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Damien Derrouch, Bruno Chauvel, Stéphane Cordeau, Fabrice Dessaint

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1 **Functional shifts in weed community composition following adoption of conservation**
2 **agriculture**

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5 **Damien Derrouch¹, Bruno Chauvel¹, Stéphane Cordeau¹, Fabrice Dessaint¹**

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¹Agroécologie, AgroSup Dijon, INRAE, Univ. Bourgogne, Univ. Bourgogne-Franche-Comté,
F-21000 Dijon, France

10 Correspondence

11 Bruno Chauvel, Agroécologie, AgroSup Dijon, INRAE, Univ. Bourgogne, Univ. Bourgogne-
12 Franche-Comté, 17 rue Sully, BP 86510, F-21065 Dijon Cedex
13 Email: bruno.chauvel@inrae.fr

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33 **Abstract:**

34 To better understand the changes in weed communities following the adoption of
35 conservation agriculture (CA), we investigated the functional composition of weed
36 communities in fields implementing CA continuously from 1 to 21 years.
37 Weed surveys were conducted in 100 winter wheat fields of 53 farmers in the Bourgogne-
38 Franche-Comté region, Eastern France. Ten response traits were selected to highlight changes
39 in the functional composition of weed communities, using weighted mean value for
40 quantitative traits and an approach based on composition analysis for qualitative traits. Out of
41 the ten traits, four were impacted by the time following the adoption of CA significantly,
42 while two only showed trends. Specific leaf area, leaf dry matter content, seed dispersal mode
43 and soil seedbank longevity did not change over time following adoption of CA, whereas
44 changes were observed for plant type, Raunkiær's life forms, Ellenberg's indicator value for
45 light and germination and flowering periods. Phanerophyte and geophyte life forms, summer-
46 germinating species, and spring- and summer-flowering species increased with time following
47 adoption of CA. Shade-tolerant species, not present in field recently converted to CA,
48 established later. Community-weighted mean of seed mass and the percentage of graminoids
49 tended to increase with time following adoption of CA. Some functional shifts in weed
50 communities occurred quicker than others (i.e. summer-germinating species increased after at
51 least ten years of continuous application of CA principles). These results can be used to
52 inform farmers moving towards CA about expected changes.

53

54 **KEYWORDS**

55 Response trait, community weighted mean, community assembly processes, transition phase,
56 no-tillage, direct seeding, field network

57

58

59 **1 INTRODUCTION**

60

61 In agroecosystems, cropping practices play a key role in assembling weed communities.
62 Together with ecological and environmental conditions, they act as filters and shape the
63 composition of weed communities (Booth and Swanton, 2002). Hence, viewed within a
64 community assembly framework, drastic changes in farming practices can either constrain or
65 promote the representation of species within the subsequent weed community. Considering
66 that arable lands have been tilled since the industrialization of agriculture, the adoption of
67 conservation agriculture by farmers could be considered, from a weed science point of view,
68 as one the main evolution in cropping strategies in recent decades. Conservation agriculture
69 (CA) changes farming systems based on the simultaneous and continuous application of three
70 principles: minimum soil disturbance (no-tillage), permanent residue cover on the soil surface
71 (cover crops or mulch) and a high crop rotation diversification (Reicosky, 2015).

72 The response of weed communities to changes in cropping practices was often studied
73 from the taxonomic perspective (Légère et al., 2005; Fried et al., 2008). Recently, the use of
74 functional traits has been proposed as an effective method for identifying general rules
75 governing community assembly (Armengot et al., 2016; Gaba et al., 2017). Most studies
76 using a functional approach have focused on the response of weed communities to the
77 reduction in tillage intensity (Zanin et al., 1997; Armengot et al., 2016). By lowering the
78 intensity of a major disturbance of weed community and modifying the vertical distribution of
79 seeds in the soil (Clements et al., 1996), reduced tillage leads to the development of
80 perennials (Zanin et al., 1997) and select for smaller seeds that can easily penetrate the soil
81 (Armengot et al., 2016). Wind-disseminated species, known as rapid colonizers, and
82 graminoid species seem to be favoured in no-till systems (Debaeke and Orlando, 1991; Zanin
83 et al., 1997; Young and Thorne, 2004; Murphy et al., 2006). However, the functional
84 responses of weed communities to CA which include two other CA principles (i.e. residue
85 cover on the soil surface and crop rotation diversification) in addition to no-till are not as well
86 documented (Gunton et al., 2011; Mahaut et al., 2019). By maximizing the soil coverage,
87 farmers intend to increase the competition between sown species (crops and cover crops) and
88 weeds (Teasdale, 1996), selecting for more competitive and shade-tolerant weeds. Since crop
89 diversification can create also new temporal niches, one would also expect to observe a
90 diversification of weed life cycle periods.

91 Of all the weed community studies conducted in CA, only Trichard et al. (2013)
92 reported the functional responses of weed communities to the simultaneous and the

93 continuous application of the three CA principles during the five first years following CA
94 adoption (for most of the fields). During these first years of CA, the authors confirmed results
95 observed on reduced tillage systems, such as the increase in perennial and graminoid species.
96 More recently, Derrouch et al. (2021) showed that higher functional homogeneity of weed
97 communities occurred in CA fields only ten years after continuous application of CA. Thus,
98 the effects of CA practices on weeds communities present in fields during the first years could
99 be masked by a buffering effect of the seedbank whose composition is related to cultural
100 practices carried out before the adoption of CA.

