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Weed community diversity in conservation agriculture: post-adoption changes

Damien Derrouch[a], Fabrice Dessaint[a], Guillaume Fried[b], Bruno Chauvel[a]

[a]Agroécologie, AgroSup Dijon, INRAE, Univ. Bourgogne, Univ. Bourgogne Franche-Comté, F-21000 Dijon, France

[b]Unité Entomologie et Plantes Invasives, Laboratoire de la Santé des Végétaux, Anses, 34988 Montferrier-sur-Lez, France

Corresponding author: Damien Derrouch

Email address: damien.derrouch@inrae.fr

Present address: INRAE, UMR Agroécologie, 17 rue Sully, BP 86510, 21065 Dijon, France

Abstract

Conservation agriculture has been identified as one of the farming systems likely to deliver sustainable agriculture but its effects over time on the diversity and composition of weed communities are poorly documented. Using a network of 100 winter wheat fields selected to encompass a gradient of years in conservation agriculture from 1 to 20 years in the Bourgogne-Franche-Comté region (France), we analysed the changes that occurred in the diversity of weed communities over several years, both in α- and β-diversity using a taxonomic (species level) and functional (10 response traits) approach. Based on three weed surveys (before the last herbicide use, before harvest, before sowing the following crop), we identified weeds able to maintain and/or to produce propagules. All the observed weed communities were rich (average species richness of 23.9 species), diverse (average Shannon diversity of 2.15) and equitably composed of low-density species. The results showed an increase in species richness, total weed abundance and α-functional diversity but no change in species diversity and species evenness over time. Heterogeneity and average values of β-taxonomic and β-functional diversity between communities were high in the early years following the adoption of conservation agriculture. Heterogeneity and average β-taxonomic and β-functional diversity decreased over time, leading to a homogenization of weed community assemblages. Despite major changes in cultural practices related to conservation agriculture, homogenization of weed community was not immediate and did not concern all the traits studied.

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

1 Introduction

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

To improve the understanding of the effects of cultural practices on weed communities, Booth and Swanton (2002) proposed applying assembly theory to weed communities. By describing weed species by their biological traits, it is possible to identify general rules that drive weed community assembly. In this framework, each management practice is likely to act as a filter on weed communities by removing, limiting or favouring species depending on their trait combination values. As observed in other situations such as the transition to organic farming (Delate and Cambardella, 2004), each change in cultural practices is likely to modify the strength and mesh size of the filters and thus, the combination of selected trait values. For example, in arable crops, soil tillage is widely known as the main factor explaining the high percentage of annual species in the community. By frequently disturbing the soil surface, soil tillage filters mainly plants able to survive unfavourable perturbations in the form of seeds or, to a lesser extent, in the form of underground organs capable of vegetative propagation (e.g. rhizomes). Weed seeds buried by soil tillage remain dormant before being brought back to the soil surface by the following soil tillage. Due to the absence of soil disturbance when adopting CA, seeds remain concentrated on the soil surface and annual species are partly replaced by perennials as during plant succession (Bazzaz, 1979; Zanin et al. 1997). The presence of residues on the soil surface in CA systems modifies the conditions for germination and the emergence of weed seeds by reducing light availability and affecting the soil's characteristics (humidity, pH and temperature) (Holland, 2004). When the cover crop is alive, other processes such as competition for nutrients and allelopathy can affect germination and the emergence of some weed species (Teasdale, 1996). The diversification of crop succession with the adoption of CA modifies all the disturbances and stress events that shape communities, thus limiting the development of weed populations with phenological and physiological similarities to the crop as observed in simple crop sequences (Cardina et al. 1998).

Most of the studies describing the response of weed communities to CA focused on the response of weed species to one or two of the CA principles, with opposing results sometimes occurring between studies. In most cases, the reduction of tillage and crop diversification seemed to increase weed diversity. The effects on weed abundance seemed different for each of these two CA principles: the reduction of tillage tends to increase weed abundance while crop diversification tends to decrease it. (Mahaut et al. 2019; Travlos et al. 2018; Weisberger et al. 2019). The use of cover crops decreased weed abundance (Buchanan et al. 2016) and potentially the weed richness when the cover crop biomass is high (Smith et al. 2015a). Concerning changes identified in weed community composition when adopting one or the other of the CA principles, the results vary according to the system, although a strong tendency towards the filtering for perennial (no disturbance of perennial weed organs), wind disseminated and graminoid species was highlighted in CA systems (Trichard et al. 2013; Young and Thorne, 2004). To date, no study examined whether the adoption of CA on the long-term leads to a homogenisation of weed communities or, on the contrary, to an increase of dissimilarity between communities. Changes in dissimilarity between communities (β-diversity) in the literature are accessed through two main approaches (Brice et al. 2017; Fried et al. 2016; Rooney et al. 2004). The first approach is mainly used when comparing communities over time. In this case, an homogenization or a convergence of weed communities refers to the process by which β-diversity between communities decreases over time (Olden and Rooney, 2006). The second approach is mainly used to compare different communities in different groups along an ecological gradient. In this case, homogenization refers to a decrease of β-diversity between communities belonging to the same group, *i.e.* in similar ecological conditions (Brice et al. 2017).

