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

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Abstract

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

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

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Introduction

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

Farming practices such as crop type, tillage regime, herbicide and fertiliser use are the main factors shaping weed community composition and structure (Andersson & Milberg 1998; Cordeau et al. 2017b; Fried, Norton & Reboud 2008; Stevenson et al. 1997). It is often suggested that the edge of arable fields, which corresponds to the small disturbed area between the adjacent perennial field margin and the first row of the crop, could play a major role in the maintenance of weed diversity at the field scale (Rotchés-Ribalta et al. 2015). These edges have been shown to shelter up to twice as many weed species as the adjacent field cores (Cordeau, Petit, Reboud & Chauvel 2012b) and although this differential can vary greatly depending on the farming practices conducted in the field (de Snoo 1997; José-María, Armengot, Chamorro & Xavier Sans 2013). Poggio, Chaneton and Ghersa (2013) thus showed field edge a higher richness of geophyte and therophyte species than the interior of the field. A current limitation in our understanding of the role of field edges in the maintenance of functional weed diversity in arable landscapes stems from the fact that comparisons between weed communities in field edges and their adjacent field cores have only been documented for few crop types. Moreover, weed survey is usually conducted for one year and for one crop type (Bourgeois, Gaba, Plumejeaud & Bretagnolle 2020; Metcalfe, Hassall, Boinot & Storkey 2019; Pinke & Gunton 2014). This most likely underestimates weed functional diversity as crop type is a strong environmental filter allowing a small portion of the weed seedbank diversity to be observed as emerged plants in a particular year (Fried, Norton & Reboud 2008). A field survey over a diversified crop succession would provide a more reliable basis for comparing the weed flora in the core and in the edge of the same field. A pooling of data collected in the same location over consecutive annual surveys would give a more accurate picture of the differences in the diversity and composition of the weed flora in the two habitats, closer to the composition of the soil seedbank (Sjursen 2001), which is associated with the past farming practices applied in the field (Hawes et al. 2010; Rotchés-Ribalta, Sans, Mayer & Mäder 2020).

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

One way to assess the relative contribution of these two processes and the real contribution of field edges in functional weed diversity is to compare the taxonomic and functional composition of field edge weed flora to field core communities. Functional weed ecology approaches have proven successful in investigating how different factors select for or against different types of weeds, resulting in different levels of weed diversity (*e.g.* José-María et al. (2011); Ryan et al. (2010); Storkey et al. (2010); Cordeau et al. (2017a)). Comparisons of the distribution of key weed response traits in field edges and field cores could help deciphering the relative role of the ecological processes at play. For example, the spillover of species from the grass margin to the field edge would be reflected by a high proportion of perennials such as geophytes and hemicryptophytes (*e.g.* Grime’s competitive and competitive/ruderal strategies). Field edges could also shelter species expressing a shade avoidance syndrome (high height and low specific leaf area) not observed in field cores (Perronne, Gaba, Cadet & Le Corre 2014).

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

Materials and methods

Study system

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

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

Weed surveys

Weed surveys were carried out annually between 2008 and 2013 in the 60 fields. The timing of the survey was adapted to the crop type and conducted after most of the weeding operations (*i.e.* March for winter crops, April for spring crops and June for summer crops). In each field and year, weed communities were surveyed the same day in the core and the edge of the field, leading to a dataset of 720 annual weed surveys (60 fields x 2 locations x 6 years). As described by Yvoz, Petit, Biju-Duval & Cordeau (2020), weeds were recorded in the field core following a “W” pattern within a 2000 m² area (50 m by 40 m, real prospected area 130 m by 1.5 m) located 20 m away from the adjacent perennial field margin (Fig. 1). Weeds were recorded in the field edge in a 50 m linear transect alongside the adjacent perennial field margin, in front of the field core sampled area. The width of this sampled area corresponded to the space between the first row of the crop and the grass margin, *i.e.* averaging 30 cm width. The prospected areas differed between both locations because i) our sampling design required both sampled areas to be in front of each other to ensure a meaningful comparison of weed flora and ii) because field edge harboured higher weed richness and abundance than the field core in the study area, thus allowing a smaller prospected area to assess the composition of weed flora (*e.g.* 80% of the weed diversity) (He & Legendre 2002). In both areas, weeds were identified to the species level except for 16 taxa of the 147 identified, and named according to Jauzein (1995). Their abundance was estimated visually using the scale developed by Barralis (1976) with six classes of density (one individual in the prospected area, <1, 1-2, 3-20, 21-50, and 51-100 individuals.m^{-2}). The total weed abundance was computed using the centre of each density class (0.0005, 0.5, 1.5, 11.5, 35.5, and 75.5 individuals.m^{-2}, respectively) to be able to sum species densities. To study the global effect of the within-field location (field core or field edge) and the crop management strategy on the weed functional traits, independently of the effects of the crop and the year, we focussed on the cumulated weed surveys over the six-year period. Thus, for the core and the edge of the 60 fields, we averaged the abundance of the six annual surveys for each species (null abundance when the species was not observed). Subsequent analyses were applied on these 120 weed assemblages over six years (60 fields x 2 locations), called hereafter cumulated weed surveys.