101 In this article, we studied the functional shifts of weed communities following the
102 adoption of CA, analyzing the functional composition or value of ten response traits
103 (Raunkiaer's life form, soil seedbank longevity, plant type, time of flowering, time of
104 germination, seed dispersal, Ellenberg's indicator value for light, seed mass, specific leaf area
105 and leaf dry matter content) of weed communities surveyed in 100 winter wheat fields of 53
106 farmers that had been implementing CA continuously for 1 to 21 years. We hypothesized that
107 the adoption of CA will favour the development of non-therophyte life forms, graminoids,
108 rapid colonizers such as anemochore or zoochore species, smaller seeds and more shade-
109 tolerant species. We hypothesized the average soil seedbank longevity of the community to
110 decrease with time since the adoption of CA because no-till and cover crop place seeds in
111 non-favourable conditions to germinate on the soil surface. We expected also an unfavourable
112 filtering for species with high internal conductivity (high specific leaf area) and low
113 investment in structural tissues (low leaf dry matter content), due to a higher competition for
114 light. Crop rotation diversification and lack of soil disturbance during the intercropping period
115 was expected to increase summer- and/or fall- germinating or flowering species. Finally, we
116 expected that most of the functional shifts would be observed in fields that have been in CA
117 for more than five years, due to the buffering effect of the weed seedbank and to an adaptation
118 of weed management by farmers after this period, such as the inclusion of summer crops
119 (Derrouch et al., 2020a).

120

121 **2 MATERIALS AND METHODS**

122

123 **2.1 Study site**

124

125 The study area was located in Bourgogne-Franche-Comté, a temperate oceanic zone located
126 in the northeaster of France, where yearly rainfall and daily temperatures average 756 mm and

127 10.9°C, respectively (<https://www.insee.fr/fr/statistiques/4176857>). Based on a network of 53
128 farmers, we selected 100 winter wheat (*Triticum aestivum* L.) fields under annual crop
129 production (i.e. without temporary meadows) for at least four years, that had been
130 implementing CA continuously for one to 21 years. Fields were grouped into four groups of
131 age since CA adoption. Age group boundaries were chosen according to the periods during
132 which changes in weed community structure were observed (Derrouch et al., 2021) and which
133 changes were observed in a national survey on weed management practices (Derrouch et al.,
134 2020a). Fields of group “1” with one year of time since CA adoption (12 fields) constituted
135 the initial state. Fields of group “2-5” had a time since CA adoption from two to five years (42
136 fields). Fields of group “6-10” had a time since CA adoption from six to ten years (32 fields)
137 and represented a period during which French CA farmers generally adapt their weed
138 management (summer crops added, shift to post-emergence herbicide application) (Derrouch
139 et al., 2020a). Finally, the group “>10” grouped fields with a time since CA adoption more
140 than 10 years (14 fields) and represented the period during which weed communities become
141 significantly more similar and homogeneous (Derrouch et al., 2021). Weed management
142 changes made during the six to ten first years of CA were retained after ten years of CA.

143

144 **2.2 Weed data collection**

145

146 Weed surveys were conducted in each field in 2018 (51 fields) and 2019 (49 fields) over three
147 periods: early March (before the last post-emergent herbicide use), mid-June (before harvest),
148 and early September (intercropping period before sowing of the following crop). In all
149 surveys, weeds were recorded on a 40x50 m area, located 50 m away from field boundaries,
150 following a W-shaped walked path (2 persons, 30-40 minutes for each survey). Most plants
151 were identified at the species level and named according to French taxonomic referential
152 (TaxRef V13, (Gargominy et al., 2019)). The genus level was used only for immature plants
153 or because of the lack of distinguishing criteria (e.g. *Lolium* sp.). The abundance of each
154 species was estimated according to a modified Barralis' scale (Barralis, 1976): [+] found once
155 in the 2,000 m² plot; [1] less than 1; [2] 1 to 2; [3] 3 to 10; [3.5] 11 to 20; [4] 21–50 and [5]
156 51 to 60 individuals m⁻². The percentage of stage of development (seedling, vegetative,
157 flowering, fructification) of each species was also estimated. Based on information provided
158 by the farmers, species that were sown in the current or preceding year were not considered in
159 the analysis, thus excluding most of cover crop species and volunteer crop plants.

160 To better explained the changes in community assembly processes induced by the
161 application of CA, only weeds with a successful establishment, *i.e.* able of producing
162 propagules or of maintaining during the crop cycle were selected (see Appendix S1 for
163 details), selecting 226 out of the 256 weed species observed (see the full list of species with
164 their occurrence and abundance in Table S1).

