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1 Weed community diversity in conservation agriculture: post-adoption changes

2

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12

13 Abstract

14 Conservation agriculture has been identified as one of the farming systems likely to deliver sustainable
15 agriculture but its effects over time on the diversity and composition of weed communities are poorly
16 documented. Using a network of 100 winter wheat fields selected to encompass a gradient of years in
17 conservation agriculture from 1 to 20 years in the Bourgogne-Franche-Comté region (France), we
18 analysed the changes that occurred in the diversity of weed communities over several years, both in α -
19 and β -diversity using a taxonomic (species level) and functional (10 response traits) approach. Based
20 on three weed surveys (before the last herbicide use, before harvest, before sowing the following
21 crop), we identified weeds able to maintain and/or to produce propagules. All the observed weed
22 communities were rich (average species richness of 23.9 species), diverse (average Shannon diversity
23 of 2.15) and equitably composed of low-density species. The results showed an increase in species
24 richness, total weed abundance and α -functional diversity but no change in species diversity and
25 species evenness over time. Heterogeneity and average values of β -taxonomic and β -functional
26 diversity between communities were high in the early years following the adoption of conservation
27 agriculture. Heterogeneity and average β -taxonomic and β -functional diversity decreased over time,
28 leading to a homogenization of weed community assemblages. Despite major changes in cultural

29 practices related to conservation agriculture, homogenization of weed community was not immediate
30 and did not concern all the traits studied.

31 Keywords: α -diversity; β -diversity; no-tillage; weed survey; functional convergence

32 1 Introduction

33 With a growing world population, one of the major challenge of agriculture is to improve production
34 while preserving the environment and the biodiversity present in agroecosystems (Robertson and
35 Swinton, 2005). Among the different farming systems that can provide productive and sustainable
36 agriculture, conservation agriculture (CA) has been identified as one of the most favourable options
37 (Hobbs et al. 2008). Based on an objective of preserving agricultural soils, CA is characterized by the
38 simultaneous and continuous application of three principles: minimum soil disturbance (no-tillage);
39 residue cover on the soil surface (cover crops or dead mulch) and diverse crop successions and cover
40 crop mixes (Reicosky, 2015). Widely used in some countries (USA, Brazil, Argentina, Canada,
41 Australia), it was only adopted in France in the 2000s with a production of around 300,000 hectares in
42 2014 (Kassam et al. 2018), approximately 1.6 % of the utilised agricultural area. The choice to convert
43 to CA has been made by farmers from different farming systems using different combinations of
44 cultural practices but the adoption of CA leads to a reduction of the range of usable cultural practices
45 and to less divergent weed management strategies between farmers (Derrouch et al. 2020a). Although
46 the majority of farmers had already reduced the frequency or depth of tillage practices prior to
47 adoption, the complete abandonment of tillage and the related soil disturbances represent the major
48 change for the weed communities at the time of adopting CA (Derrouch et al. 2020b).

49 To improve the understanding of the effects of cultural practices on weed communities, Booth and
50 Swanton (2002) proposed applying assembly theory to weed communities. By describing weed
51 species by their biological traits, it is possible to identify general rules that drive weed community
52 assembly. In this framework, each management practice is likely to act as a filter on weed
53 communities by removing, limiting or favouring species depending on their trait combination values.
54 As observed in other situations such as the transition to organic farming (Delate and Cambardella,
55 2004), each change in cultural practices is likely to modify the strength and mesh size of the filters and
56 thus, the combination of selected trait values. For example, in arable crops, soil tillage is widely
57 known as the main factor explaining the high percentage of annual species in the community. By
58 frequently disturbing the soil surface, soil tillage filters mainly plants able to survive unfavourable

59 perturbations in the form of seeds or, to a lesser extent, in the form of underground organs capable of
60 vegetative propagation (e.g. rhizomes). Weed seeds buried by soil tillage remain dormant before being
61 brought back to the soil surface by the following soil tillage. Due to the absence of soil disturbance
62 when adopting CA, seeds remain concentrated on the soil surface and annual species are partly
63 replaced by perennials as during plant succession (Bazzaz, 1979; Zanin et al. 1997). The presence of
64 residues on the soil surface in CA systems modifies the conditions for germination and the emergence
65 of weed seeds by reducing light availability and affecting the soil's characteristics (humidity, pH and
66 temperature) (Holland, 2004). When the cover crop is alive, other processes such as competition for
67 nutrients and allelopathy can affect germination and the emergence of some weed species (Teasdale,
68 1996). The diversification of crop succession with the adoption of CA modifies all the disturbances
69 and stress events that shape communities, thus limiting the development of weed populations with
70 phenological and physiological similarities to the crop as observed in simple crop sequences (Cardina
71 et al. 1998).

72 Most of the studies describing the response of weed communities to CA focused on the response of
73 weed species to one or two of the CA principles, with opposing results sometimes occurring between
74 studies. In most cases, the reduction of tillage and crop diversification seemed to increase weed
75 diversity. The effects on weed abundance seemed different for each of these two CA principles: the
76 reduction of tillage tends to increase weed abundance while crop diversification tends to decrease it.
77 (Mahaut et al. 2019; Travlos et al. 2018; Weisberger et al. 2019). The use of cover crops decreased
78 weed abundance (Buchanan et al. 2016) and potentially the weed richness when the cover crop
79 biomass is high (Smith et al. 2015a). Concerning changes identified in weed community composition
80 when adopting one or the other of the CA principles, the results vary according to the system, although
81 a strong tendency towards the filtering for perennial (no disturbance of perennial weed organs), wind
82 disseminated and graminoid species was highlighted in CA systems (Trichard et al. 2013; Young and
83 Thorne, 2004). To date, no study examined whether the adoption of CA on the long-term leads to a
84 homogenisation of weed communities or, on the contrary, to an increase of dissimilarity between
85 communities. Changes in dissimilarity between communities (β -diversity) in the literature are accessed

86 through two main approaches (Brice et al. 2017; Fried et al. 2016; Rooney et al. 2004). The first
87 approach is mainly used when comparing communities over time. In this case, an homogenization or a
88 convergence of weed communities refers to the process by which β -diversity between communities
89 decreases over time (Olden and Rooney, 2006). The second approach is mainly used to compare
90 different communities in different groups along an ecological gradient. In this case, homogenization
91 refers to a decrease of β -diversity between communities belonging to the same group, *i.e.* in similar
92 ecological conditions (Brice et al. 2017).

93 Using a network of 100 winter wheat fields covering an age gradient from 1 to 20 years since CA
94 adoption, the present paper explored the responses of weed communities over time under new filtering
95 pressures, using different scales (within the field and between fields) at both taxonomic and functional
96 levels. More specifically, we investigated (1) how weed α -diversity changed according to time in CA,
97 (2) whether these changes have led to change in β -diversity and (3) how many years were required to
98 observe pronounced changes in β -diversity since the adoption of CA. As the adoption of CA reduces
99 the range of cultural practices and weed management practices, we expected taxonomic and functional
100 β -diversity to decrease over time. Because CA brings together farmers from different farming systems
101 prior to adoption, we expected high mean values of β -diversity and a high heterogeneity between
102 communities in the first years of CA. Alternatively, as the strength of the "soil disturbance" filter is
103 reduced in CA, it can be expected that the diversity of the weed flora will be more dependent on
104 landscape structures around plots and therefore differs more from plot to plot. The main objective of
105 this work was to test whether the continuous application of cultural practices linked to the application
106 of CA principles, resulted in a global homogenization of weed communities.

107

108 2 Materials and methods

109 2.1 Study site

110 The study area was set up in the Bourgogne-Franche-Comté region in north-eastern France, one of the
111 main emerging areas of CA use. The study area was located in a temperate oceanic zone according to

112 the Köppen-Geiger classification, with an average rainfall of 756 mm and an average temperature of
113 10.9°C (<https://www.insee.fr/fr/statistiques/4176857>). Since 2018, however, drier and warmer seasons
114 than usual have been observed. Two types of soil are predominant in the region: clay-limestone soils
115 and deep loamy soils with a more or less significant clay gradient (<https://bourgogne.websol.fr/carto>).
116 In this study area, a network of 53 farmers belonging to different CA groups or organisations was
117 created. A hundred winter wheat (*Triticum aestivum*) fields were selected in which farmers complied
118 with CA principles and on the basis of the number of years since adopting this farming system (age
119 gradient from 1 to 21 years). Due to the gradual adoption of CA in the study area, the distribution of
120 fields along the age gradient was not homogenous, with a higher number of fields with a recent CA
121 adoption. For analytical purposes, the oldest fields were grouped together according to age in CA. We
122 regrouped fields from 11, 12 and 13 years in CA as “12 years”, fields from 14, 15, 16 years as “15
123 years” and fields from 18, 20, 21 years as “20 years”. The distribution of the 13 “age groups” in the
124 study area is represented in Figure 1. In the field network, farming systems prior to the adoption of CA
125 were mainly based on reduced tillage (76 of the 100 fields) but exact intensity of reduced tillage was
126 not known. The management of the remaining fields was based on soil tillage (21 fields) or on no-till
127 (3). Although herbicide use may vary among fields, farmers, and over the years in CA (Derrouch et
128 al., 2020a), in this study all farmers used herbicides for weed control. The fields were mainly located
129 in a landscape dominated by crops. No prior selections were made on soil type, even though the nature
130 of the soil can influence the presence of weed species (Fried et al. 2008).

