European Journal of Agronomy 133 (2022) 126438

Contents lists available at ScienceDirect

European Journal of Agronomy

journal homepage: www.elsevier.com/locate/eja

Cropping system diversification does not always beget weed diversity

Guillaume Adeux[a,1], Séverin Yvoz[a,1], Luc Biju-Duval[a], Emilie Cadet[a], Pascal Farcy[b], Guillaume Fried[c], Jean-Philippe Guillemin[a], Dominique Meunier[a], Nicolas Munier-Jolain[a], Sandrine Petit[a], Stéphane Cordeau[a,*]

[a] Agroécologie, AgroSup Dijon, INRAE, Univ. Bourgogne, Univ. Bourgogne Franche-Comté, F-21000 Dijon, France
[b] INRAE, U2E, Unité Expérimentale du Domaine d'Epoisses, F-21000 Dijon, France
[c] Unité Entomologie et Plantes Invasives, Laboratoire de la Santé des Végétaux, Anses, 34988 Montferrier-sur-Lez, France

ARTICLE INFO

Keywords:
Functional diversity
Taxonomic diversity
Traits
Composition
Crop rotation
Tillage
Herbicides
Long-term experiment

ABSTRACT

Cropping system (CS) diversification appears as a promising solution to increase CS sustainability. However, weed community response to different options of CS diversification remains poorly documented. Moreover, these effects are expected to be more pronounced in experimental than commercial farms because experimental farms explore more diverse combinations of farming practices. We hypothesized that (i) CS diversification would increase weed diversity at multiple spatio-temporal scales but that (ii) different options of CS diversification would select different weed communities and that (iii) responses could differ between experimental and commercial farms. Hence, weed density per species was measured over a 6-year time period in a CS experiment and in a farmers' network (both resorting to diverse CSs that were numerically summarized to allow their comparison, *i.e.* different positions along gradients of tillage intensity, herbicide use, crop rotation length *etc.*). Weed density measures were used to compute weed diversity indices (taxonomic and functional, at annual and plurennial scales) and community weighted means on key response traits for each CS. All experimented alternative CSs (diversified crop sequences with coherent but different combinations of weed management tools) showed that diverse combinations of agronomic tools are available to increase weed diversity, as highlighted by a 3 and 2-fold increase in species richness at the annual and plurennial scales, respectively. In contrast, only one farmer CS (3-year rotation, low tillage intensity, intermediate herbicide reliance) showed significantly higher levels of weed diversity, possibly because the reduced tillage intensity was not compensated by other agronomic levers (*e.g.* increase of herbicide use and/or crop rotation diversity). Such outcomes were attributed to (i) reduced CS complexity in commercial compared to experimental farms and (ii) high herbicide reliance in commercial farms, irrespectively of CS complexity. Across both experimental and commercial farms, tillage, weed management and crop type appeared as the main factors structuring weed communities. Systems with reduced tillage were associated with a higher percentage of grasses and perennials. Systems with spring/summer crops and/or mechanical weeding were associated with a higher proportion of spring/summer and perennial species. These results suggest that solutions are readily available for farmers to implement sustainable weed management, but supports are required to address the factors hindering the adoption of these experimented CS in commercial conditions.

1. Introduction

The oversimplification of cropping systems (CSs) (low crop diversity coupled with intensive use of tillage, herbicides and nitrogen fertilizers) has led to a drastic decline in weed diversity (Stoate et al., 2001; Albrecht et al., 2016). This loss of within field weed diversity has generated an erosion of the natural capital on which sustainable crop production is founded (Marshall et al., 2003; Storkey and Neve, 2018). Indeed, weeds represent the base of food chains in agroecosystems, and therefore support all higher trophic levels (*e.g.* beneficial insects and birds), responsible for a wide set of agroecosystem services, such as pollination and biological control (Pocock et al., 2012; Blaix et al.,

* Corresponding author.
E-mail address: stephane.cordeau@inrae.fr (S. Cordeau).
[1] These authors contributed equally to this work.

https://doi.org/10.1016/j.eja.2021.126438
Received 31 May 2021; Received in revised form 24 November 2021; Accepted 26 November 2021
Available online 9 December 2021
1161-0301/

2018). On the other hand, weeds can generate severe yield losses at high levels of abundance, which has justified their management (Cousens, 1985; Milberg and Hallgren, 2004). Therefore, identifying CSs which maintain weed diversity while preventing important yield losses was cited as a top research priority in weed science (Neve et al., 2018).

CS diversification (*i.e.* crop rotation and farming operations associated with each crop) has been proposed as a key approach to increase the sustainability of weed management (Liebman et al., 2001; Wezel et al., 2014), *i.e.* to maintain weed diversity while alleviating weed:crop competition (see the review of Colbach et al., 2020). CS diversification can be carried out at both the annual and plurennial scales (Wezel et al., 2014). For example, conventional winter wheat (*Triticum aestivum* L.), which involves summer bare soil before sowing and chemical weed control, can be diversified at the annual scale through the adoption of cover crops or false seedbed operations, cultivar or crop mixtures and a combination of mechanical and site-specific chemical weeding (Jabran et al., 2017). At the plurennial scale, short winter-cereal based rotations can be diversified with crops of different botanical families (*e.g.* winter faba bean, *Vicia faba* L.), sowing periods (*e.g.* spring barley, *Hordeum vulgare* L.) or even life cycle duration (*e.g.* alfalfa, *Medicago sativa* L., or other perennial legumes such as common sainfoin, *Onobrychis viciifolia* Scop.) (Cirujeda et al., 2019; Weisberger et al., 2019). The integration of new crops in the crop sequence is usually associated with a diversification of selection pressure on weeds because crops largely determine tillage timing, sowing date, fertilizer rate, type of herbicides and/or mechanical weeding, *etc.* (Fried et al., 2008; Koocheki et al., 2009). Hence, focusing on coherent sets of agronomic practices, rather than apprehending them individually and independently, should provide a greater understanding of how weed communities are shaped in real farming conditions (Swanton and Weise, 1991).

Cropping system effects on weed diversity should be considered at different spatio-temporal scales. Studies which have focused on annual snapshots of weed flora in a given crop (*e.g.* Fried et al., 2008 and Schumacher et al., 2018) may have identified farming practices that promote annual weed diversity (*e.g.* reduced fertilization rate or herbicide dose) but have provided little information concerning how CSs may be designed to promote weed diversity at both the annual and plurennial scales while limiting yield losses. Different management practices may promote weed diversity at different spatial scales in a given year (*e.g.* quadrat, lowest hierarchical level of weed sampling or plot:year scale, pool of all quadrats for a given plot and year) and over time (*e.g.* plot scale, pool of all quadrats for a given plot over time). This is of considerable importance because weed diversity at the quadrat and plot:year scales do not necessarily provide the same type of agroecosystem services. Weed diversity at the quadrat scale could mitigate weed:crop competition through complementarity in resource use in space and time (Adeux et al., 2019b) whereas weed diversity at the plot:year scale could maintain a greater diversity of mobile organisms, such as pollinators and/or natural enemies (Nicholls and Altieri, 2013; Schuldt et al., 2019). Greater inter-annual variability of crop types and management practices is expected to increase the diversity of habitats favorable to different weed species (Weibull et al., 2003), which should be reflected through higher cumulated weed diversity at the plot scale. Finally, the growing recognition that ecosystem processes depend on species' traits rather than on species richness (Hooper et al., 2005) has led researchers to characterize diversity through the extent of trait dissimilarity within the community, *i.e.* functional diversity (Garnier and Navas, 2012). Therefore, an additional focus on functional diversity could shed light on whether more diversified CSs promote more functionally diverse weed communities (Mahaut et al., 2019), thereby potentially maximizing ecosystem multifunctionality (Gross et al., 2017).

Different combinations of agronomic practices may lead to similar levels of taxonomic or functional diversity through the selection of different sets of functional response traits (Légère et al., 2005). Indeed, assembly rules in weed community ecology state that each set of farming practices will act as a set of filters on weed species traits (Booth and Swanton, 2002). However, different combinations of agronomic practices may reflect different farming objectives (*e.g.* maximizing economic profitability and/or enhancing soil health and/or minimizing reliance on external inputs). CSs tend to be designed to maximize profitability in commercial farming conditions (Colbach et al., 2020), whereas experimenters tend to explore more alternative strategies designed according to different and more diverse sets of objectives (Deytieux et al., 2012). Indeed, farmers tend to give more importance to the negative facet of weeds (*e.g.* yield loss) than experimenters (Vissoh et al., 2007; Wilson et al., 2008), usually resulting in higher management intensity in commercial farming conditions than in experimental farms. Combing such datasets could allow to investigate whether the volume of CS diversification space explored in commercial farms is sufficient to modify weed communities or if more complex changes (as explored in experimental farms) are required (Deytieux et al., 2016; Lechenet et al., 2017a). To our knowledge, no study has investigated the long-term effect of different options of CS diversification on weed communities (albeit different options across commercial and experimental farms), from both a taxonomic and functional perspective, and at different spatio-temporal scales.

The objectives of this study are (i) to identify if different options of CS diversification – that were previously confirmed as viable (*i.e.* low weed:crop competition), either in an experimental station (Adeux et al., 2019a) or on a farmers' network (Yvoz et al., 2020b) – could promote weed diversity at different spatial scales (*i.e.* quadrat, plot:year, plot) and (ii) to investigate the response traits of the corresponding weed communities in order to identify potential weed community assembly rules at the CS level. We hypothesized that (1) taxonomic and/or functional weed diversity could be promoted at different spatial scales through different options of CS diversification but (2) that each option would select weed communities with an adapted set of functional attributes. The study was based on weed surveys originating from two neighboring sites of the same production situation: an integrated weed management CS experiment aiming to reduce herbicide reliance through four alternative CSs (in comparison to a regional reference) and a network of farmers implementing various CSs to maximize economic profitability. Each dataset combined six years of weed samplings (weed density and biomass per species, after weeding, in all crops) and management practices over the same period.

2. Materials and methods

Both sites are located in the same production situation (47°14′11.2′N, 5°05′56.1′E) in southern Burgundy, France (Fig. 1), which is subject to a semi-continental climate, characterized by cold wet winters (average daily temperature of 4 °C and average monthly precipitation of 43 mm) and warm summers (average daily temperature of 18 °C and average monthly precipitation of 69 mm).

2.1. Cropping system experiment

The study focused on the last six years (harvest 2012 to harvest 2017) of a long-term CS experiment initiated in 2000 at the INRAE experimental farm in Bretenière, France (Adeux et al., 2019a). The experiment was set up as a randomized complete block design. For each of the five experimental CSs (ECSs), the set of decision rules was replicated on two blocks, separated by a distance of 1 km (Fig. 1) and characterized by clay soils (40–50%) of medium depth (50–90 cm). The will to implement ECSs in farm scale conditions (plot size = 1.7 ha) led to experimental limitations. Hence, only one term of the rotation was present for a given combination of block:year:ECS. Moreover, two different entry points (*i.e.* crop) were chosen for the two plots of a given CS to limit, to some extent, complete overlap between ECS:year and ECS:year:crop effects (Lechenet et al., 2017b).

Main characteristics of the five ECSs are presented in Table 1. The reference CS (ECS1), typical of the Burgundy region, was designed to

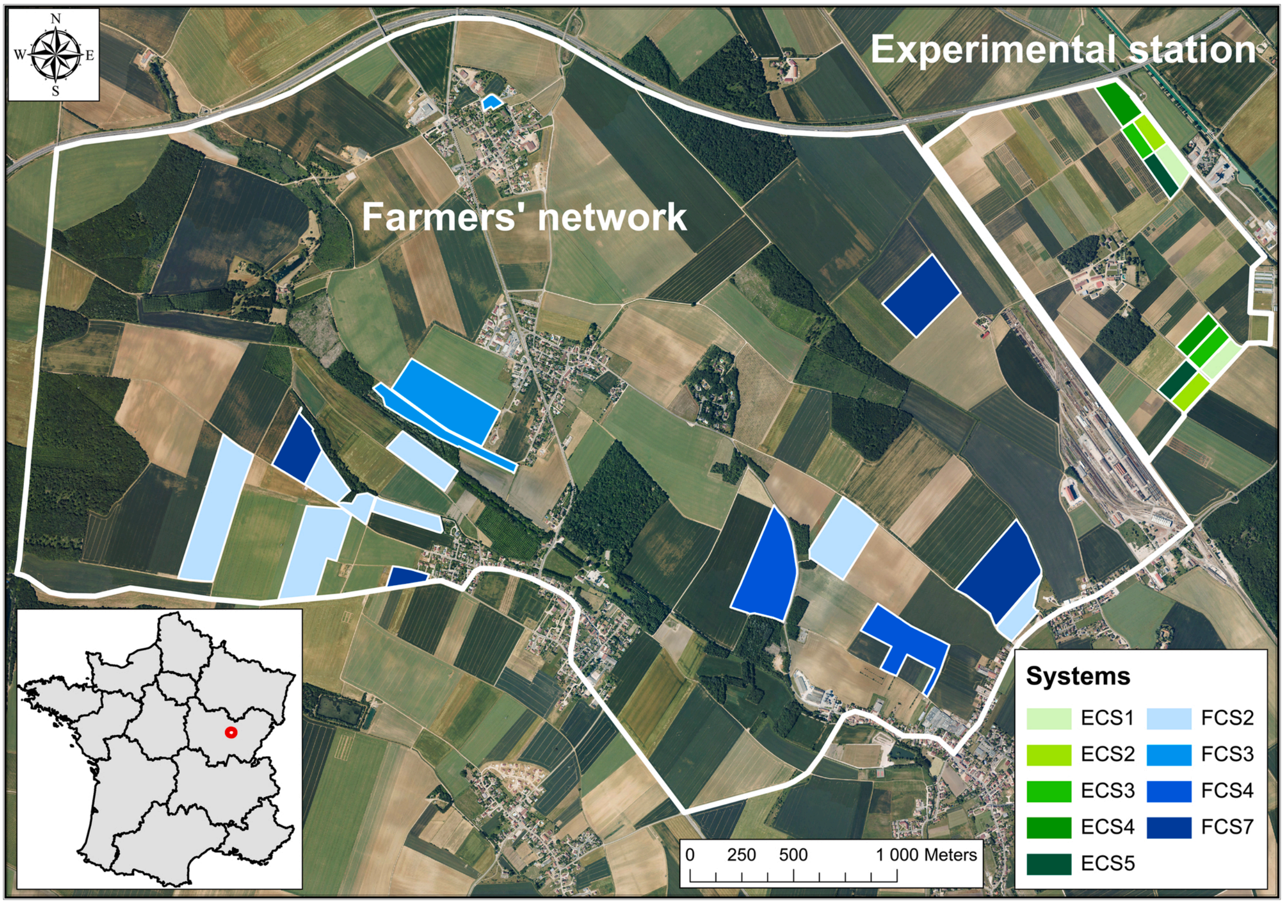

Fig. 1. Satellite image highlighting the vicinity of the experimental station (and experimented cropping systems, ECS) with the farmer's network (and farmer cropping systems, FCS).

