was formed by 13 weed species (Appendix A: Fig.

331 3C) mainly associated with grass species (Fig. 4). The group FG4 included 62 species
332 (Appendix A: Fig. 3C) with low Height, Germ.onset and Flow.onset values, and high SLA
333 values (Fig. 4). Forb and therophyte species were over-represented in this group. Finally, the
334 group FG5 included 10 species (Appendix A: Fig. 3C), mainly therophytes, with low Height,
335 Germ.onset, Flow.onset and high SLA, Ellenberg.N, Germ.dur and Flow.dur values (Fig. 4).
336 The relative distribution of the five functional groups within the 120 cumulated weed surveys
337 varied by Within-field location, Crop management strategy and their interaction (Fig. 5). FG1,
338 FG3 and FG5 were significantly under-represented in field cores, while FG4 was over-
339 represented (p -values < 0.05). FG1 was mostly found in S2 and S3 and much less in S5 and
340 S8. FG2 was not well represented in S5 but commonly found in S7. FG3 was minor in S2 and
341 S5 but widely found in S7. FG4 was not well represented in S2 and FG5 was more often
342 observed in S5 and S8. For all strategies except S8, FG4 occurred significantly more in field
343 cores and less in field edges (test of independence in Appendix A: Fig. 4). FG1 and FG3 were
344 found more often in field edges and less often in field cores of S5 and S7. FG1 and FG2 were
345 under-represented in field cores of S2, FG5 in field cores of S5 where FG2 was over-
346 represented in field cores of S8 (Appendix A: Fig. 4).

347 *Interannual stability of the weed functional groups*

348 The interannual stability of the functional groups was significantly different between field
349 edges and field cores, except for FG3 (Appendix A: Fig. 5). The coefficient of variation was
350 higher in field cores than in field edges for FG1, FG2 and FG5, whereas it was the opposite
351 for FG4 (Appendix A: Fig. 5). The mean coefficient of variation ranged from 0.6 to 1.1 and
352 from 0.3 to 1.8 for the five functional groups in field edges and cores, respectively. The
353 effects of the Crop management strategy and the interaction with the Within-field location
354 were never significant.

355 **Discussion**

356 Our analysis of weed surveys cumulated at a pluri-annual scale confirmed the findings of
357 previous studies conducted at an annual scale, namely that field edges are significantly richer
358 and more diverse in species than their associated field cores. Besides, the smaller area of the
359 survey in field edge compared to field core should negatively impact the species richness
360 estimation, thus the differences between locations may be higher. However, we showed that
361 different processes acting simultaneously lead to a higher weed species functional diversity in
362 field edges in comparison to field cores. The edge of fields harboured species with particular
363 combination of traits (*i.e.* FG1 and FG3) generally associated with the adjacent perennial field

364 margin, and their occurrence in field edges was almost constant across years. In addition, field
365 edges also sheltered species typically observed in field cores (*i.e.* FG4), and in much larger
366 numbers than field cores. Our pluri-annual analysis also revealed that core and edge weed
367 surveys differed less, taxonomically and functionally, when the crop management strategy
368 implemented in the field was less intensive. The observed higher taxonomic and functional
369 diversity and the higher temporal stability of the weed flora of field edges converge to
370 highlight their role in the maintenance of weed diversity in agricultural landscapes, especially
371 when crop management intensity is high.

372 ***The composition of field edge weed surveys***

373 Several studies have suggested that the higher weed richness observed in field edges can
374 result from the spillover of species from the adjacent perennial field margins (Dutoit, Gerbaud
375 & Ourcival 1999; Metcalfe, Hassall, Boinot & Storkey 2019). Such species are rarely
376 observed in field cores (or are very transient) and are mostly competitive species tolerant to
377 mowing (Cordeau, Petit, Reboud & Chauvel 2012a; Marshall 1989). Here, we indeed
378 identified three functional groups adapted to the ecological conditions of field margins (FG1:
379 tall geophyte species with big seeds and low SLA, FG2: tall hemicryptophyte species with
380 low SLA and FG3: grass species). Plants with such a conservative strategy (*i.e.* investing a lot
381 of energy to produce long-lived stem and leaves) were very well represented in the field edge
382 surveys of our study area but rarely observed in the field cores.

383 It is also often suggested that the high weed richness observed in field edges results from the
384 lower level of disturbance of these habitats compared to the core of the fields (Pinke &
385 Gunton 2014). Our analysis of trait distributions aligns with this explanation. We observed
386 higher seed mass and height in field edge surveys, indicative of a less intense soil disturbance,
387 since small plants with high production of small seeds are highly adapted to soil tillage (Gaba
388 et al. 2017). The wider distribution of some traits in field edges compared to field cores,
389 particularly the germination duration and the flowering onset, also suggests that the ecological
390 niche in field cores is smaller than that of field edges. Under intensive crop management, the
391 standard deviation of traits is reduced (Bourgeois et al. 2019) and the number of species able
392 to survive as well. Indeed, we showed here that field cores were dominated by ruderal species
393 (FG4), while field edges expressed more even distribution of the five weed functional groups.
394 Surprisingly, we found that indicator values for Nitrogen (Ellenberg.N) were higher in field
395 edges than in field cores. This could be explained by the combination of two factors: a high
396 quantity of in-crop nitrogen fertilisation (Kleijn & van der Voort 1997) and a low crop use in
397 the edge of the field compared to the core, leading to more resources available for

398 nitrophilous weed species. The study area is indeed characterised by a high proportion of
399 highly nitrogen-demanding winter crops such as oilseed rape, mustard and winter cereals.
400 Similarly, we expected field edge surveys to exhibit a higher affinity for light (*i.e.*
401 Ellenberg.L) than field core surveys, as the amount of photosynthetically active radiation is
402 higher in the field edge than in the field core of the studied fields (Yvoz, Cordeau, Zuccolo &
403 Petit 2020). The lack of such signal could result from the variability of the growing conditions
404 over time linked to the succession of crops with various heights and growth habits, combined
405 with a variability of surrounding vegetation and semi-natural habitats leading to a high
406 competition for light, even in field edges (Seifert, Leuschner, Meyer & Culmsee 2014). This
407 would be in line with the results of Perronne et al. (2014) showing a shade-tolerant syndrome
408 in weeds both in field edges and field cores. Finally, we cannot exclude that the Ellenberg-N
409 and L values of weed communities in field edges may have been influenced by the spillover
410 of species coming from the adjacent perennial grass margin. In our study, most weed species
411 occurring in field edges were present every year over the 6-year sequence. This could result
412 from a continuous influx of propagules from the adjacent perennial grass margin (Blumenthal
413 & Jordan 2001). Alternatively, these species could establish more permanently in the field
414 edges, which would imply that their traits are adapted to the ecological filters acting in field
415 edges, notably herbicide applications and tillage operations.

