Stochastic processes and crop types shape weed community assembly in arable fields

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Abstract

Aims: In agro-ecosystems, crop types, i.e., the crop species and its associated agricultural practices, have been shown to influence the taxonomic as well as functional composition of weed communities. However, the processes underlying weed community assembly within a crop type are poorly understood, especially regarding the contributions of local factors and stochastic processes. In this study, we investigate the effects of the crop type in shaping local weed communities.

Location: LTER Zone Atelier Plaine et Val de Sèvre, an intensive cereal system in western France.

Methods: We selected 105 fields of five crop types and investigated the functional structure of weed communities for those traits that define the Leaf–Height–Seed (L-H-S) strategy as well as phenological traits. We compared the observed trait distribution to trait distributions expected under random assembly. The trait distributions were described by the range, the community-weighted mean and the dispersion of each trait, and simulated communities were generated with a null model approach that randomizes the 'species × traits' matrix to maintain equiprobable the occurrence of each trait combination. The relationship between trait values and species abundance within each community was investigated using Kendall rank correlation tests.

Results: Our results showed that, in ca. 90% of the fields, the functional diversity of weed communities did not differ from what would be expected under random assembly. Departures from random expectations essentially resulted from shifts in weighted mean values for phenological traits. Weed communities of sunflower, maize and spring pea had later onsets of emergence and flowering than randomly expected. Communities of winter wheat had smaller species and earlier onset of flowering, and communities from oilseed rape had a larger duration of the emergence period and earlier onset of flowering. In addition, we found a positive significant relationship between species abundance and trait values for phenology for spring pea, sunflower and maize, suggesting that species with a later onset of emergence and flowering period have higher performance in these weed communities.

Conclusions: At landscape scale, weed communities generally showed patterns of functional diversity in accordance with those expected under random community assembly, except for phenological traits in spring and summer crops, where patterns were rather consistent with environmental filtering.

Introduction

How plant communities assemble is one of the oldest questions in ecology. Its recent revival may be credited to the neutral theory, which turns out to explain a surprising range of complex patterns despite extremely simple mechanisms being involved, i.e., dispersal and demographic stochasticity (Hubbell 2001; Alonso et al. 2006). Recently, the consensus that has emerged among most community ecologists is that niche-based and stochastic processes

jointly affect community assembly (Chave 2004; Tilman 2004; Leibold & McPeek 2006). The neutral theory seems to better explain species-rich community assembly where stochastic processes (i.e., at the local scale, the stochastic balance between immigration and extinction) are presumably more important than competitive ability differences among species (Hubbell 2001). In contrast, niche theory considers that stabilizing niche differences and relative fitness differences are essential to understand community assembly at a fine scale, and better explains species-poor communities (Chave 2004). However, species generally interact in a network of local communities where spatial dynamics can also affect their structure (Leibold et al. 2004). The metacommunity theory seeks to investigate how spatial and local dynamics affect local species diversity by altering local community processes that feed back to the regional scale processes (Leibold et al. 2004). Among the paradigms proposed in this theory, three take into account the relative importance of dispersal and niche-based processes, constituting special cases of species sorting (Winegardner et al. 2012). Since the 'patch dynamics' paradigm assumes homogeneous environmental conditions among communities, hereafter we only consider the 'mass effects' and 'species sorting' paradigms. Under the 'mass effects' paradigm, dispersal predominates over local niche-based processes, allowing poorly adapted species to persist locally, whereas under the 'species sorting' paradigm, local environmental conditions and interactions among species represent the predominant factors.

In agro-ecosystems, the processes underlying weed assembly remain to be established. Agro-ecosystems can be seen as a mosaic of crop types characterized by specific environmental conditions. Crop type, which refers to the combination of the crop species and its associated management practices, has been shown to strongly influence taxonomic and functional aspects of weed communities (Hallgren et al. 1999; Fried et al. 2008; Smith et al. 2008; Gunton et al. 2011). Weed functional traits (seed weight, canopy height and phenological traits) have been shown to be related to sowing season or crop architecture, emphasizing the strong role of crop phenology in weed community composition (Gunton et al. 2011). More generally, specific weed traits have been identified and described as a syndrome characterizing both rare and common species responses to crop type characteristics (Storkey et al. 2010; Fried et al. 2012). Together, these results suggest that crop types exert a filtering effect that structures local weed communities according to the species functional traits. Moreover, at the regional landscape scale, association between variation in the composition of weed communities and landscape structure suggests that dispersal processes can have a large effect on weed communities (Gaba et al. 2010). In addition, weed communities usually display classic species-abundance distributions, i.e., with few abundant and numerous subordinate species (Dornelas et al. 2009), a pattern that can be predicted from both neutral and niche models (Chave 2004).

Weed community assembly can therefore result from (i) stochastic dispersal and demographic processes, here considering no functional differences among species; or (ii) differences in species' performances in each set of given local environmental conditions, thus considering both the biotic and abiotic context (respectively, the competition with the crop and local pedoclimatic conditions as well as agricultural practices). Under the predominance of the first scenario, no association is expected between patterns of local species abundances and variations of functional traits. Considering the second scenario, an association is expected between the local abundances of species and their performance-related functional traits. However, based on current knowledge about the assembly of weed communities, the weed community within a field can be viewed as the result of the interaction between local filtering processes due to biotic (competition with the crop) and abiotic factors (pedoclimatic conditions and agricultural practices), and dynamics involving spatial dispersal (Petit et al. 2013) and seed persistence in the seed bank (Bàrberi et al. 1998). This scenario takes into account the relative importance of dispersal and niche-based processes. Under this third scenario, the most abundant species have a range of response trait values allowing them to persist and grow despite local filtering, reflecting their adaptations to specific biotic and abiotic local conditions. In contrast, the less abundant species are those that display suboptimal trait values preventing the persistence of large populations, and their presence is driven mainly by non-local factors, such as random dispersal and demographic processes.