Table 1
Overview of the main characteristics (black cells) of the different experimented (ECS) or farmer (FCS) cropping systems present in this study.

	Cropping system experiment					Farmers' network			
	ECS1	ECS2	ECS3	ECS4	ECS5	FCS2	FCS3	FCS4	FCS7
Crop diversification		■	■	■	■			■	■
No-till		■							
Reduced tillage							■		
Ploughing	■		■	■	■	■	■	■	■
Chemical weeding	■	■	■	■		■	■	■	■
Mechanical weeding				■	■				■
False seed bed practices			■	■	■	■	■	■	■
Increased sowing density		■	■	■	■				
Reduced N fertilization		■	■	■	■				■
Delayed sowing of winter cereals		■	■	■	■				

maximize financial return. It was characterized by a triennial oilseed rape (*Brassica napus* subsp. *napus* L.) – winter wheat – winter barley rotation, near-systematic moldboard plowing (in autumn due to high clay content), early sowing of winter cereals, herbicides as sole curative weed management tool, and high nitrogen fertilization (Table 2). All alternative CSs (ECS2 to ECS5) were designed to mimic farmers aiming to reduce herbicide reliance through different agronomic options and resulted in more diversified 6-year rotations (Table 2), which included

Table 2
Differences in terms of farming practices between experimented cropping systems (over the 2012–2017 period) and farmer cropping systems (over the 2008–2013 period). Effects were determined through F-tests on linear models. Values (observed means ± standard error) were computed over the crop sequence and standardized at the annual scale. Cropping systems sharing identical letters are not significantly different at $P < 0.05$ (p-values in bold). HTFI: Herbicide Treatment Frequency Index (average number of herbicide applications at the recommended dose).

	Cropping system experiment						Farmers' network				
	Experimented cropping system effect (df=4)	ECS1	ECS2	ECS3	ECS4	ECS5	Farmer cropping system effect (df=3)	FCS2	FCS3	FCS4	FCS7
Ploughing frequency	**F=47.67, P=0.001**	0.83±0.00 a	0.00±0.00 c	0.42±0.12 b	0.42±0.12 b	0.67±0.00 ab	F=2.19, P=0.14	0.66±0.11 a	0.34±0.17 a	1.00±0.21 a	0.50±0.15 a
Average number of false seedbed operations year^{-1}	**F=7.24, P=0.041**	1.75±0.12 ab	0.00±0.00 b	2.58±0.59 a	2.67±0.24 a	2.08±1.30 ab	**F=8.20, P=0.003**	2.39±0.10 c	1.78±0.17 ab	2.50±0.20 bc	1.67±0.14 a
Frequency of delayed sowing of winter cereals	**F=12.53, P=0.016**	0.00±0.00 b	0.75±0.35 a	0.83±0.24 a	1.00±0.00 a	0.58±0.12 ab	F=0.33, P=0.81	0.02±0.02 a	0.00±0.03 a	0.00±0.03 a	0.00±0.02 a
Average HTFI year^{-1}	**F=32.31, P=0.003**	1.34±0.18 ab	1.97±0.18 a	0.82±0.26 bc	0.50±0.16 c	0.00±0.00 c	F=0.66, P=0.59	1.51±0.08 a	1.63±0.13 a	1.42±0.16 a	1.41±0.11 a
Average HTFI before sowing year^{-1}	**F=639.7, P<0.0001**	0.02±0.02 b	1.05±0.06 a	0.02±0.03 b	0.01±0.01 b	0.00±0.00 b	F=1.73, P=0.21	0.01±0.03 a	0.15±0.05 a	0.06±0.06 a	0.05±0.05 a
Average HTFI after sowing year^{-1}	**F=13.32, P=0.014**	1.32±0.16 a	0.92±0.12 a	0.80±0.29 ab	0.49±0.17 ab	0.00±0.00 b	F=0.67, P=0.58	1.49±0.08 a	1.48±0.13 a	1.36±0.15 a	1.32±0.11 a
Average number of herbicide applications year^{-1}	**F=23.77, P=0.005**	1.25±0.12 b	2.42±0.35 a	1.42±0.35 ab	0.83±0.00 bc	0.00±0.00 c	**F=6.88, P=0.005**	1.08±0.07 b	1.61±0.11 a	1.50±0.14 ab	1.38±0.10 ab
Average number of herbicide applications before sowing year^{-1}	**F=13.72, P=0.013**	0.08±0.12 b	1.17±0.23 a	0.17±0.23 b	0.08±0.12 b	0.00±0.00 b	F=0.72, P=0.56	0.02±0.04 a	0.11±0.06 a	0.08±0.07 a	0.08±0.05 a
Average number of herbicide applications after sowing year^{-1}	F=3.26, P=0.14	1.17±0.00 a	1.25±0.59 a	1.25±0.59 a	0.83±0.00 a	0.00±0.00 a	**F=9.02, P=0.002**	1.06±0.05 b	1.5±0.108 a	1.42±0.10 a	1.29±0.07 ab
Average number of mechanical weeding operations year^{-1}	**F=37.38, P=0.002**	0.00±0.00 b	0.00±0.00 b	0.17±0.24 b	1.83±0.00 a	2.92±0.58 a	F=1.10, P=0.38	0.00±0.01 a	0.00±0.02 a	0.00±0.03 a	0.04±0.02 a
Average nitrogen fertilisation kg N year^{-1}	**F=29.14, P=0.003**	154±8 a	94±6 b	96±5 b	109±2 b	79±12 b	**F=4.06, P=0.03**	149±5 ab	163±7 a	145±9 ab	130±6 b
Proportion of non-fertilised crops	F=5.67, P=0.06	0.00±0.05 a	0.25±0.05 a	0.25±0.05 a	0.17±0.05 a	0.25±0.05 a	**F=0.00, P=0.00**	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a	0.00±0.00 a
Proportion of autumn-sown crops	F=6.00, P=0.055	0.67±0.04 b	0.50±0.04 ab	0.50±0.04 ab	0.50±0.04 ab	0.42±0.04 a	F=1.42, P=0.28	0.60±0.05 a	0.67±0.08 a	0.42±0.10 a	0.63±0.07 a
Proportion of winter-sown crops	F=6.00, P=0.055	0.00±0.04 b	0.17±0.04 ab	0.17±0.04 ab	0.17±0.04 ab	0.25±0.04 a	F=3.00, P=0.07	0.10±0.06 a	0.00±0.09 a	0.25±0.12 a	0.33±0.08 a
Proportion of spring-sown crops	**Perfect fit***	0.00±0.00 b	0.17±0.00 a	0.17±0.00 a	0.17±0.00 a	0.17±0.00 a	**F=13.20, P=0.0003**	0.00±0.02 b	0.00±0.03 b	0.25±0.04 a	0.04±0.03 b
Proportion of summer-sown crops	**Perfect fit***	0.33±0.00 a	0.17±0.00 b	0.17±0.00 b	0.17±0.00 b	0.17±0.00 b	**F=23.96, P<0.0001**	0.29±0.02 b	0.33±0.04 b	0.08±0.05 a	0.00±0.03 a
Number of crops	**F=8.60, P=0.03**	3.00±0.35 b	5.00±0.35 ab	5.50±0.35 a	5.00±0.35 ab	5.50±0.35 a	**F=5.51, P=0.01**	3.75±0.18 b	3.33±0.30 b	3.50±0.36 ab	4.75±0.26 a
Number of botanical families	**Perfect fit***	2.00±0.00 c	4.00±0.00 a	3.00±0.00 b	4.00±0.00 a	3.00±0.00 b	F=1.78, P=0.20	2.00±0.11 a	2.00±0.18 a	2.50±0.22 a	2.25±0.16 a
Number of sowing periods	**Perfect fit***	2.00±0.00 b	4.00±0.00 a	4.00±0.00 a	4.00±0.00 a	4.00±0.00 a	**F=3.60, P=0.04**	2.25±0.15 a	2.00±0.24 a	3.00±0.29 a	2.75±0.21 a
Number of crop types	**F=31.0, P=0.003**	2.00±0.22 b	5.00±0.22 a	4.50±0.22 a	5.00±0.22 a	4.00±0.22 a	**F=5.96, P=0.009**	2.50±0.23 b	2.00±0.37 b	3.50±0.45 ab	3.75±0.32 a
Functional diversity of crop sequence**	**F=7.06, P=0.04**	0.05±0.01 b	0.08±0.01 ab	0.08±0.01 ab	0.09±0.01 a	0.08±0.01 ab	**F=5.58, P=0.01**	0.08±0.00 b	0.07±0.00 ab	0.09±0.01 b	0.06±0.00 a

*Perfect fit denotes a model where each level of the factor shows no variability, *i.e.* $R^2 = 1$.
**Functional diversity of the crop sequence (1 value per plot over the period) was computed with Rao's quadratic entropy on 9 traits: life form (annual *vs.* perennial), sowing period (autumn, winter, spring, summer), number of cotyledons (monocotyledonous *vs.* dicotyledonous), nitrogen fixing ability (yes/no), seed mass, length of growing cycle, crop height at flowering, crop architecture (graminoïd, multi-stem, rosette, single stem), and flowering onset. Rao's quadratic index was computed with the FD (functional diversity) function of the R FD package (Laliberté and Legendre, 2010) and weighted by frequency in the crop sequence (mixtures were partitioned according to the number of species). Seed mass, length of growing cycle and crop height at flowering were log transformed before the analysis.

one autumn-sown oilseed rape crop, three winter crops (mainly cereals), one spring sown crop (mainly barley) and one summer sown crop (Table 2). In ECS5, alfalfa, a perennial forage crop, was included in order to manage Canada thistle (*Cirsium arvense* (L.) Scop.) through repeated mowing. The introduction of legume crops was the main driver of reduced nitrogen fertilization (−29 to −49%) at the CS scale for all alternative ECSs (Table 2).

The alternative CSs (ESC2–5) also differed by their tillage type and weed management strategies, including a wide array of preventive and cultural weed management tools, such as false seedbed technique, delayed sowing of winter cereals, and increased crop density (Table 2). ECS2 was a transition from reduced tillage (*i.e.* no inversion tillage from 2001 to 2010) to permanent no-till (2010–2017 in conservation agriculture) whereas ECS3, ECS4 and ECS5 implemented moldboard plowing about every two years (Table 2). ESC2 and ECS3 resorted exclusively to herbicides for curative weed control (50% corresponding to burndown applications of glyphosate in ECS2, Table 2) whereas ECS5 resorted exclusively to mechanical weeding (Table 2). ECS4 aimed to be the typical integrated weed management system, resorting preferentially to mechanical weeding, post-emergence applications of specialized herbicides on target species remaining possible when weather conditions were not suitable for mechanical weeding or to control weeds with low sensibility to mechanical weeding (*e.g. Galium aparine* L.).