416 ***Response of field edge weed surveys to crop management strategies***

417 Our results highlight that although field edges are richer due to the spillover of species from
418 the close boundary, they are also part of the field and as such are affected by the crop
419 management strategy implemented in the adjacent crop. Indeed, field edges were
420 characterised by a surprisingly high turnover of weed species between consecutive years.
421 Since crop type is a major factor shaping weed communities (Fried, Norton & Reboud 2008),
422 changes in the composition of field edge weed surveys from one year to the next could partly
423 be explained by the change in the crop grown in the field. In addition, the high coefficient of
424 variation of the proportion of ruderal species (FG4) suggests that species associated with field
425 cores vary with the field management and especially the crop grown.

426 It is likely that crop management strategies affected field edge weed diversity in this study, as
427 shown in previous studies (Romero, Chamorro & Sans 2008). The fact that we used weed data
428 surveyed over six consecutive years enabled us to detect signals regarding weed response to
429 long-term management strategies, including the type of crop rotation. Mahaut et al. (2019)
430 showed indeed that the crop rotation diversification generally leads to a decrease of the
431 species richness at the annual scale but an increase at the pluri-annual scale. Our five crop

432 management strategies differed in terms of tillage intensity (Yvoz, Petit, Biju-Duval &
433 Cordeau 2020), and our results suggest that low ploughing frequency (such as in strategies S5,
434 S7 and S8) enhanced weed species richness in field edges and field cores, as shown in
435 previous studies (Murphy et al. 2006). The five crop management strategies also differed in
436 terms of herbicide use (Yvoz, Petit, Biju-Duval & Cordeau 2020). In a recent study, Metcalfe
437 et al. (2019) showed that after herbicide application (*i.e.* at the timing we surveyed weeds),
438 the effect of the crop, which also reflects herbicide selectivity (*e.g.* anti-grass herbicide
439 applied on forb crops and vice versa), is a key factor driving field edge weed diversity at the
440 annual scale. These effects at the annual scale transcribed into effects at the pluri-annual scale
441 since we showed here that functional differences between field edges and cores varied
442 according to the intensity of farming practices. The most marked contrast between field edge
443 and field core surveys was detected in fields managed with the most intensive strategy (S2,
444 with the lowest crop diversity and highest use of external inputs) whereas the least marked
445 contrast was observed in the most diversified crop successions, either using less herbicide
446 (S7) or tillage (S8).

447 The taxonomic composition of weed surveys in the edge also responded to the crop
448 management strategy implemented in the field. Although we detected no interaction between
449 Strategy and Within-field location, we observed that field edge weed surveys were
450 significantly less dispersed than field core surveys. Besides, the impact of Crop management
451 strategy on the distribution of the functional groups was generally more marked in the core
452 than in the edge of fields. Indeed, ruderal species (FG4) were more dominant in the field core
453 of the most conventional/intensive strategies (S2, S3 and S5) while conservative species
454 (FG2) were favoured in field cores conducted under strategies expressing low herbicide use
455 (S7) or tillage intensity (S8). Species generally associated with field cores (FG4) were less
456 present in the core of fields managed with strategies relying exclusively on herbicide and
457 implementing few tillage operations (S8). Indeed, weed communities from the core of fields
458 in conservation agriculture tend to be more persistent (Trichard, Alignier, Chauvel & Petit
459 2013), leading to few differences between the core and the edge of the field. Thus, the
460 proportion of ruderal species in field edges of S8 was higher than in the other strategies and
461 close to field cores. These results were congruent with previous studies (Cordeau, Petit,
462 Reboud & Chauvel 2012a; José-María et al. 2010). Contrary to the hypothesis that practices
463 performed in the field, including herbicide or fertiliser use, might affect the field edge flora
464 (Boutin & Jobin 1998), our results supported those from Cordeau et al. (2010) in field
465 margins and suggested that herbicide drift did not highly decrease weed diversity in field
466 edges (De Snoo & Van der Poll 1999), particularly in crop management strategies with higher

467 herbicide use. However, field edges of conventionally managed arable fields remain rich and
468 diverse habitats in agricultural landscapes.

469 **Conclusions**

470 Our study shows that field edges are rich and diverse habitats, both from a taxonomic and a
471 functional perspective, harbouring species with typical functional profiles of those associated
472 with the adjacent perennial field margins and those associated with field cores. Field edges
473 also act as refugia for many species that are filtered out from field cores by intensive crop
474 management strategies. Our pluri-annual analysis shows that species temporal turnover
475 between successive years, while lower than in field cores, is quite high in field edges,
476 suggesting on the one hand a significant impact of crop management strategy on the field
477 edge weed flora, and on the other hand that some species originating from adjacent
478 boundaries or field cores are transient. Despite the limited acreage field edges represent in the
479 agricultural landscape compared to field cores, the higher richness, diversity and stability of
480 their weed flora call for future studies assessing their role in the provision of ecosystem
481 services.

482

483

484 **Acknowledgements**

485 We would like to thank Luc Biju-Duval who conducted the farmers' interviews and farmers
486 of the Fénay study area for providing crop management information and for granting access to
487 their fields. We are grateful to Remi Perronne (INRAE) for his advice for the trait distribution
488 analysis. Séverin Yvoz was funded by the European Union's Horizon 2020 research and
489 innovation program under grant agreement No 727321 (IWM PRAISE) and the INRAE
490 metaprogram ECOSERV "ecosystem services". Authors acknowledge financial support from
491 INRAE.

492 **Author contributions**

493 EC collected the weed data, FD and EC developed the weed database. SY, SP and SC
494 designed the analyses and SY, FD and SC analysed the data. SY, SP and SC contributed to
495 the writing of the manuscript. SP coordinates the Fénay study area and funded the research.

496 **Data availability**

497 The data that support the findings of this study and the code used to analyse the data and
498 produce the figures are available from the corresponding author upon request.