131

132 2.2 Weed data collection and selection

133 For each field, weed communities were surveyed either in 2018 (51 fields) or in 2019 (49 fields) on a
134 50x40 m area, which was representative of the weeds present in the whole field according to the
135 farmers. The area was located 50 m away from field boundaries to avoid field edge effects. Weed data
136 were collected at three periods: in early March (before the last post-herbicide use), in mid-June (before
137 harvest, *i.e.* a period of potential weed seed production) and in early September during the
138 intercropping period (before sowing of the following crop). The sampling protocol was similar for all

139 periods. All species were recorded within the 2,000 m² surveyed area and following a W-shaped
140 walked path (two persons, 30-40 min for each survey). For each period, seven to eight days were
141 required to collect all the data. Most plants were identified at species level according to Jauzein
142 (1995). Taxonomy was corrected according to the TAXREF Taxonomic repository v13.0 (Gargominy
143 et al. 2019). For some vegetative plants, plants were noted at the genus level (e.g. *Lolium* sp.) due to a
144 lack of relevant distinguishing criteria at the seedling and/or vegetative stages. The abundance of each
145 weed species was estimated using a modified Barralis scale of abundance (Barralis, 1976): [+] found
146 once 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] 51 to
147 60 individuals m⁻². For each period, the percentage of each stage of development (seedling, vegetative,
148 flowering, fructification) was also estimated for each species. Only plants that were not intentionally
149 sown by farmers in the given year or the preceding year were considered. Plants used for cover crop in
150 the given year but also volunteers from the preceding year were excluded.

151 The aim of the three successive weed surveys was to provide an overview of all the species present
152 during the crop period (from winter outgrowth to intercropping period) which cannot be captured via a
153 single survey. Thanks to scoring based on stage of development, our survey could distinguish weed
154 species able to produce propagules but also weed species not able to reproduce, *i.e.* species present
155 only at a seedling or a vegetative stage. It was therefore possible to reduce the statistical noise due to
156 casual species by selecting only weeds able to maintain and/or to produce propagules during a winter
157 crop cycle. This selection was made in each field and for each species, and took into account density
158 (centre of abundance classes), stage percentages, the survey period and Raunkiaer's life-form
159 categorization (scheme shown in Figure 2). For therophytes species, *i.e.* species that persist only by
160 seeds, only those with a flowering or fructification stage in either March, June or September were
161 selected (example of species 1, 2 and 4 in Figure 2). As records of mature individuals of the same
162 annual species during different surveys over time undoubtedly represent different cohorts, we summed
163 the densities of selected weed species in order to obtain a single density measure for each species in a
164 given field. Therophyte species observed in the seedling or vegetative stages were not retained
165 (example for species 3 in Figure 2), recognizing that early spring flowering species (*Scandix pecten-*

166 *veneris*, *Anthriscus caucalis*) could be more affected than others species by the applied selection
167 method. For perennial weed species (hemicryptophytes, geophytes, chamaephytes and phanerophytes),
168 able to survive for several years and/or produce propagules (sexual and/or vegetative reproduction),
169 the selection was carried out regardless of their stage of development. Since similar individual plants
170 were present in the plot over several survey periods (weed surveys conducted exactly at the same
171 location), we used the average density value for each species to further obtain a single density measure
172 (species 5, 6, 7 and 8 in Figure 2). Of the 257 identified weed species, 30 therophytes species were
173 never found in a flowering or fructification stage and were therefore excluded for analysis. This
174 selection also reduced the weight of weed species present in many fields but predominantly at the
175 vegetative stage. This was the case of *Sonchus asper*, *Fallopia convolvulus*, *Geranium dissectum* and
176 *Lapsana communis*. The differences in species abundance and frequency between the original data set
177 and the retained data set are presented in Table S1. Over the 100 fields, 227 weed species out of the
178 257 recorded species were considered in the analysis (see Table S1 for the list of weed species).
179 Hereafter the term “community” will comprise species recorded in a plot field.

180

181 2.3 Trait data

182 Ten response traits (Table 1) were selected based on a reference list of functional traits for arable
183 weeds (Booth and Swanton, 2002; Gaba et al. 2014, Gaba et al. 2017) and on articles related to CA or
184 no-till systems (Armengot et al. 2016; Trichard et al. 2013). Traits were selected for their key role in
185 the weed dynamic. Raunkiaer’s life-form (Raunkiaer et al. 1934) and the number of cotyledons
186 (graminoids, eudicotyledons) referred to plant life-form. The Raunkiaer’s life form was used to capture
187 the potential effect of an absence of mechanical soil disturbance on weed communities. The trait
188 "number of cotyledons" was chosen due to the important effect of herbicide application on the
189 proportion of monocotyledons or eudicotyledons in the weed community. Because farmers can
190 specifically target graminoids and/ or eudicotyledons weeds through herbicide application, this trait
191 can refer to some possible changes in weed management with CA duration. Time of germination
192 (season) and time of flowering (season) gave indications on weed life cycle and thus could capture the

193 effects of CA on temporal niches, but also a possible change in weed management. Soil seedbank
 194 longevity (years), mode of seed dispersal (four classes) and seed mass (mg) referred to either temporal
 195 or spatial weed seed dispersion. In CA, vertical seed movements in the soil due to the abandonment of
 196 tillage are reduced which could therefore induce changes regarding the values of these three traits that
 197 will be favoured under this system. Specific leaf area ($\text{mm}^2.\text{mg}^{-1}$), leaf dry matter content ($\text{mg}.\text{g}^{-1}$) and
 198 Ellenberg's indicator value for light (five classes) represented weed resource use (see Table 1 for
 199 source, and Table S2 for attributes and more information about data selection from databases). For
 200 weed species identified at genus level, trait values were from the most common species from the same
 201 genus in the initial database. For trees and shrubs, traits values were based on the most common
 202 species in the region (Bardet et al. 2008). Finally, to enable analysis, missing values (see Table S2 for
 203 the number of missing values per trait) were completed with expert opinion, taking into account the
 204 closest attributed values.

205 Table 1 : Response traits used

Traits	Number of attributes	Trait role	Main associated principle or change induced by the adoption of CA*	Data source
Raunkiaer's life-form	5	Plant life-form	P1	1 (2)
Number of cotyledons	2	Plant life-form	P1, P2, P3: Low use of specific grass-weed herbicide treatment (Trichard et al. 2013)	3
Time of germination	9	Life cycle	P2; P3; shift towards post herbicide application (Derrouch et al. 2020a); longer crop cycle period (intercropping period)	4
Time of flowering	6	Life cycle	P3; longer crop cycle period (intercropping period)	3 (1)
Soil seedbank longevity	6	Dispersion	P1	5 (6)
Seed dispersal	4	Dispersion	P1	3
Seed mass	6	Dispersion	P1	7 (5)
Specific leaf area	7	Resource use	P1; P2	5 (6)
Leaf dry matter content	6	Resource use	P1; P2	5 (6)

Ellenberg light	6	Resource use	P2	3 (8,2)
-----------------	---	--------------	----	---------

*P1: minimum soil disturbance (no-tillage); P2: residue cover on the soil surface (cover crops or dead mulch); P3: diverse crop successions and cover crop mixes
 1 (Bardet et al. 2008); 2 (Bocci, 2015), 3 (Julve, 1998); 4 (Mamarot and Rodirguez, 2014);
 5 (Kleyer et al. 2008); 6 (Tavşanoğlu and Pausas, 2018); 7 (Royal Botanic Gardens Kew,
 2020); 8 (Hill et al. 1999)