Weed species traits and ecological descriptors

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

Statistical analyses

All statistical analyses were implemented with the R software version 4.0.2 (R Core Team 2020). The 120 cumulated weed surveys were first described by five metrics: species richness (Sp_Richness), total abundance (Abundance), Pielou's equitability index (Evenness), Rao's functional diversity (Rao_FD) and inter-annual species turnover (Turnover) (See correlations between metrics in Appendix A: Fig. 1). The functional diversity was calculated as the Rao's quadratic entropy (Botta-Dukát 2005) computed from the species-species distance matrix based on the eleven functional traits (Table 1) using the dbFD function from the [FD] package. The turnover was calculated as $(b + c)/(a + b + c)$, where b and c are the number of species gained and lost between two successive years, respectively, and a the number of species observed in both years, (*i.e.* 2008/2009, 2009/2010, 2010/2011, 2011/2012, 2012/2013). The turnover was computed using the function turnover from the package [codyn], then averaged for each weed survey over the six-year period. Turnover ranges from 0 to 1 and is high when the proportion of species shared between two successive years is low.

Weed survey composition

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

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

Trait distributions

We compared the distribution of the eleven functional traits (Table 1) between field edge and field core surveys for each crop management strategy. Within each of the five crop management strategies we compared the distribution of the nine quantitative traits (Gaussian kernel density estimation weighted by the relative abundance of each species calculated with the *density* function in R) between the core and the edge of the field using the approach described by Perronne et al. (2014) and Bourgeois et al. (2019). We computed the dissimilarity of traits distribution by calculating the proportion of the distributions in common between the two within-field locations (overlapTrue function from the [overlap] package). We used a randomization method to test whether the overlap between within-field locations in each crop management strategy was significantly lower than the null hypothesis (random layout of the weed surveys between within-field locations). The randomization procedure was implemented within each crop management strategy by random permutations of the cumulated weed surveys between field edges and field cores. Thus, we generated 10 000 random distributions and implemented a one-tailed direct test of significance for the non-random structure (p-values < 0.05). P-values were estimated as the proportion of random distributions having an overlap value lower than the observed overlap. Adjustments based on the calculation of the false discovery rate (Benjamini & Hochberg 1995) were applied per functional trait to deal with multiple comparisons within the five crop management strategies. For the two qualitative traits, we assessed the differences in category distributions between the edge and the core of each crop management strategy by Monte-Carlo simulation tests based on 10,000 replicates.

Weed functional groups

To integrate simultaneously all eleven traits, we classified the 147 observed weed species into functional groups and compared their relative representation according to Within-field locations and Crop management strategies. Firstly, we implemented a Hill and Smith multivariate analysis (Hill & Smith 1976) on the eleven quantitative and qualitative functional traits (Table 1) with the *dudi.hillsmith* function from the [ade4] package. Quantitative traits were centred and standardised before implementing the multivariate analysis. Based on the distance matrix from the Hill and Smith analysis, we then identified species functional groups using a Hierarchical Clustering Analysis (HCA) with the *HCPC* function from the [FactoMineR] package. Functional groups were identified by an agglomerative hierarchical clustering following the Ward's method and clusters were not consolidated. The number of clusters kept was decided after examination of the dendrogram and confirmed using the gain of explained variance when increasing the number of clusters. Trait levels belonging to each functional group were finely described using a one-way analysis of variance (*catdes* function from the [FactoMineR] package). Secondly, we compared the relative distribution of the functional groups between the field edge and the field core of the five crop management strategies. The effects of Strategy, Within-field location and their interaction on the distribution of the functional groups were carried out using a test of independence with the *mosaic* function from the [vcd] package. Significance of the effects was tested using a Pearson Chi-squared test with the *assocstats* function from the [vcd] package.

Interannual stability of the weed functional groups

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

Results

Weed survey structure and composition

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

Compositions of the 120 weed surveys differed between Within-field location and Strategy (Appendix A: Fig. 2A, p-values < 0.001), but not by their interaction. Field edge surveys were more associated with grass species (*e.g. Elytrigia repens*, *Alopecurus myosuroides*, *Bromus* sp., *Lolium* sp., *Poa annua*) and perennials (*e.g. Daucus carota*, *Galium mollugo*, *Achillea millefolium*) than field core surveys (Appendix A: Fig. 2B). Overall, all species were more associated with field edges than field cores due to their higher abundance in field edges. Field cores of S7 and S8, were characterised by summer-germinated species (*i.e. Aethusa cynapium*, *Persicaria maculosa* and *Solanum nigrum*). The analysis of variance homogeneity showed no significant differences between strategies nor between combinations of Within-field location and Strategy (p-values > 0.05). However, the composition of weed surveys in field cores was more variable than those of field edges (p-value < 0.001), as shown by the wider ellipses for field cores (Appendix A: Fig. 2A).