499 **ORCID**

500 Séverin Yvoz: <https://orcid.org/0000-0003-3814-4117>

501 Sandrine Petit: <https://orcid.org/0000-0001-8781-8873>

502 Fabrice Dessaint: <https://orcid.org/0000-0001-9135-598X>

503 Stéphane Cordeau: <https://orcid.org/0000-0003-1069-8388>

504

505 References

506

- 507 Aebischer, N. (1991). Twenty years of monitoring invertebrates and weeds in cereal fields in
508 Sussex. In: L. Firbank, N. Carter, J. Darbyshire, & G. Potts (Eds.), *The Ecology of*
509 *temperate cereal fields* (pp. 305-331): Oxford, Blackwell Scientific.
- 510 Anderson, M.J. (2001). A new method for non-parametric multivariate analysis of variance.
511 *Austral Ecology*, 26, 32-46.
- 512 Anderson, M.J. (2006). Distance-based tests for homogeneity of multivariate dispersions.
513 *Biometrics*, 62, 245-253.
- 514 Andersson, T.N., & Milberg, P. (1998). Weed flora and the relative importance of site, crop,
515 crop rotation, and nitrogen. *Weed Science*, 46, 30-38.
- 516 Andreasen, C., Stryhn, H., & Streibig, J. (1996). Decline of the flora in Danish arable fields.
517 *Journal of Applied Ecology*, 33, 619-626.
- 518 Barralis, G. (1976). Méthode d'étude des groupements adventices des cultures annuelles. *Ve*
519 *Colloque International sur l'Ecologie et la Biologie des Mauvaises herbes* (pp. 59-68).
520 Paris (France): COLUMA.
- 521 Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: a practical and
522 powerful approach to multiple testing. *Journal of the Royal statistical society: series B*
523 *(Methodological)*, 57, 289-300.
- 524 Blaix, C., Moonen, A.C., Dostatny, D., Izquierdo, J., Le Corff, J., Morrison, J., Von Redwitz,
525 C., Schumacher, M., & Westerman, P. (2018). Quantification of regulating ecosystem
526 services provided by weeds in annual cropping systems using a systematic map
527 approach. *Weed Research*, 58, 151-164.
- 528 Blumenthal, D., & Jordan, N. (2001). Weeds in field margins: a spatially explicit simulation
529 analysis of Canada thistle population dynamics. *Weed Science*, 49, 509-519.
- 530 Botta-Dukát, Z. (2005). Rao's quadratic entropy as a measure of functional diversity based on
531 multiple traits. *Journal of Vegetation Science*, 16, 533-540.
- 532 Bourgeois, B., Gaba, S., Plumejeaud, C., & Bretagnolle, V. (2020). Weed diversity is driven
533 by complex interplay between multi-scale dispersal and local filtering. *Proceedings of*
534 *the Royal Society B*, 287, 20201118.
- 535 Bourgeois, B., Munoz, F., Fried, G., Mahaut, L., Armengot, L., Denelle, P., Storkey, J., Gaba,
536 S., & Violle, C. (2019). What makes a weed a weed? A large-scale evaluation of
537 arable weeds through a functional lens. *American Journal of Botany*, 106, 90-100.
- 538 Boutin, C., & Jobin, B. (1998). Intensity of agricultural practices and effects on adjacent
539 habitats. *Ecological Applications*, 8, 544-557.
- 540 Cordeau, S., Petit, S., Reboud, X., & Chauvel, B. (2012a). The impact of sown grass strips on
541 the spatial distribution of weed species in adjacent boundaries and arable fields.
542 *Agriculture Ecosystems & Environment*, 155, 35-40.
- 543 Cordeau, S., Petit, S., Reboud, X., & Chauvel, B. (2012b). Sown grass strips harbour high
544 weed diversity but decrease weed richness in adjacent crops. *Weed Research*, 52, 88-
545 97.
- 546 Cordeau, S., Reboud, X., & Chauvel, B. (2010). Relative importance of farming practices and
547 landscape context on the weed flora of sown grass strips. *Agriculture Ecosystems &*
548 *Environment*, 139, 595-602.
- 549 Cordeau, S., Ryan, M.R., Bohan, D.A., Reboud, X., & Chauvel, B. (2017a). Which traits
550 allow weed species to persist in grass margin strips? *Weed Science*, 65, 381-394.
- 551 Cordeau, S., Smith, R.G., Gallandt, E.R., Brown, B., Salon, P., DiTommaso, A., & Ryan,
552 M.R. (2017b). Timing of tillage as a driver of weed communities. *Weed Science*, 65,
553 504-514.