206

207 2.4 Data analysis

208 2.4.1 α -diversity

209 Potential changes in diversity of weed communities were first studied at the plot scale using indices
 210 referring directly to α -diversity (species diversity, functional diversity) or more generally to
 211 community description (species richness, species evenness and abundance). Abundance, represented
 212 here by a density measure, was the total abundance of all species present per m² in a given field. For
 213 weed diversity, Shannon's (H') and Simpson's (D) diversity indices were calculated with $H' =$
 214 $-\sum_{i=1}^S pi(\ln pi)$, where pi is the proportion of individuals belonging to the i species and S is the total
 215 number of species and $D = \sum_{i=1}^S p_i^2$ where p_i is the proportional abundance of i species. Each index
 216 provided different information. While the Shannon index is strongly influenced by rare species and
 217 species richness, the Simpson index gives more weight to common species and evenness. The
 218 evenness of weed communities was represented by the Pielou index (J'), with $J' = \frac{H'}{H'max}$, where H' is
 219 the Shannon diversity index and $H'max$ the maximum possible value of H' . Functional diversity was
 220 represented by the functional diversity index developed by Cardoso et al. (2014) which corresponds to
 221 the total length of branches of a community tree linking all species present in a given plot. The
 222 functional diversity was estimated using all functional traits (227 species x 10 functional traits). The
 223 community tree was obtained by multiple correspondence analysis on the "species x traits" matrix
 224 followed by clustering analysis. The community tree was constructed on the basis of Euclidean
 225 distances with the Ward algorithm and considering all axes of the multiple correspondence analysis.
 226 To create a community tree, the three quantitative traits (seed mass, specific leaf area, and leaf dry
 227 matter content) were divided into classes (see Table S2 for attributes). Diversity and evenness indices
 228 were obtained using the "vegan" package (Oksanen et al. 2019) of R software (R Development Core

229 Team, 2020). Functional diversity estimations were provided by the “BAT” package (Cardoso et al.
230 2020).

231 Relationships between the number of years of conversion to CA and indices were tested by robust
232 regression using function `rlm()` in the MASS package (Venables and Ripley, 2002) in R. In robust
233 regressions, the effects of outliers on the model are reduced giving less weight to large residuals
234 (Rousseeuw and Leroy, 1987).

235

236 2.4.2 β -diversity

237 Potential changes in the diversity of weed communities were then studied using a between community
238 scale. In order to do so, pairwise dissimilarities were estimated. At the taxonomic level, taxonomic β -
239 diversity ($T\beta_{\text{total}}$) was calculated using the Jaccard dissimilarity index based on the presence/absence of
240 species with $T\beta_{\text{total}} = \frac{b+c}{a+b+c}$ where a is the number of species shared by both communities, b the
241 number of species unique to the first community and c , the number of species unique to the second
242 community. Following the approach proposed by Podani and Schmera (2011), $T\beta_{\text{total}}$ was decomposed
243 into richness difference ($T\beta_{\text{rich}}$), with $T\beta_{\text{rich}} = \frac{|b-c|}{a+b+c}$ and into replacement ($T\beta_{\text{repl}}$) with $T\beta_{\text{repl}} =$
244 $\frac{2\min(b,c)}{a+b+c}$. While $T\beta_{\text{total}}$ represents the total taxonomic dissimilarity, $T\beta_{\text{repl}}$ gives the variation resulting
245 from species replacement (turnover) and $T\beta_{\text{rich}}$ accounts for the variation resulting from differences in
246 species richness induced by species loss/gain. Using the framework developed by Cardoso et al.
247 (2014) and the same community tree used for functional α -diversity, we quantified functional β -
248 diversity ($F\beta_{\text{total}}$) and its components, *i.e.* functional difference ($F\beta_{\text{rich}}$) and functional replacement
249 ($F\beta_{\text{repl}}$). All estimates for functional diversity and β -diversity were obtained using the BAT package
250 (Cardoso et al. 2020).

251 To access changes in β -diversity within and between age groups, both mean value and heterogeneity
252 of dissimilarities measures were taken into account. Differences in heterogeneity between age groups
253 were tested using an analysis of multivariate homogeneity of group dispersions (PERMDISP,

254 Anderson et al. 2006). Using square root of dissimilarities indices, the “betadisper()” function from the
255 “vegan” package (Oksanen et al. 2019) calculated the median spatial distance of fields belonging to
256 the same age group to the group centroid in a multivariate space. The difference in mean
257 dissimilarities measures between age groups was tested using a permutational non-parametric
258 multivariate analysis of variance (PERMANOVA, Anderson, 2001) which tested for location
259 differences between centroids. The “adonis()” function, an analogous test to non-parametric
260 MANOVA was used with 9,999 permutations. Because PERMANOVA is sensitive to differences in
261 multivariate dispersion (*i.e.* a significant result may be due to the difference in variation rather than
262 differences in the centroid location), only indices with homogeneous dispersion were tested
263 (PERMDISP not significant). Finally, for all significant PERMDISP tests, group mean dispersions
264 were compared using the Tukey post-hoc pairwise comparison test (function
265 “TukeyHSD.betadisper()” from the “vegan” package). In order to identify the number of years
266 required in CA before identifying noticeable changes since adoption, the pairwise comparison was
267 only performed between age “1” and other ages groups. Analysis of β -diversity was performed on all
268 β -diversity indices ($T\beta_{total}$, $T\beta_{rich}$, $T\beta_{repl}$, $F\beta_{total}$, $F\beta_{rich}$ and $F\beta_{repl}$).

269 After been studied with all the traits (10 traits), α - and β -functional diversity were also estimated using
270 four trait combinations referring to the trait roles presented in Table 1: plant life-form (2 traits), life
271 cycle (2 traits), dispersion (3 traits), and resource use (3 traits). A new community tree was built for
272 each trait combination. This approach allowed us to examine whether the response was the same for
273 all traits or whether some trait combinations responded differently.

274

275 3 Results

276 3.1 Weed species

277 Of the 227 species retained from the initial database, nearly half of them (43.6 %) were therophyte
278 species (50.2 % from the initial database) and hemicryptophyte species represented 38.8 %. Graminoid
279 species represented 15 %. The most abundant plant families were Poaceae (32.1 % of weeds),
280 Asteraceae (16.1 %) and Amaranthaceae (13.5 %). The three most frequent species with an occurrence
281 (number of fields where species was present) higher than 75 % were *Taraxacum officinale* (84 %),
282 *Chenopodium album* (78 %) and *Alopecurus myosuroides* (78 %). In the fields where these species
283 were recorded, their mean abundance was comprised between 0.83 and 1.79 plants m⁻². The most
284 common species were not the most abundant species, which were represented by *Veronica hederifolia*
285 (occurrence of 5 % and mean abundance of 7.55 plants m⁻²), *Digitaria sanguinalis* (occurrence of
286 17 % and mean abundance of 7.32 plants m⁻²) and *Setaria pumila* (occurrence of 20 % and mean
287 abundance of 6.43 plants m⁻²) (Table S1). The mean abundance of most of species (91.7 %) was
288 represented by less than one plant m⁻². Half of the species (114) were found in less than five fields
289 (5 %). Some species, not usually found in the core area of arable crops were recorded, such as woody
290 (*Hedera helix*, *Euonymus europaeus*, *Acer* sp.) or field border species (*Heracleum sphondylium*,
291 *Vulpia myuros*, *Jacobaea vulgaris*, *Bromus commutatus*) and some species previously used as cover
292 that persisted in fields (e.g. *Medicago sativa*, *Lotus corniculatus*, *Vicia sativa*). Five rare or threatened
293 species listed on the National Action Plan for the conservation of segetal flora (Cambecèdes et al.
294 2012) have been recorded (see Table S1), with at least two species (*Bromus secalinus*, *Bromus*
295 *arvensis*) with higher frequency than observed in a weed survey of mainly conventional fields in the
296 same region (Fried et al. 2016). No failure situations (crop destruction, major yield loss) due to weeds
297 were observed in any of the studied fields.

298

299 3.2 α -diversity

300 The weed species richness varied greatly from field to field and ranged from 6 to 69 species with a
 301 global mean of 23.9 species (± 12.7 SD). Its value increased significantly ($F=9.76$, $P=0.002$) with the
 302 number of years of CA (Figure 3a) from a mean of 19.2 to a mean of 31.0 species after 20 years. The
 303 trend was similar for functional diversity estimated with all traits ($F=10.8$, $P=0.001$, Figure S1) and
 304 with the four trait combinations (Figure S2). The relationship between species richness and the
 305 estimation of functional diversity with all traits revealed a high correlation ($r_p=0.99$, $P<0.001$),
 306 indicating that each species has a unique trait combination (hardly any functional redundancy) (Figure
 307 3b). Results obtained with others estimations of functional diversity also showed a strong correlation
 308 with species richness for trait combinations related to dispersion, life cycle and resource use (r_p
 309 comprised between 0.88 and 0.95, $P<0.001$). The relationship appeared less significant for traits
 310 referring to plant life-form ($r_p=0.62$, $P<0.001$).