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

2 Materials and methods

2.1 Study site

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

2.2 Weed data collection and selection

For each field, weed communities were surveyed either in 2018 (51 fields) or in 2019 (49 fields) on a 50x40 m area, which was representative of the weeds present in the whole field according to the farmers. The area was located 50 m away from field boundaries to avoid field edge effects. Weed data were collected at three periods: in early March (before the last post-herbicide use), in mid-June (before harvest, *i.e.* a period of potential weed seed production) and in early September during the intercropping period (before sowing of the following crop). The sampling protocol was similar for all periods. All species were recorded within the 2,000 m^2 surveyed area and following a W-shaped walked path (two persons, 30-40 min for each survey). For each period, seven to eight days were required to collect all the data. Most plants were identified at species level according to Jauzein (1995). Taxonomy was corrected according to the TAXREF Taxonomic repository v13.0 (Gargominy et al. 2019). For some vegetative plants, plants were noted at the genus level (e.g. *Lolium* sp.) due to a lack of relevant distinguishing criteria at the seedling and/or vegetative stages. The abundance of each weed species was estimated using a modified Barralis scale of abundance (Barralis, 1976): [+] found once in the 2,000 m^2 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 60 individuals m^{-2}. For each period, the percentage of each stage of development (seedling, vegetative, flowering, fructification) was also estimated for each species. Only plants that were not intentionally sown by farmers in the given year or the preceding year were considered. Plants used for cover crop in the given year but also volunteers from the preceding year were excluded.

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

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

2.3 Trait data

Ten response traits (Table 1) were selected based on a reference list of functional traits for arable weeds (Booth and Swanton, 2002; Gaba et al. 2014, Gaba et al. 2017) and on articles related to CA or no-till systems (Armengot et al. 2016; Trichard et al. 2013). Traits were selected for their key role in the weed dynamic. Raunkiaer’s life-form (Raunkiær et al. 1934) and the number of cotyledons (graminoids, eudicotyledons) referred to plant life-form. The Raunkiær’s life form was used to capture the potential effect of an absence of mechanical soil disturbance on weed communities. The trait "number of cotyledons" was chosen due to the important effect of herbicide application on the proportion of monocotyledons or eudicotyledons in the weed community. Because farmers can specifically target graminoids and/ or eudicotyledons weeds through herbicide application, this trait can refer to some possible changes in weed management with CA duration. Time of germination (season) and time of flowering (season) gave indications on weed life cycle and thus could capture the effects of CA on temporal niches, but also a possible change in weed management. Soil seedbank longevity (years), mode of seed dispersal (four classes) and seed mass (mg) referred to either temporal or spatial weed seed dispersion. In CA, vertical seed movements in the soil due to the abandonment of tillage are reduced which could therefore induce changes regarding the values of these three traits that will be favoured under this system. Specific leaf area (mm².mg^{-1}), leaf dry matter content (mg.g^{-1}) and Ellenberg's indicator value for light (five classes) represented weed resource use (see Table 1 for source, and Table S2 for attributes and more information about data selection from databases). For weed species identified at genus level, trait values were from the most common species from the same genus in the initial database. For trees and shrubs, traits values were based on the most common species in the region (Bardet et al. 2008). Finally, to enable analysis, missing values (see Table S2 for the number of missing values per trait) were completed with expert opinion, taking into account the closest attributed values.