Our aims in the present study were to assess (i) whether crop types shape arable weed communities with regard to their functional traits and cause non-random patterns in the distribution of weed functional trait values among crop types; and (ii) whether a relationship between trait values and species abundances exists in these different crop types, considering that local abundances reflect the success of species in passing through the filtering effects of the local environmental factors. First, to detect filtering processes using a trait-based approach, we relied on a null model approach (Stubbs & Wilson 2004), which required testing for alternative null structure of community combined with functional metrics describing the mean, the spread and the range of the functional trait distributions (e.g., Mouchet et al. 2010). Second, we investigated whether there was a significant correlation between trait values and species abundances within each community, following Cornwell & Ackerly (2010). We investigated these two questions in five annual crops (i.e., winter oilseed rape, winter wheat,

spring pea, sunflower and maize) and analysed three functional traits commonly used to define the Leaf–Height–Seed (L-H-S) strategy scheme (Westoby 1998). One of these traits is related to seed dispersal and establishment, i.e., seed weight, whereas the two others are related to plant performance (resource acquisition and competitive ability). In addition, we analysed three phenological traits, considered as important descriptors of weed communities in view of the recent literature (Storkey et al. 2010; Gunton et al. 2011; Fried et al. 2012; Gaba et al. 2014).

Methods

Study site and farming practices

The survey was carried out in 2006, between 20 March in winter oilseed rape and 8 June in sunflower, in an agricultural landscape located in central-western France. The study site is the LTER Zone Atelier Plaine et Val de Sèvre (http://www.zaplainevaldesevre.fr/), an intensive cereal agro-ecosystem area (450 km², 190 00 fields), located in the Poitou-Charentes region, south Deux-Sèvres district (46.23°N, 0.41 W). Cereal crops are dominant (44.6% of the cultivated area in 2011), in particular winter wheat (39.6%), but winter oilseed rape, maize and sunflower also constitute important annual crops (ca. 10–14% each). Average annual precipitation is 890 mm and mean temperature 6 °C in January and 18 °C in June. The regional scale was chosen to minimize the possible influence of precipitation and temperature differences among localities and to ensure relative homogeneity of soil conditions (i.e., mainly shallow, stony calcareous soils such as Rendzic Leptosols; see Table 1 for details) while encompassing a large number of farms corresponding to the diversity of agricultural practices. The main crop sequence (65% of fields; Table 1) can be summarized as 'winter wheat – oilseed rape – winter wheat – sunflower'. The other crop sequences were either based on maize (e.g., maize monoculture or dominance of maize in the crop sequence) or contained a significant proportion of spring pea.

Weed sampling and species selection

Plant surveys were performed at least 3 wk after the last herbicide treatment. Weeds were sampled in five different crop types, which represent the diversity of conventional agricultural practices, for a total number of 105 fields (i.e., 21 fields per crop type): winter wheat (WW), winter oilseed rape (OR), spring pea (SP), maize (MA) and sunflower (SU). Weed occurrence was sampled on an eight arms, star-shaped sampling design. On each arm, four 4 m² (2 m × 2 m) plots located at 4, 12, 38 and 60 m from the centre of the star were sampled (see Gaba et al. 2010 for details). The outermost plot of the array was at least

5 m from any field margin. Thus all plots were located within the core of each field. Presence–absence data recorded in the 32 plots were cumulated to calculate species frequency – ranging from 0 to 32 – at the field scale, and considered as a reasonable proxy for the relative abundance of each species in the following analyses.

Based on expert assessment (B. Chauvel pers. comm.), we deleted woody plants and species specific to roadsides that could have colonized arable fields from their margins (i.e., 11 species). We excluded these species that are not arable weeds *per se*. Four taxa known to be inconsistently identified at the seedling stage were grouped at the genus level and were assigned the trait values from the species that is regionally the most common (i.e., *Lolium multiflorum*, *Mentha spicata*, *Panicum miliaceum*, *Valerianella locusta*). Temporary grassland species and volunteer crops were retained. For each field, we calculated the species richness and species evenness (Hill 1973; Table 1).

Functional traits

We chose several widely used vegetative (canopy height and specific leaf area, hereafter SLA) and dispersal-related reproductive traits (seed weight). These traits define the L-H-S strategy scheme proposed by Westoby (1998), and were shown to respond to different crop types and their associated management practices (Gaba et al. 2014). SLA is considered as a surrogate for plant ability to use light efficiently, depending on its position relative to the crop canopy (Storkey 2005), while canopy height characterizes the ability to compete for light with neighbouring plants and especially with crop individuals (Cudney et al. 1991). Seed weight is related to dispersal, including colonization and persistence capabilities (Moles & Westoby 2006). We also selected three phenological traits: onset of emergence period, onset of flowering period and duration of emergence period. These traits determine the adequacy of the weeds' life cycle with the cultivation period of each crop and their ability to escape from potentially destructive farming practices such as herbicides (Storkey et al. 2010; Gunton et al. 2011; Fried et al. 2012; Gaba et al. 2014).

Functional trait values were mainly retrieved from the LEDA trait database (Kleyer et al. 2008). Trait values measured under arable field conditions when available in the literature were added (Storkey 2005; Storkey et al. 2010). Expert assessments were used to more precisely characterize phenological traits per a time step of 10 d. As the onset of emergence period of weeds is related to sowing date of crops, and given the differences between crop types, we chose to code this phenological trait from the first 10 d of September, the average date of emergence of oilseed rape in the area (following the codification of Fried et al. 2012). In the same way, the onset of flowering is based on the first

Table 1. Field characteristics according to crop type. Pedology: major soil groups in the area based on World Reference Base for Soil Resources (1998). Crop succession type: group of fields with a similar crop sequence based on the last 5 yrs. The main crop sequence can be summarized as a 'winter wheat – oilseed rape – winter wheat – sunflower' sequence, and also includes more complex but less represented variants (e.g., one crop with a higher return period). The other crop sequences were either based on maize (e.g., maize monoculture or dominance of maize in the crop sequence) or contained a significant proportion of spring pea or, to a lesser extent, pluri-annual crops. For 'pedology' and 'crop succession type', numbers refer to the number of relevant fields. Taxonomic metrics: for each crop and each metric, the mean and SD are given.