Functional traits distribution

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

Weed functional groups

The 147 weed species were grouped into five functional groups (Appendix A: Fig. 3). All traits, except Ellenberg.N and Ellenberg.L significantly contributed to the grouping (p-values < 0.001). The functional group FG1 included 14 weed species (Appendix A: Fig. 3C) with low SLA and Flow.dur values, but high Height and Seed.mass values (Fig. 4). Geophyte species were over-represented in this group. The group FG2 was composed of48 weed species (Appendix A: Fig. 3C) with low SLA, Germ.dur and Flow.dur values, but high Height, Germ.onset and Flow.onset values (Fig. 4). Forb and hemicryptophyte species were over-represented in this group. The group FG3 was formed by13 weed species (Appendix A: Fig.

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

Interannual stability of the weed functional groups

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

Discussion

Our analysis of weed surveys cumulated at a pluri-annual scale confirmed the findings of previous studies conducted at an annual scale, namely that field edges are significantly richer and more diverse in species than their associated field cores. Besides, the smaller area of the survey in field edge compared to field core should negatively impact the species richness estimation, thus the differences between locations may be higher. However, we showed that different processes acting simultaneously lead to a higher weed species functional diversity in field edges in comparison to field cores. The edge of fields harboured species with particular combination of traits (*i.e.* FG1 and FG3) generally associated with the adjacent perennial field margin, and their occurrence in field edges was almost constant across years. In addition, field edges also sheltered species typically observed in field cores (*i.e.* FG4), and in much larger numbers than field cores. Our pluri-annual analysis also revealed that core and edge weed surveys differed less, taxonomically and functionally, when the crop management strategy implemented in the field was less intensive. The observed higher taxonomic and functional diversity and the higher temporal stability of the weed flora of field edges converge to highlight their role in the maintenance of weed diversity in agricultural landscapes, especially when crop management intensity is high.

The composition of field edge weed surveys

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

It is also often suggested that the high weed richness observed in field edges results from the lower level of disturbance of these habitats compared to the core of the fields (Pinke & Gunton 2014). Our analysis of trait distributions aligns with this explanation. We observed higher seed mass and height in field edge surveys, indicative of a less intense soil disturbance, since small plants with high production of small seeds are highly adapted to soil tillage (Gaba et al. 2017). The wider distribution of some traits in field edges compared to field cores, particularly the germination duration and the flowering onset, also suggests that the ecological niche in field cores is smaller than that of field edges. Under intensive crop management, the standard deviation of traits is reduced (Bourgeois et al. 2019) and the number of species able to survive as well. Indeed, we showed here that field cores were dominated by ruderal species (FG4), while field edges expressed more even distribution of the five weed functional groups.

Surprisingly, we found that indicator values for Nitrogen (Ellenberg.N) were higher in field edges than in field cores. This could be explained by the combination of two factors: a high quantity of in-crop nitrogen fertilisation (Kleijn & van der Voort 1997) and a low crop use in the edge of the field compared to the core, leading to more resources available for nitrophilous weed species. The study area is indeed characterised by a high proportion of highly nitrogen-demanding winter crops such as oilseed rape, mustard and winter cereals. Similarly, we expected field edge surveys to exhibit a higher affinity for light (*i.e.* Ellenberg.L) than field core surveys, as the amount of photosynthetically active radiation is higher in the field edge than in the field core of the studied fields (Yvoz, Cordeau, Zuccolo & Petit 2020). The lack of such signal could result from the variability of the growing conditions over time linked to the succession of crops with various heights and growth habits, combined with a variability of surrounding vegetation and semi-natural habitats leading to a high competition for light, even in field edges (Seifert, Leuschner, Meyer & Culmsee 2014). This would be in line with the results of Perronne et al. (2014) showing a shade-tolerant syndrome in weeds both in field edges and field cores. Finally, we cannot exclude that the Ellenberg-N and L values of weed communities in field edges may have been influenced by the spillover of species coming from the adjacent perennial grass margin. In our study, most weed species occurring in field edges were present every year over the 6-year sequence. This could result from a continuous influx of propagules from the adjacent perennial grass margin (Blumenthal & Jordan 2001). Alternatively, these species could establish more permanently in the field edges, which would imply that their traits are adapted to the ecological filters acting in field edges, notably herbicide applications and tillage operations.