- 554 De Snoo, G., & Van der Poll, R. (1999). Effect of herbicide drift on adjacent boundary
555 vegetation. *Agriculture, Ecosystems & Environment*, 73, 1-6.
- 556 de Snoo, G.R. (1997). Arable flora in sprayed and unsprayed crop edges. *Agriculture,*
557 *Ecosystems & Environment*, 66, 223-230.
- 558 Dutoit, T., Gerbaud, E., & Ourcival, J.-M. (1999). Field boundary effects on soil seed banks
559 and weed vegetation distribution in an arable field without weed control (Vaucluse,
560 France). *Agronomie*, 19, 57-590.
- 561 Fried, G., Kazakou, E., & Gaba, S. (2012). Trajectories of weed communities explained by
562 traits associated with species' response to management practices. *Agriculture,*
563 *Ecosystems & Environment*, 158, 147-155.
- 564 Fried, G., Norton, L.R., & Reboud, X. (2008). Environmental and management factors
565 determining weed species composition and diversity in France. *Agriculture,*
566 *Ecosystems & Environment*, 128, 68-76.
- 567 Fried, G., Petit, S., Dessaint, F., & Reboud, X. (2009). Arable weed decline in Northern
568 France: Crop edges as refugia for weed conservation? *Biological Conservation*, 142,
569 238-243.
- 570 Fuller, R., J, Gregory, R., D, Gibbons, D., Marchant, J., Wilson, J., Baillie, S., Royal, &
571 Carter, N. (1995). Population declines and range contractions among lowland
572 farmland birds in Britain. *Conservation Biology*, 9, 1425-1441.
- 573 Gaba, S., Perronne, R., Fried, G., Gardarin, A., Bretagnolle, F., Biju-Duval, L., Colbach, N.,
574 Cordeau, S., Fernández-Aparicio, M., & Gauvrit, C. (2017). Response and effect traits
575 of arable weeds in agro-ecosystems: a review of current knowledge. *Weed Research*,
576 57, 123-147.
- 577 Hawes, C., Squire, G., Hallett, P., Watson, C., & Young, M. (2010). Arable plant
578 communities as indicators of farming practice. *Agriculture, Ecosystems &*
579 *Environment*, 138, 17-26.
- 580 He, F., & Legendre, P. (2002). Species diversity patterns derived from species–area models.
581 *Ecology*, 83, 1185-1198.
- 582 Hill, M., & Smith, A. (1976). Principal component analysis of taxonomic data with multi-
583 state discrete characters. *Taxon*, 249-255.
- 584 Holland, J.M., Hutchison, M.A.S., Smith, B., & Aebischer, N.J. (2006). A review of
585 invertebrates and seed-bearing plants as food for farmland birds in Europe. *Annals of*
586 *Applied Biology*, 148, 49-71.
- 587 Jauzein, P. (1995). *Flore des champs cultivés*. SOPRA-INRA Ed. 898 pages.
- 588 José-María, L., Armengot, L., Blanco-Moreno, J.M., Bassa, M., & Sans, F.X. (2010). Effects
589 of agricultural intensification on plant diversity in Mediterranean dryland cereal fields:
590 Agriculture intensity & plant diversity. *Journal of Applied Ecology*, 47, 832-840.
- 591 José-María, L., Armengot, L., Chamorro, L., & Xavier Sans, F. (2013). The conservation of
592 arable weeds at crop edges of barley fields in northeast Spain: Arable plants at crop
593 edges. *Annals of Applied Biology*, 163, 47-55.
- 594 José-María, L., Blanco-Moreno, J.M., Armengot, L., & Sans, F.X. (2011). How does
595 agricultural intensification modulate changes in plant community composition?
596 *Agriculture, Ecosystems & Environment*, 145, 77-84.
- 597 Julve, P. (1998). Baseflor. Index botanique, écologique et chorologique de la Flore de France.
598 Version 28/09/2010. Programme Catminat.
599 <http://perso.wanadoo.fr/philippe.julve/catminat.htm> Accessed: August 20, 2017.
- 600 Kleijn, D., & van der Voort, L.A.C. (1997). Conservation headlands for rare arable weeds: the
601 effects of fertilizer application and light penetration on plant growth. *Biological*
602 *Conservation*, 81, 57-67.
- 603 Kleyer, M., Bekker, R., Knevel, I., Bakker, J., Thompson, K., Sonnenschein, M., Poschlod,
604 P., Van Groenendael, J., Klimeš, L., & Klimešová, J. (2008). The LEDA Traitbase: a

605 database of life-history traits of the Northwest European flora. *Journal of Ecology*, *96*,
606 1266-1274.

607 Klotz, S., Kühn, I., & Durka, W. (2002). BIOLFLOR - Eine Datenbank zu biologisch-
608 ökologischen Merkmalen der Gefäßpflanzen in Deutschland. *Schriftenreihe für*
609 *Vegetationskunde*, *38* - Bonn: Bundesamt für Naturschutz.

610 Kovács-Hostyánszki, A., Batáry, P., Báldi, A., & Harnos, A. (2011). Interaction of local and
611 landscape features in the conservation of Hungarian arable weed diversity. *Applied*
612 *Vegetation Science*, *14*, 40-48.

613 Mahaut, L., Gaba, S., & Fried, G. (2019). A functional diversity approach of crop sequences
614 reveals that weed diversity and abundance show different responses to environmental
615 variability. *Journal of Applied Ecology*, *56*, 1400-1409.

616 Mamarot, J., & Rodriguez, A. (2014). *Mauvaises herbes des cultures*. (4 ed.). Paris (France):
617 ACTA.

618 Marshall, E.J.P., Brown, V.K., Boatman, N.D., Lutman, P.J.W., Squire, G.R., & Ward, L.K.
619 (2003). The role of weeds in supporting biological diversity within crop fields. *Weed*
620 *Research*, *43*, 77-89.

621 Marshall, E.J.P., & Moonen, A.C. (2002). Field margins in northern Europe: their functions
622 and interactions with agriculture. *Agriculture, Ecosystems & Environment*, *89*, 5-21.

623 Marshall, J.P. (1989). Distribution patterns of plants associated with arable field edges.
624 *Journal of Applied Ecology*, *26*, 247-257.

625 Metcalfe, H., Hassall, K.L., Boinot, S., & Storkey, J. (2019). The contribution of spatial mass
626 effects to plant diversity in arable fields. *Journal of Applied Ecology*, *56*, 1560-1574.

627 Murphy, S.D., Clements, D.R., Belaoussoff, S., Kevan, P.G., & Swanton, C.J. (2006).
628 Promotion of weed species diversity and reduction of weed seedbanks with
629 conservation tillage and crop rotation. *Weed Science*, *54*, 69-77.

630 Perronne, R., Gaba, S., Cadet, E., & Le Corre, V. (2014). The interspecific and intraspecific
631 variation of functional traits in weeds: diversified ecological strategies within arable
632 fields. *Acta Botanica Gallica: Botany Letters*, *161*, 243-252.

633 Pinke, G., & Gunton, R.M. (2014). Refining rare weed trait syndromes along arable
634 intensification gradients. *Journal of Vegetation Science*, *25*, 978-989.

635 Poggio, S.L., Chaneton, E.J., & Ghera, C.M. (2013). The arable plant diversity of intensively
636 managed farmland: Effects of field position and crop type at local and landscape
637 scales. *Agriculture, Ecosystems & Environment*, *166*, 55-64.

638 R Core Team. (2020). R: A language and environment for statistical computing. Vienna,
639 Austria.: R Foundation for Statistical Computing.

640 Romero, A., Chamorro, L., & Sans, F.X. (2008). Weed diversity in crop edges and inner
641 fields of organic and conventional dryland winter cereal crops in NE Spain.
642 *Agriculture, Ecosystems & Environment*, *124*, 97-104.

643 Roschewitz, I., Gabriel, D., Tschardtke, T., & Thies, C. (2005). The effects of landscape
644 complexity on arable weed species diversity in organic and conventional farming.
645 *Journal of Applied Ecology*, *42*, 873-882.