	Oilseed Rape	Winter Wheat	Spring Pea	Sunflower	Maize
Pedology					
Cambisols (Eutric to Hypereutric)	1	2	2	3	0
Cambisols (Calcaric and Hypereutric)	2	2	2	0	0
Fluvisols	1	2	0	1	5
Rendzic Leptosols	4	7	6	12	5
Rendzic Leptosols and Cambisols (Calcaric)	13	8	10	5	11
Crop Succession Type					
Main Crop Sequence	19	14	8	18	5
Others	2	5	12	2	16
Taxonomic Metrics					
Species Richness	15.76 (±4.49)	15.86 (±5.90)	18.71 (±6.66)	16.57 (±4.32)	15.43 (±6.82)
Species Evenness	0.48 (±0.09)	0.48 (±0.11)	0.49 (±0.10)	0.46 (±0.09)	0.48 (±0.08)
Total Species Richness	69	68	67	62	67

10 d of January. SLA values were not available for one species among the 114 species observed in our study (*Silybum marianum*); this species was thus removed from the analyses. We applied a $\log_{10}$ transformation on seed weight data in order to reach normality in distribution.

Comparisons of weed taxonomic community composition among crop types

We compared the species pool of one crop type to the species pool of each of the other four crop types with pair-wise comparisons. The species pool for a given crop type was composed of all the species found in the 21 fields of this crop type. We used the Sørensen dissimilarity metric (formula 1 – S8 in Legendre & Legendre 1998) and the Bray-Curtis dissimilarity metric (formula 1 – S17 in Legendre & Legendre 1998) to compute dissimilarity between species pools based on species presence–absence or relative abundance, respectively. A $\log(1 + x)$ transformation was applied before Bray-Curtis calculation following Legendre & Legendre (1998). The significance of the dissimilarity among crop type species pools was analysed using a randomization procedure, which maintains both species richness and species abundance distribution per crop type species pool. We generated 10 000 species pools per crop type by randomly sampling species based on the combined list of species observed in the two chosen pools. Then, for each pair-wise comparison of the crop type species pools, the observed dissimilarity was compared with the distribution of 10 000 dissimilarity values calculated for randomly sampled species pools. We used a one-tailed direct test with a significant threshold of $P < 0.05$, and applied a sequential Bonferroni adjustment to account for multiple

pair-wise comparisons (Holm 1979). Taxonomic dissimilarity metrics were computed using the package 'vegan' (http://cran.r-project.org/web/packages/vegan/) of the software R 2.15.1 (R Foundation for Statistical Computing, Vienna, AT).

Comparisons of functional traits distributions and functional diversity among crop types

Weed community functional diversity was characterized using the range, the mean (i.e., community-level weighted mean, CWM; Garnier et al. 2004) and the spread (functional dispersion index, FDis; Laliberté & Legendre 2010) of the trait distribution. The comparisons of the five crop types for each metric × trait combination were made with a non-parametric Kruskal-Wallis test associated with a *post-hoc* test for multiple pair-wise comparisons. All the traits studied are quantitative. Functional metrics were computed using the R package 'FD' (http://cran.r-project.org/web/packages/FD/).

In order to test the potential unwanted effects of cropping history and soil properties, we performed a preliminary single-trait linear model analysis on CWM and FDis metrics for each trait. Model selection was based on AIC, and sum to zero contrasts were applied to fit the model (see App. S1 for further details). The analyses revealed a highly significant effect of crop type for eight of the 12 'metric × trait' combinations, and no or only a marginal effect of crop history and soil, respectively (App. S1). Linear models were performed using the R package 'car' (http://cran.r-project.org/web/packages/car/). In addition, we tested for spatial autocorrelation among sites separately for each diversity metric using Moran's I statistic, available

in the R package 'ape' (http://cran.r-project.org/web/packages/ape/).

Null model approach to test the filtering effect of the crop type

For each field separately, 10 000 'species × traits' matrices were generated by randomizing trait values among all species from the regional species pool. The regional species pool corresponds to all species observed in at least one of the fields. This null model procedure, also proposed by Spasojevic & Suding (2012), ensures that each species within the regional species pool was equally likely to act as a functionally influential species in each null community, corresponding to an equiprobable randomization. The observed occurrences and abundances of species within communities were fixed, while the trait values were randomized, following the Tokeshi principle (Tokeshi 1986), implying that every feature of the randomized data set must be maintained, except the one which is the focus of the test. The null model breaks the link between species abundance and trait values within the community, following the hypothesis that each crop type is characterized through a community with trait values reflecting specific local factors. We then calculated the range, the CWM and the FDis for each randomized matrix. Significant differences between observed and randomized trait distributions were based on the number of fields with metric values lower or higher than expected under a random assembly hypothesis using a two-tailed test with threshold P-values of 2.5% and 97.5%.

Relationship between species abundance and trait values

To test for a non-random association between trait values and species abundance at the field scale, we computed a Kendall rank correlation coefficient test for each field and each trait separately. For each crop type, we compared the Kendall's correlation coefficients to the null expectation of zero with a two-tailed one-sample Wilcoxon test, following Cornwell & Ackerly (2010).