2.2. Farmers' network

The present study also focuses on six years of data (harvest 2008 to harvest 2013) originating from farmer's fields located within the Fénay platform, near Dijon (north-eastern France), which borders the INRAE experimental station (Fig. 1), and thus shares similar weather and soil conditions. The Fénay platform represents a 950 ha zone of contiguous fields cultivated by 23 farmers, where weed communities and farming practices are recorded since 2004 by INRAE. The fields of the area were previously classified into eight crop management strategies (here denoted FCS for farmer CS), based on 14 indicators describing the diversity of crop sequences and the intensity of practices such as plowing, tillage, nitrogen and pesticide use over the 2004–2016 period (Yvoz et al., 2020b). For this study, only the fields in which weeds were surveyed after all weeding operations every year over the 2008–2013 period were retained (N = 17). Therefore, the final layout (Fig. 1) did not correspond to any experimental or sampling design (hence considered as completely randomized in following statistical section). This sub-dataset comprised 4 FCSs, whose main characteristics are summarized in Table 1. FCS2 (N = 8 fields) and FCS3 (N = 3 fields) were characterized by short rotations dominated by autumn-sown crops, but differed by the frequency of moldboard plowing (highest in FCS2), the use of secondary tillage (lowest in FCS3) and their reliance on herbicides (highest in FCS3, particularly before sowing, Table 2). FCS4 (N = 2 fields) was characterized by moderately diversified crop sequences based on systematic moldboard plowing, but relatively low reliance on herbicides and secondary tillage operations. FCS7 (N = 4 fields) was characterized by a diversified crop sequence, low reliance on moldboard plowing and herbicides and was the unique FCS implementing mechanical weeding (Table 2).

2.3. Weed sampling

In the CS experiment, weed density was counted per species in 8 randomly positioned 0.36 m^2 quadrats in each plot each year at crop flowering (*i.e.* few weeks after final weeding operations). Sampling quadrats were placed anew each year in a given plot. Crop volunteers were not included in the counts so as to focus on natural vegetation. Aboveground weed biomass was sampled per weed species concurrently. Biomass samples were then oven dried for 48 h at 80 °C and weighed. Weed biomass and density of each species was pooled at the quadrat level to obtain total weed biomass and density per quadrat. In the farmers' network, weed density was visually estimated per species within one 2000 m^2 area (50 m * 40 m, located 20 m away from the field margin and fixed in time) each year in each field before crop elongation stage and after weeding (*i.e.* early spring for winter cereals, late spring for spring crops and mid-summer for summer crops). Weed density was visually estimated using a slightly modified version of the scale of abundance developed by Barralis (1976), which proposes 6 classes of abundance (one individual in the 2000 m^2 area, < 1, 1–2, 3–20, 21–50, and 51–100 individuals m^{-2}). Total weed abundance was then computed using the center of each density class (*i.e.* 0.0005, 0.5, 1.5, 11.5, 35.5, and 75.5 individuals m^{-2}, respectively) following the methodology of previous studies (Fried et al., 2009; Trichard et al., 2013; Chamorro et al., 2016).

2.4. Numerical and statistical analyses

The two datasets were analysed separately so as to account for their differences in structure and sampling methodology. All the results presented in the main text are based on density as the measure was common to both datasets but additional results based on biomass are also provided as Supplementary Materials for the CS experiment.

2.4.1. Weed community descriptors

All diversity indices were computed at three different scales: the quadrat scale, the plot:year scale (the 8 quadrats for a given combination of plot:year were summed, *i.e.* 60 plot:year observations in total for the CS experiment) and the plot scale (the 48 quadrats for a given plot were summed across years, *i.e.* 10 plot observations in total for the CS experiment; the 6 annual surveys for a given plot were summed across years, *i.e.* 17 plot observations in total for the farmers' network). Quadrat and plot:year scale are referred to as the annual scale whereas the plot scale is referred to as the plurennial scale.

Weed diversity was characterized through two taxonomic indices (species richness and Shannon diversity index) and one index of functional dispersion (Rao's quadratic entropy). Species richness was computed as the number of species and Shannon diversity index was computed as $H' = -\sum_{i=1}^{S} p_i x ln(p_i)$ where p_i represents the relative abundance of species i and S represents species richness (Scheiner, 2012). Rao's quadratic entropy (Botta-Dukát, 2005) was computed with the functional diversity function (FD) of the R FD package (Laliberté and Legendre, 2010) on eight attributes reflecting plant strategies: 1) life cycle duration (annual *vs.* perennial), 2) number of cotyledons (grasses *vs.* broadleaves), 3) growth form (rosette, hemirosette or erosulate (*i.e.* no rosette during the whole plant cycle)), 4) germination period (non-seasonal, strict spring, strict summer, staggered germination from spring to summer, autumn and spring with no preference, autumn and spring with a preference for autumn), 5) specific leaf area, 6) flowering period (indifferent, spring/summer, summer, summer/autumn), 7) average height and 8) seed mass. Rao's quadratic entropy was weighted by density so as to account for the potential dominance of species with specific functional attributes (otherwise the indicator is simply based on absence/presence and a species representing 75% of abundance has as much weight on the analysis as a species representing 5%). Average height and seed mass were ln-transformed prior to the computation of Rao's quadratic entropy to reduce skewness. All attributes were either extracted from the LEDA (Kleyer et al., 2008), BiolFlor (Kühn et al., 2004) or Kew Gardens databases (Kew, 2020). Monospecific or empty surveys were attributed the lowest possible value of both Shannon diversity index (*i.e.* 0) and Rao's quadratic entropy (*i.e.* 0). These surveys were maintained because their removal would have inflated the average level of weed diversity, and hence, would have lacked to reflect the real level of weed diversity, particularly at the quadrat scale.

Community weighted means (CWM, average value of a given attribute weighted by the relative abundance of each species) were also computed on five attributes (life cycle duration, number of cotyledons, average height, seed mass, germination period) reflecting weed community response to agricultural practices (Lavorel et al., 2008; Ricotta and Moretti, 2011). CWM of life cycle duration, number of cotyledons, height and seed mass were computed at the plot:year scale to account for the patchy distribution of certain weed species with key response traits. CWM of germination periods was computed at the plot scale in order to encompass the whole crop sequence.

2.4.2. Data analysis

All statistical analyses were carried out with the R software version 3.6.2 (R Core Team, 2016). Generalized linear mixed effect models were fitted with the R glmmTMB package (Brooks et al., 2017) in order to account for the nature of certain response variables (*e.g.* Poisson distribution for species richness), the hierarchical design of the data (*e.g.* repeated sampling in a given field in time and space) and/or zero inflation to account for the excess zeroes (with respect to Tweedie distribution) in Shannon diversity index at the quadrat scale for the CS experiment (where ECS1 showed a high proportion of empty quadrats). The list of all the fitted models can be found in Supplementary Table 1. All response variables (weed biomass, weed density, diversity indicators, CWMs) were modeled as a function of block (for the CS experiment only) and CSs (ECS or FCS) in order to highlight potential differences between CSs. Statistical models were fitted at the quadrat, plot:year and plot scale (except the plot scale for the CS experiment due to lack of statistical power (N = 10, d.f. CS effect = 4)). Temporal coverage was identical for all three scales for a given dataset (2012–2017 for the CS experiment and 2008–2013 for the farmers' network) and no data was missing. Year (as factor), plot, block:year (CS experiment only), and CS:year were considered as random effects at both the quadrat and plot:year scales. A unique plot:year identifier was added as a random effect for analyses carried out at the quadrat scale in order to account for pseudoreplication (CS experiment only). Significance of CS effects (*i.e.* ECS or FCS) were determined through likelihood ratio tests. Model diagnostics (*i.e.* QQ plot residuals, quantile regression of residual *vs.* fitted, overdispersion, zero-inflation) were visualized using the DHARMa package (Hartig, 2020). Contrasts were adjusted using the emmeans package (Lenth, 2019). Magnitude and significance of correlations between diversity variables at different scales were assessed through the Spearman correlation coefficient and test, respectively.

Partial canonical correspondence analysis (pCCA) was performed at the plot:year scale to determine the percentage of variance in weed community data which could be explained by ECS or FCS, after accounting for the covariates year (both datasets) and block (CS experiment dataset, pCCA #1, covariates are shown in parenthesis). The response matrix consisted of 60 or 102 rows (the plot:years) by 38 and 40 columns (one for each species observed in more than one plot:year), respectively for the CS experiment and farmers' network. In the CCA analysis, weed densities were ln(X + 1)-transformed to reduce the influence of dominants. The following CCA analyses were conducted:

pCCA #1: weed communities ~ ECS or FCS + (block) + (year).

The proportion of partial variance explained by crop type was determined by replacing ECS or FCS in pCCA #1 by crop type (pCCA #2):

pCCA #2: weed communities ~ crop type + (block) + (year).

To determine whether ECS or FCS effects were simply due to the integration of new crop types (combination of botanical family and sowing period), the percentage of partial variation explained by pCCA #1 was compared to the percentage of partial variation explained by the joint effect of ECS or FCS and crop type (pCCA #3):

pCCA #3: weed communities ~ ECS or FCS + crop type + (block) + (year).

The difference in explained variance between pCCA #3 and #2 can be interpreted as ECS or FCS effects which cannot simply be explained by crop type, whereas the difference between pCCA #3 and #1 can be interpreted as the net effect of crop type which cannot be explained by associated agricultural operations. To identify whether ECS or FCS effects were identical across all crops, the percentage of variance explained by the joint effect of ECS or FCS and crop type (pCCA #3) was compared to the percentage of variance explained by the interaction between ECS or FCS and crop type (*i.e.* pCCA #4, where "*" denotes all simple effects and the first order interaction).

pCCA #4: weed communities ~ ECS or FCS*crop type + (block) + (year).

Due to the lack of a complete experimental design (*e.g.* all phases of the crop rotation of a given CS were not present every year in each block), meaningful (*i.e.* restricted) permutations were not feasible and hence, only percentages of explained variance were retained. The ordination diagrams were produced with the CANOCO software (Šmilauer and Lepš, 2014).

3. Results

In the CS experiment, 46 taxa were observed over the 2012–2017 period. The dominant weed species were *Alopecurus myosuroides* Huds., *Viola arvensis* Murray, *Fallopia convolvulus* (L.) A.Löve, *Galium aparine*, *Lysimachia* spp. (*arvensis* (L.) U.Manns & Anderb. and *foemina* (Mill.) U. Manns & Anderb.) and *Polygonum aviculare* L., representing 15%, 14%, 12%, 8%, 7% and 6% of total weed density after weeding, respectively (Fig. 2A). Over half (*i.e.* 53%) of the quadrats sampled in ECS1 did not contain any weed species at crop flowering, *i.e.* after weeding (*vs.* 2–12% in ECS2-ECS5). Average weed density after weeding (plant $m^{-2} \pm$ SE) at the quadrat scale was greater in ECS2 (39.0 ± 11.0), ECS3 (51.2 ± 14.3), ECS4 (34.7 ± 9.8) and ECS5 (53.4 ± 14.9) than in ECS1 (7.3 ± 2.3). Equivalent information based on biomass for the ECS can be found in Supplementary materials (Supplementary Tables 2–4, Supplementary Figs. 1–3). Weed biomass was comprised between 8 and 23 g m^{-2} for ECS2 to ECS5 and nearly null (< 1 g m^{-2}) for ECS1.

In the farmers' network, 61 taxa were observed over the 2008–2013 period. The dominant weed species were *V. arvensis*, *F. convolvulus*, *Solanum nigrum* L., *Veronica hederifolia* L., *A. myosuroides*, *Geranium dissectum* L., *Aethusa cynapium* L. and *Scandix pecten-veneris* L., representing 29%, 14%, 10%, 8%, 5%, 4%, 4% and 3% of the total weed density after weeding, respectively (Fig. 2B). Average weed density after weeding (plant $m^{-2} \pm$ SE) at the plot:year scale was generally low and not significantly different between FCS (FCS2 = 3.8 ± 1.2, FCS3 = 5.5 ± 1.9, FCS4 = 6.1 ± 2.3 and FCS7 = 4.7 ± 1.7).

3.1. Taxonomic and functional diversity at different scales

In the CS experiment, CS had a significant effect on weed species richness, Shannon diversity index and Rao's quadratic entropy at both the quadrat and the plot:year scales (Table 3). All alternative CSs (ECS2-ECS5) generated greater diversity values than the reference system (ECS1) at all three scales. Even though less pronounced, differences tended to persist at the plot scale for species richness, Shannon diversity index and Rao's quadratic entropy (no statistical test performed, Table 3). Correlations between weed diversity indicators were all significant between each other at both the quadrat and plot:year scales but not at the plot scale (Supplementary Table 3). For a given combination of plot and year, average weed diversity at the quadrat scale showed to be highly correlated with weed diversity computed across all quadrats (Supplementary Table 3). However, only average species richness at the plot:year scale was significantly correlated with its reciprocal at the plot scale (Supplementary Table 3).

In the farmers' network, CS had a significant effect on weed species richness, Shannon diversity index and Rao's quadratic entropy at both the plot:year and the plot scale, excepted for Rao's quadratic entropy at the plot scale (Table 3). FCS3 expressed higher weed diversity values than the 3 other CSs at the plot:year scale, although less pronounced at the plot scale (Table 3). Weed diversity indicators were significantly correlated between each other, except for species richness and Rao's quadratic entropy at the plot scale (Supplementary Table 3).