311 Total weed abundance per field ranged from 2 to 80 plants m^{-2} with a mean of 21 plant m^{-2} (± 19 SD).
 312 Although the robust regression result was not significant ($F=3.55$, $P=0.062$), total abundance of weed
 313 tended to increase over time. The means of Shannon and Simpson diversities were relatively high
 314 (2.15 ± 0.74 SD and 8.54 ± 7.58 SD respectively). Pielou's evenness ratio ranged from 0.16 to 0.99
 315 with a mean value of 0.7 (± 0.21 SD). For all these indices, no relationships with age groups were
 316 found (Table 2).

317 Table 2: Values of slopes of robust linear regression model based on all 100 fields with ages of CA as
 318 explanatory variable and the index as response variable. In bold, significant results ($p < 0.05$)

Index	Estimate	SE	F	P
Species richness	0.807	0.258	9.76	0.002
Abundance	0.574	0.304	3.55	0.062
Shannon diversity	0.021	0.017	1.57	0.214
Simpson diversity	0.096	0.125	0.59	0.443
Pielou evenness	-0.003	0.005	0.26	0.611
Functional diversity (all traits)	3.39	1.03	10.8	0.001

319 Shown are standard errors (*SE*), F-statistic values (*F*) and probability values (*P*).

320 3.3 β -diversity

321 Across all CA fields and age groups, $T\beta_{total}$ ranged between 0.47 and 1.00, with a mean of 0.82. $T\beta_{repl}$
322 was higher than $T\beta_{rich}$ indicating that taxonomic β -diversity among fields was driven more by species
323 replacement (59.5 %) than species loss or gain (40.5 %). $F\beta_{total}$ estimated with all traits was lower than
324 $T\beta_{total}$ and ranged between 0.37 and 0.90, with a mean of 0.70. Concerning its components, $F\beta_{repl}$ and
325 $F\beta_{rich}$, the same pattern was observed as with β -taxonomic diversity. $F\beta_{repl}$ drove 56.8 % of functional
326 β -diversity and $F\beta_{rich}$ 43.2 %. According to the PERMDISP analysis, dispersion of β -diversity values
327 within age groups differed significantly among age for $T\beta_{total}$ ($F= 5.42$, $P < 0.001$) and $F\beta_{total}$ ($F=5.50$,
328 $P < 0.001$, all traits) but not for the other β -diversity indices (Table 3). The relationship between
329 dispersion measured as median distance to centroid and the number of years in CA showed that
330 dispersion within age groups tended to decrease over time for $T\beta_{total}$ and $F\beta_{total}$ (all traits). Median
331 distances to centroids decreased from 0.61 to 0.5 for $T\beta_{total}$ and from 0.56 to 0.47 for $F\beta_{total}$ (all traits)
332 after 20 years in CA. However, the decrease was not linear (Figure 4). The same global decreasing
333 trend was observed for the average $T\beta_{total}$ and $F\beta_{total}$ values over time (Figure S3). β -diversity mean
334 values decreased slightly from 0.82 to 0.76 after 20 years in CA for $T\beta_{total}$ and from 0.69 to 0.63 for
335 $F\beta_{total}$.

336 For indices that were homogeneous for dispersion, PERMANOVA found no significant difference in
337 group centroids for $T\beta_{repl}$, $T\beta_{rich}$, $F\beta_{rich}$ and $F\beta_{repl}$ (Table 3).

338 Results gained from analysis with β -diversity indices obtained with the four trait combinations showed
339 different results according to the combinations. Results showed similar trends to those revealed for
340 functional diversity indices obtained with all traits for traits referring to dispersion (seed mass, seed
341 dispersal, soil seedbank longevity), life cycle (time of germination and time of flowering), and
342 resource use (specific leaf area, leaf dry matter content and Ellenberg light) (Table S3). However, for
343 traits referring to plant life-form (Raunkiaer's life-form and number of cotyledons), PERMDISP
344 analysis showed no difference in dispersion of β -diversity values within age groups and
345 PERMANOVA found a significant difference in group centroids for $F\beta_{total}$ and $F\beta_{rich}$ (Table S3) but no
346 trend was identified over time (figure not shown).

347 Table 3: Values of permutational non-parametric multivariate analysis of variance (PERMANOVA)
 348 and analysis of multivariate homogeneity of group dispersions (PERMDISP) with ages of CA as
 349 explanatory variable and the β -diversity as response variable. Functional β -diversity indices present in
 350 the table were estimated with all traits. In bold, significant results ($p < 0.05$)

	PERMANOVA						PERMDISP			
	Df	SS	MSS	F	R ²	P	SS	MSS	F	P
T β_{total}							0.075	0.0063	5.42	<0.001
T β_{repl}	12	1.84	0.153	1.13	0.135	0.334	0.124	0.0104	0.44	0.942
T β_{rich}	12	1.22	0.101	1.37	0.159	0.155	0.233	0.0195	1.26	0.257
F β_{total}							0.091	0.0076	5.50	<0.001
F β_{repl}	12	1.24	0.104	1.13	0.135	0.345	0.096	0.0080	0.39	0.963
F β_{rich}	12	1.16	0.097	1.62	0.183	0.072	0.299	0.0249	1.74	0.073

351 Shown are factor and residual degrees of freedom (*Df*), sum of squares (*SS*), mean sum of squares (*MSS*), *F*-
 352 statistic values (*F*), proportion of explained variance (*R*²) and probability values (*P*). For T β_{repl} and F β_{repl} ,
 353 negative values were changed to zero distances for PERMDISP test

354

355 For all age groups, Tukey's post-hoc pairwise comparisons revealed similar or lower heterogeneity of
 356 values relating to age group 1. According to Figure 5, only the values from age groups 8, 15 and 20
 357 were significantly less heterogeneous for T β_{total} and from age groups 15 and 20 for F β_{total} (all traits).
 358 The first five years in CA showed values with a similar degree of heterogeneity for T β_{total} and F β_{total}
 359 (all traits). Although not significantly different with regard to age group 1, the values for both indices
 360 tended to be less heterogeneous after 6 to 7 years of CA. This trend appeared to be reversed after 9 and
 361 10 years in CA, before decreasing again after 12 years in CA.

362 Results of Tukey's post-hoc pairwise comparisons on F β_{total} obtained with the other trait combinations
 363 (dispersion, life cycle and resource use) showed similar but less pronounced results to those obtained
 364 with all traits. The values from age group 15 were significantly less heterogeneous for F β_{total} than for

365 age group 1 for traits related to dispersion and resource use, as well as the values from age group 20
366 for resources use traits (Figure S4).

367

368 4 Discussion

369 The results focused only on weed species able to maintain and/or to produce propagules in the field.
370 The hypothesis is that those weed species better explain the effects of cultural practices on the changes
371 in the community than casual species. With this selection of species and on the basis of three weed
372 surveys, CA winter wheat fields showed rich plant communities. The number of species (mean of 23.9
373 species) was higher than usually recorded in conventional or no-till fields. To compare, Alarcón et al.
374 (2018) found less than 14 species in cereal crops in minimum or no-till systems, Armengot et al.
375 (2016) recorded a species richness comprised between 2 and 15 species according to the country and
376 the system (conventional or reduced tillage), and Hernandez Plaza et al. (2011) a species richness
377 comprised between 6 and 9 species. The high number of species we found may be the result of the
378 three weeds surveys conducted. By covering a larger period than is usually carried out in other studies
379 and thus covering more temporal niches, we highlighted a higher level of species richness. However,
380 the number of species remained higher to those found by Trichard et al. (2013) with a similar number
381 of weed surveys in no-till fields (mean species richness of 19 species). The species diversity values
382 obtained with the Shannon (mean of 2.15) and Simpson (mean of 8.54) indices were also outside the
383 range of values usually reported for weed communities, thus describing the weed communities found
384 on the CA fields as very diverse communities. Usually, the Shannon index is <2 (Hernandez Plaza et
385 al. 2011; Légère et al. 2005; Smith and Gross, 2007). The Simpson index is less frequently used than
386 the Shannon index but Alarcón et al. (2018) reported values <6.5 .