646 Rotchés-Ribalta, R., Blanco-Moreno, J.M., Armengot, L., Chamorro, L., & Sans, F.X. (2015).
647 Both farming practices and landscape characteristics determine the diversity of
648 characteristic and rare arable weeds in organically managed fields. *Applied Vegetation*
649 *Science*, *18*, 423-431.

650 Rotchés-Ribalta, R., Sans, F.X., Mayer, J., & Mäder, P. (2020). Long-term farming systems
651 and last crop sown shape the species and functional composition of the arable weed
652 seed bank. *Applied Vegetation Science*, *23*, 428-440.

653 Royal Botanic Gardens Kew. (2020). Seed Information Database (SID). Version 7.1. URL
654 <http://data.kew.org/sid/> (accessed 17 Apr 2020).

- 655 Ryan, M.R., Smith, R.G., Mirsky, S.B., Mortensen, D.A., & Seidel, R. (2010). Management
656 filters and species traits: weed community assembly in long-term organic and
657 conventional systems. *Weed Science*, 58, 265-277.
- 658 Seifert, C., Leuschner, C., Meyer, S., & Culmsee, H. (2014). Inter-relationships between crop
659 type, management intensity and light transmissivity in annual crop systems and their
660 effect on farmland plant diversity. *Agriculture, Ecosystems & Environment*, 195, 173-
661 182.
- 662 Sjursen, H. (2001). Change of the weed seed bank during the first complete six-course crop
663 rotation after conversion from conventional to organic farming. *Biological Agriculture
664 & Horticulture*, 19, 71-90.
- 665 Stevenson, F.C., Legere, A., Simard, R.R., Angers, D.A., Pageau, D., & Lafond, J. (1997).
666 Weed species diversity in spring barley varies with crop rotation and tillage, but not
667 with nutrient source. *Weed Science*, 45, 798-806.
- 668 Storkey, J., Moss, S.R., & Cussans, J.W. (2010). Using assembly theory to explain changes in
669 a weed flora in response to agricultural intensification. *Weed Science*, 58, 39-46.
- 670 Tela Botanica. (2020). (continuously updated): Tela Botanica. Flore électronique. Flores en
671 ligne, France métropolitaine. <https://www.tela-botanica.org/> [accessed 16 April 2020].
- 672 Trichard, A., Alignier, A., Chauvel, B., & Petit, S. (2013). Identification of weed community
673 traits response to conservation agriculture. *Agriculture, Ecosystems and Environment*,
674 179, 179-186.
- 675 Van Swaay, C., & Warren, M. (1999). *Red data book of European butterflies (Rhopalocera)*.
676 Council of Europe.
- 677 Wilson, P.J., & Aebischer, N.J. (1995). The distribution of dicotyledonous arable weeds in
678 relation to distance from the field edge. *Journal of Applied Ecology*, 32, 295-310.
- 679 Winfree, R., Aguilar, R., Vázquez, D.P., LeBuhn, G., & Aizen, M.A. (2009). A meta-analysis
680 of bees' responses to anthropogenic disturbance. *Ecology*, 90, 2068-2076.
- 681 Yvoz, S., Cordeau, S., Zuccolo, C., & Petit, S. (2020). Crop type and within-field location as
682 sources of intraspecific variations in the phenology and the production of floral and
683 fruit resources by weeds. *Agriculture, Ecosystems and Environment*, 302, 107082.
- 684 Yvoz, S., Petit, S., Biju-Duval, L., & Cordeau, S. (2020). A framework to type crop
685 management strategies within a production situation to improve the comprehension of
686 weed communities. *European Journal of Agronomy*, 115, 126009.

687

688 **Tables**

689 **Table 1.** Functional traits used and their description. Range [minimum – maximum] of the
 690 traits for the 147 studied weed species. A detailed justification of trait selection with
 691 references can be found in Appendix A: Table 2.

Traits or Indicator values	Unit	Description	Source	Range [min-max]
Maximum height	cm	Ability to compete for light; negatively correlated with soil tillage and disturbance; proxy of the competitive strategy	(Mamarot & Rodriguez 2014; Tela Botanica 2020)	[12-250]
Specific leaf area (SLA)	m ² /kg	High for ruderal plants from disturbed area: efficiency of light interception; correlated with growth rate; increase with light competition	LEDA Traitbase (Kleyer et al. 2008)	[8.6-48.5]
Seed mass	mg	Negatively correlated with soil disturbance; linked to seed dormancy and persistency	Seed information database (Royal Botanic Gardens Kew 2020)	[0.01-33.5]
Germination onset	1=Sept. 12=Aug.	Correlated with the crop sowing date	(Mamarot & Rodriguez 2014)	[1-9]
Germination duration	month	Higher in rotations with varying crop sowing dates; ability to respond to disturbance events	(Mamarot & Rodriguez 2014)	[3-12]
Flowering onset	1=Jan. 12=Dec.	Correlated with the crop flowering date; earlier in disturbed area and intensive system	(Mamarot & Rodriguez 2014; Tela Botanica 2020)	[1-8]
Flowering duration	month	Ability to respond to disturbance events	(Mamarot & Rodriguez 2014; Tela Botanica 2020)	[1-12]
Ellenberg.N		Response to the soil nitrogen availability; indicator of the type of habitat, especially arable crop	Baseflor (Julve 1998)	[1-9]
Ellenberg.L		Response to the light resource availability; impacted by the sowing density or row spacing	Baseflor (Julve 1998)	[4-9]
Plant class		Associated with the type of herbicide use; more grass species when the tillage intensity is reduced	BiolFlor (Klotz, Kühn & Durka 2002)	Grass Forb
Raunkiaer's life form		Associated with the tillage intensity; more hemicryptophyte and geophyte when tillage is reduced; therophyte adapted to soil disturbance; associated with the crop sowing date	BiolFlor (Klotz, Kühn & Durka 2002)	Therophyte Hemi-cryptophyte Geophyte

692

693 **Figures and captions**

694 **Fig. 1.** Weed sampling design implemented annually in each field core (“W” pattern of about
695 130 m long by 1.5 m width in a 2000 m² area) and field edge (linear transect of about 50 m
696 long by 0.3 m width). Green lines represent the prospected area in both within-field locations.
697 Grey lines represent the crop rows for an example of crop type, showing that the field edge is
698 the habitat located between the grass margin and the first crop row.