Response of field edge weed surveys to crop management strategies

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

It is likely that crop management strategies affected field edge weed diversity in this study, as shown in previous studies (Romero, Chamorro & Sans 2008). The fact that we used weed data surveyed over six consecutive years enabled us to detect signals regarding weed response to long-term management strategies, including the type of crop rotation. Mahaut et al. (2019) showed indeed that the crop rotation diversification generally leads to a decrease of the species richness at the annual scale but an increase at the pluri-annual scale. Our five crop management strategies differed in terms of tillage intensity (Yvoz, Petit, Biju-Duval & Cordeau 2020), and our results suggest that low ploughing frequency (such as in strategies S5, S7 and S8) enhanced weed species richness in field edges and field cores, as shown in previous studies (Murphy et al. 2006). The five crop management strategies also differed in terms of herbicide use (Yvoz, Petit, Biju-Duval & Cordeau 2020). In a recent study, Metcalfe et al. (2019) showed that after herbicide application (*i.e.* at the timing we surveyed weeds), the effect of the crop, which also reflects herbicide selectivity (*e.g.* anti-grass herbicide applied on forb crops and vice versa), is a key factor driving field edge weed diversity at the annual scale. These effects at the annual scale transcribed into effects at the pluri-annual scale since we showed here that functional differences between field edges and cores varied according to the intensity of farming practices. The most marked contrast between field edge and field core surveys was detected in fields managed with the most intensive strategy (S2, with the lowest crop diversity and highest use of external inputs) whereas the least marked contrast was observed in the most diversified crop successions, either using less herbicide (S7) or tillage (S8).

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

Conclusions

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

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Author contributions

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

Data availability

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

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Tables

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

Traits or Indicator values	Unit	Description	Source	Range [min-max]
Maximum height	cm	Ability to compete for light; negatively correlated with soil tillage and disturbance; proxy of the competitive strategy	(Mamarot & Rodriguez 2014; Tela Botanica 2020)	[12-250]
Specific leaf area (SLA)	m²/kg	High for ruderal plants from disturbed area: efficiency of light interception; correlated with growth rate; increase with light competition	LEDA Traitbase (Kleyer et al. 2008)	[8.6-48.5]
Seed mass	mg	Negatively correlated with soil disturbance; linked to seed dormancy and persistency	Seed information database (Royal Botanic Gardens Kew 2020)	[0.01-33.5]
Germination onset	1=Sept. 12=Aug.	Correlated with the crop sowing date	(Mamarot & Rodriguez 2014)	[1-9]
Germination duration	month	Higher in rotations with varying crop sowing dates; ability to respond to disturbance events	(Mamarot & Rodriguez 2014)	[3-12]
Flowering onset	1=Jan. 12=Dec.	Correlated with the crop flowering date; earlier in disturbed area and intensive system	(Mamarot & Rodriguez 2014; Tela Botanica 2020)	[1-8]
Flowering duration	month	Ability to respond to disturbance events	(Mamarot & Rodriguez 2014; Tela Botanica 2020)	[1-12]
Ellenberg.N		Response to the soil nitrogen availability; indicator of the type of habitat, especially arable crop	Baseflor (Julve 1998)	[1-9]
Ellenberg.L		Response to the light resource availability; impacted by the sowing density or row spacing	Baseflor (Julve 1998)	[4-9]
Plant class		Associated with the type of herbicide use; more grass species when the tillage intensity is reduced	BiolFlor (Klotz, Kühn & Durka 2002)	Grass Forb
Raunkiaer's life form		Associated with the tillage intensity; more hemicryptophyte and geophyte when tillage is reduced; therophyte adapted to soil disturbance; associated with the crop sowing date	BiolFlor (Klotz, Kühn & Durka 2002)	Therophyte Hemi-cryptophyte Geophyte

Figures and captions

Fig. 1. Weed sampling design implemented annually in each field core (“W” pattern of about 130 m long by 1.5 m width in a 2000 m^2 area) and field edge (linear transect of about 50 m long by 0.3 m width). Green lines represent the prospected area in both within-field locations. Grey lines represent the crop rows for an example of crop type, showing that the field edge is the habitat located between the grass margin and the first crop row.