387 With regard to all species, annual species represented only 43.6 % of the observed weed species
388 whereas conventional fields are usually composed of around 80 % of annual species (Jauzein, 1995).
389 This result indicated that CA allows favourable conditions for both annual and perennial species and
390 could explain the higher overall diversity and the presence of woody or field border species (Armengot

391 et al. 2016; Trichard et al. 2013; Zanin et al. 1997). Although we did not investigate the same fields in
392 a time series but different fields of different CA ages at the same time, some species were common to
393 all fields, as *Taraxacum officinale*, a perennial species. This species has also been considered as one
394 on the most common weed species in no-till system by Trichard et al. (2013). *T. officinale* has the
395 ability to disperse over long distances due to its wind-disseminated seeds (Benvenuti, 2007). This seed
396 dispersal mechanism makes this weed species a rapid colonizer, which could explain its presence at
397 low density in 84 % of the CA fields. Since anemochory is a characteristic of Asteraceae family, this
398 could also explain the important presence of Asteraceae weeds in CA (Fried et al. 2012; Young and
399 Thorne, 2004; Zanin et al. 1997). Poaceae weeds are also well represented in CA fields (32.1 % of
400 weeds plants), through one of the most common species (*Alopecurus myosuroides*) or through the
401 most abundant species (*Digitaria sanguinalis*, *Setaria pumila*). As found in the literature (Debaeke
402 and Orlando, 1991; Murphy et al. 2006; Trichard et al. 2013), Poaceae weeds are favored by the
403 reduction of soil tillage. If *A. myosuroides* is generally affiliated to winter-sown crops (Fried et al.
404 2008), *D. sanguinalis* and *S. pumila* are two summer weed species. Their presence in high densities
405 could result from a development during the intercropping period, as well as for *Chenopodium album*.
406 Although competition is increased during the intercropping period by the use of cover crops, more
407 than half of CA French farmers use herbicides (mainly glyphosate) to simultaneously destroy the
408 cover crop and the weeds (Derrouch et al. 2020b), so short time before the sowing of the next crop.
409 Thus, after the harvest of the crop, some summer weeds species can take advantage of the absence of
410 chemical or mechanical disturbance to develop.

411 In our study, evenness values described most of weed communities as equitably composed and
412 suggested no evidence of truly dominant species. Pielou's evenness ratio was quite variable from a
413 community to another (values ranged from 0.16 to 0.99) but its mean value (0.7) was quite close to
414 those found by Hernandez Plaza et al. (2011) for no-till or minimum tillage systems (around 0.62) and
415 for conventional systems (0.64). Weed communities were equitably composed of many low-density
416 species (91.7 % of the species with a mean abundance less than 1 plant m⁻²). This result is consistent
417 with the value of abundance of weed plants (< 3 plants m⁻²) observed in no-till fields with a similar

418 number of weed surveys by Trichard et al. (2013). However, globally, the mean of total abundance
419 nonetheless reached 21 plants m⁻² able to maintain and/or to produce propagules over the entire crop
420 period. These communities with a high number of plants m⁻², although distributed throughout the
421 entire crop period, can become complex for farmers to manage. Such communities may theoretically
422 represent an advantage in terms of competition between crops and weeds compared to weed
423 communities dominated by just a few species, which are more likely to have weeds that share similar
424 trait combinations with the crop (Adeux et al. 2019).

425 4.1 Variation of α -diversity over time in conservation agriculture

426 Our results showed a moderate increase of species' richness (approximately one species per year) over
427 time since conversion to CA. This result is consistent with results found in some studies focused on
428 soil tillage reduction (Dorado and López-Fando, 2006; Mulugeta et al. 2001; Teresa Mas and Verdú,
429 2003) and on the crop diversification (Mahaut et al. 2019; Satorre et al. 2020). By adopting CA,
430 farmers modified both the intensity and the diversity of filters that may impact the weed communities.
431 These filter changes appeared favourable for new species to establish. The observed establishment of
432 species could result either from seed and vegetative propagule dispersal or from unintentional human
433 mechanical dispersal such as crop harvests or seed exchanges between farmers (Benvenuti, 2007).

434 As few functional redundancies were found between species using all traits or only combinations of
435 these traits, functional diversity also increased along the CA age gradient. The establishment of
436 species with new combinations of biological traits may progressively lead to a change in the functional
437 composition of the community over time as observed in no-till systems by Trichard et al. (2013), but
438 spotlights the necessity to study farming systems over a longer period. Functional redundancy was
439 lower for the combination of plant life-form traits but this observation could result from the few
440 numbers of attributes for both Raunkiaer's life-form (four attributes) and the number of cotyledons
441 (two attributes), leading to fewer possible combinations than for other trait combinations.

442 We expected an increase of species diversity over time due to the reduction of soil tillage (Dorado and
443 López-Fando, 2006; Murphy et al. 2006; Santín-Montanyá et al. 2013; Teresa Mas and Verdú, 2003;

444 Travlos et al. 2018) and due to the diversification of crop successions (Mahaut et al. 2019) but no
445 change in species diversity for both Shannon and Simpson indices was observed over time. In fact,
446 although the number of species increased over time, species evenness did not vary, leading to the
447 absence of change in both the Shannon and Simpson indices. These results are consistent with others
448 studies that compared different systems and found no (Alarcón et al. 2018; Hernandez Plaza et al.
449 2011) or few differences (Légère et al. 2005) in community diversity. The increased use of herbicide
450 applications with the adoption of CA (only during to intercropping period application) by French CA
451 farmers (Derrouch et al. 2020a) could also have masked the effects of abandonment of tillage, and thus
452 the possible changes on weed diversity, as observed by Derksen et al. (1995).

453 Although the separate application of the different CA principles generally lead to antagonistic effects
454 on species abundance, their simultaneous application tended to increase the total abundance of weeds
455 over the CA duration. The reduction of soil tillage is generally linked to an increase of species
456 abundance (Santín-Montanyá et al. 2013; Travlos et al. 2018), although this result may be dependent
457 on certain species (*i.e.* only the perennials species according to Armengot et al. (2016)). The crop
458 diversification generally reduces the abundance of weeds by increasing the time required for weeds to
459 meet their optimal development conditions (Mahaut et al. 2019; Weisberger et al. 2019). The presence
460 of a cover crop can, during the intercropping period, reduce the abundance of weed species (Baraibar
461 et al. 2018; Buchanan et al. 2016; Fisk et al. 2001; MacLaren et al. 2019) through competition
462 (Lawley et al. 2012) or by modifying the conditions of germination and emergence of weeds (Buhler
463 et al. 1996; Teasdale and Mohler, 1993). Our results showed that when applied simultaneously, the
464 effect of the abandonment of tillage on weed abundance outweighed the effect of the two other
465 principles (residue cover and crop rotation).

466

467 4.2 Variation of β -diversity since conversion to conservation agriculture

468 Our results showed that the winter wheat weed communities converged over time, both taxonomically
469 and functionally. The dispersion (and probably the mean value) within age groups of $T\beta_{total}$ and $F\beta_{total}$

470 (with all traits) decreased over time and weed communities after 20 years in CA were more similar and
471 less heterogeneous than those in first years of CA.

472 The decrease of heterogeneity between values within age groups observed for both $T\beta_{total}$ and $F\beta_{total}$
473 (with all traits) showed that the CA cultural practices (as filtering process) tend, in the long-term, to
474 act on weed communities in a similar way in all fields. Because CA brought together farmers with
475 different systems prior to adoption (tillage, reduced tillage and no-till) and therefore with different
476 weed communities, we took as reference a high degree of heterogeneity in weed communities for the
477 new farmers in CA. When adopting CA, farmers reduce the range of usable cultural practices and
478 weed management practices (Derrouch et al. 2020a), and the related filtering pressures. Thus, over the
479 CA duration, the high degree of heterogeneity found in the first year of CA decreased, meaning that
480 species that established in fields over time were similar through the different fields, although the local
481 species pool may be different. The establishment of similar species in CA fields induced a functional
482 convergence over time.