699 **Fig. 2.** Effects of Crop management strategy (S2 to S8), Within-field location (FC: field core,
700 FE: field edge) and their interaction on the five metrics (*i.e.* species richness (A), total
701 abundance (B and C), Evenness (D), functional diversity as the Rao's quadratic entropy (E)
702 and species turnover (F)) describing the 120 cumulated weed surveys. Table shows the
703 significance of the effects tested by a type II ANOVA applied on linear and generalised linear
704 mixed models (Appendix A: Table 3) (p-values < 0.05 are in bold). Within each graph,
705 boxplots with no letters in common are significantly different, based on a least significant
706 difference analysis. Weed surveys were done in FC following a “W” pattern of about 130 m
707 long by 1.5 m width in a 2000 m² area) and in FE following linear transect of about 50 m long
708 by 0.3 m width, resulting in different sampled areas (see Fig. 1).

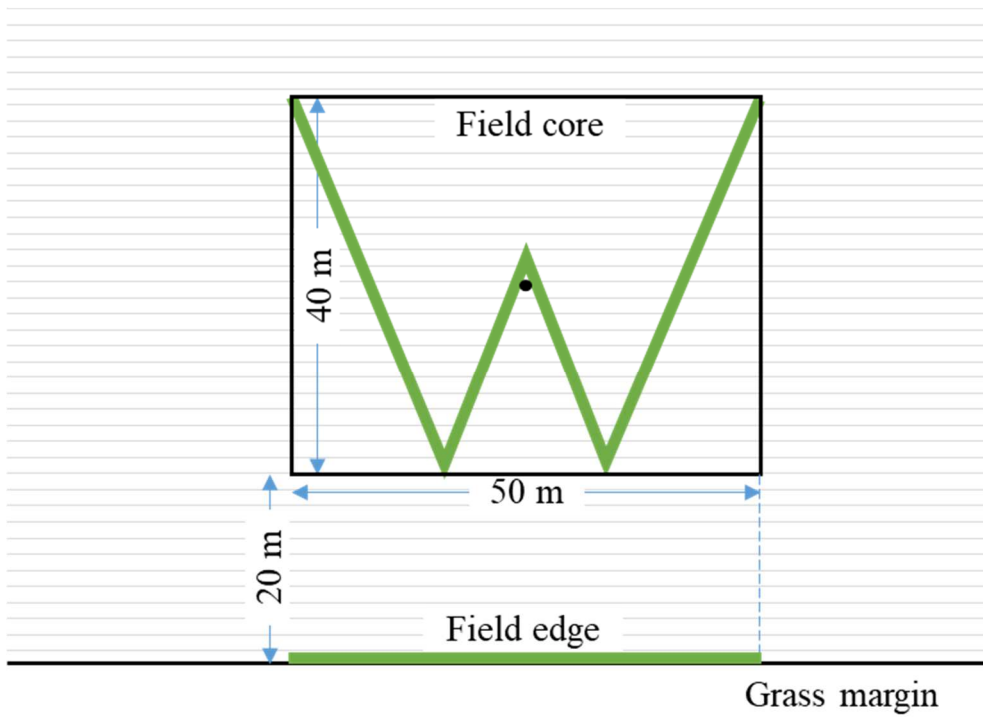
709 **Fig. 3.** Effects of the Within-field location (FC: field core, FE: field edge) on the distribution
710 of the nine quantitative and two qualitative traits (Table 1 for details and units) within the five
711 Crop management strategies. Overlaps (Ov) of trait distributions between within-field
712 locations were compared within strategy to the null hypothesis using a one-tailed direct test of
713 significance for non-random distribution, based on 10 000 randomizations of weed surveys.
714 Significant associations between Within-field locations and qualitative trait categories were
715 evaluated within Crop management strategy by Pearson Chi-square tests. P-values in bold are
716 significant (p-values < 0.05). NS: p > 0.1.

717 **Fig. 4.** Functional traits describing the five weed functional groups. Green (v.test values > 0)
718 and red (v.test values < 0) bars indicate the traits that are positively correlated (quantitative
719 traits)/over-represented (qualitative traits) and negatively correlated (qualitative)/under-
720 represented (quantitative traits) to each functional group, respectively. V.test represents the
721 normalised difference to the mean associated with the individuals belonging to a specific
722 category. P-values were calculated using a one-way analysis of variance or a Chi-square test
723 for quantitative and qualitative response variable, respectively (*: p < 0.05, **: p < 0.01,
724 ***: p < 0.001).

725 **Fig. 5.** Relative abundance of the five functional groups (FG) in the edge (FE) and the core
726 (FC) of the 60 fields farmed with one of the five Crop management strategies (S2 to S8).
727 Numbers above the bars indicate the sum of average field:year weed abundance (individual.m⁻²)
728 per Crop management strategy and Within-field location.