3.2. Associations between cropping systems, weed species and functional traits

In the CS experiment, ECS alone explained 25.7% of partial variation (after the removal of year and block effect, which explained 14.5% of total variation, pCCA #1) whereas crop type alone explained 30.6% of

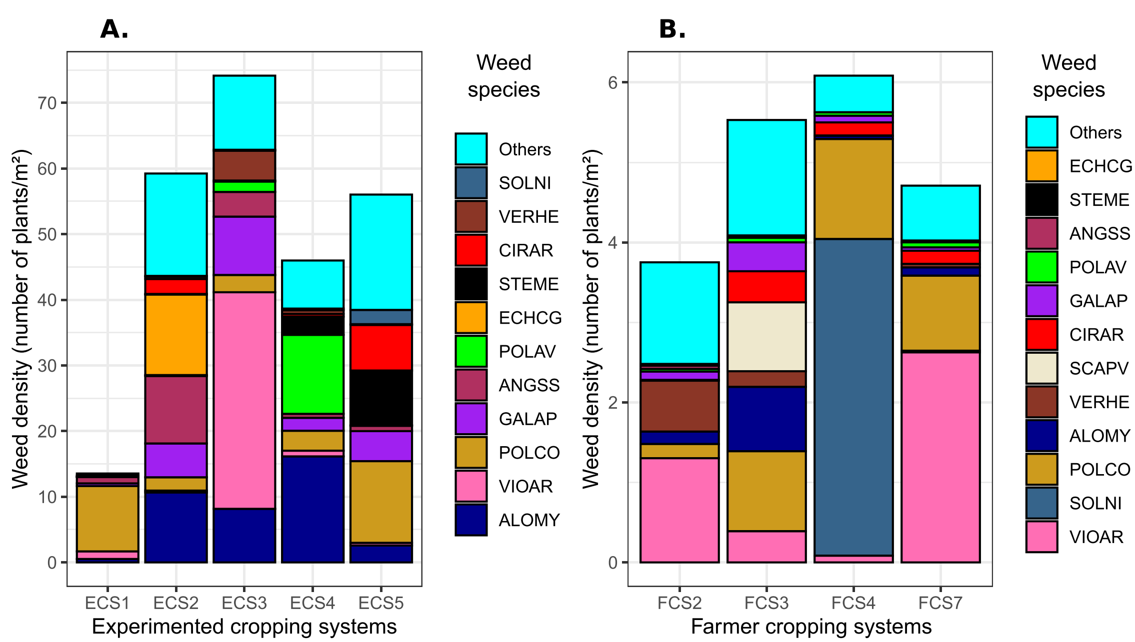

Fig. 2. Observed mean weed density per species (named by to their EPPO code, https://gd.eppo.int/) after weeding (*i.e.* at crop flowering for A. and prior to crop elongation for B.) between A) experimented cropping systems (ECS1 to ECS5) over the 2012–2017 period and between B) farmer cropping systems (FCS2 to FCS7) over the 2008–2013 period.

Table 3
Effect of experimented or farmer cropping systems on weed diversity (species richness, Shannon diversity index, and Rao's quadratic entropy, the last two weighted by density) at three different scales (quadrat for the cropping system experiment, plot:year and plot for the cropping system experiment and farmers' network) over the 2012–2017 and 2008–2013 period, respectively. Values represent least square means (± standard error) whereas values for the cropping system experiment at the plot scale represent observed means (± standard deviation). Effects were determined by likelihood ratio tests. Experimented or farmer cropping systems sharing identical letters are not significantly different at $P < 0.05$ (p-values in bold).

		Cropping system experiment							Farmers' network					
Diversity indicator	Scale	Experimented cropping system effect (df=4)	N	ECS1	ECS2	ECS3	ECS4	ECS5	Farmer cropping system effect (df=3)	N	FCS2	FCS3	FCS4	FCS7
Species richness	Quadrat	**χ2=20.43, P=0.0004**	480	0.62±0.13 b	2.49±0.45 a	3.48±0.62 a	2.65±0.48 a	3.40±0.61 a	NA		NA	NA	NA	NA
	Plot:year	**χ2=21.41, P=0.0003**	60	3.29±0.56 b	9.54±1.09 a	10.19±1.14 a	8.53±1.02 a	9.61±1.10 a	**χ2=22.27, P=0.0007**	102	3.6±0.50 b	7.6±1.32 a	3.1±0.74 b	3.7±0.64 b
	Plot	Not tested*	10	9.00±5.66	21.50±2.12	23.50±6.37	19.00±4.24	22.00±0.00	**χ2=10.20, P=0.017**	17	10.8±1.16 b	18.0±2.45 a	11.0±2.35 ab	11.0±1.66 ab
Shannon diversity index	Quadrat	**χ2=14.53, P=0.006**	480	0.05±0.04 c	0.61±0.09 b	0.97±0.07 a	0.77±0.10 ab	0.93±0.08 a	NA		NA	NA	NA	NA
	Plot:year	**χ2=22.83, P=0.0001**	60	0.59±0.11 b	1.45±0.17 a	1.62±0.18 a	1.50±0.17 a	1.41±0.17 a	**χ2=20.73, P=0.0001**	102	0.77±0.09 b	1.62±0.26 a	0.49±0.13 b	0.90±0.14 b
	Plot	Not tested*	10	1.14±0.33	2.04±0.24	2.02±0.39	1.83±0.02	2.04±0.05	**χ2=11.86, P=0.008**	17	1.39±0.12 a	2.09±0.25 a	1.16±0.23 a	1.27±0.17 a
Rao's quadratic entropy	Quadrat	**χ2=20.59, P=0.0004**	480	0.00±0.00 b	0.03±0.01 a	0.04±0.01 a	0.03±0.01 a	0.04±0.01 a	NA		NA	NA	NA	NA
	Plot:year	**χ2=15.86, P=0.003**	60	0.03±0.00 b	0.08±0.01 a	0.06±0.01 a	0.06±0.01 a	0.05±0.01 a	**χ2=19.89, P=0.0002**	102	0.03±0.00 bc	0.07±0.01 a	0.02±0.01 c	0.04±0.01 ab
	Plot	Not tested*	10	0.04±0.01	0.08±0.00	0.06±0.00	0.07±0.02	0.07±0.00	χ2=7.37, P=0.06	17	0.04±0.01 a	0.07±0.02 a	0.03±0.01 a	0.04±0.01 a

NA: not applicable, *i.e.* no data collected at this scale.
*No tests were performed at the plot scale due to lack of statistical power (N = 10, d.f. cropping system effect = 4).

partial variation (pCCA #2, Fig. 3). ECS and crop type (pCCA #3) jointly explained 50% of partial variation, indicating that ECS had a unique effect on weed community composition on top of crop type (*i.e.* 50–30.6 = 19.4% of partial variation). The interaction between ECS and crop type (pCCA #4) explained 64.9% of partial variation, highlighting important variations in weed community composition across ECS for a given crop type.

When the analysis was solely constrained by ECS (after the removal of year and block effects, pCCA #1), the first and second axis explained 9.4% and 9% of partial variation, respectively (Fig. 4A). The first axis clearly discriminated ECS2 (no-till) from the other plowing-based systems and could therefore be associated with the presence or absence of plowing (Table 2). Weed species associated with no-till (ECS2) were *Echinochloa crus-galli* (L.) P.Beauv., *Convolvulus arvensis* L., *Lapsana communis* L., *Plantago lanceolata* L., *Senecio vulgaris* L., *Sonchus* spp. (*asper* L. and *oleraceus* L.), *Myosotis arvensis* (L.) Hill, *C. arvense*, *Taraxacum officinale* F.H.Wigg., and *Lolium perenne* L. Weed species associated with tillage (ECS1, ECS3, ECS4, ECS5) were *P. aviculare*, *Euphorbia exigua* L., *Fumaria officinalis* L., *Chaenorhinum minus* (L.) Lange, *and Thlaspi arvense* L. The second axis clearly discriminated ECS5 (mechanical weeding) from ECS3 (chemical weeding), and was associated with weed management type in spring/summer crops (Table 2). Weed species associated with mechanical weeding in spring/summer crops (ECS5) were *Polygonum* spp. (*persicaria* L., *lapathifolium* L., and *aviculare* L.), *Rumex* spp. (*obtusifolius* L. and *crispus* L.), *S. nigrum, Chenopodium album* L., *C. arvense,* and *Lipandra polysperma* (L.) S.Fuentes, Uotila & Borsch.

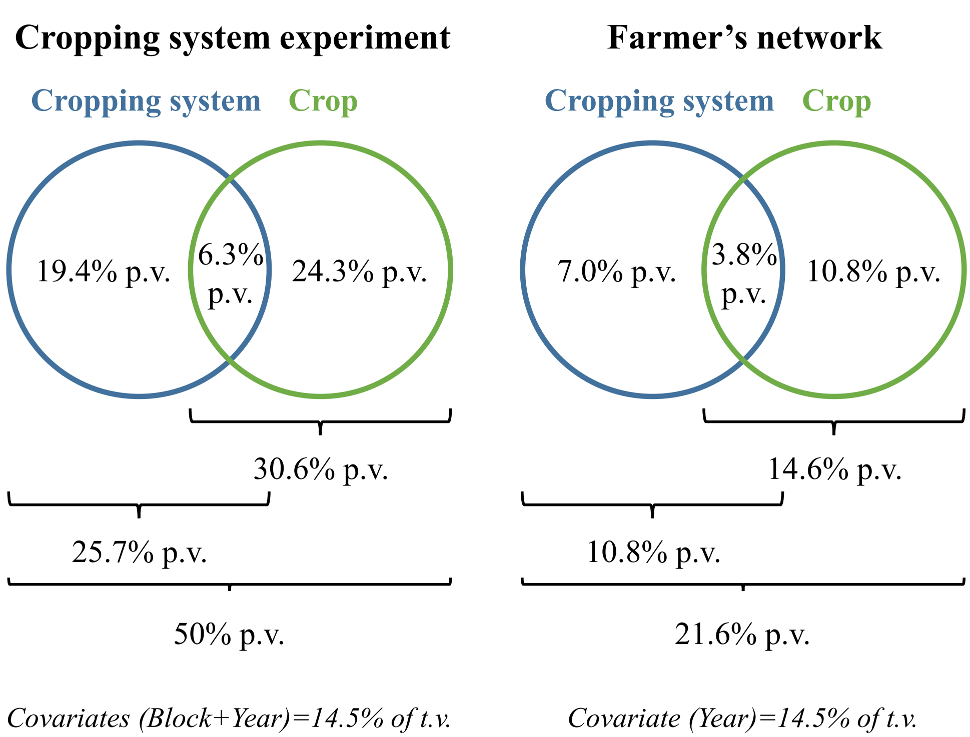

Fig. 3. Gross and net effects of cropping system and crop on weed community composition for A) the cropping system experiment and for B) the farmers' network. t.v.: total variation; p.v.: partial variation.

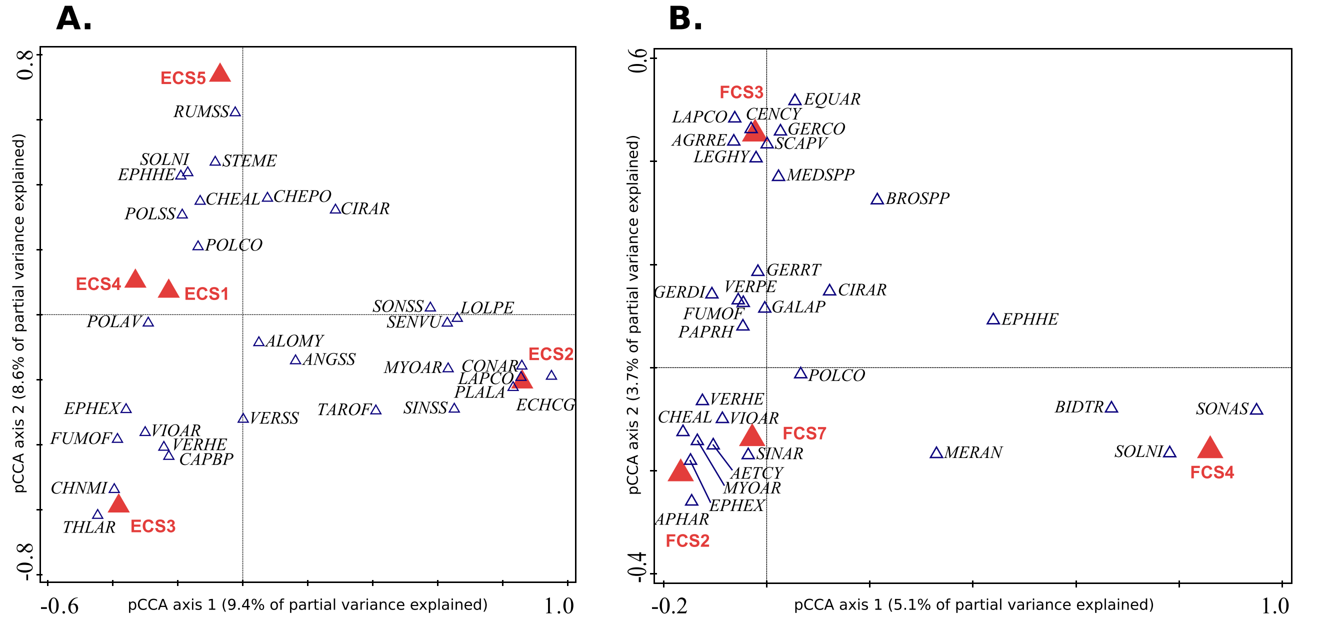

Fig. 4. Partial canonical correspondence analyses highlighting the relationship between (A) experimented cropping systems or (B) farmer cropping systems (red triangles) and weed species (empty blue triangles, named by to their EPPO codes, https://gd.eppo.int/) after the removal of block (A) and year (A and B) effects. The response matrix consisted of 60 (A) and 102 (B) plot:years and weed density per species. Only the 30 best fitting species are represented for graphical purposes. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Weed species associated with chemical weed control (ECS3) were *T. arvense*, *C. minus*, *Capsella bursa-bastoris* (L.) Medik., *V. arvensis* and *Veronica hederifolia* L.