165

166 **2.3 Biological traits**

167

168 Based on a reference list of functional traits for arable weeds (Booth and Swanton, 2002;
169 Gaba et al., 2017) and articles on no-till (Debaeke and Orlando, 1991; Young and Thorne,
170 2004; Murphy et al., 2006) and CA (Trichard et al., 2013), we selected ten responses traits.
171 Seven were categorical: Raunkiær's life form, soil seedbank longevity (six classes), plant type
172 (graminoid/eudicotyledon), germination and flowering periods, seed dispersal mode and
173 Ellenberg's indicator value for light (EIV-l). Three traits were quantitative: seed mass (mg),
174 specific leaf area ($\text{mm}^2 \cdot \text{mg}^{-1}$) and leaf dry matter content ($\text{mg} \cdot \text{g}^{-1}$). Raunkiær's life form
175 (Raunkiær et al., 1934), seed mass and soil seedbank longevity were related to the reduction
176 of soil disturbances. Raunkiær's life form was used to capture the potential effect of an
177 absence of mechanical soil disturbance on the development of non-therophytes life forms. The
178 traits referring to seeds (seed mass and soil seedbank longevity) were used to assess the effect
179 of a change in the vertical distribution of seeds in the soil on seed characteristics and their
180 ability to persist in the seedbank. Plant type was selected to confirm the shift towards more
181 graminoids species observed in the literature (Debaeke and Orlando, 1991; Trichard et al.,
182 2013). This response trait can also be used to observe the response of weed communities to a
183 potential change in weed management, as farmers can use herbicide specifically targeting
184 either graminoids or eudicotyledons. The periods of germination and flowering were chosen
185 to capture the effect of CA on temporal niches. Seed dispersal was used to assess the ability of
186 plants to colonize fields (Benvenuti, 2007). The use of Ellenberg's indicator value for light
187 was used to capture a potential filtering of more shade-tolerant species. The specific leaf area
188 and the leaf dry matter content were used to capture the effect of both changing internal
189 dynamics of communities and reducing disturbances.

190 All trait values were extracted from databases (Table S2 for selection details and data
191 sources). For weed species identified at genus level, we selected the trait value of the most
192 common species belonging to the same genus. For trees and shrubs, traits values were based
193 on the most common species in the region (Bardet et al., 2008).

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2.5 Statistical analysis

To obtain a value representative of each trait at the community level, we started by computing the community-level weighted mean (quantitative traits) or the weighted proportion (categorical traits) of trait attributes (CWM). For the seven categorical traits, we obtained the weighted proportions of each attribute. This form of data, composed of non-negative components whose sum was 1 (or 100 %) for each trait, causes some problems with classical methods of analysis based on Euclidean geometry (Jackson, 1997) and several authors have pointed out the risks of using classical methods with this type of data. So, we used the CoDa (compositional data) approach proposed by Aitchison (2003). As zero counts represented a problem for the analysis of compositional data, they were imputed according to a Bayesian paradigm proposed by Palarea-Albaladejo and Martin-Fernandez (2015) and implemented in the `cmultRepl()` function of the `{zCompositions}` package. We reported compositional descriptive statistics and variance for traits proportions as the closed geometric mean and variance matrix of centred log-ratio (clr) transformed data set. The geometric mean better represents the centre of compositional data points than the arithmetic mean, and dispersion of compositional data is summarized using a variance matrix of pairwise log-ratios (Aitchison, 2003).

Principal component analysis on clr transformed data was used to examine variance in the proportions of traits (Aitchison and Greenacre, 2002). In this analysis, the PCA axes were plotted using a biplot in which the length of the link (*i.e.*, distance between arrowheads) along a component relates to the standard deviation (SD) of the log-ratio of two components. Thus, the distance between links was used to evaluate relative variation between components. We used compositional analysis in acomp geometry as proposed by Van-den-boogaart et al. (2020) in `{compositions}` package.

To examine differences in traits composition between the four groups of CA adoption, we used a permutation-based MANOVA (PERMANOVA) on Euclidean distance matrix calculated on the clr-transformed data for categorical traits and Euclidean distance on the CWM values for quantitative traits. For these analysis we used the `adonis()` function implemented in the `{vegan}` package (Oksanen et al., 2019). All the analysis were done with R version 4.0.2 (R Development Core Team, 2021).

228 **3 RESULTS**

229

230 Weed communities were composed of an average of 23.9 species per 2,000 m² plot (\pm 12.7
231 SD). The most frequent species were *Taraxacum officinale* F.H.Wigg. (present in 84% of the
232 fields), *Alopecurus myosuroides* Huds. (78%) and *Chenopodium album* L. (78%). Half of the
233 226 species were present in less than five fields. Most species showed low average abundance
234 (less than one plant m⁻² or even one plant per 2,000m²). The most abundant species, *Veronica*
235 *hederifolia* L. (7.55 plants per m² on average), *Digitaria sanguinalis* (L.) Scop. (7.32 plants
236 per m²), *Setaria pumila* (Poir.) Roem. & Schult. (6.43 plants per m²) and *Amaranthus*
237 *hybridus* L. (5.23 plants per m²) were not the most frequent species (occurrence between 5
238 and 22 %) (Table S1). Some species, more commonly found in others habitats such as
239 woodlands (*Acer* sp., *Euonymus europaeus* L., *Hedera helix* L., *Juglans* sp.), field edges
240 (*Rubus* sp., *Heracleum sphondylium* L., *Cornus* sp.) or meadows (*Rumex obtusifolius* L.,
241 *Plantago lanceolata* L., *Plantago media* L.) were also present in weed communities.