Results

Comparison of weed taxonomic community composition among crop types

The number of species within the regional species pool (105 fields) was 113. Species richness varied from five to 31 species per field, and on average from 15.43 ± 6.82 in maize to 18.71 ± 6.66 in sunflower. Evenness, on average 0.48 ± 0.09, also varied slightly among crop types (Table 1). There were no significant differences among crop types in both species richness and evenness based on Kruskal-Wallis non-parametric comparisons (Table 1). In addition, no significant spatial autocorrelation was detected for any of the 20 diversity metrics used (two taxonomic metrics: species richness and species evenness, and three functional metrics: CWM, FDis and range, computed for each of six traits), with the sole exception of CWM of the onset of emergence period. Permutation tests on dissimilarity metrics showed significant differences between all crop type pairs, for both presence–absence and abundance data (App. S2). Thus, the species pools that characterized each crop type differed more in their composition than expected by chance.

Comparisons of functional traits and functional diversity among crop types

The CWM of all traits, except SLA, significantly differed among crop types (Fig. 1), while only FDi values of the onset and duration of emergence were significantly different among crop types (Fig. 2). Moreover, the range of values also showed significant differences for the onset of emergence and the onset of flowering period (data not shown). The onset of flowering and emergence period differed significantly between winter and summer crops – spring pea having intermediate values (Fig. 1). In addition, weed communities in maize showed a less variable onset and duration of emergence period compared to other crop types (Fig. 2), mainly because of the predominance of spring germinating weed species.

Filtering effect of crop types

The comparison between the observed metrics and their expectations under random assembly revealed 14.1%, 5.8% and 3.3% significant deviations, respectively, for CWM, FDi and range (Table 2). The range was characterized by a lack of significant departure for all the traits (Table 2, top), suggesting that all species from the regional species pool can establish in all the crops, regardless of their trait values. Few deviations from the null hypothesis were observed for trait dispersion, i.e., FDis (Table 2, middle). However, we observed trends of under-dispersion for seed weight in winter wheat (24%, corresponding to five of 21 fields) and spring pea (19%) and for the onset of emergence in maize (29%), and trends of over-dispersion in oilseed rape for the onset of flowering period (19%) and duration of emergence period (19%). High deviations from the hypothesis of random assembly were observed for the CWM of the onset of emergence period (up to 90% in maize) and for flowering period (around 40% in both sunflower and maize; Table 2, bottom). Deviations were also
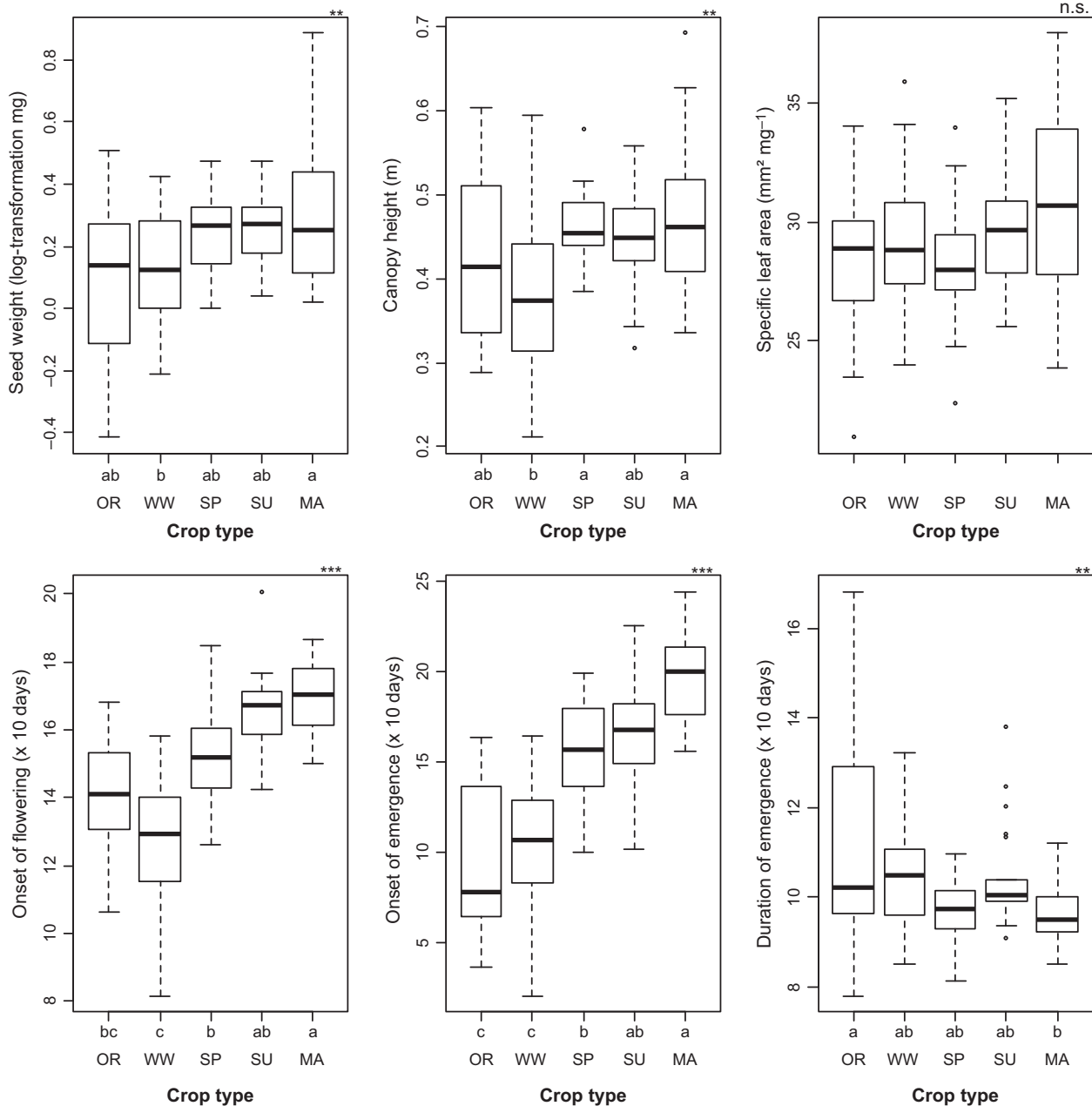
Fig. 1. Abundance-weighted means per trait split by crop type ($n = 21$). For each boxplot, the box was delimited by the interquartile values (25–75% lie within the box), the median is indicated as a horizontal line in bold, while the minimum and maximum values of the distribution are shown as the whiskers. Crop types are presented below as OR for oilseed rape, WW for winter wheat, SP for spring pea, SU for sunflower and MA for maize. Results of Kruskal–Wallis tests are presented. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, n.s. not significant. Letters indicate significantly different values according to non-parametric *post-hoc* tests.

observed for the duration of the emergence period in oilseed rape, where species showed a longer period than expected under the random assembly hypothesis (24%). Few deviations of the CWM were observed for L-H-S traits, although smaller species tend to be more frequent in winter wheat than expected under random sampling from the regional species pool (24%).