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

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

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

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

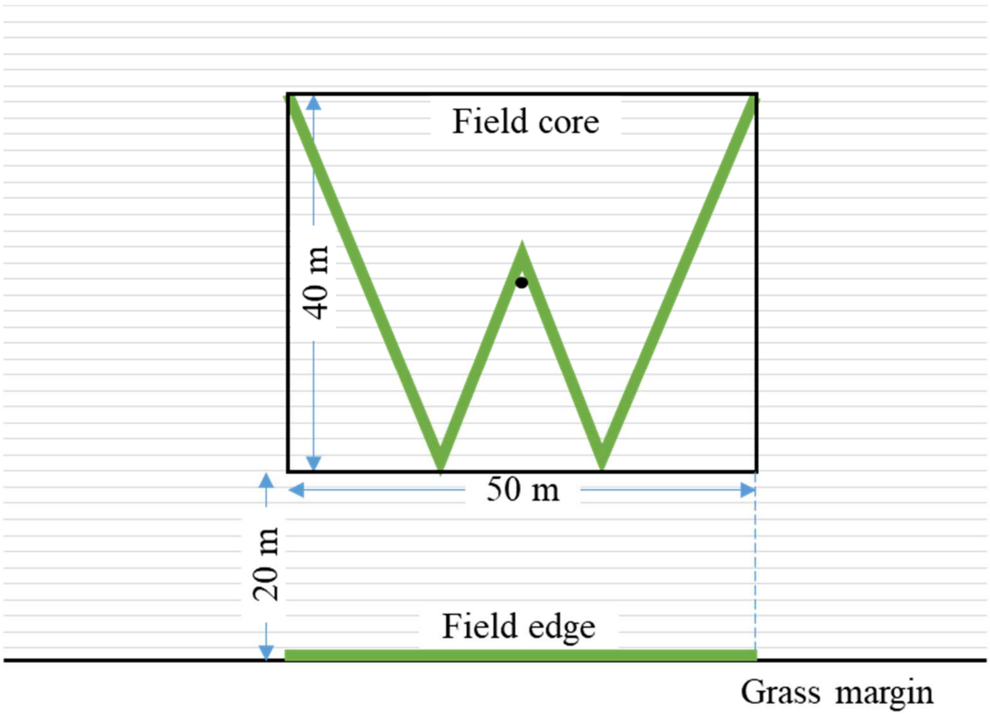
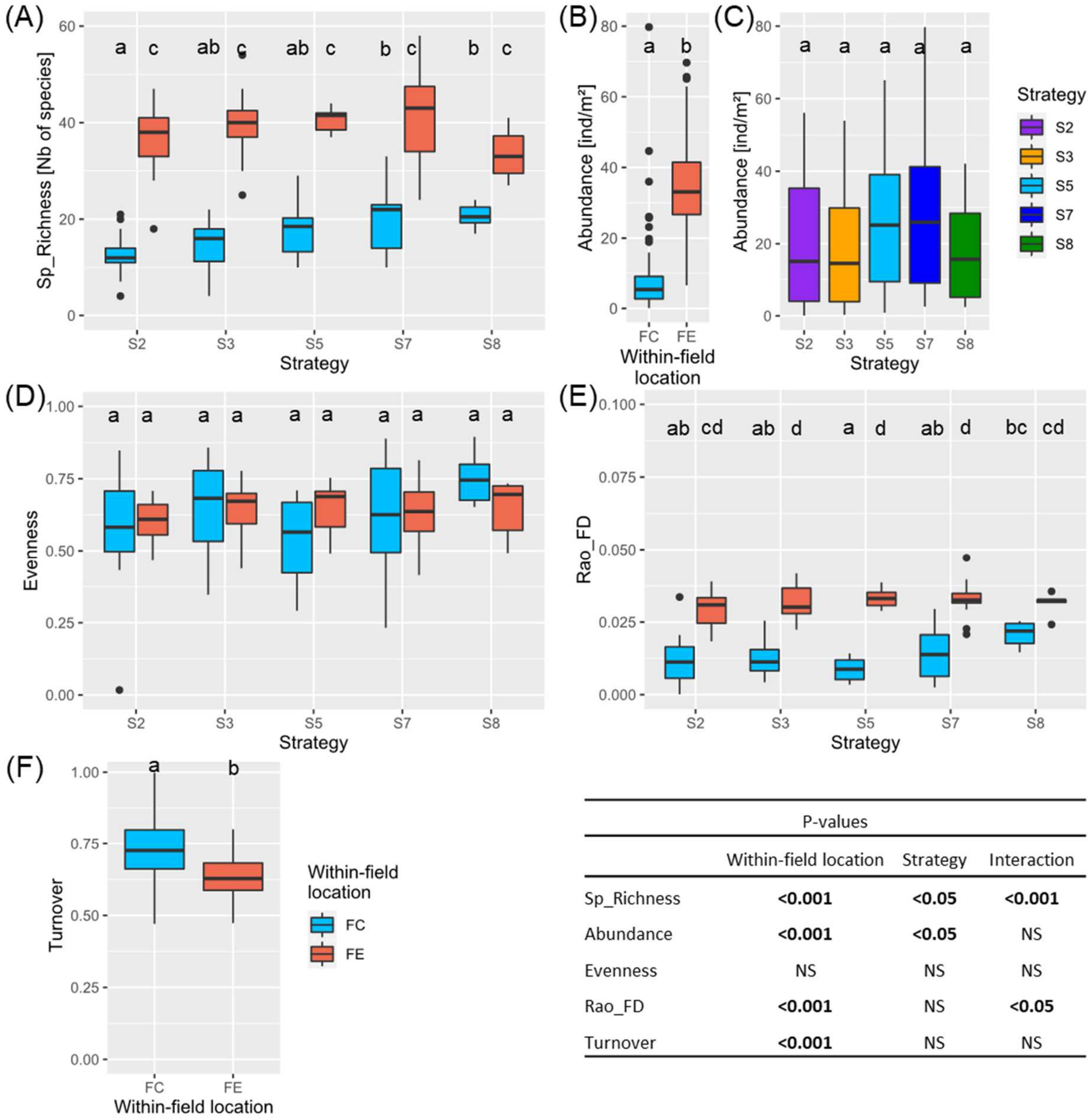


Fig. 1.