242

243

244 **3.1 Overall trait representation**

245

246 Weed communities were mainly composed of therophyte (98 species) or hemicryptophyte (88
247 species). Annual weeds (71.2% of plants) were more abundant than perennials in the weed
248 communities. Hemicryptophytes (23.1% of plants) represented most of perennial weeds
249 (Table 1). Around half of species had a transient soil seedbank (a maximum one-year survival
250 in the soil). These species accounted for 35.8% of plants in the weed communities. Most of
251 the plants on weed communities (70.2%) had a seed survival in soil less than five years
252 (transient, transient to short term and short term attributes). Only 33 species were graminoids
253 but these species accounted for about 27% of individuals in weed communities. Slightly less
254 than half of the weeds (42%) had a flowering period during the intercropping period (summer
255 to autumn). Species with a spring to summer and a spring to autumn flowering period (48 and
256 53 species, respectively) were also well represented in weed communities (28.7% and 20.4%
257 of individuals, respectively). About 23.6% of the weeds were able to germinate all year round.
258 For most of the remaining weeds, germination occurred either at the beginning (autumn to
259 spring) or at the end (spring to summer) of the winter crop. Although represented by 52
260 species, only 7.5% of the weeds had a spring germination period. Seed dispersal modes were
261 fairly well distributed by species with no particular dispersion mechanisms (73 species),

262 anemochorous (62) and zoochorous species (83). However, considering their abundance,
263 almost half of weeds produced seeds that remained in the field (no dispersion mechanism).
264 Most species (195) and high percentage of weeds (88.8%) were heliophilous (Ellenberg's
265 indicator value for light of 7, 8 or 9). Mean values for seed mass, specific leaf area and leaf
266 dry matter content were 4.9 mg, 25.4 mm².mg⁻¹, and 187.2 mg.g⁻¹, respectively. Although the
267 mean CWM values for specific leaf area and the leaf dry matter content traits were fairly
268 stable (low coefficient of variation across communities: 12% and 14%), the mean CWM value
269 of the seed mass was more variable across weed communities (coefficient of variation of
270 79%).

271

272 *Table 1 near here*

273

274 **3.2 Functional shifts by CA age groups**

275

276 Time since CA adoption appeared to have important effect on functional composition of weed
277 communities. For categorical traits, PERMANOVA results (Table 2) identified a significant
278 effect of time since CA adoption on the weed community composition for the Raunkiær's life
279 form (F= 4.06, p= 0.001), the time of flowering (F= 3.422, p= 0.001), the time of germination
280 (F= 2.719, p= 0.013) and the Ellenberg's indicator value for light (F= 3.105, p= 0.002). A
281 non-significant trend was also observed for the plant type (F= 2.425, p= 0.059). For
282 quantitative traits, only a trend towards an effect of time since CA adoption was observed for
283 the seed mass (F= 2.446, p= 0.065).

284

285 *Table 2 near here*

286

287 **3.2.1 Raunkiær's life form**

288

289 The first component of the Raunkiær's life form PCA biplot (Figure 1a) was associated with
290 differences in ratio of phanerophytes to geophytes and explained 51.6% of the variance. The
291 second component, explaining 38.5% of the variance, separated chamaephytes, therophytes
292 and hemicryptophytes from phanerophytes and geophytes. The greatest link distance occurred
293 between phanerophytes, geophytes and chamaephytes, indicating that the most relative
294 variation occurred between these three attributes. The shortest link, indicating consistency in
295 their ratio over communities, was found between therophytes and hemicryptophytes. By

296 interpreting the position of ellipses, we identified a higher ratio of chamaephytes, therophytes
297 and hemicryptophytes vs phanerophytes and geophytes weeds for the age group 1 and a
298 reverse trend for old fields in CA (age group > 10).

299

300 *Fig 1 near here*

301

302 **3.2.2 Germination period**

303

304 The first component of PCA biplot (58.1% of the variance) was associated with a difference
305 in ratios between summer-germinated plants and all other plants (Figure 1b). The second
306 component (25.2% of variance) was associated with the difference in ratios between spring-
307 germinated plants and plants with germination mainly in fall to spring or spring to summer.
308 These changes in ratios appeared to have little link with the time since the conversion. The
309 fields that had been in CA for more than 10 years, had relatively more plants with summer
310 germination than the other groups of fields.

311

312 **3.2.3 Flowering period**

313

314 The first component of PCA biplot (32.7%) discriminated between weed communities with
315 higher ratio of plants with a summer flowering vs plants able to flower all year (Figure 1c).
316 The second dimension (29.4%) was affiliated with the differences in ratios between spring
317 and a group of attributes (summer to autumn, spring to summer, and spring to autumn).
318 Communities of age group 1 showed a relatively higher proportion of plants capable of
319 flowering all year round while the other age groups had higher proportions of summer
320 flowering plants. Weed communities for age group >10 also appeared to have a relatively
321 higher proportion of spring flowering plants.