Relationship between species abundance and trait values

When a significant filtering effect by crop type was detected, we expected that it primarily involved the most abundant species, while the presence of the less abundant species should be mainly explained through stochastic
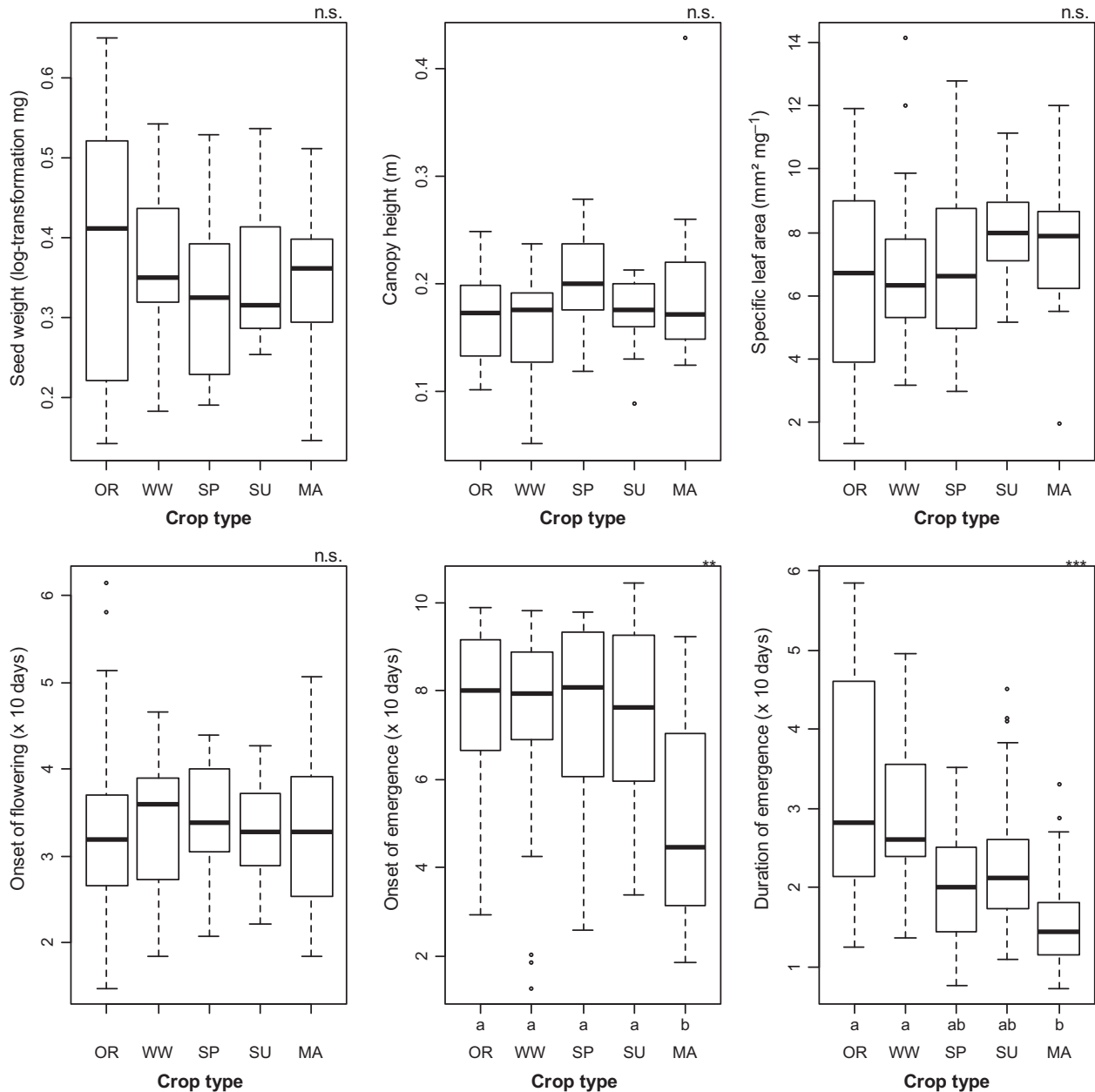
Fig. 2. Functional dispersion index per trait split by crop type (n = 21). For each boxplot, the box is delimited by the interquartile values (25–75% lie within the box), the median is indicated as a horizontal line in bold, while the minimum and maximum values of the distribution are shown as the whiskers. Crop types are presented below as OR for oilseed rape, WW for winter wheat, SP for spring pea, SU for sunflower and MA for maize. Results of Kruskal–Wallis tests are presented. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, n.s. not significant. Letters indicate significantly different values according to non-parametric *post-hoc* tests.

processes. Under this hypothesis, abundant species should have distinct trait values. Trait values were significantly correlated (either positively or negatively) with species abundances for several crop types and traits (Fig. 3). Weed communities in summer crops (i.e., sunflower and maize) and spring pea showed a significant positive correlation, both for the onset of emergence and flowering period

(Fig. 3). In these crop types, abundant species thus showed a later onset of emergence and flowering than the other species in the weed communities. In winter crops (i.e., oilseed rape and winter wheat), a significant relationship was observed between onset of emergence and species abundance (Fig. 3). Some relationships were also observed for the L-H-S traits: a significant positive correlation with

Table 2. Number of significant deviations from the null model for the functional assembly of weed communities. The values given are the number of fields showing a value of the metric (range, FDis or CWM) significantly different from expected by assuming an independent relationship between species abundances and species trait values. For FDis and CWM, thresholds for significance were set at 2.5% (values lower than expected) and 97.5% (values higher than expected) and indicated by '<' and '>', respectively. For the range, only the number of fields showing lower values than expected can be interpreted in terms of filtering process and are given. Values in bold indicate significant trends over > 15% of fields.