P-values			
	Within-field location	Strategy	Interaction
Sp_Richness	**<0.001**	**<0.05**	**<0.001**
Abundance	**<0.001**	**<0.05**	NS
Evenness	NS	NS	NS
Rao_FD	**<0.001**	NS	**<0.05**
Turnover	**<0.001**	NS	NS

Fig. 2.

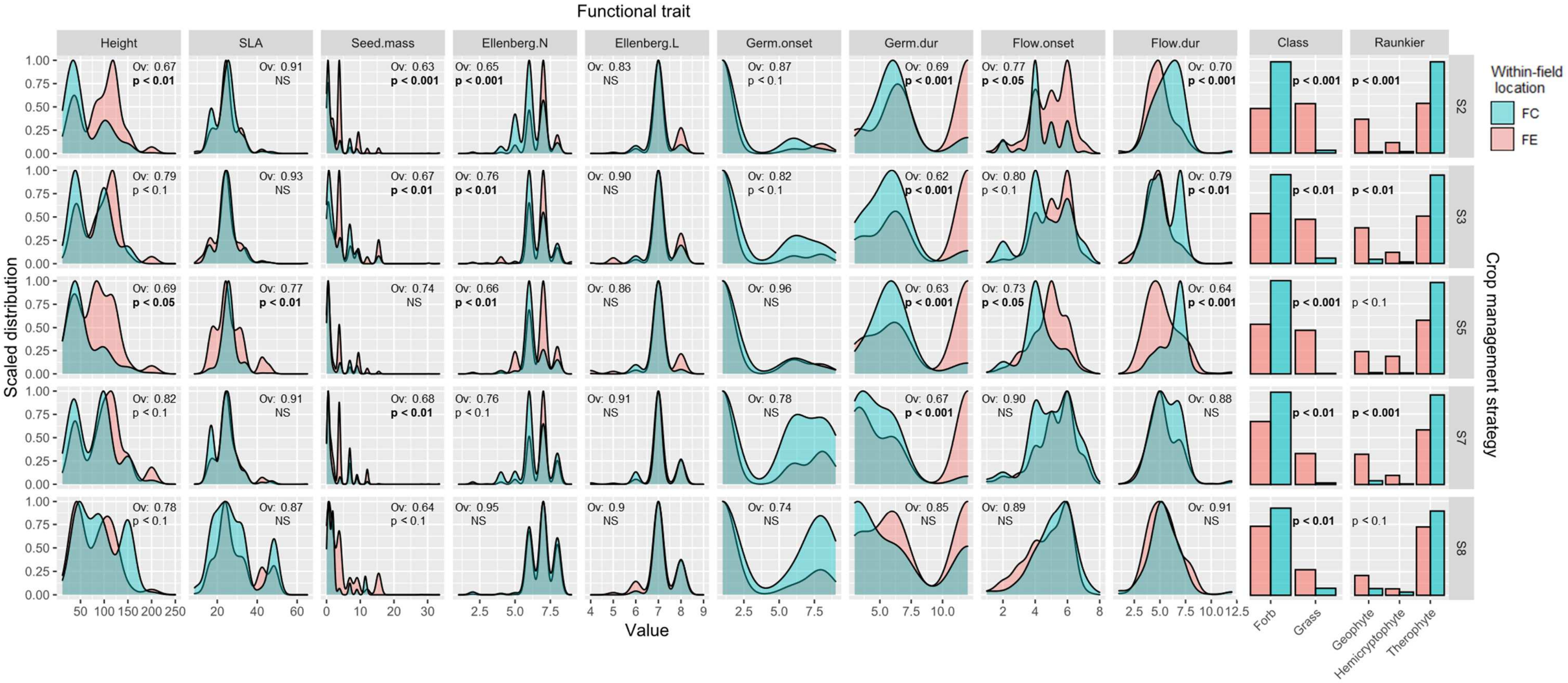

Functional trait
Height
SLA
Seed.mass
Ellenberg.N
Ellenberg.L
Germ.onset
Germ.dur
Flow.onset
Flow.dur
Class
Raunkier
Within-field location
FC
FE
Crop management strategy
S2
S3
S5
S7
S8
Scaled distribution
1.00
0.75
0.50
0.25
0.00
Value
Ov: 0.67 p < 0.01
Ov: 0.91 NS
Ov: 0.63 p < 0.001
Ov: 0.65 p < 0.001
Ov: 0.83 NS
Ov: 0.87 p < 0.1
Ov: 0.69 p < 0.001
Ov: 0.77 p < 0.05
Ov: 0.70 p < 0.001
p < 0.001
p < 0.001
Ov: 0.79 p < 0.1
Ov: 0.93 NS
Ov: 0.67 p < 0.01
Ov: 0.76 p < 0.01
Ov: 0.90 NS
Ov: 0.82 p < 0.1
Ov: 0.62 p < 0.001
Ov: 0.80 p < 0.1
Ov: 0.79 p < 0.01
p < 0.01
p < 0.01
Ov: 0.69 p < 0.05
Ov: 0.77 p < 0.01
Ov: 0.74 NS
Ov: 0.66 p < 0.01
Ov: 0.86 NS
Ov: 0.96 NS
Ov: 0.63 p < 0.001
Ov: 0.73 p < 0.05
Ov: 0.64 p < 0.001
p < 0.001
p < 0.1
Ov: 0.82 p < 0.1
Ov: 0.91 NS
Ov: 0.68 p < 0.01
Ov: 0.76 p < 0.1
Ov: 0.91 NS
Ov: 0.78 NS
Ov: 0.67 p < 0.001
Ov: 0.90 NS
Ov: 0.88 NS
p < 0.01
p < 0.001
Ov: 0.78 p < 0.1
Ov: 0.87 NS
Ov: 0.64 p < 0.1
Ov: 0.95 NS
Ov: 0.9 NS
Ov: 0.74 NS
Ov: 0.85 NS
Ov: 0.89 NS
Ov: 0.91 NS
p < 0.01
p < 0.1
50 100 150 200 250
20 40 60
0 10 20 30
2.5 5.0 7.5
4 5 6 7 8 9
2.5 5.0 7.5
5.0 7.5 10.0
2 4 6 8
2.5 5.0 7.5 10.0 12.5
Forb
Grass
Geophyte
Hemicryptophyte
Therophyte

Fig. 3.