322

323 **3.2.4 Ellenberg's indicator value for light**

324

325 The first component of the Ellenberg's indicator value for light biplot (Figure 1d) explained
326 41.8 % of the variance and was affiliated with the difference between the ratios of the score 5
327 and the score 6. The second component was affiliated with the difference in ratios of
328 heliophile (7, 8, and 9) and shade-tolerant species (4 and 5). The second component explained
329 27.7 % of the variance. The strongest links were found between the score 4 and 5. Weed

330 communities of the age group 1 appeared to have less variability in the ratios of attributes
331 than others age groups. More heliophilous weeds were linked to the age group 1, while
332 proportions of shade-affiliated weeds (scores 4 and 5) were higher in the other age groups.

333

334 **3.2.5 Plant type**

335

336 Attribute ratios for the age groups 1 and 2-5 appeared to be more variables within the age
337 groups in comparison with others age groups. The figure 2a also showed a trend to an increase
338 of graminoids proportions during the first ten years of CA (age groups 2-5 and 6-10) and in
339 the oldest systems (age group >10).

340

341

342 **3.2.6 Seed mass**

343

344 The CWM of the seed mass tended to increase continuously over the CA age groups (Figure
345 2b). Median values of the CWM seed mass increased from 2.62 mg in the age group 1 to 5.19
346 mg in the age group >10. Weed communities with very high CWM values (up to 20 mg)
347 appeared for the age groups 6-10 and >10.

348

349

350 **4 DISCUSSION**

351

352 The results presented above on successfully established weeds (able to maintain and/or to
353 reproduce) confirmed that not all functional responses of weed communities to the adoption
354 of CA are visible during the first years of CA. Indeed, some functional shifts were spread over
355 the 21-year age gradient of continuous application of CA.

356

357 Of all the traits included in this study, the specific leaf area and the leaf dry matter
358 content were found to be the least influenced traits by the time since CA adoption. We
359 expected an unfavourable filtering for species with high internal conductivity (high specific
360 leaf area) and low investment in structural tissues (low leaf dry matter content), as it has been
361 observed in field margins (Carlesi et al., 2013). Unlike others traits, these traits can be
362 extremely variable within species (Kichenin et al., 2013). In this study, results suggested that
363 the observed intraspecific variability would be mostly due to phenotypic plasticity. Using data
from the database, we only captured the possible response of weed communities to CA

364 resulting from a change in composition, thus excluding an intraspecific adaptation in plant
365 physiology. We can therefore conclude that the weed composition changes that may occur
366 along the age gradient of CA, did not alter the capacity of plants to use resources or to
367 compete. A similar result was found by Armengot et al., (2016) for specific leaf area in a no-
368 till system. Although no change was observed for both traits, the results for seed mass could
369 indicate a change in competitive ability at the early stage of weed development. It was
370 expected that there would be a filtering towards smaller seeds, capable of natural seed burial,
371 as it has been observed for reduced or no-tillage systems (Hernández Plaza et al., 2015;
372 Armengot et al., 2016). On the contrary, our results showed an opposite trend, i.e an increase
373 of the CWM value of seed mass with time since CA adoption. This increase of seed mass can
374 correspond to a progressive shift toward smaller seeds with high colonizing capacity in early
375 years of CA to larger seeds with high competition capacity in the oldest age groups, as
376 observed in secondary succession on meadows (Zhang et al., 2018). The presence of
377 permanent residue cover on the soil surface (cover crops or dead mulch) could have
378 contributed to this shift by requiring additional resources for weed seeds to germinate
379 (Teasdale, 1996), thus favouring weeds with larger seeds. The CWM values of this trait
380 appeared quite variables, especially in the oldest systems (age groups 6-10 and >10), meaning
381 that there were differences between communities, which could result from variations in weed
382 management.

383 Regarding the mode of seed dispersion, we expected to find more wind-disseminated
384 species in the youngest CA fields, which are typically rapid colonizers of undisturbed
385 agroecosystems (Zanin et al., 1997; Young and Thorne, 2004). We also expected an increase
386 of seed dispersion mechanisms dependents of others communities such as zoochory due to a
387 better soil life activity in CA (Henneron et al., 2015). However, although anemochory and
388 zoochory represented an important part of seed dispersion mechanisms of weed communities
389 (19.9 and 30.8%, respectively), no change was observed with CA age. Since most farmer
390 using CA in France use reduced tillage systems before adopting CA (Derrouch et al., 2020b)
391 and because reduced tillage is also known to favour anemochore species (Swanton et al.,
392 1993), we hypothesize that changes in seed dispersal mechanisms may have been masked by
393 the legacy effects of past practices before adoption of CA. Some anemochorous and
394 zoochorous species may have colonized the fields before the adoption of CA and persisted
395 over time, as illustrated by the most frequent species in the dataset, i.e. *T. officinale*.