Metric × Trait Combination		Crop Type				
Metric	Trait	OR	WW	SP	SU	MA
Range	log (SW)	3	1	0	0	1
	CH	2	2	1	2	2
	SLA	2	0	0	0	0
	OFP	0	0	0	0	0
	OEP	1	2	0	0	0
	DEP	0	0	0	0	2
FDis	log (SW)	2 (<)	**5** (<)	**4** (<)	0	0
	CH	1 (<)	2 (<)	0	0	1 (>)
	SLA	2 (<)	1 (>)	0	0	0
	OFP	**4** (>)	0	0	0	0
	OEP	1 (<)	1 (<)	0	1 (<)	**6** (<)
	DEP	**4** (>)	1 (>)	1 (<)	0	0
CWM	log (SW)	1 (>)	0	1 (>)	1 (>)	1 (>)
	CH	1 (<)	**5** (<)	0	0	0
	SLA	1 (<)	1 (>)	0	0	1 (>)
	OFP	**5** (<)	**5** (<)	2 (>)	**8** (>)	**9** (>)
	OEP	1 (<)	1 (<)	**7** (>)	**11** (>)	**19** (>)
	DEP	**6** (>)	1 (>)	0	1 (>)	0

OR, oilseed rape; WW, winter wheat; SP, spring pea; SU, sunflower; MA, maize. SW, seed weight; CH, canopy height; SLA, specific leaf area; OFP, onset of flowering period; OEP, onset of emergence period; DEP, duration of emergence period.

species abundance was detected for the seed weight in spring pea and sunflower, and for SLA in sunflower and maize, suggesting that these crop types promote species with high values of these traits (Fig. 3).

Discussion

In this study, we aimed to detect (i) whether different crop types shape different weed communities and (ii) whether there is a relationship between trait values and species abundance in these different crop types. Broad taxonomic and functional patterns differences were observed between crop types, in accordance with previous results (e.g., Gunton et al. 2011). However, we only detected a few deviations from the random patterns expected on the hypothesis of random assembly of weed species among crop types from the regional species pool. The largest proportion of fields deviating from the random assembly hypothesis was detected for phenological traits. Our study also reveals that in spring and summer crops, the most

abundant species display a distinct range of trait values compared to the less abundant species in the community. These complementary results give insights in demonstrating the interactions between local weed communities due to heterogeneity in the local environmental conditions (i.e., crop type) and effects of dispersal in shaping weed communities. The heterogeneous habitats provided by crop types across the agricultural landscape may ensure the regional coexistence of weed species with different abilities to respond to the local factors (i.e., biotic interactions with the crop and disturbances induced by agricultural practices), while dispersal may promote local coexistence by ensuring the maintenance of less competitive species. Our results emphasize the important role of both crop type and dispersal, rather in accordance with the 'species sorting' perspective of metacommunity theory, *sensu* Leibold et al. (2004). However, multiple complex scenarios could be envisaged on weed metacommunity dynamics and diversity depending on the level of heterogeneity across the agricultural landscape, and further investigations are needed to extend and strengthen our results.