The proportion of monocotyledonous species was greater in ECS2 than in ECS1 (Table 4), which is coherent with ECS2′s association with *Echinochloa crus-galli* and *Lolium perenne* (Fig. 4A), and the dominance of *P. convolvulus* in ECS1 (74% of total abundance, Fig. 2A). The proportion of perennials was greater in ECS2 and ECS5 than in ECS1 (Table 4), which is coherent with ECS2 association with *L. perenne* , *C. arvensis*, *P. lanceolata*, *T. officinale*, and ECS5′s association with *Rumex* spp. and *C. arvense* (Fig. 4A). Community weighted mean of height was greater in ECS1 and ECS5 than in ECS3 (Table 4), which is coherent with ECS5′s association with *Rumex* spp., *C. arvense*, *C. album*, *S. nigrum*, and *L. polysperma* and ECS3′s association with *V. arvensis* or *V. hederifolia* (Fig. 4A). Community weighted mean of seed mass was greater in ECS1 than in all other ECS (Table 4), mostly as a result of *P. convolvulus*.

ECS could be classified into three main categories according to weed germination period profiles (Fig. 5A): 1) those with a high proportion of autumn and/or spring germinating species (ECS1, ECS3, and ECS4), 2) those with a high proportion of indifferent or summer (mainly due to *Echinochloa crus-galli*) germinating species (ECS2) and 3) those with a high proportion of spring and/or summer germinating species (ECS5).

In the farmers' network, FCS alone explained 10.8% of partial variation (after the removal of year effect, which explained 6.6% of total variation, pCCA #1) whereas crop type alone (pCCA #2) explained 14.6% of partial variation. FCS and crop type (pCCA #3) jointly explained 21.5% of partial variation, indicating that FCS had a unique effect on weed community composition on top of crop type (*i.e.* 21.5–14.6 = 6.9% of partial variation). The interaction between FCS and crop type (pCCA #4) explained 31% of partial variation, highlighting slight variations in weed community composition across FCS for a given crop type.

When the analysis was solely constrained by FCS (after the removal of year effect, pCCA #1), the first and second axis explained 5.1% and 3.6% of partial variation, respectively (Fig. 4B). The first axis clearly discriminated FCS4 (high frequency of spring-sown crops, Table 2) from the other FCS and could therefore be associated with crop diversification through the introduction of spring-sown crops. Weed species associated with the introduction of spring-sown crops (FCS4) were *Euphorbia helioscopia* L., *S. asper*, *Bidens tripartita* L., *Mercurialis annua* L., and *S. nigrum*.

Table 4
Effect of cropping systems on community weighted means (CWM weighted by density) of different weed response traits. Values represent least square means (± standard error). Effects were determined by likelihood ratio tests. Experimented or farmer cropping systems sharing identical letters for each response variable are not significantly different at $P < 0.05$ (p-values in bold).

Response variable	Cropping system experiment								Farmers' network						
	Scale	Experimented cropping system effect (df=4)	N	ECS1	ECS2	ECS3	ECS4	ECS5	Scale	Farmer cropping system effect (df=3)	N	FCS2	FCS3	FCS4	FCS7
Proportion of monocotyledonous species	Plot:year	**χ2=9.34, P=0.05**	60	0.12±0.04 b	0.41±0.08 a	0.22±0.06 ab	0.24±0.06 ab	0.17±0.05 ab	Plot:year	χ2=0.82, P=0.84	102	0.11±0.04 a	0.09±0.06 a	0.06±0.05 a	0.07±0.04 a
Proportion of perennial species	Plot:year	**χ2=11.73, P=0.02**	60	0.04±0.02 b	0.16±0.05 a	0.04±0.02 ab	0.04±0.02 ab	0.17±0.05 a	Plot:year	**χ2=10.01, P=0.02**	102	0.05±0.01 b	0.12±0.03 a	0.08±0.03 ab	0.08±0.02 ab
CWM height	Plot:year	**χ2=11.81, P=0.02**	60	49.1±3.32 ab	44.6±3.08 bc	36.8±2.81 c	43.1±3.03 bc	56.1±3.53 a	Plot:year	**χ2=9.22, P=0.03**	102	35.3±2.4 b	45.1±4.7 a	46.9±6.0 a	46.4±4.2 a
CWM seed mass	Plot:year	**χ2=13.77, P=0.008**	60	5.33±0.81 a	2.62±0.39 b	2.27±0.33 b	2.38±0.35 b	2.84±0.42 b	Plot:year	**χ2=8.23, P=0.05**	102	2.12±0.32 b	4.12±0.87 a	2.78±0.78 ab	3.38±0.64 ab

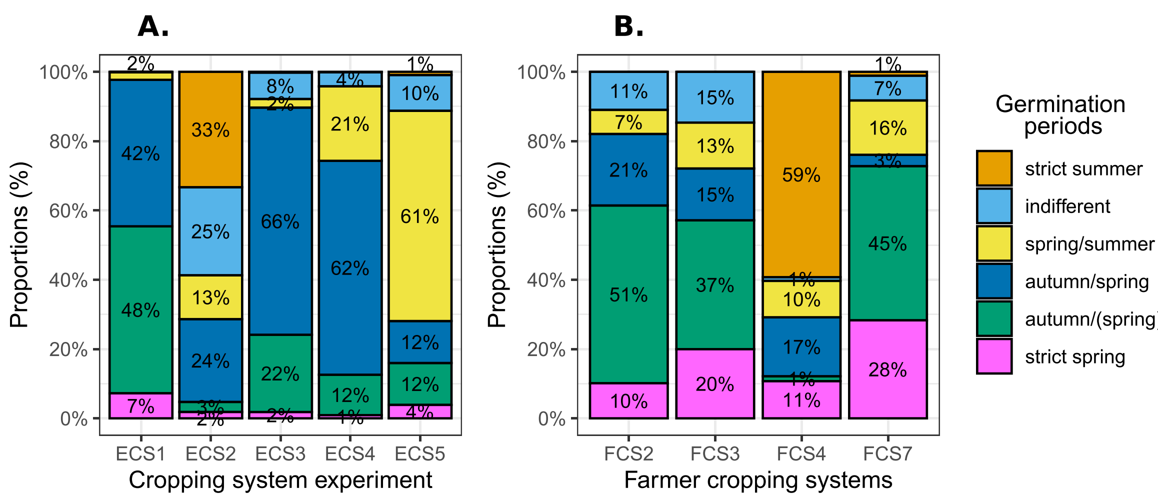

Fig. 5. Proportion of weed germination periods (weighted by density) between (A) experimented cropping systems and between (B) farmer cropping systems. Note: autumn/(spring) refers to species which show a peak of germination during autumn that partially extends into the spring whereas autumn/springs refers to species which do not show any preference between autumn and spring.

The second axis clearly discriminated FCS3 from FCS2 and FCS7, and could therefore be associated with a combination of weed management type and tillage intensity (*i.e.* minimum tillage, pre-sowing herbicide and in-crop herbicide applications at low dose in FCS3 *vs.* plowing and few herbicide applications at high dose in FCS2/FCS7, Table 2). Weed species associated with low tillage intensity, pre-sowing herbicides and in-crop herbicide applications at low dose (FCS3) were *L. communis* , *Elymus repens* (L.) Gould, *Legousia hybrida* (L.) Delarbre, *Equisetum arvense* L., *Cyanus segetum* Hill, *Geranium columbinum* L., *S. pecten-veneris*, and *Medicago* spp. Weed species associated with plowing and few herbicide applications at high dose (FCS2, FCS7) were *V. hederifolia*, *V. arvensis*, *C. album*, *Aphanes arvensis* L., *E. exigua*, *M. arvensis*, and *A. cynapium*.

The proportion of monocotyledonous species was not significantly different across FCS (Table 4). The proportion of perennials was greater in FCS3 than in FCS2 (Table 4), which is coherent with FCS3′s association with *E. repens*, *E. arvense* and *Medicago* spp. (Fig. 4B). Community weighted mean of height tended to be lower in FCS2 but was not significantly different across FCS (Table 4). Community weighted mean of seed mass was greater in FCS3 than in FCS2 (Table 4).

FCS could be classified into two main categories according to weed germination period profiles (Fig. 5B): 1) those with a high proportion of autumn and/or spring germinating species (FCS2, FCS3, and FCS7), and 2) those with a high proportion of summer germinating species (FCS4).

4. Discussion

4.1. *Various options of cropping diversification promote taxonomic and functional weed diversity*

4.1.1. *Diversity at the annual (quadrat and plot:year) scale*

All alternative ECSs (ECS2 to ECS5) and one FCS (FCS3), which were previously shown to limit crop yield losses to low levels (Albrecht et al., 2016; Adeux et al., 2019a; Yvoz et al., 2020b), illustrated that multiple agronomic options were possible to promote high weed diversity at the annual scale (*i.e.* quadrat and plot:year scales). Higher weed density in all alternative experimented cropping systems (ECS2–5) did not transcribe into levels of weed biomass susceptible of generating significant crop yield losses (Adeux et al., 2019a) because weed management tactics targeted the most competitive weed species (*e.g. Galium aparine, Alopecurus myosuroides, Cirsium arvense*) and because a high proportion of total weed density was represented by late germinating weeds (possibly promoted by mechanical weeding and/or late sampling). Weed densities in the farmers' network were too low (< 7 plants m-2) to generate any significant yield loss (Quinio et al., 2017; Yvoz et al., 2020b). Competitive species were observed well below their 5% yield loss threshold (Wilson and Wright, 1990).

The regional reference (ECS1) and three of the four FCS (FCS2, FCS4 and FCS7) were illustrative of the dramatically low level of weed diversity present in intensively managed agricultural fields in the study region, and with studies from other central and northern European countries (Andreasen et al., 1996; Sutcliffe and Kay, 2000; Baessler and Klotz, 2006; Fried et al., 2009; Albrecht et al., 2016). Fields managed under ECS1 principles showed less than one species per quadrat on average and fields managed under FCS2, FCS4 and FCS7 principles harbored only three to four species per field on average each year. These results could be attributed to the oversimplified and intensive practices implemented in ECS1 and FCS2, namely low crop diversity, near systematic plowing, repeated use of pre- and post-emergence broad spectrum herbicides, and high nitrogen fertilization (Gressel and LeBaron, 1982; Haas, 1982; Nikolich et al., 2012). However, low weed diversity could not be attributed to the same reasons for FCS4 and FCS7, which resorted to a more diversified crop sequence. The detailed characterization of farming practices highlighted that FCS remained intensive on a yearly basis, with nitrogen and herbicide use being as important as in ECS1 (mechanical weeding being insignificant). In contrast, all alternative ECS (ECS2 to ECS5) showed three species per quadrat and FCS3 averaged 7.9 species per field each year. Such results are of considerable importance because they stress that diverse strategies are available to promote weed diversity while preventing yield loss (Adeux et al., 2019a). Moreover, higher weed diversity at the local scale (*i.e.* quadrat) could mitigate crop yield losses (for a given level of weed biomass) through more complementary use of resources in space and time (Adeux et al., 2019b) and promote other organisms sustaining ecosystem services (Marshall et al., 2003; Blaix et al., 2018).

The adopted CS approach did not allow to disentangle the relative effects of crop sequence, tillage, and weed control on weed diversity. Nevertheless, greater weed diversity at the annual scale in the different agronomic options cited above most likely resulted either from less intensive in-crop weed control in the CS experiment (Doucet et al., 1999; Légère et al., 2005), or from inefficient long-term weed management in FCS3 (Colbach et al., 2020; Yvoz et al., 2020b). Increased weed diversity in ECS3 (chemical weeding only) highlights that a well-balanced rotation including a diverse suite of weed management tactics (targeted use of post-emergence herbicide included) can reduce total herbicide use (−40% compared to ECS1), increase weed diversity and limit yield losses due to competitive dominants, as shown in (Adeux et al., 2019b) on the same CSs. To reach similar levels of performance in terms of weed diversity while limiting yield losses, ECS5 (mechanical weeding only) had to resort to more than twice as many weeding operations. Indeed, weed management strategies in alternative CSs relied on a combination of non-chemical weed management tools with partial effect rather than broadcast use of broad spectrum herbicides (Swanton and Weise, 1991), as it was the case for the farmers' network. Higher weed diversity in all alternative ECSs may also have resulted from reduced nitrogen fertilization (which was not the case in the farmers' network) and crop productivity (Albrecht et al., 2016; Adeux et al., 2019a). Indeed, higher nitrogen fertilization in ECS1 and all FCS may have exerted a strong competitive effect on weed species susceptible to shading (Kleijn and van der Voort, 1997), thereby reflecting potential antagonisms between weed diversity and crop productivity in highly productive agricultural contexts (Albrecht et al., 2016).