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)

2.4 Data analysis

2.4.1 α-diversity

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

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

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

2.4.2 β-diversity

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

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

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

3 Results

3.1 Weed species

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

3.2 α-diversity

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

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

Table 2: Values of slopes of robust linear regression model based on all 100 fields with ages of CA as 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**

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

3.3 β-diversity

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

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

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

Table 3: Values of permutational non-parametric multivariate analysis of variance (PERMANOVA) and analysis of multivariate homogeneity of group dispersions (PERMDISP) with ages of CA as explanatory variable and the β-diversity as response variable. Functional β-diversity indices present in 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
$T\beta_{total}$							0.075	0.0063	5.42	**<0.001**
$T\beta_{repl}$	12	1.84	0.153	1.13	0.135	0.334	0.124	0.0104	0.44	0.942
$T\beta_{rich}$	12	1.22	0.101	1.37	0.159	0.155	0.233	0.0195	1.26	0.257
$F\beta_{total}$							0.091	0.0076	5.50	**<0.001**
$F\beta_{repl}$	12	1.24	0.104	1.13	0.135	0.345	0.096	0.0080	0.39	0.963
$F\beta_{rich}$	12	1.16	0.097	1.62	0.183	0.072	0.299	0.0249	1.74	0.073

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

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

Results of Tukey's post-hoc pairwise comparisons on $F\beta_{total}$ obtained with the other trait combinations (dispersion, life cycle and resource use) showed similar but less pronounced results to those obtained with all traits. The values from age group 15 were significantly less heterogeneous for $F\beta_{total}$ than for age group 1 for traits related to dispersion and resource use, as well as the values from age group 20 for resources use traits (Figure S4).

4 Discussion

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

With regard to all species, annual species represented only 43.6 % of the observed weed species whereas conventional fields are usually composed of around 80 % of annual species (Jauzein, 1995). This result indicated that CA allows favourable conditions for both annual and perennial species and could explain the higher overall diversity and the presence of woody or field border species (Armengot et al. 2016; Trichard et al. 2013; Zanin et al. 1997). Although we did not investigate the same fields in a time series but different fields of different CA ages at the same time, some species were common to all fields, as *Taraxacum officinale*, a perennial species. This species has also been considered as one on the most common weed species in no-till system by Trichard et al. (2013). *T. officinale* has the ability to disperse over long distances due to its wind-disseminated seeds (Benvenuti, 2007). This seed dispersal mechanism makes this weed species a rapid colonizer, which could explain its presence at low density in 84 % of the CA fields. Since anemochory is a characteristic of Asteraceae family, this could also explain the important presence of Asteraceae weeds in CA (Fried et al. 2012; Young and Thorne, 2004; Zanin et al. 1997). Poaceae weeds are also well represented in CA fields (32.1 % of weeds plants), through one of the most common species (*Alopecurus myosuroides*) or through the most abundant species (*Digitaria sanguinalis, Setaria pumila*). As found in the literature (Debaeke and Orlando, 1991; Murphy et al. 2006; Trichard et al. 2013), Poaceae weeds are favored by the reduction of soil tillage. If *A. myosoroides* is generally affiliated to winter-sown crops (Fried et al. 2008), *D. sanguinalis* and *S. pumila* are two summer weed species. Their presence in high densities could result from a development during the intercropping period, as well as for *Chenopodium album*. Although competition is increased during the intercropping period by the use of cover crops, more than half of CA French farmers use herbicides (mainly glyphosate) to simultaneously destroy the cover crop and the weeds (Derrouch et al. 2020b), so short time before the sowing of the next crop. Thus, after the harvest of the crop, some summer weeds species can take advantage of the absence of chemical or mechanical disturbance to develop.

In our study, evenness values described most of weed communities as equitably composed and suggested no evidence of truly dominant species. Pielou’s evenness ratio was quite variable from a community to another (values ranged from 0.16 to 0.99) but its mean value (0.7) was quite close to those found by Hernandez Plaza et al. (2011) for no-till or minimum tillage systems (around 0.62) and for conventional systems (0.64). Weed communities were equitably composed of many low-density species (91.7 % of the species with a mean abundance less than 1 plant m^{-2}). This result is consistent with the value of abundance of weed plants (< 3 plants m^{-2}) observed in no-till fields with a similar number of weed surveys by Trichard et al. (2013). However, globally, the mean of total abundance nonetheless reached 21 plants m^{-2} able to maintain and/or to produce propagules over the entire crop period. These communities with a high number of plants m^{-2}, although distributed throughout the entire crop period, can become complex for farmers to manage. Such communities may theoretically represent an advantage in terms of competition between crops and weeds compared to weed communities dominated by just a few species, which are more likely to have weeds that share similar trait combinations with the crop (Adeux et al. 2019).