396 The lack of effect of the CA age on the soil seedbank longevity is consistent with
397 results found by Armengot et al. (2016) on no-till systems. In agroecosystems, soil tillage has

398 a major influence on soil seedbank dynamics (Cordeau et al., 2017). By burying the seeds,
399 soil tillage induces dormancy, thus lengthening seed persistence over time (Albrecht and
400 Auerswald, 2009). Without tillage, most seeds remain localized near the soil surface
401 (Clements et al., 1996), a condition deemed to be unfavourable to weed seed germination
402 because of poor seed-soil contact (et al.1984) but suitable for predation (Petit et al., 2017).
403 Consequently, their persistence in the soil should decrease. The lack of change observed with
404 time since CA adoption could result from an increase in soil life activity in CA fields
405 (Henneron et al., 2015). By facilitating biological seed burial, macrofauna and megafauna
406 may have replaced part of superficial tillage effect (Smith et al., 2005). In addition, the
407 potential decrease in the longevity of soil seedbanks could have been masked by the fact that
408 short-lived seeds are more rapidly affected by changes in filtering pressure than persistent
409 seeds (Albrecht and Auerswald, 2009).

410 The effect of the maximum soil coverage on weed communities can also be observed
411 through the changes identified in the Ellenberg's indicator value for light. In the first year
412 after CA adoption, the weed communities appeared to be composed only of heliophile species
413 (scores of 7, 8 and 9). By voluntarily decreasing the available light for weeds, farmers
414 allowed colonizing species with an intermediate light affinity (Ellenberg's indicator value for
415 light of 4, 5) to establish and reproduce in fields. Although the results showed an increase in
416 weed species more tolerant to shade, the majority of the CA weeds community remained
417 composed of heliophile weeds.

418 Regarding the Raunkiær's life forms, with the decrease in mechanical soil
419 disturbances, an increase of all perennial life forms (Zanin et al., 1997; Trichard et al., 2013)
420 was expected. Nevertheless, the proportions of hemicryptophytes and chamaephytes were
421 higher in the age group 1. This observation could be the result of the progressive soil tillage
422 reduction chosen by farmers before adopting CA (Derrouch et al., 2020b). Age groups 2-5
423 and 6-10 appeared as an intermediate state between the other groups, with higher proportions
424 of geophytes and phanerophytes than age group 1 and higher proportions of therophytes,
425 hemicryptophytes and chamaephytes than age group >10. Although the proportion of
426 geophytes and phanerophytes increased with continuous application of CA, the proportion of
427 therophytes in the weed communities in CA remains unaffected. Most of the common (*A.*
428 *myosuroides*, *C. album*) and abundant species (*V. hederifolia*, *D. sanguinalis*, *S. pumila*, *A.*
429 *hybridus*) were therefore therophyte species.

430 The results showed a tendency toward an increase of graminoids with CA age. Weed
431 communities in the age groups 6-10 and >10 appeared to be less variables in their proportions

432 of eudicotyledons/ graminoids and composed of a higher proportion of graminoids. This trend
433 has already been observed in systems with reduced tillage (Murphy et al., 2006) or in CA
434 (Trichard et al., 2013) and may result from a smaller range of chemical solutions that can be
435 used on grasses on wheat crop.

436 Both the germination and flowering periods were affected by the time since CA
437 adoption. The age groups 2-5, 6-10 and >10 had a higher proportion of summer flowering
438 than the age group 1 and the oldest age group (> 10) showed a higher proportion of species
439 germinating in summer. This filtering towards summer life span weeds in CA could be due to
440 the opportunity for weeds to establish during the intercropping period. In CA, due to the
441 absence of post-harvest disturbance by tillage and to the use of chemical weeding mainly
442 before the sowing of the next crop, the intercropping period represents a new temporal niche
443 for weeds. In addition, these changes could have been facilitated by the third principle of CA,
444 the crop diversification. This crop diversification, applied by half of farmers when adopting
445 CA (Derrouch et al., 2020a) is generally optimized by farmers after the first five years of CA
446 to achieve sustainable weed management (Derrouch et al., 2020a). The introduction of spring
447 and summer crops during the post-adoption period, could explain the observed increase in
448 summer germination proportions in the age group >10. Thus, in a wheat crop (from late
449 winter to intercropping period), summer weeds (*C. album*, *D. sanguinalis*, *S. pumila*, *A.*
450 *hybridus*) generally more affiliated to summer crops such as maize (*Zea mays* L.) or soybean
451 (*Glycine max* (L.) Merr.) have the opportunity to develop and reproduce.

452

453 **5 Conclusions**

454

455 The objective of this study was to identify functional shifts in weed communities over a 21-
456 year age gradient since CA adoption. Results showed that functional shifts observed in fields
457 recently converted to CA (two to five years) remain visible in the older ones. This was
458 particularly the case for shifts towards more phanerophyte and geophyte life forms,
459 graminoids, weeds with larger seeds, spring- to summer- germinating and summer-flowering
460 species. Nevertheless, some functional shifts occurred later, i.e. ten year after CA adoption,
461 such as an increase of summer-germinating and spring-flowering weeds. As changes in weed
462 community functional composition could potentially worsen current weed management
463 efficacy, this work could therefore provide knowledge to CA farmers and farmers moving
464 towards CA to redesign the weed management tactic according to expected weed community
465 evolution.