Surprisingly, ECS2 (no-till) promoted higher weed diversity at the annual scale even though total herbicide use was 47% greater than in ECS1. The same trends were observed in the farmers' network: FCS3 (reduced-tillage) showed the highest weed diversity at the annual scale even through total herbicide use was 8–15% greater than in the other FCS. Three complementary hypotheses could be formulated to explain this result. First, ECS2 and FCS3 showed the greatest proportion of glyphosate in total herbicide use, a systemic non-residual herbicide used for burn-down weed control prior to crop sowing, which had no direct effect on weed seedlings emerging after sowing (due to the timing of application and mode of action). This hypothesis is in line with Plaza et al. (2011), Dorado and Lopez-Fando (2006), Murphy et al. (2006) and Víllora et al. (2019) and numerous other authors whom reported no difference in weed diversity between tillage systems, or greater weed diversity in no-till, although no-till resorted to glyphosate applications for burn-down control in addition to the other in-crop herbicides used in the other systems. Second, in-crop herbicide use was actually 30% lower in ECS2 than ECS1. No pre-emergence herbicides were applied in ECS2, due to their low efficacy in no-till systems, where organic matter is concentrated on top of the soil surface (Peter and Weber, 1985; Blumhorst et al., 1990). Such weeding constraints could have allowed a greater diversity to establish in the crop. This second hypothesis cannot be applied to FCS3, which presented similar herbicide use after sowing than the three other FCS. Third, no-till (ECS2) or superficial tillage (FCS3) generate a concentration of the weed seedbank in the top soil layers (Mohler et al., 2006), thereby increasing the probability of weed seed recruitment, except for species exhibiting decreased germination on the soil surface (Cordeau et al., 2015).

4.1.2. Diversity at the plurennial scale

Differences in annual weed diversity across CSs clearly persisted at the plurennial scale (*i.e.* plot scale) when considering species richness. Increasing crop diversity while reducing herbicide use increased species diversity in all alternative ECSs, which harbored twice as many species as ECS1 over the course of the experiment. Such results could be attributed to a greater diversity of sowing periods which allowed the development of weed species with different germination requirements (Gunton et al., 2011). Indeed, Mahaut et al. (2019) showed across a large-scale French weed monitoring network encompassing 1045 crop sequences that greater variability of sowing dates was associated with greater weed species richness at the plurennial scale. Murphy et al. (2006) and Sosnoskie et al. (2006) also reported a more diverse weed seedbank after a 3-year rotation integrating summer and winter-sown crops than after a 2-year rotation integrating only summer crops or a monoculture. Furthermore, a diverse set of studies spanning different continents report clear associations between crops (and hence sowing dates) and weed species (Hyvönen and Salonen, 2002; Poggio et al., 2004; Ryan et al., 2010; Andrade et al., 2017), suggesting that a greater turnover in crops species (and hence sowing dates) can favor weed species turnover in time. In the farmers' network, herbicide use remained high, irrespectively of crop diversity, thereby generating little differences in weed diversity across FCS (exception made of FCS3). Higher weed diversity in FCS3 could rather be attributed to the combination of low crop diversity, low tillage intensity and moderate use of in-crop herbicides. Little variation could be observed across ECSs or FCSs in terms of Shannon diversity and of Rao's quadratic entropy at the plurennial scale. Such outcomes could arise from the fact that (i) a species with high abundance a given year can lead to dominance at the CS scale if total abundance is low the other years, even if species relative abundance is evenly distributed within the other years, and that (ii) the most abundant and frequent weed species were able to maximize weed functional trait space in the CS experiment (based on the selected traits extracted from databases). Ecosystem services associated with weeds also depend on species abundance (Tarjuelo et al., 2019), thereby questioning the capacity of ECS1 and all FCS to provide ecosystem services with extremely low levels of weed abundance.

4.2. Different options of cropping system diversification generate different combinations of weed traits

Different options of CS diversification reached similar levels of weed diversity through the selection of weed communities with different functional attributes. In accordance with previous studies, tillage, crop and weed control methods appeared as major filters on the functional composition of weed communities (Légère et al., 2005; Ryan et al., 2010; Gunton et al., 2011; Fried et al., 2012; Trichard et al., 2013). The first and second axis of the ordination of the CS experiment and the farmers' network, respectively, clearly illustrated the role of plowing (*i.e.* inversion tillage) in structuring weed communities. The lack of soil disturbance in ECS2 and reduced tillage in FCS3 was reflected by their association with perennials and wind-disseminated *Asteraceae* species (confounded with indifferent species, *i.e.* non-seasonal species), and the association of ECS2 with grasses, as previously reported by *e.g.* Froud--Williams (1988), Thomas et al. (2004) or Mirsky et al. (2013) in other reduced or no-till systems. In accordance with previous studies (Dorado and Lopez-Fando, 2006; Giambalvo et al., 2012; Hernández Plaza et al., 2015; Pardo et al., 2019), weed communities in ECS1 (near systematic plowing) were characterized by species with more important seed mass than all other ECS (which ranged from a plowing frequency of 0.5 for ECS3–5–0 for ECS2). Under systematic conventional tillage, high seed mass could confer species an advantage in terms of germination depth and competitive ability (Turnbull et al., 1999; Gardarin et al., 2009) whereas under permanent no-till, greater seed mass could limit seed:soil contact and hence weed seed imbibition and recruitment (Chauhan et al., 2012). The lack of differences between ECS2 (systematic no-till) and ECS3–5 (plowing once every two years) or the opposite trends observed in farmers' network (the community with the highest seed mass was found in the FCS with the lowest plowing frequency) could point out to intense filtering of seed mass in absence of soil disturbance (systematic plowing *vs.* no-till) but a more diverse set of winning strategies at higher levels (Hernández Plaza et al., 2015). Indeed, Fried et al. (2012) highlighted that low seed mass (and hence high seed production) could also confer species an advantage to cope with frequent soil disturbances. Such discrepancies could arise from the data type that was used to compute CWM: density (as in Fried et al., 2012) could give more weight to ruderal species with low seed mass and high seed production, whereas biomass, as in Bàrberi et al. (2018), could give more weight to competitive species with high seed mass (*e.g. A. myosuroides* and *G. aparine*). Finally, it is important to stress that CSs act on multiple species traits at once (some of which may be correlated) and that higher seed mass in ECS1 may simply be confounded with other traits which conferred *G. aparine* or *F. convolvulus* an advantage (*e.g.* herbicide tolerance).

The second and first axis of the ordination of the CS experiment and farmers' network, respectively, revealed an association between spring/summer and strict spring weed species (*e.g. C. arvense*, *C. album*, *P. aviculare*, *S. nigrum*, *Persicaria* spp.) and high proportion of spring crops in the rotation for ECS4/ECS5 and FCS4. Such effects could not only be attributed to crop diversification as ECS4 (6-year rotation) was closely associated with ECS1 (3-year rotation) in the ordination. Rather, we hypothesize that (i) mechanical weeding (main and unique technique for direct weed control in ECS4 and ECS5) was not as efficient as chemical weeding on species in spring/summer crops, possibly due to staggered germinations or quick growth rate, (ii) late mechanical weeding operations in cereal crops stimulated new germinations (Mohler, 1993; Benvenuti et al., 2021), and (iii) that high herbicide use in ECS1 (3-year rotation with winter crops) selected against autumn/-winter germinating species and for species capable of germinating after herbicide applications (*i.e.* strict spring weed species).

The high proportion of perennials in ECS5 and FCS3 could not be attributed to the same reasons. First, herbicides in ECS1/ECS3/ECS4 and FCS2/FCS4/FCS7 allowed an efficient management of *C. arvense/Rumex* spp. and *P. lanceolata/C. vulgare*, the two dominant couples of perennials in the CS experiment and farmers' network, respectively. Second, technical difficulties in one of the two ECS5 plot did not allow a successful establishment of alfalfa, which has previously been shown to be an efficient weed management tool (*i.e.* through repeated mowing operations) against perennials in herbicide-free CSs (Lukashyk et al., 2008; Lacroix et al., 2021). Finally, the proportion of perennials was high in FCS3 because reduced tillage intensity was not coherently compensated by other efficient agronomic levers such as a diversified crop sequence including cover cropping, as farmers do when transitioning to conservation agriculture (Chauhan et al., 2012; Derrouch et al., 2020).

4.3. Insights on how and when to assess weed diversity

One of the originalities of our study was to assess weed diversity from a taxonomic and functional point of view, based on density or biomass, and at the quadrat, plot:year and plurennial scales. The results provide insights for future works to guide weed sampling and computation of diversity indices.

4.3.1. Gain to move from a taxonomic to a functional point of view

Our results showed that functional diversity provided little additional insight compared to taxonomy-based diversity indicators (*i.e.* species richness and Shannon diversity index). The ranking between ECS or FCS was highly consistent across all taxonomic and functional diversity indicators. In the CS experiment, Rao's quadratic entropy and taxonomy-based indicators showed highly significant correlations (see Supplementary Table 3). This can be explained by the relatively small species pool of our study sites and the fact that the five most abundant species of the experiment were functionally unique. Therefore, an increase in species richness was necessarily associated with an increase in functional diversity. However, it is important to note that intraspecific trait variability was not considered (Kazakou et al., 2014; Yvoz et al., 2020a).

4.3.2. Describing weeds by their density or biomass

All the alternative ECSs showed greater weed diversity values than ECS1, whether indices were based on density or on biomass. Nevertheless, diversity indices based on density tended to magnify these differences. The species producing the most biomass within a CS were not necessarily the species found at greatest density (*e.g.* in ECS3, *A. myosuroides* was dominant in terms of biomass whereas *V. arvensis* was dominant in terms of density). Sampling weed biomass per species is often considered time consuming and is therefore substituted by weed density (Fried et al., 2008; Santín-Montanyá et al., 2013; Trichard et al., 2013; Mahaut et al., 2019) or weed cover (Hiltbrunner et al., 2008; Ulber et al., 2009), even though some authors have argued biomass as more relevant to compute diversity indices (Guo and Rundel, 1997). However, such considerations could have important implications. Density-based indicators do not reflect species' competitive ability, whereas biomass-based indicators gave more weight to competitive species. Therefore, density indicators appear relevant for species centered analysis (*i.e.* the diversity of successful reproductive strategies) whereas biomass indicators appear more suitable for agroecosystem centered analysis (*i.e.* the diversity of species which contributed to agroecosystem functioning, weed-crop competitive relationships).

4.3.3. Relation between diversity at different spatio-temporal scales

The assessment of weed diversity at different scales allowed us to appreciate weed diversity turnover between quadrats at the plot:year scale and between years at the plot scale. Species richness increased by roughly a 3-fold from the quadrat to the plot:year scale for all ECSs and by a 3- and 2-fold from the plot:year scale to the plot scale for ECS1/all FCS and all other ECS, respectively. Such low species turnover at the plot scale could be associated with generalist species which can tolerate a wide range of agronomic practices (Fried et al., 2010) or to weed samplings positioned late in the crop cycle causing an overlap between two crop seasons (Hanzlik and Gerowitt, 2016). This multi-scale approach also allows to conclude that all alternative ECSs (ECS2 to ECS5) harbored as many weed species a given year as ECS1 harbored over the whole length of the crop sequence. This was also the case in the farmers' network, in which FCS3 harbored as many weed species a given year as FCS2/FCS4/FCS7 harbored over the whole length of the crop sequence.

4.4. Differences between experimented and farmer cropping systems

All alternative ECS harbored higher weed diversity than the reference system, and were previously shown to limit yield losses due to weeds (Adeux et al., 2019a). All these alternative ECS expressed similar levels of weed diversity but weed functional response was dependent on the combination of the adopted farming practices. Conversely, weed diversity did not increase with crop diversification in the farmer's network. All FCSs expressed levels of weed diversity similar to ECS1, except FCS3. This could be explained by the short length of the CS diversification gradient explored in the farmers' network, in comparison with the CS experiment which resorted to highly differentiated agronomic options. Moreover, all FCS relied on high herbicide use, similar to that of ECS1. Nevertheless, previous studies have reported contradictory results concerning the effect of herbicide use on species richness: certain authors report little effect (Mahn and Helmecke, 1979; Derksen et al., 1995), while others highlight a negative effect (José-María et al., 2013).

The CS experiment highlighted that different options of CS diversification are available to increase weed diversity without deteriorating weed management. However, farmers remain reluctant to implement such innovative systems. Results collected in experimental stations can differ from those collected in farms because experimenters tend to explore extreme alternative strategies without having to assume the economic consequences (Deytieux et al., 2012). Reducing herbicide reliance requires long-term strategic weed management, which aims to prevent rather than to control weed infestations (Mace et al., 2007), while the current mainstream practices focus on control rather than on prevention (Wilson et al., 2008). Risk aversion also influences weed management strategies: farmers tend to minimize the risk of failure, even at the cost of reducing their economic performance (Doohan et al., 2010), while experimenters accept failure as a response of the agronomic practices tested. This is coherent with previous studies reporting higher herbicide use and lower weed diversity in commercial farming conditions than in experimental stations (Colbach and Cordeau, 2018).