4.1 Variation of α-diversity over time in conservation agriculture

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

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

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

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

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

4.2 Variation of β-diversity since conversion to conservation agriculture

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

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

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

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

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

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

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

Whereas abandoning tillage represents an immediate change in the farming system and thus rapidly modifies the filtering pressure on weeds (Clements et al. 1996), a buffer effect of the seedbank produced during the previous farming systems may persist. In CA, because of the soil seedbank is mainly located near the soil surface, a larger proportion of the seeds are subject to germination (Benech-Arnold et al. 2000; Benvenuti et al. 2001) or to abiotic deterioration and predation (Petit et al. 2017) than when buried. The soil seedbank is therefore expected to decline more rapidly. The time required for this decline in the soil seedbank is therefore dependent on species seed longevity in the soil seedbank. According Murphy et al. (2006), soil seedbank declined after six years in no-till systems from 41 000 to 8 000 seeds m^{-3}, which corresponds to the number of years before heterogeneity within age groups started to decrease in our results. However, this soil seedbank decline is possible in no-till systems only if the emerged weeds are well managed (Légère et al. 2011).

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

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Declaration of Competing Interest

The authors reported no potential conflict of interest.

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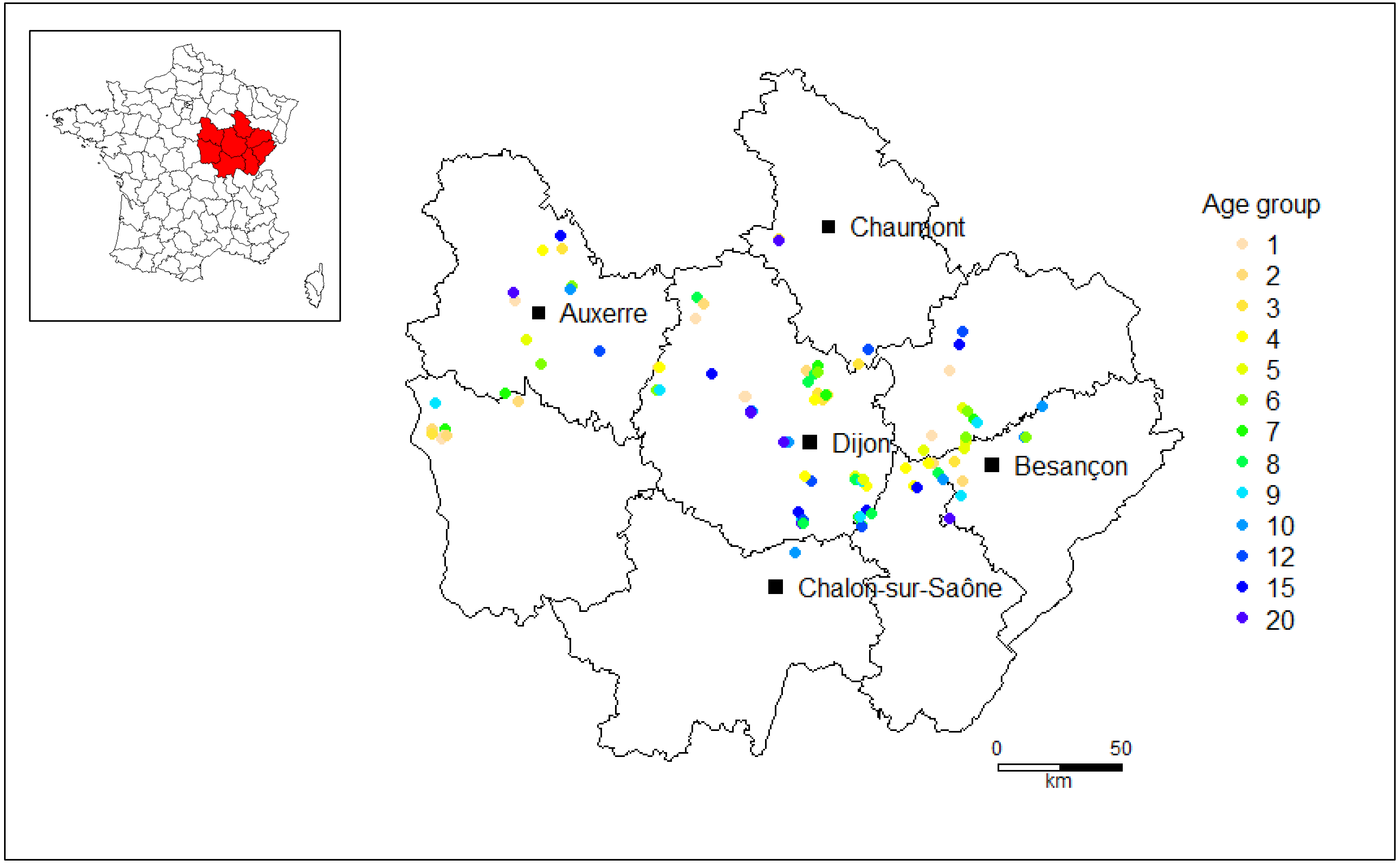
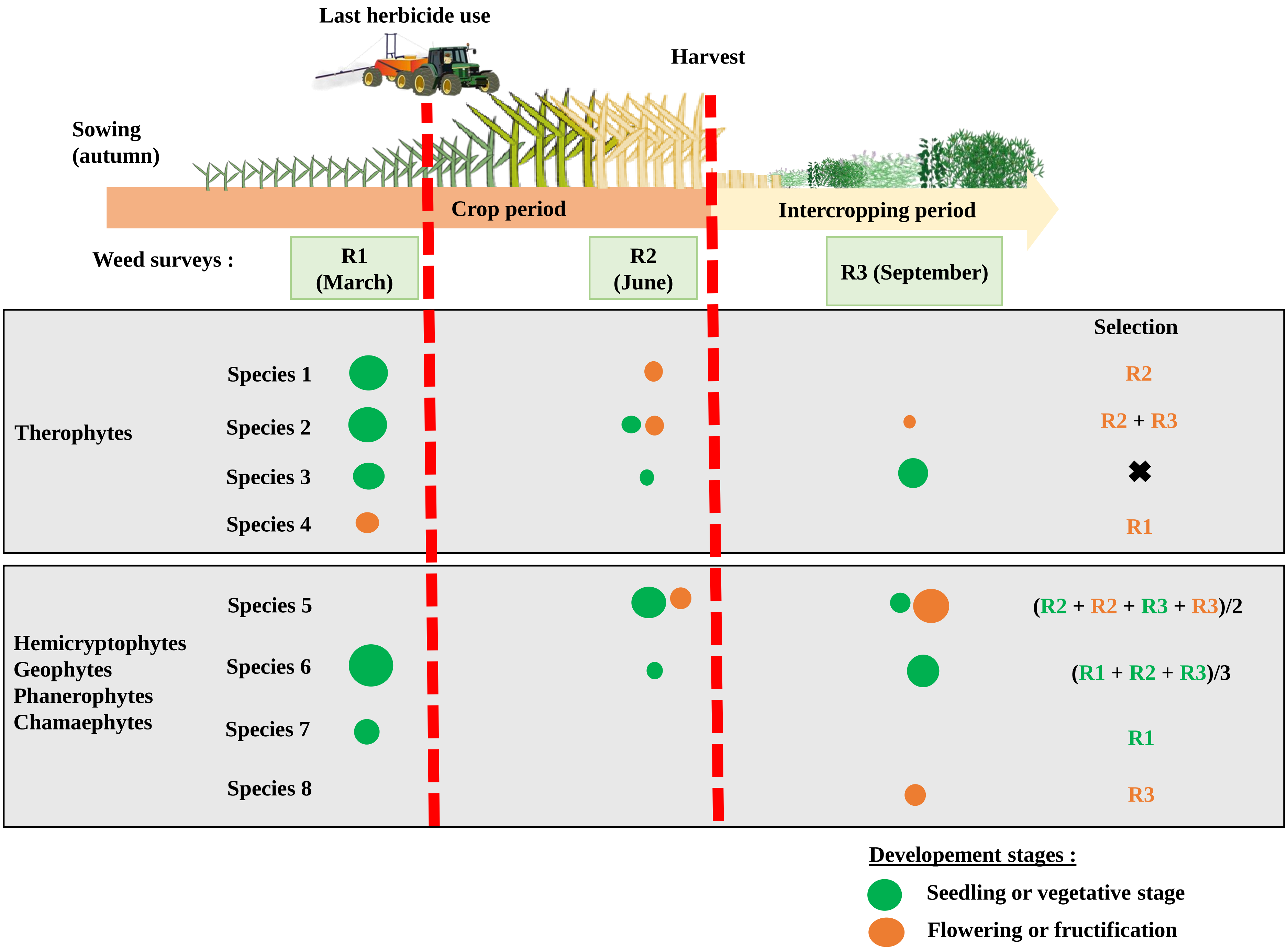
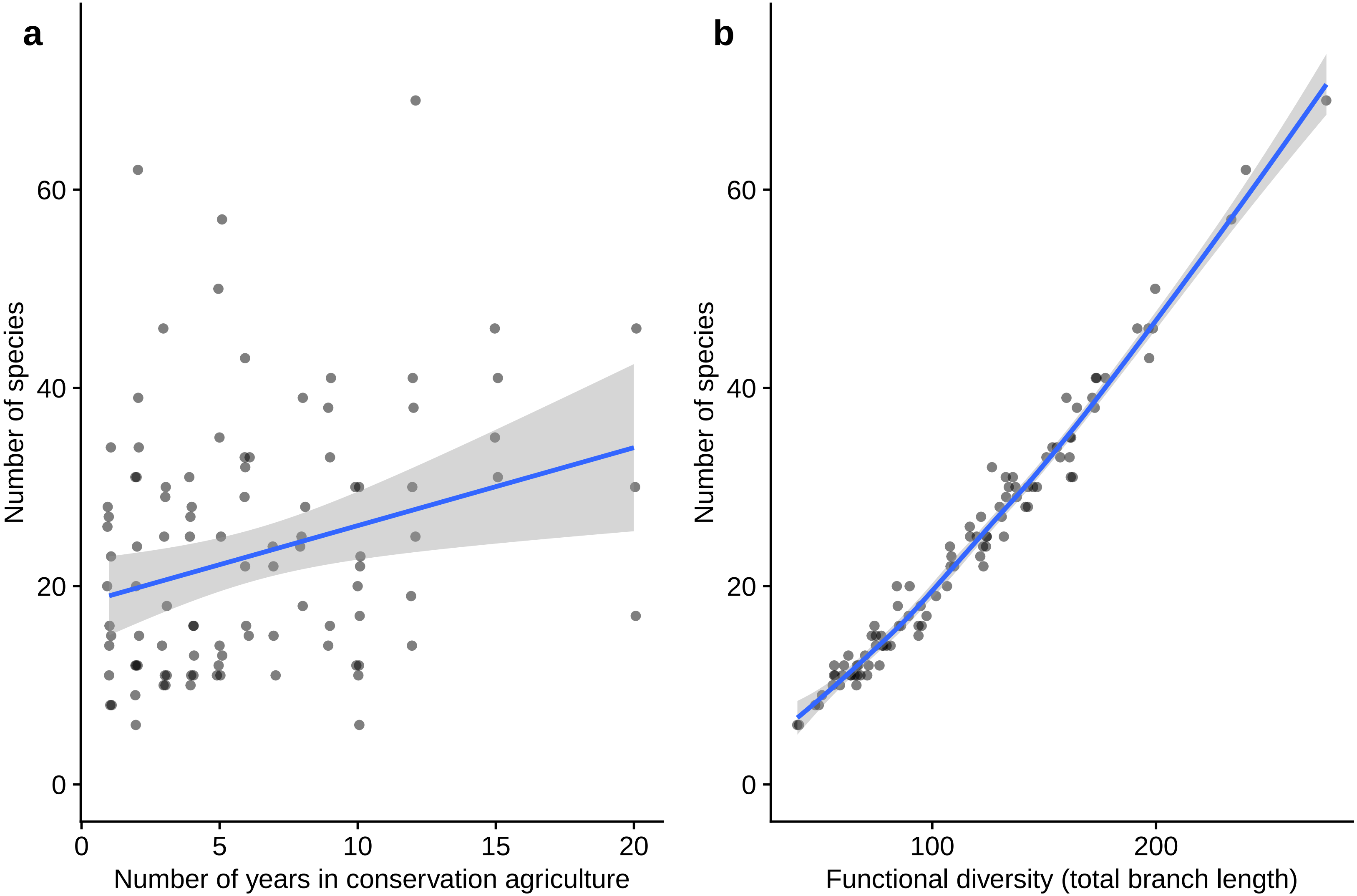
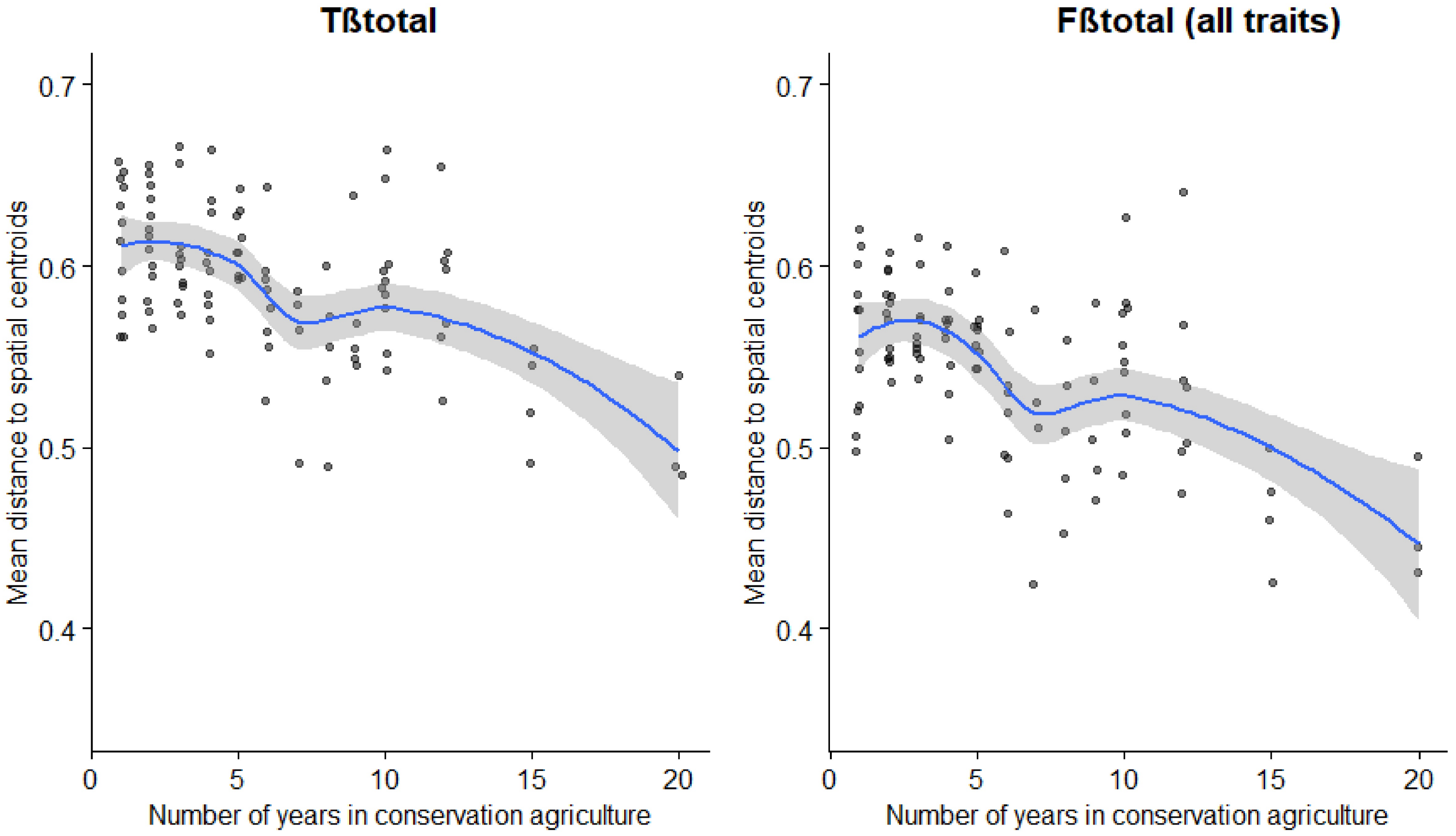
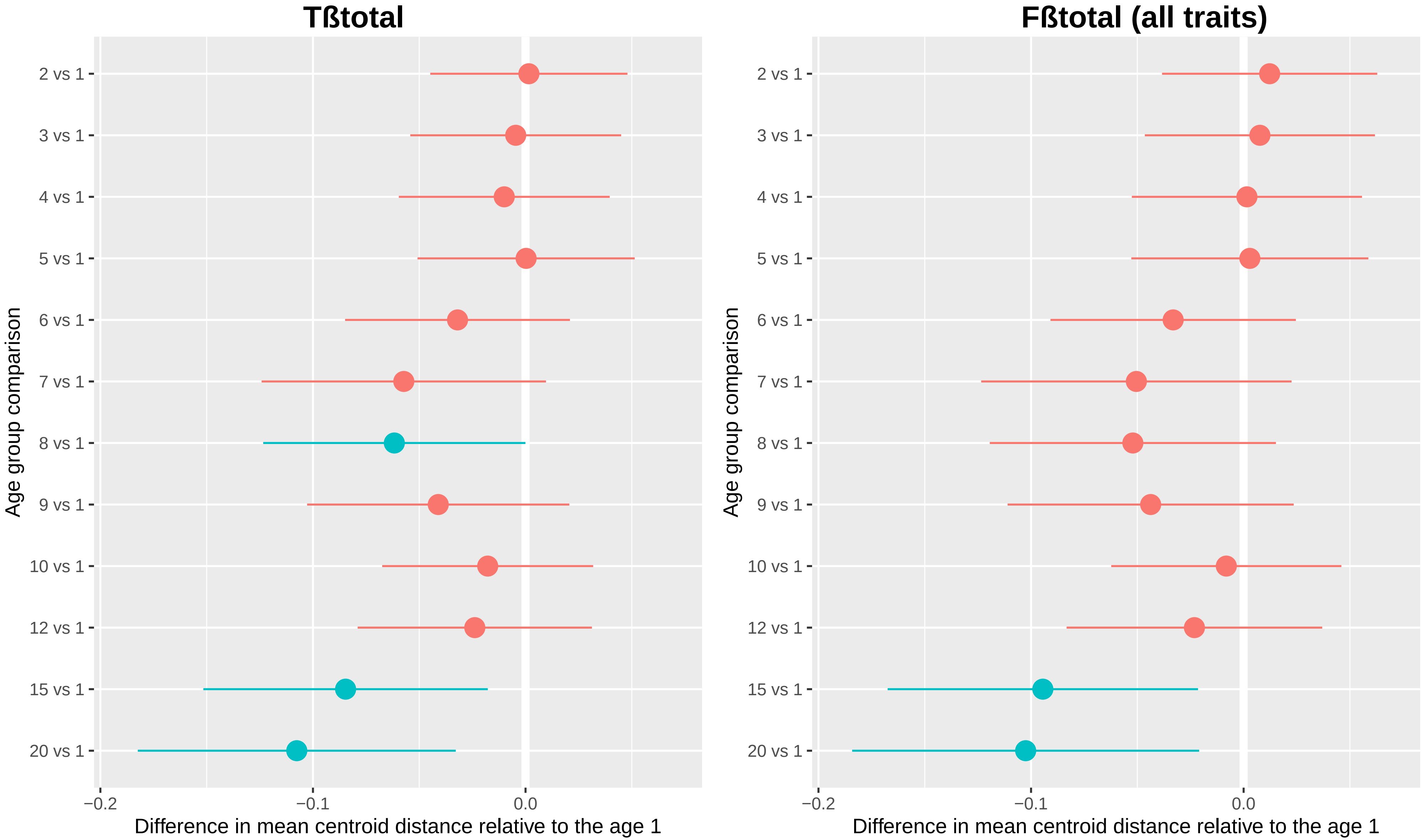