483 Changes in β -diversity revealed a process of filtering that is not only relevant to CA but concern all
484 continuous applications of farming systems (Murphy and Lemerle, 2006). In CA fields, the vertical
485 seed movement on the soil due to the abandonment of tillage is reduced, although some soil
486 organisms, such as earthworms, can bring to the soil surface a significant amount of buried seeds
487 (Forey et al. 2011; Smith et al. 2005b). Only the seeds presented near the soil surface are able to
488 germinate (Baskin and Baskin, 1985; Benech-Arnold et al. 2000). For the most part, these seeds were
489 produced during the previous harvest or came from neighbouring plots (species easily dispersed over
490 long distances). This reduction of vertical seed movement near the soil could have accelerated the
491 convergence of weed communities over time in CA, compared to a conventional system (Fried et al.
492 2016). Despite this observed β -diversity decreasing trend after 20 years of CA, it is important to note
493 that β -diversity values were still quite high, meaning that weed communities were still significantly
494 different from one another. Lower values of $F\beta_{total}$ (with all traits) relative to $T\beta_{total}$ showed less
495 functional differences between communities, although each species had its own combination of
496 biological traits. Partitioning β -diversity into replacement and richness difference showed that both

497 fractions were important components of β -diversity, with a more significant replacement effect, as also
498 found by Fried et al. (2016).

499 The use of different trait combinations for estimating functional β -diversity demonstrated that the
500 functional convergence observed using all traits did not occur for all trait combinations. The functional
501 convergence over time in CA was observed for traits referring to spatial or temporal dispersion (seed
502 mass, seed dispersal and soil seedbank longevity), plant life cycle (time of germination and time of
503 flowering), and resource use traits (specific leaf area leaf dry matter content and Ellenberg light).
504 However, the estimation of functional β -diversity using only traits referring to plant life-form
505 (Raunkiaer's life-form and number of cotyledons) did not show a functional convergence over time in
506 CA. The tendency towards the addition of perennial and graminoid species to annual eudicotyledons
507 observed for CA systems (Trichard et al. 2013; Young and Thorne, 2004) and for systems with
508 minimum tillage (Debaeke and Orlando, 1991; Murphy et al. 2006) did not concern all CA fields. The
509 persistence of annual species could be explained by disturbances related to the seeding and harvesting
510 periods. As herbicide application represents a main part of the weed management in CA for French
511 farmers (Derrouch et al. 2020a), some differences between the use of herbicides (date of application,
512 spectrum, dose) could explain the absence of convergence for the traits related to plant life-form, and
513 more particularly for the number of cotyledons which represent an important indication of the use of
514 herbicides by farmers.

515

516 4.3 Non-immediate convergence in the assembly of communities between fields

517 As shown by our results, heterogeneity within age groups did not decrease during the first years and
518 tended to decrease only after six years before being significantly less heterogeneous after eight years
519 for $T\beta_{\text{total}}$.

520 Whereas abandoning tillage represents an immediate change in the farming system and thus rapidly
521 modifies the filtering pressure on weeds (Clements et al. 1996), a buffer effect of the seedbank
522 produced during the previous farming systems may persist. In CA, because of the soil seedbank is

523 mainly located near the soil surface, a larger proportion of the seeds are subject to germination
524 (Benech-Arnold et al. 2000; Benvenuti et al. 2001) or to abiotic deterioration and predation (Petit et al.
525 2017) than when buried. The soil seedbank is therefore expected to decline more rapidly. The time
526 required for this decline in the soil seedbank is therefore dependent on species seed longevity in the
527 soil seedbank. According Murphy et al. (2006), soil seedbank declined after six years in no-till
528 systems from 41 000 to 8 000 seeds m⁻³, which corresponds to the number of years before
529 heterogeneity within age groups started to decrease in our results. However, this soil seedbank decline
530 is possible in no-till systems only if the emerged weeds are well managed (Légère et al. 2011).

531 As CA represents a new farming system in France, this five-year period after adoption could also
532 represent a period during which each farmer tests his or her own system to acquire experience and
533 knowledge before stabilizing it. According to French farmers, approximately five years are necessary
534 before mastering the weed management in CA (Derrouch et al. 2020a). When reaching a mastered
535 weed management, the farmers delay applying herbicides (shift from pre to post emergence
536 application) and rely more on management practices related to the crop diversification such as
537 alternating sowing periods and crop rotation optimization (Derrouch et al. 2020a). This timeframe
538 could also explain the absence of difference in heterogeneity between weed communities during the
539 first years in CA. After nine and ten years, this decreasing trend could result from different
540 adjustments of weed management according to farmers. As CA fields remain a source of human food
541 production, farmers have continuously to deal with these changes in weed communities and to adapt
542 their management.