5. Conclusions

Through an in-depth analysis of weed communities across a complete rotation cycle, we highlighted that diverse options of CS diversification could promote weed diversity at both the annual and plurennial scales. Reduction of herbicide use through CS diversification appeared as the main driver of increased weed diversity and efficient long-term weed management. Tillage, weed management and crop type appeared as the main drivers of weed community functional structure.

Due to the limited species pool, the functional diversity approach provided little additional insight compared to taxonomy-based diversity approach. However, CS effects on weed diversity were clearer at the plot:year (*i.e.* annual) than plot (*i.e.* plurennial) scale. CS diversification did not have the same effect in the farmers' network as in the CS experiment, possibly because all FCSs relied on high levels of herbicide use. These results suggest that diverse opportunities are available to promote weed diversity in commercial farming conditions or that further research is required to identify the factors limiting the transposability of these alternative ECSs in commercial farming conditions.

CRediT authorship contribution statement

Guillaume Adeux: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Séverin Yvoz:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – review & editing. **Luc Biju-Duval:** Investigation, Resources, Data curation. **Emilie Cadet:** Investigation, Resources, Data curation. **Pascal Farcy:** Investigation, Resources, Data curation. **Guillaume Fried:** Conceptualization, Writing – review & editing. **Jean-Philippe Guillemin:** Writing – review & editing, Project administration, Funding acquisition. **Dominique Meunier:** Investigation, Resources, Data curation. **Nicolas Munier-Jolain:** Writing – review & editing, Project administration, Funding acquisition, Supervision. **Sandrine Petit:** Writing – review & editing, Project administration, Funding acquisition, Supervision. **Stéphane Cordeau:** Conceptualization, Methodology, Writing – review & editing, Project administration, Funding acquisition, Supervision.

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

Acknowledgments

We would like to thank i) all members of the INRAE experimental station in Bretenière, FR whom carried out this field experiment with dedication (Philippe Chamoy, Benjamin Pouilly, Rodolphe Hugard, Violaine Deytieux, Pascal Marget), ii) all the people who carried out the weed surveys and farmers' interviews (Marc Buthiot, Emeline Felten, Eric Vieren, Bruno Chauvel, Claude Sarrasin) and iii) all the people that provided their scientific input during the diversity indicator meeting. Guillaume Adeux was funded during his Ph.D. by the International Ph.D. Programme in Agrobiodiversity of the Scuola Superiore Sant'Anna, Pisa, IT and INRAE, FR. Séverin Yvoz was funded by the European Union's Horizon 2020 research and innovation program under Grant agreement No. 727321 (IWM PRAISE) and the INRAE metaprogram "ecosystem services". Authors acknowledge financial support from INRAE, the French Burgundy Region, the French Project CoSAC (ANR-15-CE18-0007), the French 'Investissement d'Avenir' Program and the Project ISITE-BFC 'Agroecology in BFC' (contract ANR-15-IDEX-03).

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.eja.2021.126438.

References

Adeux, G., Munier-Jolain, N., Meunier, D., Farcy, P., Carlesi, S., Barberi, P., Cordeau, S., 2019a. Diversified grain-based cropping systems provide long-term weed control while limiting herbicide use and yield losses. Agron. Sustain. Dev. 39, 42.
Adeux, G., Vieren, E., Carlesi, S., Bàrberi, P., Munier-Jolain, N., Cordeau, S., 2019b. Mitigating crop yield losses through weed diversity. Nat. Sustain. 2, 1018–1026.
Albrecht, H., Cambecèdes, J., Lang, M., Wagner, M., 2016. Management options for the conservation of rare arable plants in Europe. Bot. Lett. 163, 389–415.
Andrade, J.F., Satorre, E.H., Ermácora, C., Poggio, S.L., 2017. Weed communities respond to changes in the diversity of crop sequence composition and double cropping. Weed Res. 57, 148–158.
Andreasen, C., Stryhn, H., Streibig, J., 1996. Decline of the flora in Danish arable fields. J. Appl. Ecol. 33, 619–626.
Baessler, C., Klotz, S., 2006. Effects of changes in agricultural land-use on landscape structure and arable weed vegetation over the last 50 years. Agric. Ecosyst. Environ. 115, 43–50.
Bàrberi, P., Bocci, G., Carlesi, S., Armengot, L., Blanco-Moreno, J.M., Sans, F.X., 2018. Linking species traits to agroecosystem services: a functional analysis of weed communities. Weed Res. 58, 76–88.
Barralis, G., 1976. Méthode d'étude des groupements adventices des cultures annuelles. Ve Colloque International sur l'Ecologie et la Biologie des Mauvaises herbes. COLUMA, Paris, France, pp. 59–68.
Benvenuti, S., Selvi, M., Mercati, S., Cardinali, G., Mercati, V., Mazzoncini, M., 2021. Stale seedbed preparation for sustainable weed seed bank management in organic cropping systems. Sci. Hortic. 289, 110453.
Blaix, C., Moonen, A.C., Dostatny, D., Izquierdo, J., Le Corff, J., Morrison, J., Von Redwitz, C., Schumacher, M., Westerman, P., 2018. Quantification of regulating ecosystem services provided by weeds in annual cropping systems using a systematic map approach. Weed Res. 58, 151–164.
Blumhorst, M.R., Weber, J.B., Swain, L.R., 1990. Efficacy of selected herbicides as influenced by soil properties. Weed Technol. 4, 279–283.
Booth, B.D., Swanton, C.J., 2002. Assembly theory applied to weed communities. Weed Sci. 50, 2–13.
Botta-Dukát, Z., 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. J. Veg. Sci. 16, 533–540.
Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Machler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9, 378–400.
Chamorro, L., Masalles, R., Sans, F., 2016. Arable weed decline in Northeast Spain: does organic farming recover functional biodiversity? Agric. Ecosyst. Environ. 223, 1–9.
Chauhan, B.S., Singh, R.G., Mahajan, G., 2012. Ecology and management of weeds under conservation agriculture: a review. Crop Prot. 38, 57–65.
Cirujeda, A., Marí, A.I., Murillo, S., Aibar, J., Pardo, G., Solé-Senan, X.-O., 2019. May the inclusion of a legume crop change weed composition in cereal fields? Example of Sainfoin in Aragon (Spain). Agronomy 9, 134.
Colbach, N., Cordeau, S., 2018. Reduced herbicide use does not increase crop yield loss if it is compensated by alternative preventive and curative measures. Eur. J. Agron. 94, 67–78.
Colbach, N., Petit, S., Chauvel, B., Deytieux, V., Lechenet, M., Munier-Jolain, N., Cordeau, S., 2020. The pitfalls of relating weeds, herbicide use and crop yield: don't fall into the trap! A critical review. Front. Agron. 2. ⟨https://www.frontiersin.org/articles/10.3389/fagro.2020.615470/⟩.
Cordeau, S., Guillemin, J.P., Reibel, C., Chauvel, B., 2015. Weed species differ in their ability to emerge in no-till systems that include cover crops. Ann. Appl. Biol. 166, 444–455.
Cousens, R., 1985. A simple model relating yield loss to weed density. Ann. Appl. Biol. 107, 239–252.
Derksen, D., Thomas, A., Lafond, G., Loeppky, H., Swanton, C., 1995. Impact of post-emergence herbicides on weed community diversity within conservation-tillage systems. Weed Res. 35, 311–320.
Derrouch, D., Chauvel, B., Felten, E., Dessaint, F., 2020. Weed management in the transition to conservation agriculture: farmers' response. Agronomy 10, 843.
Deytieux, V., Nemecek, T., Freiermuth Knuchel, R., Gaillard, G., Munier-Jolain, N.M., 2012. Is integrated weed management efficient for reducing environmental impacts of cropping systems? A case study based on life cycle assessment. Eur. J. Agron. 36, 55–65.
Deytieux, V., Munier-Jolain, N., Caneill, J., 2016. Assessing the sustainability of cropping systems in single- and multi-site studies. A review of methods. Eur. J. Agron. 72, 107–126.
Doohan, D., Wilson, R., Canales, E., Parker, J., 2010. Investigating the human dimension of weed management: new tools of the trade. Weed Sci. 58, 503–510.
Dorado, J., Lopez-Fando, C., 2006. The effect of tillage system and use of a paraplow on weed flora in a semiarid soil from central Spain. Weed Res. 46, 424–431.
Doucet, C., Weaver, S.E., Hamill, A.S., Zhang, J., 1999. Separating the effects of crop rotation from weed management on weed density and diversity. Weed Sci. 47, 729–735.
Fried, G., Norton, L.R., Reboud, X., 2008. Environmental and management factors determining weed species composition and diversity in France. Agric. Ecosyst. Environ. 128, 68–76.
Fried, G., Petit, S., Dessaint, F., Reboud, X., 2009. Arable weed decline in Northern France: crop edges as refugia for weed conservation? Biol. Conserv. 142, 238–243.
Fried, G., Petit, S., Reboud, X., 2010. A specialist-generalist classification of the arable flora and its response to changes in agricultural practices. BMC Ecol. 10, 1–11.
Fried, G., Kazakou, E., Gaba, S., 2012. Trajectories of weed communities explained by traits associated with species' response to management practices. Agric. Ecosyst. Environ. 158, 147–155.
Froud-Williams, R., 1988. Changes in weed flora with different tillage and agronomic management systems. Weed Management in Agroecosystems: Ecological Approaches. CRC Press, Boca Raton, FL, pp. 213–236.
Gardarin, A., Dürr, C., Colbach, N., 2009. Which model species for weed seedbank and emergence studies? A review. Weed Res. 49, 117–130.