466

467

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469

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477

478 **CONFLICT OF INTEREST**

479 The authors reported no potential conflict of interest.

480

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605 **Figure legends**

606 **FIGURE 1:** Response traits significantly affected by time since CA adoption. In composition
607 data PCA biplot (a, b, c and d), the relevant variables are represented by the links (*i.e.* the
608 difference between two arrowheads) which correspond to the distance of log ratio between
609 two components.

610

611 **FIGURE 2:** Trend observed with time since CA adoption. Because only two attributes
612 composed the trait “plant type”, the distances of log ratio were represented with a boxplot (a).
613 For the quantitative trait “seed mass”, the CWM values were represented using a boxplot (b)

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TABLE 1 Mean community weighted mean (CWM) value or percentage of attributes

Categorical traits	Attribute	Number of species	Geometric mean (and standard deviation) in %*
Raunkiaer's life form	Therophyte	98	71.2 (± 20.1) %
	Hemicryptophyte	88	23.1 (± 18.2) %
	Geophyte	15	3.7 (± 6.1) %
	Chamaephyte	5	0.03 (± 0.2) %
	Phanerophytes	20	1.97 (± 3.8) %
Soil seedbank longevity	Transient	123	35.8 (± 22.8) %
	Transient to short term	29	15.9 (± 18.1) %
	Short term persistent	15	18.5 (± 22.8) %
	Transient to long term	34	15.7 (± 14.6) %
	Short term to long term	13	9.5 (± 14.2) %
	Long term persistent	12	4.5 (± 11.8) %
Plant type	Eudicotyledon	193	73.2 (± 24.7) %
	Graminoids	33	26.8 (± 24.7) %
Flowering period	All year	4	2.99 (± 6.5) %
	Spring	13	1.7 (± 3.4) %
	Spring to summer	48	28.7 (± 24.4) %
	Spring to autumn	53	20.4 (± 17.5) %
	Summer	22	4.3 (± 8.6) %
	Summer to autumn	86	42 (± 24.1) %
Germination period	All year	58	23.6 (± 17.7) %
	Spring	52	7.5 (± 10.3) %
	Spring to summer	34	23.3 (± 18) %
	Summer	14	10.8 (± 21.2) %
	Autumn to spring	68	34.8 (± 25.5) %
Mechanism of seed dispersal	No mechanism	73	46.9 (± 22.8) %
	Anemochory	62	19.9 (± 14.7) %
	Zoochory	83	30.8 (± 22.9) %
	Autochory	8	2.35 (± 7.9) %
Ellenberg's indicator value for light	Shadow species - 4	2	1.9(± 6.9) %
	5	13	2.4 (± 4.8) %
	6	16	6.9 (± 9.7) %
	7	102	50.3 (± 23) %
	8	87	38.4 (± 23.9) %
	Full light species - 9	6	0.1 (± 0.7) %
Quantitative traits	Unit	Mean CWM attribute (± standard deviation) on the 100 fields*	
Seed mass	mg	4.9 (± 3.9)	
Specific leaf area	mm ² .mg ⁻¹	25.4 (± 3.2)	
Leaf dry matter content	mg.g ⁻¹	187.2 (± 26.3)	

*After imputation of zero counts, see materials and methods section for the detailed method