729

730

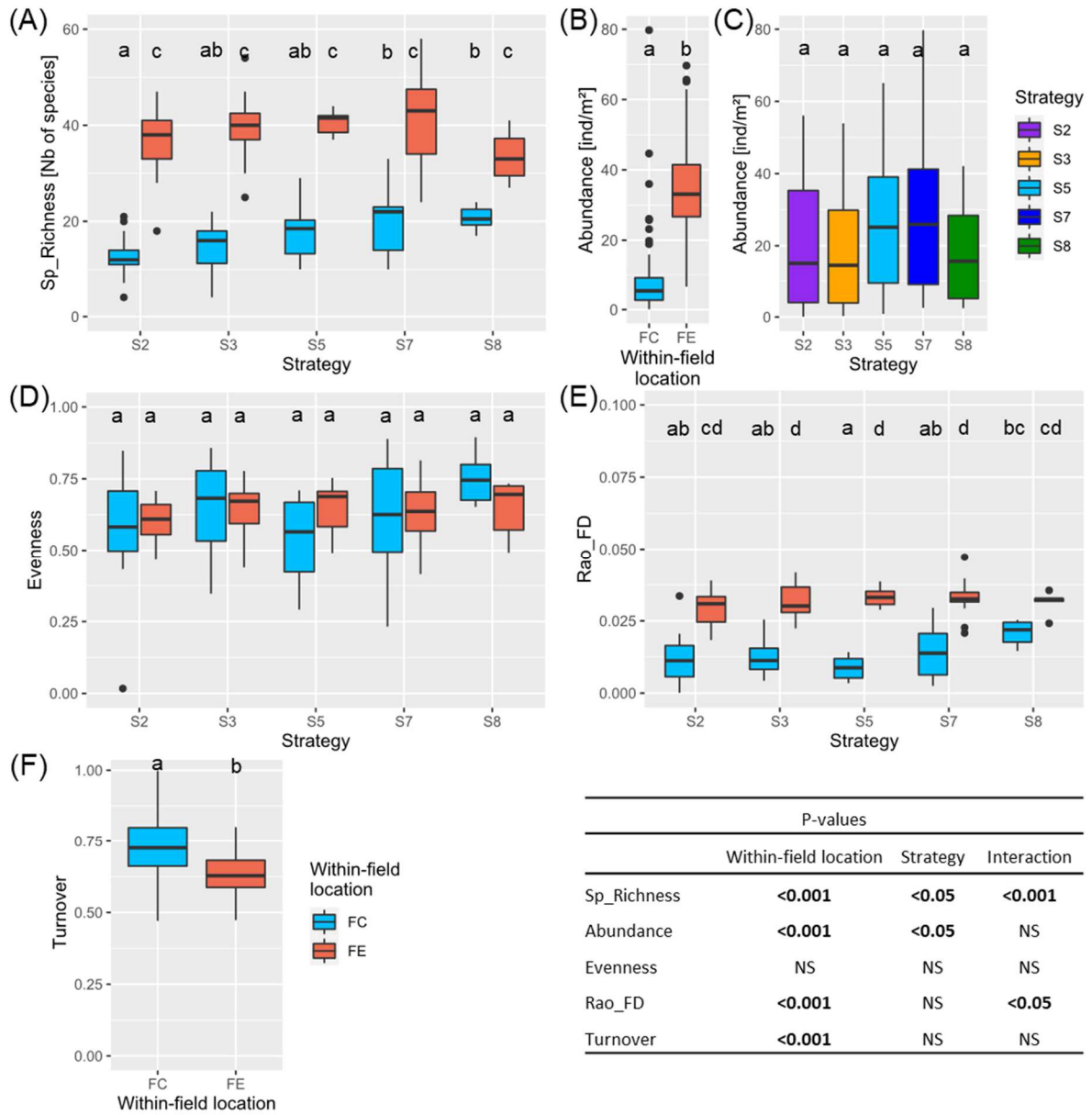


731

732 **Fig. 1.**

733

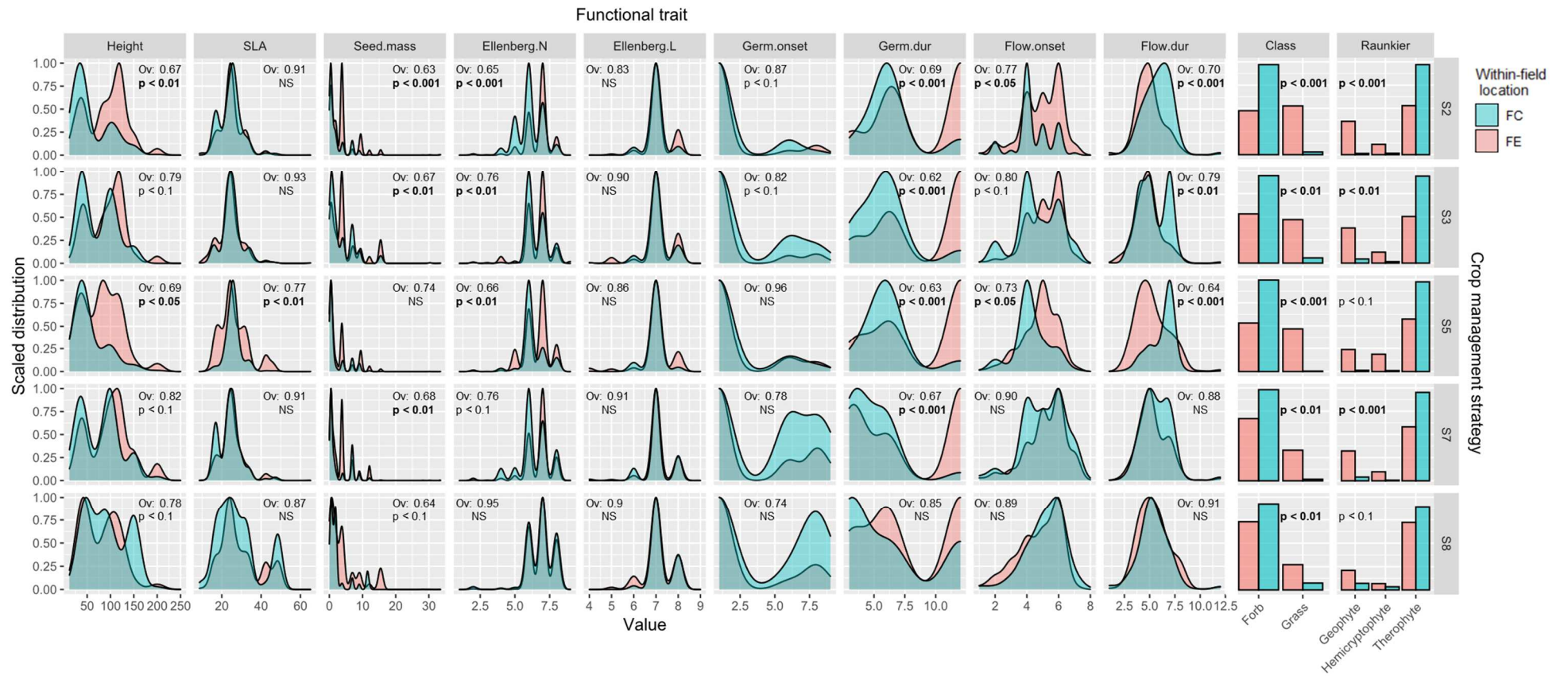
734



735

736 **Fig. 2.**

737

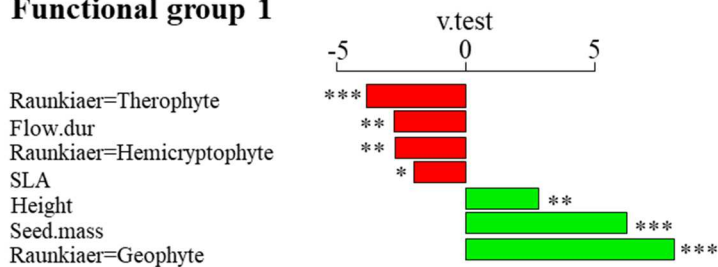


738
739

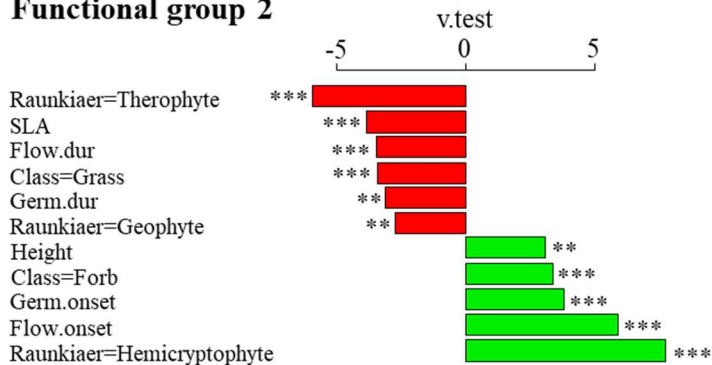
Fig.

3.

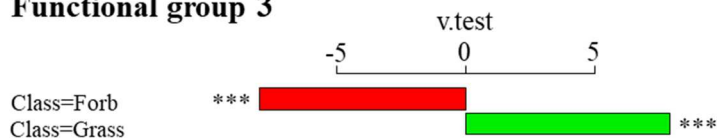