Chaumont
Auxerre
Dijon
Besançon
Chalon-sur-Saône
Age group
1
2
3
4
5
6
7
8
9
10
12
15
20
0
50
km


Last herbicide use
Harvest
Sowing (autumn)
Crop period
Intercropping period
Weed surveys :
R1 (March)
R2 (June)
R3 (September)
Selection
Therophytes
Species 1
R2
Species 2
R2 + R3
Species 3
✖
Species 4
R1
Hemicryptophytes
Geophytes
Phanerophytes
Chamaephytes
Species 5
(R2 + R2 + R3 + R3)/2
Species 6
(R1 + R2 + R3)/3
Species 7
R1
Species 8
R3
Developement stages :
Seedling or vegetative stage
Flowering or fructification


a
b
Number of species
0
20
40
60
0
5
10
15
20
Number of years in conservation agriculture
Number of species
0
20
40
60
100
200
Functional diversity (total branch length)


Tßtotal
Fßtotal (all traits)
Mean distance to spatial centroids
0.4
0.5
0.6
0.7
0
5
10
15
20
Number of years in conservation agriculture


Tßtotal
Fßtotal (all traits)
Age group comparison
2 vs 1
3 vs 1
4 vs 1
5 vs 1
6 vs 1
7 vs 1
8 vs 1
9 vs 1
10 vs 1
12 vs 1
15 vs 1
20 vs 1
−0.2
−0.1
0.0
Difference in mean centroid distance relative to the age 1