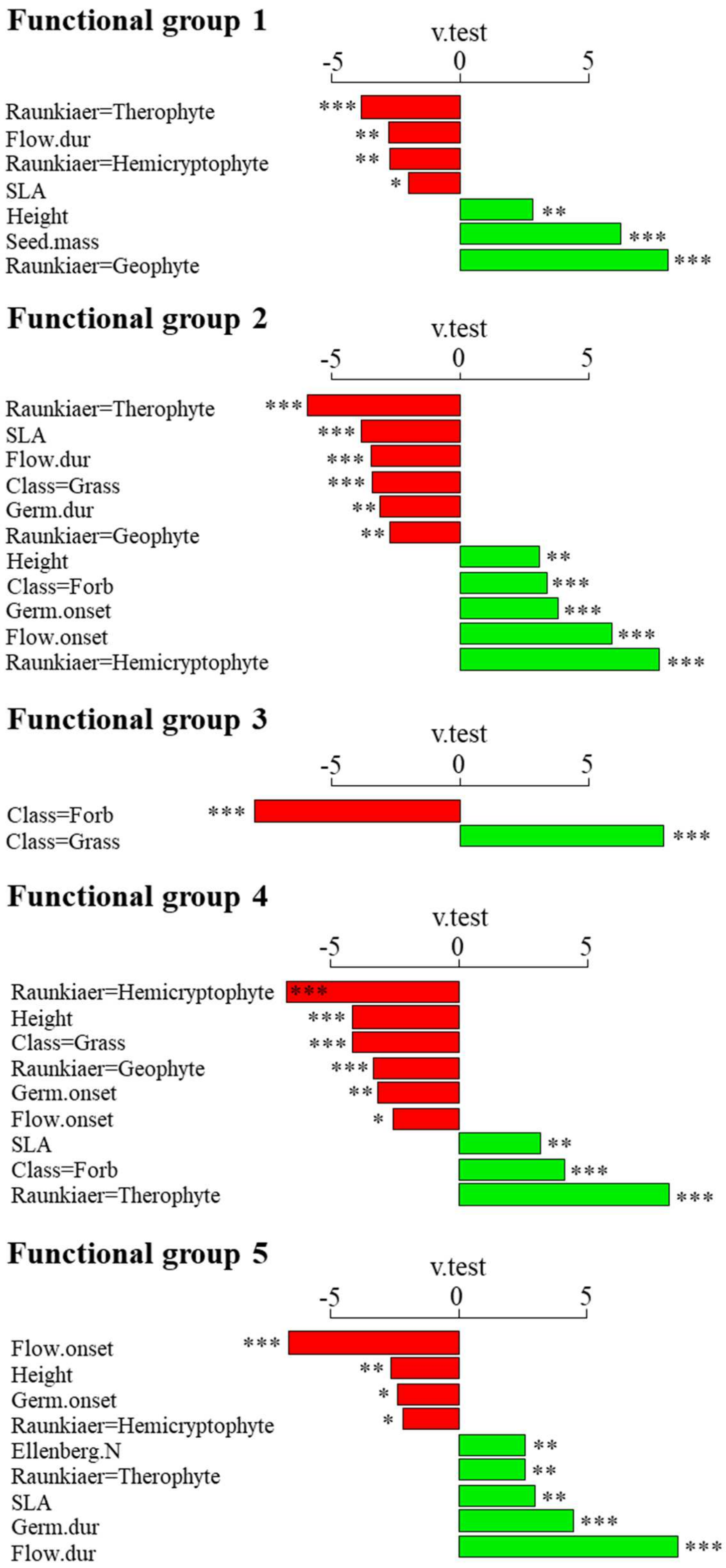
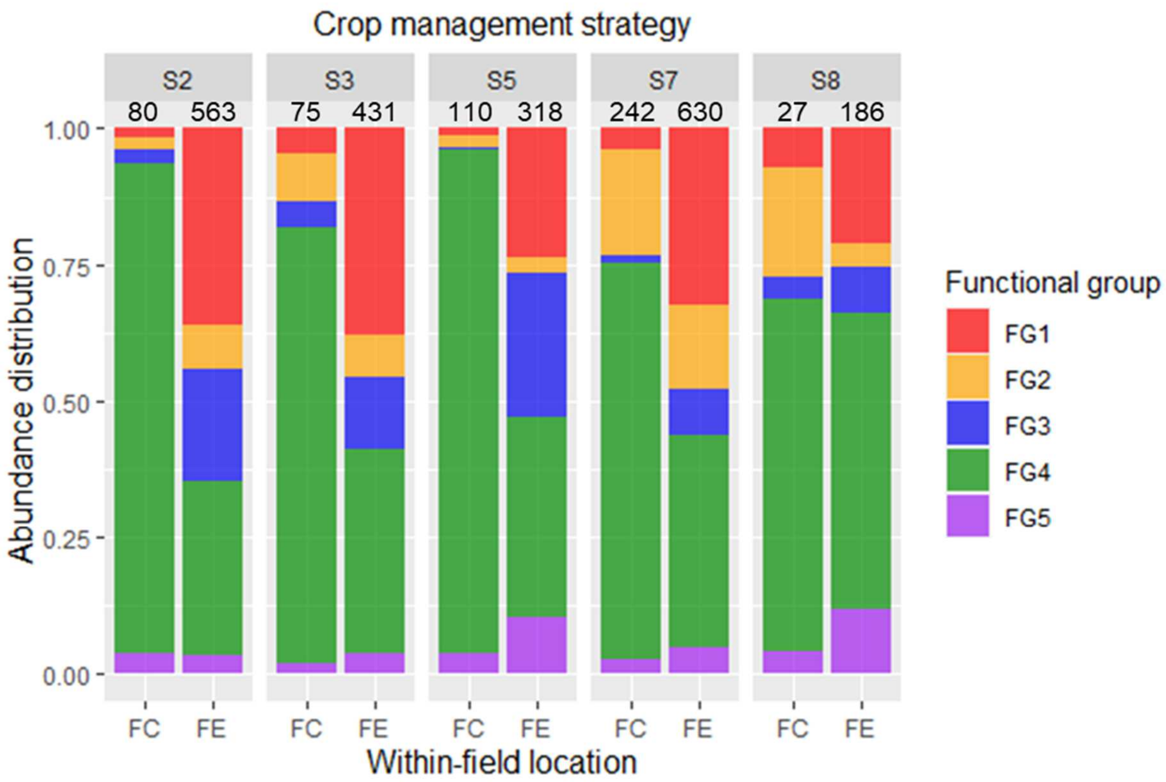

Functional group 1
v.test
-5
0
5
Raunkiaer=Therophyte ***
Flow.dur **
Raunkiaer=Hemicryptophyte **
SLA *
Height **
Seed.mass ***
Raunkiaer=Geophyte ***
Functional group 2
v.test
-5
0
5
Raunkiaer=Therophyte ***
SLA ***
Flow.dur ***
Class=Grass ***
Germ.dur **
Raunkiaer=Geophyte **
Height **
Class=Forb ***
Germ.onset ***
Flow.onset ***
Raunkiaer=Hemicryptophyte ***
Functional group 3
v.test
-5
0
5
Class=Forb ***
Class=Grass ***
Functional group 4
v.test
-5
0
5
Raunkiaer=Hemicryptophyte ***
Height ***
Class=Grass ***
Raunkiaer=Geophyte ***
Germ.onset **
Flow.onset *
SLA **
Class=Forb ***
Raunkiaer=Therophyte ***
Functional group 5
v.test
-5
0
5
Flow.onset ***
Height **
Germ.onset *
Raunkiaer=Hemicryptophyte *
Ellenberg.N **
Raunkiaer=Therophyte **
SLA **
Germ.dur ***
Flow.dur ***

Fig. 4.


Crop management strategy
S2
S3
S5
S7
S8
80
563
75
431
110
318
242
630
27
186
Abundance distribution
1.00
0.75
0.50
0.25
0.00
FC
FE
FC
FE
FC
FE
FC
FE
FC
FE
Within-field location
Functional group
FG1
FG2
FG3
FG4
FG5

743

744 **Fig. 5.**