Functional group 1



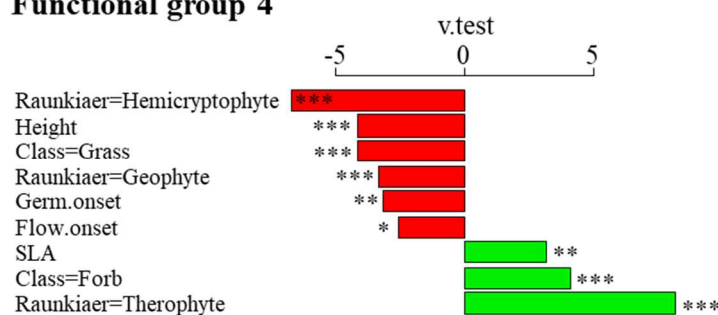
Functional group 2



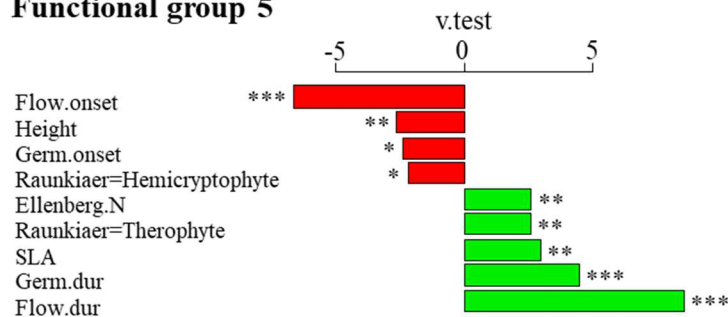
Functional group 3



Functional group 4



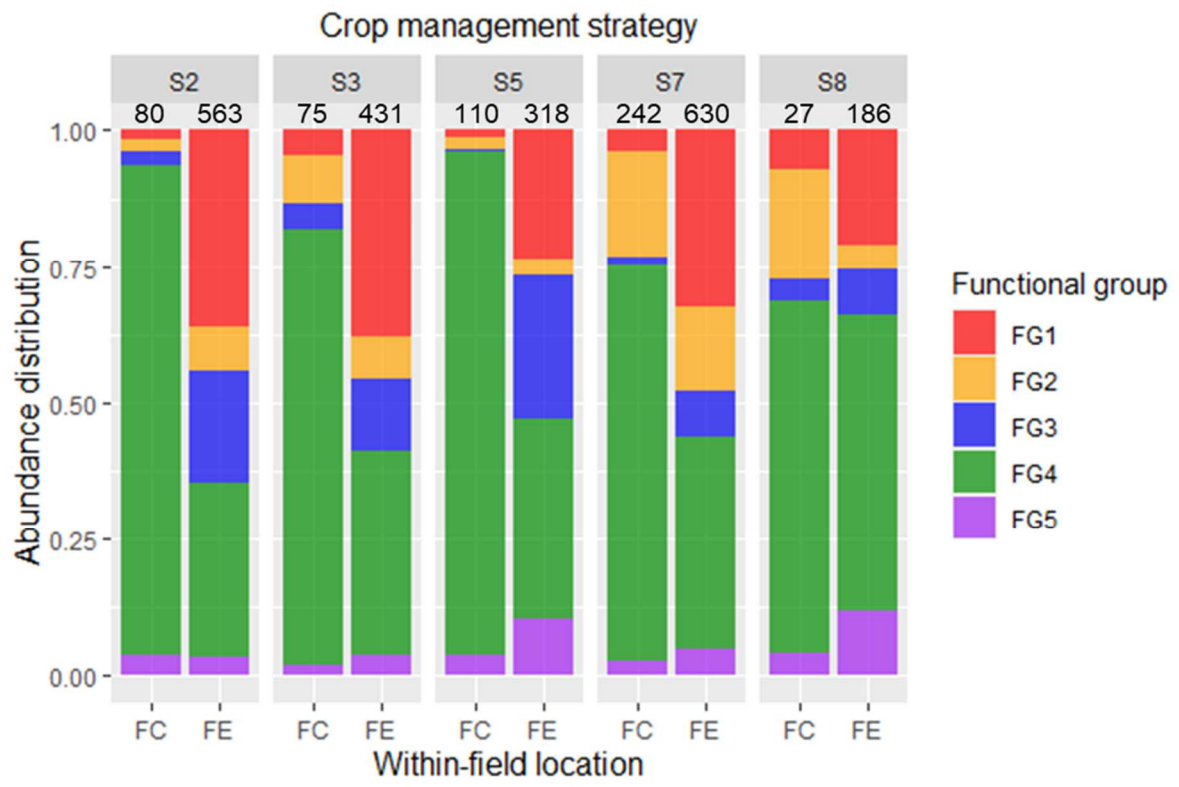
Functional group 5



740

741 **Fig. 4.**

742



743

744 **Fig. 5.**