543

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552

553 Declaration of Competing Interest

554 The authors reported no potential conflict of interest.

555

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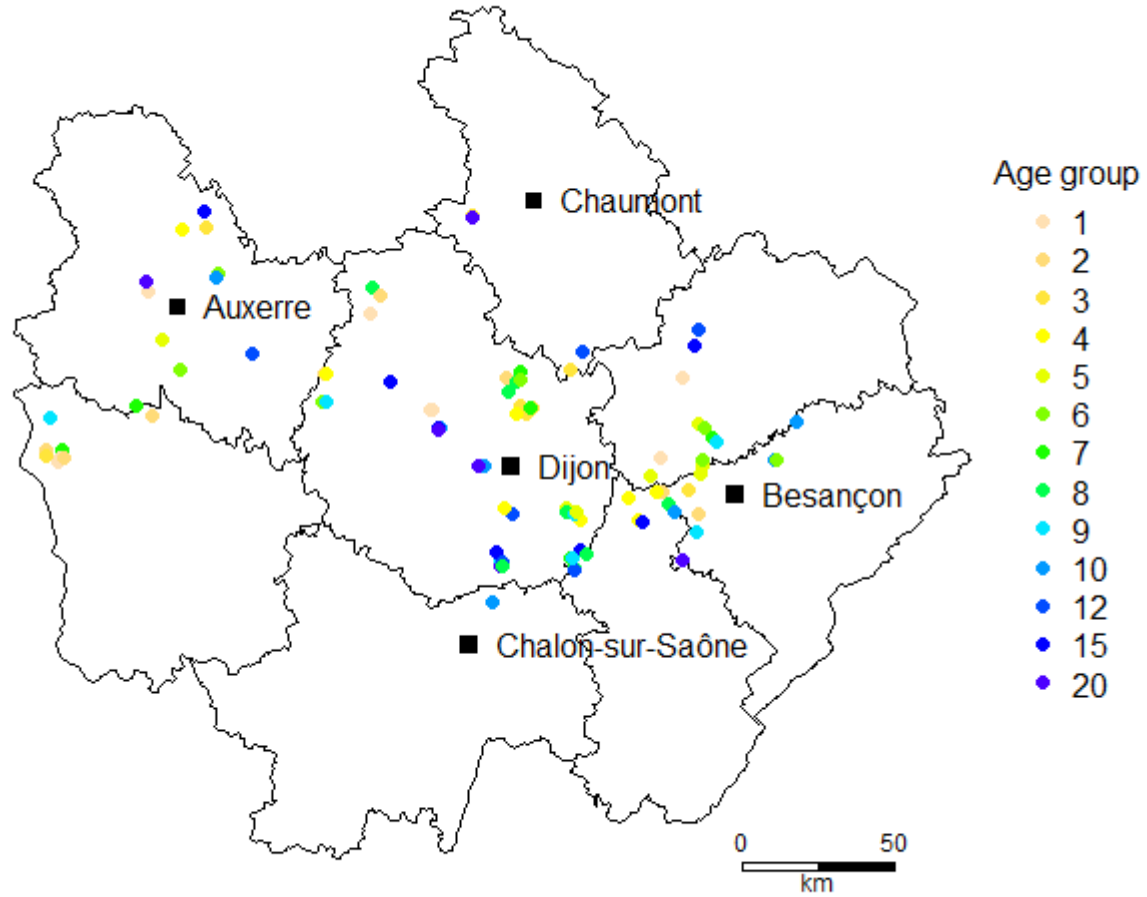
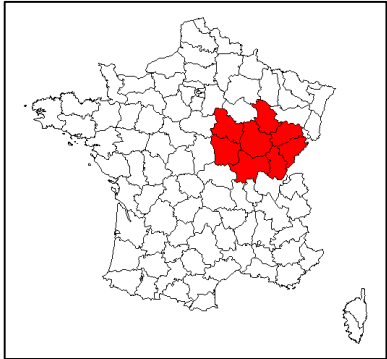
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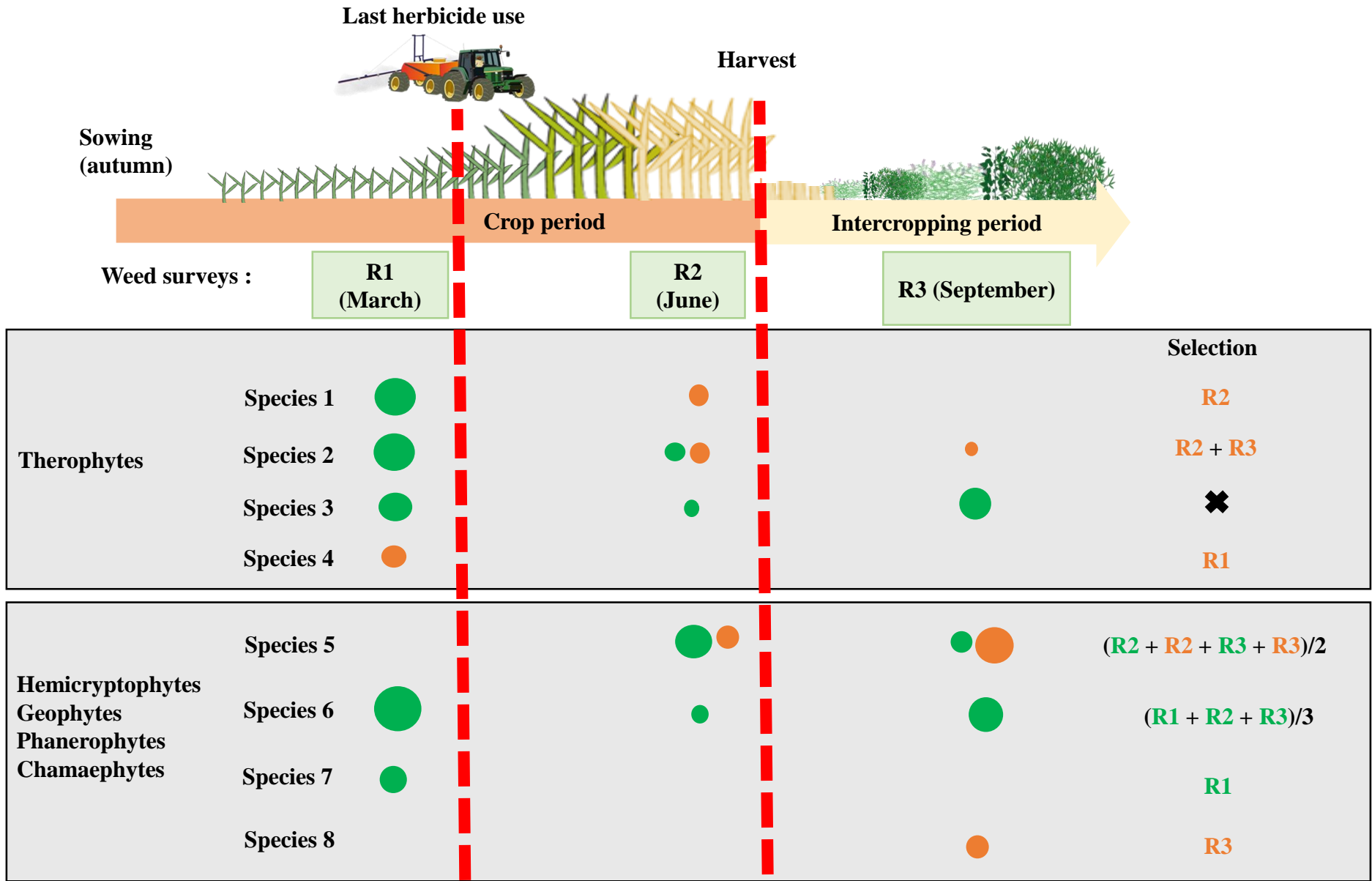
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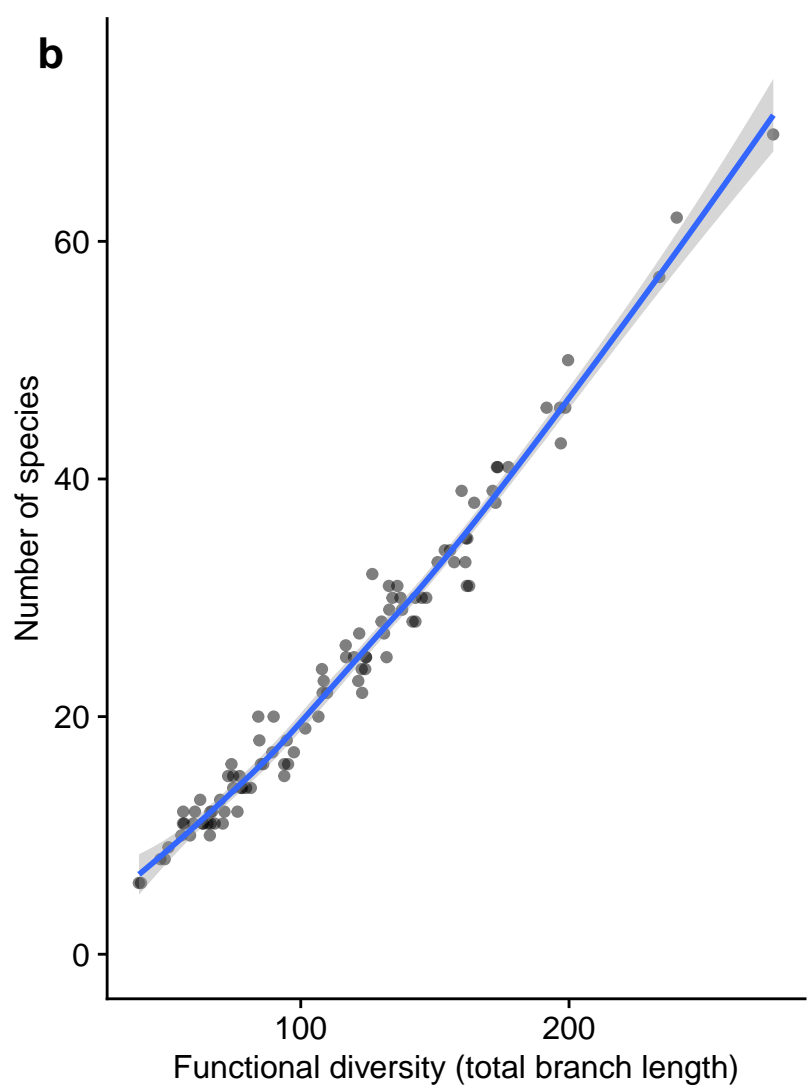
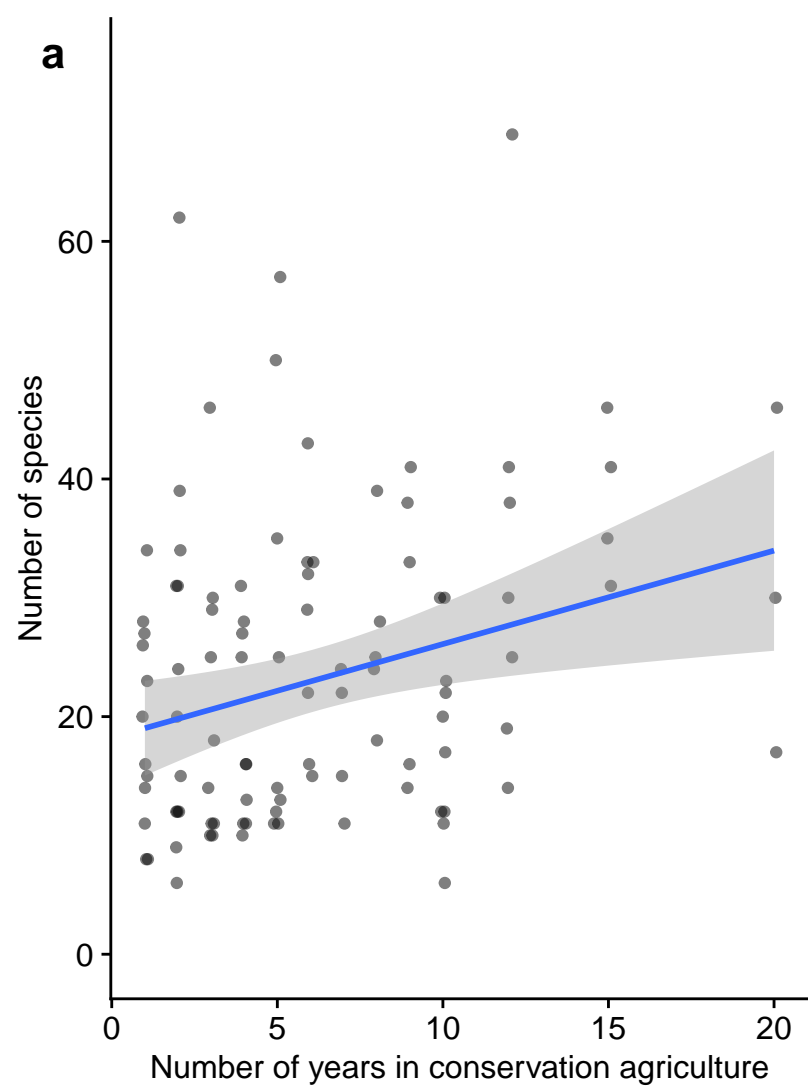
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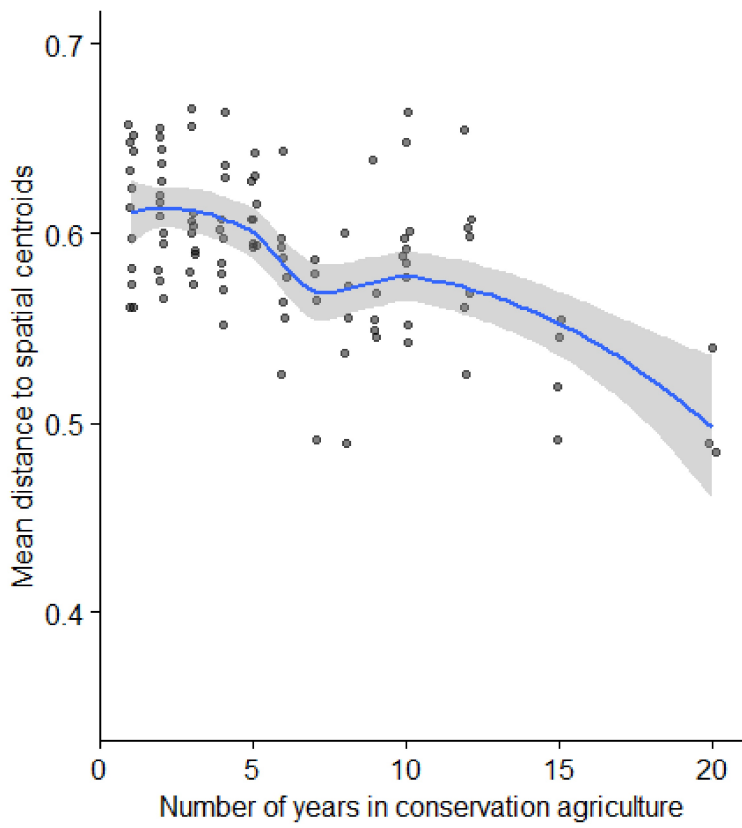