Effects of crop type on the functional diversity of weed communities

Based on the null model approach, our results revealed important differences in weed phenological traits among crop types, highlighting the important role of the crop sowing date in structuring taxonomic (Hallgren et al. 1999) and functional (Gunton et al. 2011) weed communities. In contrast, fewer differences between crop types were observed for L-H-S traits, which are commonly used in plant ecology studies in many environments (Garnier & Navas 2012). In a previous study, L-H-S traits were shown to differ widely between rare and common autumn-germinating weeds (Storkey et al. 2010). Such differences were also detected here, but to a lesser extent (Table 2). SLA is commonly used in plant ecology to detect individual response to environmental conditions, and considered as a proxy of the rate and intensity of resource acquisition. Surprisingly, we did not detect any differences in the mean, diversity and range of SLA values among crop types based on the null model approach. We suggest that considering a unique fixed mean SLA value per species may be inappropriate, as a high intraspecific variation of SLA has been reported (Pakeman 2013; Perronne et al. 2014), which may allow weed species to respond to the particular environment of different crop types. In the future, considering the intraspecific variation of L-H-S and other traits under field conditions would thus be useful to detect any non-random weed assemblages. Nevertheless, non-random patterns consisting in under-dispersion were observed for
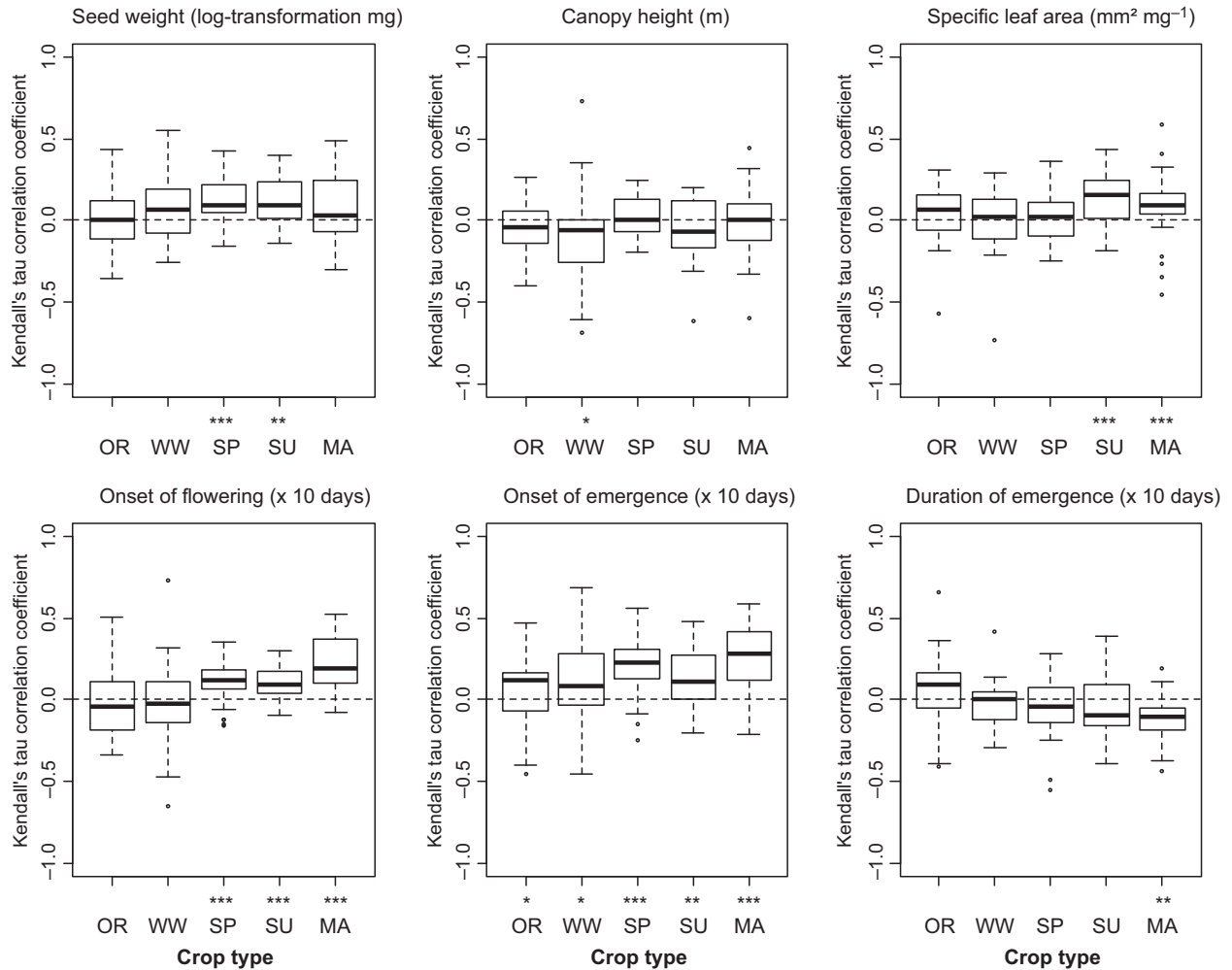
Fig. 3. Correlation between species abundance and trait values for each of the six traits per crop type ($n = 21$). Boxplots represent Kendall's tau correlation coefficients for each of the 21 fields per crop type, which are represented by OR for oilseed rape, WW for winter wheat, SP for spring pea, SU for sunflower and MA for maize. The dotted line corresponds to the null expectation ($y = 0$), while boxes of the boxplots are based on the interquartile values (25–75% lie within the box). Results of two-tailed, one-sample Wilcoxon tests, which compared the value of the Kendall's tau correlation coefficients to zero are indicated. *$P < 0.025$, **$P < 0.01$, ***$P < 0.001$.

seed weight in winter wheat and spring pea, which is consistent with some observations in other disturbed environments (e.g., Franzén 2004). Similarly, our analysis revealed a higher proportion of small weeds (lower canopy height) in winter wheat. This is consistent with the existence of a 'winning' trait combination in winter wheat, consisting of fast-growing, small-sized plants (Fried et al. 2012).

Significant responses of phenological traits to crop type have been highlighted in our study, in accordance with Gunton et al. (2011), who showed high correlations between crop sowing dates and weed phenology. This probably explains the non-random patterns of weed emergence in the two summer crops considered here, sunflower

and maize, whose communities are dominated by spring-emerging weeds, especially their most abundant species. By contrast, in oilseed rape fields, weeds are evenly divided into autumn- and spring-germinating species, including several fast-growing environmentally independent flowering weeds; this may explain the tendency towards over-dispersion of phenological trait values in this crop type. The fact that the emergence period represents the main environmental filter of community assembly has also been highlighted in other studies focusing on communities dominated by annual species (Crawley 2004; Smith 2006). Although potentially relevant, this phenological trait has rarely been considered in more stable environments. In conclusion, significant deviations were detected for

phenological traits, but rarely for L-H-S traits, which suggests a local filtering of phenological traits but not on L-H-S, and questions the relevancy of L-H-S for studying weed response to crop type.

Effect of the interaction between local factors and dispersal on functional patterns