Garnier, E., Navas, M.-L., 2012. A trait-based approach to comparative functional plant ecology: concepts, methods and applications for agroecology. A review. Agron. Sustain. Dev. 32, 365–399.
Giambalvo, D., Ruisi, P., Saia, S., Di Miceli, G., Frenda, A.S., Amato, G., 2012. Faba bean grain yield, N 2 fixation, and weed infestation in a long-term tillage experiment under rainfed Mediterranean conditions. Plant Soil 360, 215–227.
Gressel, J., LeBaron, H.M.E., 1982. Herbicide Resistance in Plants. Wiley.
Gross, N., Le Bagousse-Pinguet, Y., Liancourt, P., Berdugo, M., Gotelli, N.J., Maestre, F. T., 2017. Functional trait diversity maximizes ecosystem multifunctionality. Nat. Ecol. Evol. 1, 1–9.
Gunton, R.M., Petit, S., Gaba, S., 2011. Functional traits relating arable weed communities to crop characteristics. J. Veg. Sci. 22, 541–550.
Guo, Q., Rundel, P.W., 1997. Measuring dominance and diversity in ecological communities: choosing the right variables. J. Veg. Sci. 8, 405–408.
Haas, H., 1982. Changing patterns of weed distribution as a result of herbicide use and other agronomic factors. Herbic. Resist. Plants 57–79.
Hanzlik, K., Gerowitt, B., 2016. Methods to conduct and analyse weed surveys in arable farming: a review. Agron. Sustain. Dev. 36, 11.
Hartig, F., 2020. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R Package Version 0.2.7.
Hernández Plaza, E., Navarrete, L., González-Andújar, J.L., 2015. Intensity of soil disturbance shapes response trait diversity of weed communities: the long-term effects of different tillage systems. Agric. Ecosyst. Environ. 207, 101–108.
Hiltbrunner, J., Scherrer, C., Streit, B., Jeanneret, P., Zihlmann, U., Tschachtli, R., 2008. Long-term weed community dynamics in Swiss organic and integrated farming systems. Weed Res. 48, 360–369.
Hooper, D.U., Chapin, F.S., Ewel, J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D., Loreau, M., Naeem, S., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. 75, 3–35.
Hyvönen, T., Salonen, J., 2002. Weed species diversity and community composition in cropping practices at two intensity levels–a six-year experiment. Plant Ecol. 159, 73–81.
Jabran, K., Mahmood, K., Melander, B., Bajwa, A.A., Kudsk, P., 2017. Chapter three – weed dynamics and management in wheat. In: Sparks, D.L. (Ed.), Advances in Agronomy. Academic Press, pp. 97–166.
José-María, L., Armengot, L., Chamorro, L., Xavier Sans, F., 2013. The conservation of arable weeds at crop edges of barley fields in northeast Spain: arable plants at crop edges. Ann. Appl. Biol. 163, 47–55.
Kazakou, E., Violle, C., Roumet, C., Navas, M.L., Vile, D., Kattge, J., Garnier, E., 2014. Are trait-based species rankings consistent across data sets and spatial scales? J. Veg. Sci. 25, 235–247.
Kew, R.B.G., 2020. Seed Information Database (SID). Version 7.1.
Kleijn, D., van der Voort, L.A., 1997. Conservation headlands for rare arable weeds: the effects of fertilizer application and light penetration on plant growth. Biol. Conserv. 81, 57–67.
Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G. M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J.G., Jackel, A.-K., Kühn, I., Kunzmann, D., Ozinga, W. A., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg, O., Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E., Peco, B., 2008. The LEDA traitbase: a database of life-history traits of the Northwest European flora. J. Ecol. 96, 1266–1274.
Koocheki, A., Nassiri, M., Alimoradi, L., Ghorbani, R., 2009. Effect of cropping systems and crop rotations on weeds. Agron. Sustain. Dev. 29, 401–408.
Kühn, I., Durka, W., Klotz, S., 2004. BiolFlor: a new plant-trait database as a tool for plant invasion ecology. Divers. Distrib. 10, 363–365.
Lacroix, O., Aubertot, J.-N., Bohanec, M., Cordeau, S., Corrales, D.C., Robin, M.H., 2021. IPSIM-Cirsium, a qualitative expert-based model to predict infestations of Cirsium arvense. Front. Agron. 3, 1–16.
Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91, 299–305.
Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S., Garden, D., Dorrough, J., Berman, S., Quétier, F., Thébault, A., Bonis, A., 2008. Assessing functional diversity in the field–methodology matters! Funct. Ecol. 22, 134–147.
Lechenet, M., Dessaint, F., Py, G., Makowski, D., Munier-Jolain, N., 2017a. Reducing pesticide use while preserving crop productivity and profitability on arable farms. Nat. Plants 3, 17008.
Lechenet, M., Deytieux, V., Antichi, D., Aubertot, J.-N., Bàrberi, P., Bertrand, M., Cellier, V., Charles, R., Colnenne-David, C., Dachbrodt-Saaydeh, S., Debaeke, P., Doré, T., Farcy, P., Fernandez-Quintanilla, C., Grandeau, G., Hawes, C., Jouy, L., Justes, E., Kierzek, R., Kudsk, P., Lamichhane, J.R., Lescourret, F., Mazzoncini, M., Melander, B., Messéan, A., Moonen, A.-C., Newton, A.C., Nolot, J.-M., Panozzo, S., Retaureau, P., Sattin, M., Schwarz, J., Toqué, C., Vasileiadis, V.P., Munier-Jolain, N., 2017b. Diversity of methodologies to experiment integrated pest management in arable cropping systems: analysis and reflections based on a European network. Eur. J. Agron. 83, 86–99.
Légère, A., Stevenson, F.C., Benoit, D.L., 2005. Diversity and assembly of weed communities: contrasting responses across cropping systems. Weed Res. 45, 303–315.
Lenth, R., 2019. emmeans: Estimated Marginal Means, aka Least-Squares Means. R Package Version 1.3.5.
Liebman, M., Mohler, C.L., Staver, C.P., 2001. Ecological Management of Agricultural Weeds. Cambridge University Press.
Lukashyk, P., Berg, M., Köpke, U., 2008. Strategies to control Canada thistle (Cirsium arvense) under organic farming conditions. Renew. Agric. Food Syst. 23, 13–18.
Mace, K., Morlon, P., Munier-Jolain, N., Quere, L., 2007. Time scales as a factor in decision-making by French farmers on weed management in annual crops. Agric. Syst. 93, 115–142.
Mahaut, L., Gaba, S., Fried, G., 2019. A functional diversity approach of crop sequences reveals that weed diversity and abundance show different responses to environmental variability. J. Appl. Ecol. 56, 1400–1409.
Mahn, E.G., Helmecke, K., 1979. Effects of herbicide treatment on the structure and functioning of agro-ecosystems II. Structural changes in the plant community after the application of herbicides over several years. Agro-Ecosystems 5, 159–179.
Marshall, E.J.P., Brown, V.K., Boatman, N.D., Lutman, P.J.W., Squire, G.R., Ward, L.K., 2003. The role of weeds in supporting biological diversity within crop fields. Weed Res. 43, 77–89.
Milberg, P., Hallgren, E., 2004. Yield loss due to weeds in cereals and its large-scale variability in Sweden. Field Crop. Res. 86, 199–209.
Mirsky, S.B., Ryan, M.R., Teasdale, J.R., Curran, W.S., Reberg-Horton, C.S., Spargo, J.T., Wells, M.S., Keene, C.L., Moyer, J.W., 2013. Overcoming weed management challenges in cover crop–based organic rotational no-till soybean production in the Eastern United States. Weed Technol. 27, 193–203.
Mohler, C.L., 1993. A model of the effects of tillage on emergence of weed seedlings. Ecol. Appl. 3, 53–73.
Mohler, C.L., Frisch, J.C., McCulloch, C.E., 2006. Vertical movement of weed seed surrogates by tillage implements and natural processes. Soil Tillage Res. 86, 110–122.
Murphy, S.D., Clements, D.R., Belaoussoff, S., Kevan, P.G., Swanton, C.J., 2006. Promotion of weed species diversity and reduction of weed seedbanks with conservation tillage and crop rotation. Weed Sci. 54, 69–77.
Neve, P., Barney, J.N., Buckley, Y., Cousens, R.D., Graham, S., Jordan, N.R., Lawton-Rauh, A., Liebman, M., Mesgaran, M.B., Schut, M., Shaw, J., Storkey, J., Baraibar, B., Baucom, R.S., Chalak, M., Childs, D.Z., Christensen, S., Eizenberg, H., Fernández-Quintanilla, C., French, K., Harsch, M., Heijting, S., Harrison, L., Loddo, D., Macel, M., Maczey, N., Merotto, A., Mortensen, D., Necajeva, J., Peltzer, D.A., Recasens, J., Renton, M., Riemens, M., Sønderskov, M., Williams, M., 2018. Reviewing research priorities in weed ecology, evolution and management: a horizon scan. Weed Res. 58, 250–258.
Nicholls, C.I., Altieri, M.A., 2013. Plant biodiversity enhances bees and other insect pollinators in agroecosystems. A review. Agron. Sustain. Dev. 33, 257–274.
Nikolich, L., Milošević, D., Seremesich, S., Dalovich, I., Vuga-Janjatov, V., 2012. Diversity of weed flora in wheat depending on crop rotation and fertilisation. Bulg. J. Agric. Sci.
Pardo, G., Cirujeda, A., Perea, F., Verdú, A., Mas, M., Urbano, J., 2019. Effects of reduced and conventional tillage on weed communities: results of a long-term experiment in southwestern Spain. Planta Daninha 37, 37.
Peter, C.J., Weber, J.B., 1985. Adsorption, mobility, and efficacy of alachlor and metolachlor as influenced by soil properties. Weed Sci. 33, 874–881.
Plaza, E.H., Kozak, M., Navarrete, L., González-Andújar, J.L., 2011. Tillage system did not affect weed diversity in a 23-year experiment in Mediterranean dryland. Agric. Ecosyst. Environ. 140, 102–105.
Pocock, M.J., Evans, D.M., Memmott, J., 2012. The robustness and restoration of a network of ecological networks. Science 335, 973–977.
Poggio, S.L., Satorre, E.H., de la Fuente, E.B., 2004. Structure of weed communities occurring in pea and wheat crops in the Rolling Pampa (Argentina). Agric. Ecosyst. Environ. 103, 225–235.
Quinio, M., De Waele, M., Dessaint, F., Biju-Duval, L., Buthiot, M., Cadet, E., Bybee-Finley, A.K., Guillemin, J.-P., Cordeau, S., 2017. Separating the confounding effects of farming practices on weeds and winter wheat production using path modelling. Eur. J. Agron. 82, 134–143.
R Core Team, 2016. R: A Language and Environment for Statistical Comput-ing. R Foundation for Statistical Computing, Vienna, Austria.
Ricotta, C., Moretti, M., 2011. CWM and Rao's quadratic diversity: a unified framework for functional ecology. Oecologia 167, 181–188.
Ryan, M.R., Smith, R.G., Mirsky, S.B., Mortensen, D.A., Seidel, R., 2010. Management filters and species traits: weed community assembly in long-term organic and conventional systems. Weed Sci. 58, 265–277.
Santín-Montanyá, M.I., Martín-Lammerding, D., Walter, I., Zambrana, E., Tenorio, J.L., 2013. Effects of tillage, crop systems and fertilization on weed abundance and diversity in 4-year dry land winter wheat. Eur. J. Agron. 48, 43–49.
Scheiner, S.M., 2012. Biological diversity: frontiers in measurement and assessment. In: Magurran, Anne E., McGill, Brian J. (Eds.), The Quarterly Review of Biology, 87.
Schuldt, A., Ebeling, A., Kunz, M., Staab, M., Guimarães-Steinicke, C., Bachmann, D., Buchmann, N., Durka, W., Fichtner, A., Fornoff, F., Härdtle, W., Hertzog, L.R., Klein, A.-M., Roscher, C., Schaller, J., von Oheimb, G., Weigelt, A., Weisser, W., Wirth, C., Zhang, J., Bruelheide, H., Eisenhauer, N., 2019. Multiple plant diversity components drive consumer communities across ecosystems. Nat. Commun. 10, 1460.
Schumacher, M., Ohnmacht, S., Rosenstein, R., Gerhards, R., 2018. How management factors influence weed communities of cereals, their diversity and endangered weed species in Central Europe. Agriculture 8, 172.
Šmilauer, P., Lepš, J., 2014. Multivariate Analysis of Ecological Data using CANOCO 5. Cambridge University Press, Cambridge.
Sosnoskie, L.M., Herms, N.P., Cardina, J., 2006. Weed seedbank community composition in a 35-yr-old tillage and rotation experiment. Weed Sci. 54, 263–273.
Stoate, C., Boatman, N.D., Borralho, R.J., Carvalho, C.R., Snoo, G.R.d., Eden, P., 2001. Ecological impacts of arable intensification in Europe. J. Environ. Manag. 63, 337–365.
Storkey, J., Neve, P., 2018. What good is weed diversity? Weed Res. 58, 239–243.

Sutcliffe, O.L., Kay, Q.O., 2000. Changes in the arable flora of central southern England since the 1960s. Biol. Conserv. 93, 1–8.

Swanton, C.J., Weise, S.F., 1991. Integrated weed management: the rationale and approach. Weed Technol. 5, 657–663.

Tarjuelo, R., Morales, M.B., Arribas, L., Traba, J., 2019. Abundance of weeds and seeds but not of arthropods differs between arable habitats in an extensive Mediterranean farming system. Ecol. Res. 34, 624–636.

Thomas, A.G., Derksen, D.A., Blackshaw, R.E., Van Acker, R.C., Légère, A., Watson, P.R., Turnbull, G.C., 2004. A multistudy approach to understanding weed population shifts in medium- to long-term tillage systems. Weed Sci. 52, 874–880.

Trichard, A., Alignier, A., Chauvel, B., Petit, S., 2013. Identification of weed community traits response to conservation agriculture. Agric. Ecosyst. Environ. 179, 179–186.

Turnbull, L.A., Rees, M., Crawley, M.J., 1999. Seed mass and the competition/colonization trade-off: a sowing experiment. J. Ecol. 87, 899–912.

Ulber, L., Steinmann, H.-H., Klimek, S., Isselstein, J., 2009. An on-farm approach to investigate the impact of diversified crop rotations on weed species richness and composition in winter wheat. Weed Res. 49, 534–543.

Víllora, R.A., Plaza, E.H., Navarrete, L., Sánchez, M., Sánchez, A., 2019. Climate and tillage system drive weed communities' functional diversity in a Mediterranean cereal-legume rotation. Agric. Ecosyst. Environ. 283, 106574.

Vissoh, P., Mongbo, R., Gbèhounou, G., Hounkonnou, D., Ahanchédé, A., Röling, N., Kuyper, T., 2007. The social construction of weeds: different reactions to an emergent problem by farmers, officials and researchers. Int. J. Agric. Sustain. 5, 161–175.

Weibull, A.-C., Östman, Ö., Granqvist, Å., 2003. Species richness in agroecosystems: the effect of landscape, habitat and farm management. Biodivers. Conserv. 12, 1335–1355.

Weisberger, D., Nichols, V., Liebman, M., 2019. Does diversifying crop rotations suppress weeds? A meta-analysis. PLOS ONE 14, e0219847.

Wezel, A., Casagrande, M., Celette, F., Vian, J.-F., Ferrer, A., Peigné, J., 2014. Agroecological practices for sustainable agriculture. A review. Agron. Sustain. Dev. 34, 1–20.

Wilson, B., Wright, K., 1990. Predicting the growth and competitive effects of annual weeds in wheat. Weed Res. 30, 201–211.

Wilson, R.S., Tucker, M.A., Hooker, N.H., LeJeune, J.T., Doohan, D., 2008. Perceptions and beliefs about weed management: perspectives of Ohio grain and produce farmers. Weed Technol. 22, 339–350.

Yvoz, S., Cordeau, S., Zuccolo, C., Petit, S., 2020a. Crop type and within-field location as sources of intraspecific variations in the phenology and the production of floral and fruit resources by weeds. Agric. Ecosyst. Environ. 302, 107082.

Yvoz, S., Petit, S., Biju-Duval, L., Cordeau, S., 2020b. A framework to type crop management strategies within a production situation to improve the comprehension of weed communities. Eur. J. Agron. 115, 10.