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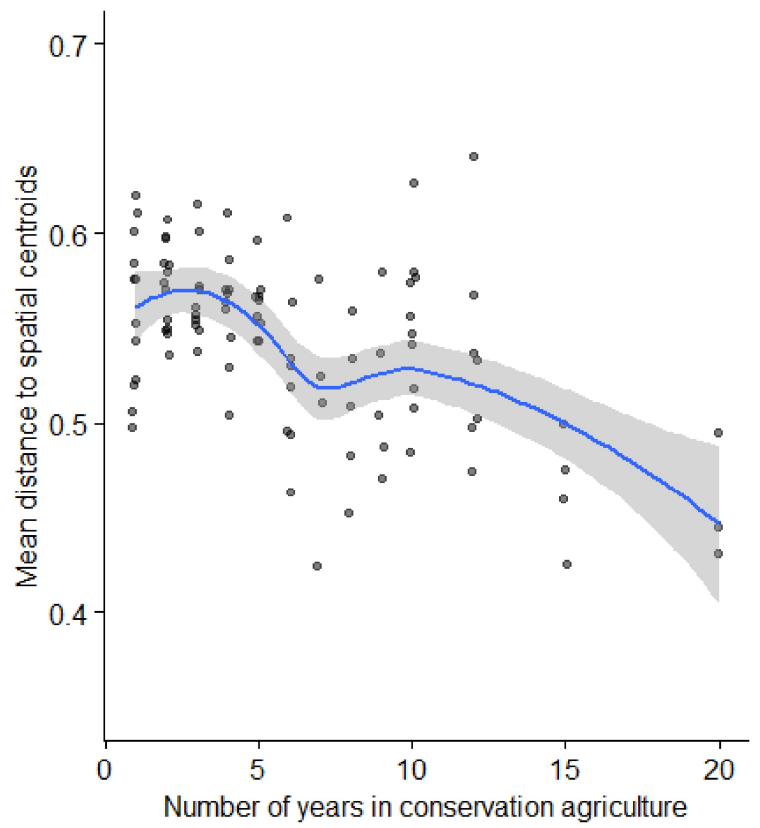
- Seedling or vegetative stage
- Flowering or fructification



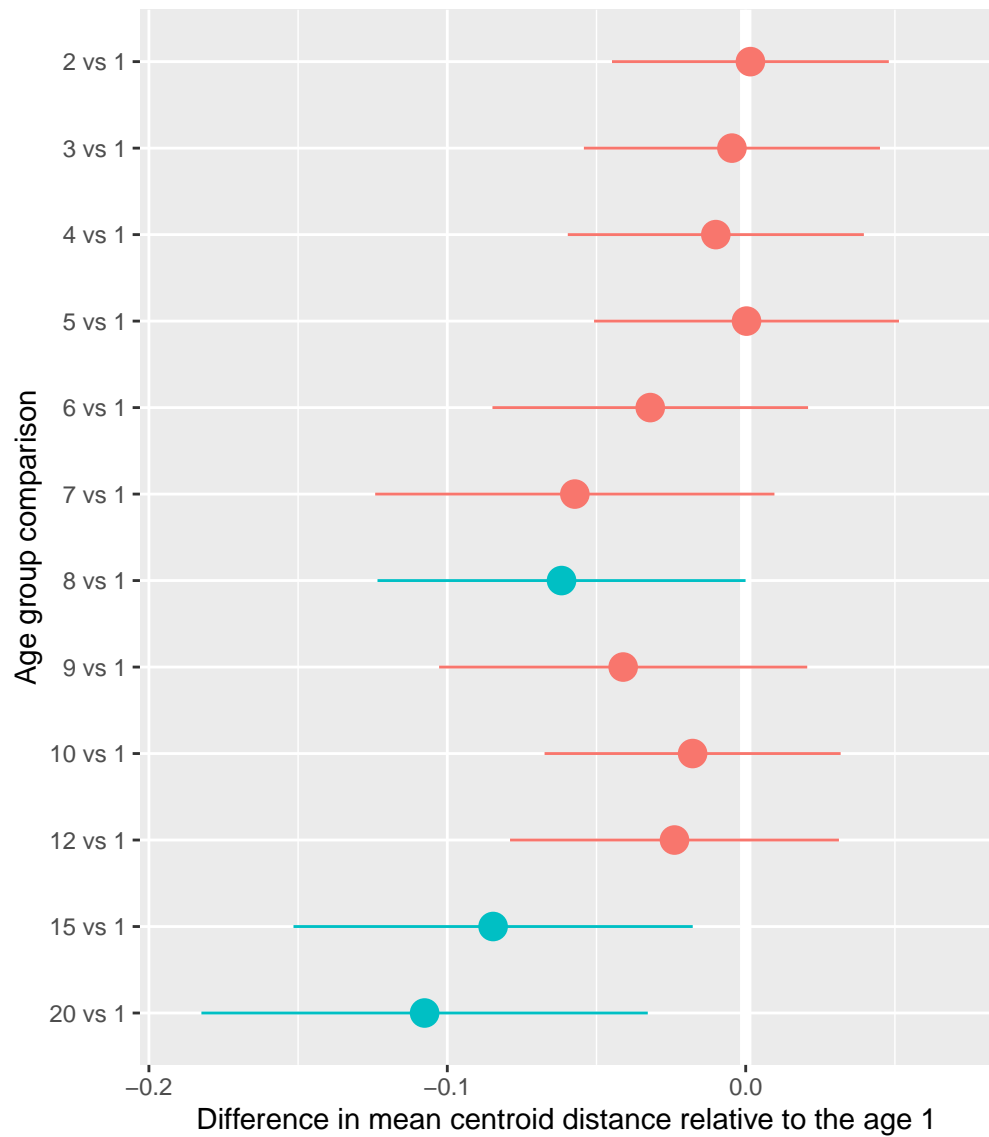
Tβtotal



Fβtotal (all traits)



Tβtotal



Fβtotal (all traits)