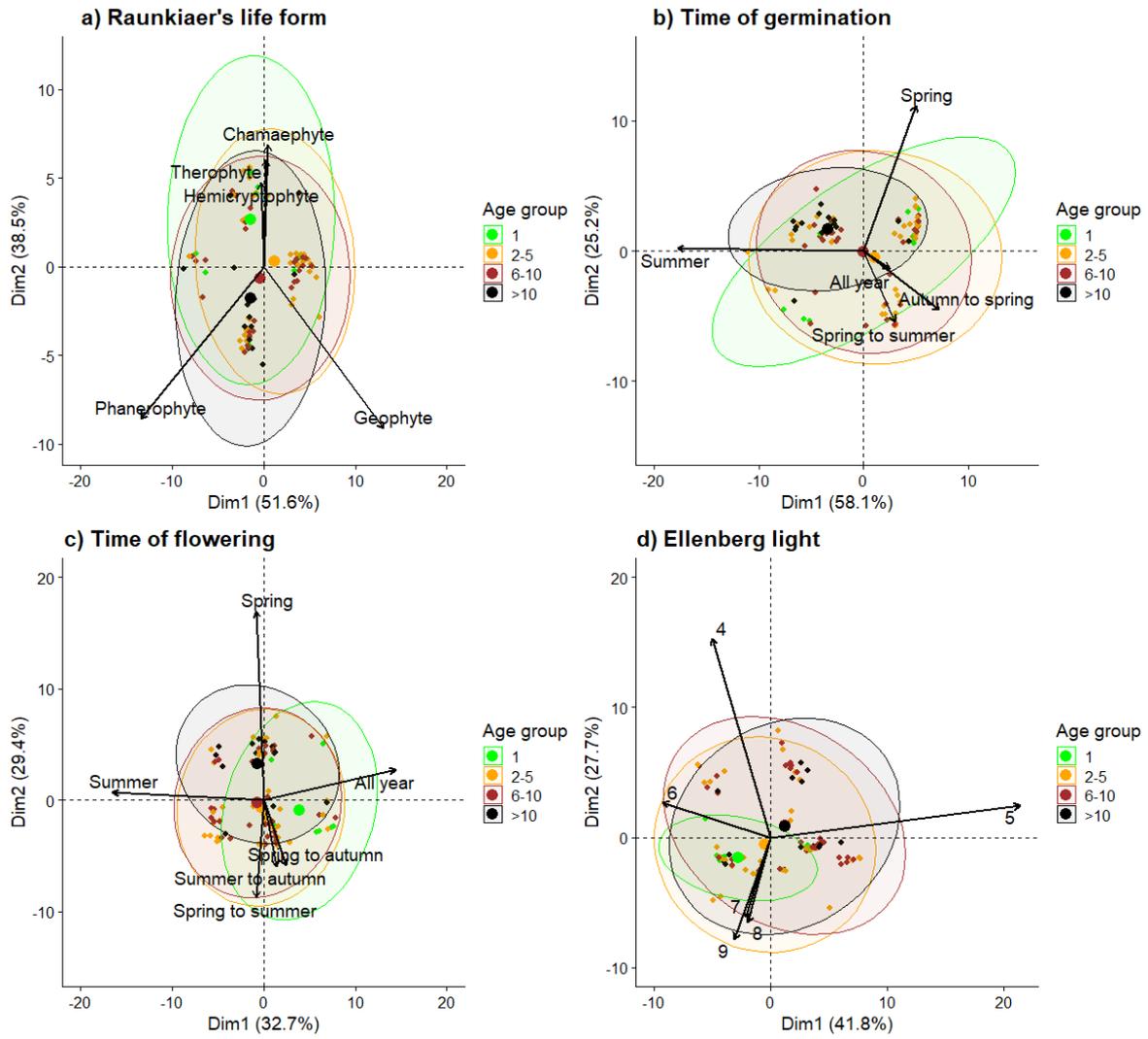
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620 **TABLE 2** Effect of the time since adoption of Conservation Agriculture (CA) on the ten
 621 traits. Values of permutational test using distance matrices (PERMANOVA) with the ten
 622 traits as responses variables and time since CA adoption as explanatory variable (4 classes of
 623 group age). In bold, significant results ($p < 0.05$).
 624

Response traits	Time since CA adoption		
	R^2	F	p
<u>Categorical traits</u>			
Raunkiær's life form	0.113	4.06	0.001
Soil seedbank longevity	0.048	1.641	0.092
Plant type	0.070	2.425	0.059
Time of flowering	0.097	3.422	0.001
Time of germination	0.078	2.719	0.013
Seed dispersal	0.024	0.781	0.614
Ellenberg's indicator value for light	0.088	3.105	0.002
<u>Quantitative traits</u>			
Seed mass	0.071	2.446	0.065
Specific leaf area	0.015	0.4997	0.681
Leaf dry matter content	0.005	0.148	0.927

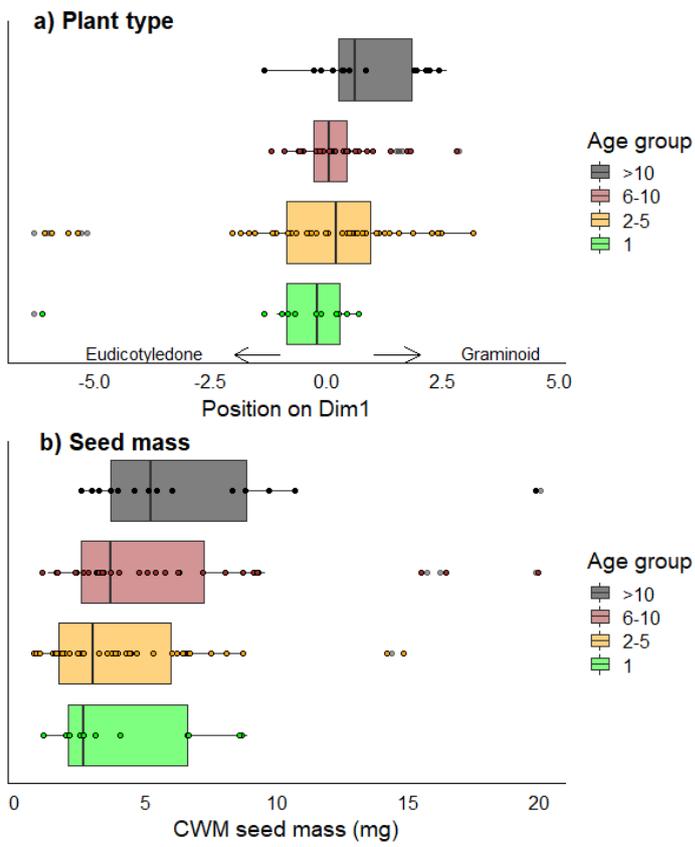
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628 **FIGURE 1**
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633 **FIGURE 2**
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