Weed communities are composed of a few abundant and numerous subordinate species (e.g., Dornelas et al. 2009). We hypothesized that local weed diversity was the result of the interaction between local filtering processes and spatio-temporal regional dynamics, under a metacommunity concept. We further hypothesized that spatio-temporal dynamics has a dominant effect on species occurrence, while local processes mainly act on their relative abundance. We therefore predicted a shift in trait values between the most abundant species and other species in the community, leading to a significant relationship between trait values and species abundance. Our hypothesis was mainly supported in three of the five crop types (spring pea, sunflower and maize). In these crop types, the most abundant species exhibited a distinct range of phenological and some L-H-S trait values compared to the other species, a result also in agreement with recent analyses (Fried et al. 2009, 2012; Storkey et al. 2010). The significant positive correlations observed for seed weight in spring pea and sunflower does not support a link between spatial dispersal ability and local abundance. Rather, it suggests some filtering acting on the success of the establishment phase and initial growth of weeds in these crops, for instance by allocating more resources to roots early in the season (Storkey et al. 2010). In addition, the more abundant species in sunflower and maize crops were those with higher SLA values. A main finding of our study is that much clearer patterns were obtained for phenological traits than for other traits. More specifically, abundant species exhibited an onset of emergence period close to the sowing date of the summer crops in the study area (early April and mid-April, respectively). This, together with the significant shift in CWM values observed in comparison with a null model, strongly suggests that the principal environmental filter set by summer crops is on the adequate time for emergence. In these crop types, two processes seem to interact: habitat filtering, for which the most abundant species positively respond, and stochastic processes that allow less abundant species to settle and grow in the fields. In the two winter crops (i.e., winter wheat and oilseed rape), our results showed a high variation from field to field in the mean trait values of the weed communities (Fig. 1), and also a high variation in trait values among species within a field, irrespective of their abundance. Low similarity between weed communities in

winter wheat fields has previously been noticed in the same cropping area (Gaba et al. 2010). In Gaba et al. (2010), the effects of landscape composition and field size were shown to affect weed diversity, suggesting an important role of weed dispersal. Spatial dispersal was also shown to contribute to maintaining species richness at local and landscape scales (Poggio et al. 2010). The predominantly random patterns observed in winter wheat and oilseed rape seemed to corroborate this hypothesis. In addition, both the seed bank – known to act as a buffer memory of past infestations (Bàrberi et al. 1998) and crop sequence (Bohan et al. 2011) – and the abilities of several cohorts to grow during the long cultivation period of winter crops may also partially explain the high trait variability among fields.

Conclusions and prospects

Our results suggest that the assembly of weed communities in different annual crops at the regional landscape scale is determined by the interaction between local factors (i.e., the local environment defined by the crop itself and associated farming practices) and spatio-temporal dynamics. In the majority of the weed communities, the patterns of functional diversity were consistent with those resulting solely from stochastic processes, independent of trait values. However, strong evidence for trait-based filtering was detected in spring and summer crops for phenology-related traits when the relationship between local abundance and trait values was examined. These results emphasize the interplay between local processes (i.e., crop type) and spatio-temporal dispersal. Since these results were established using fixed functional trait values retrieved from existing databases, further studies should, however, consider the intraspecific trait variability, which is important for several traits including L-H-S traits, and may reveal adaptations of weed plants to environmental conditions (Perronne et al. 2014). The inclusion of intraspecific variability in null models has proven its usefulness in detecting the effects of filtering processes (Jung et al. 2010; Siefert 2012). Moreover, in order to more explicitly take into account the performance of weed species in different environments, number of individuals, relative cover or biomass production could be more reliable indicators than the proxy of abundance used in the present study. Finally, to better determine the relative contribution of local, spatial and temporal processes on the observed compositional differences of weed communities, it would be helpful to investigate the effects of local biotic (mainly weed–crop competition for resources) and abiotic factors (e.g., herbicide pressure and other farming practices), while monitoring both seed bank dynamics and seed spatial dispersal.

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References

Alonso, D., Etienne, R.S. & McKane, A.J. 2006. The merits of neutral theory. *Trends in Ecology & Evolution* 21: 451–457.

Bàrberi, P., Cozzani, A., Macchia, M. & Bonari, E. 1998. Size and composition of weed seedbank under different management systems for continuous maize cropping. *Weed Research* 38: 319–334.

Bohan, D.A., Powers, S.J., Champion, G., Haughton, A.J., Hawes, C., Squire, G., Cussans, J. & Mertens, S.K. 2011. Modelling rotations: can crop sequences explain arable weed seedbank abundance? *Weed Research* 51: 422–432.

Chave, J. 2004. Neutral theory and community ecology. *Ecology Letters* 7: 241–253.

Cornwell, W.K. & Ackerly, D.D. 2010. A link between plant traits and abundance: evidence from coastal California woody plants. *Journal of Ecology* 98: 814–821.

Crawley, M.J. 2004. Timing of disturbance and coexistence in a species-rich ruderal plant community. *Ecology* 85: 3277–3288.

Cudney, D.W., Jordan, L.J. & Hall, A.E. 1991. Effect of Wild Oat (*Avena fatua*) Infestations on Light Interception and Growth Rate of Wheat (*Triticum aestivum*). *Weed Science* 39: 175–179.

Dornelas, M., Moonen, A.C., Magurran, A.E. & Bàrberi, P. 2009. Species abundance distributions reveal environmental heterogeneity in modified landscapes. *Journal of Applied Ecology* 46: 666–672.

Franzén, D. 2004. Plant species coexistence and dispersion of seed traits in a grassland. *Ecography* 27: 218–224.

Fried, G., Norton, L.R. & Reboud, X. 2008. Environmental and management factors determining weed species composition and diversity in France. *Agriculture, Ecosystems & Environment* 128: 68–76.

Fried, G., Chauvel, B. & Reboud, X. 2009. A functional analysis of large-scale temporal shifts from 1970 to 2000 in weed assemblages of sunflower crops in France. *Journal of Vegetation Science* 20: 49–58.

Fried, G., Kazakou, E. & Gaba, S. 2012. Trajectories of weed communities explained by traits associated with species' response to management practices. *Agriculture, Ecosystems & Environment* 158: 147–155.

Gaba, S., Chauvel, B., Dessaint, F., Bretagnolle, V. & Petit, S. 2010. Weed species richness in winter wheat increases with landscape heterogeneity. *Agriculture, Ecosystems & Environment* 138: 318–323.

Gaba, S., Fried, G., Kazakou, E., Chauvel, B. & Navas, M.-L. 2014. Agroecological weed control using a functional approach: a review of cropping systems diversity. *Agronomy for Sustainable Development* 34: 103–119.

Garnier, E. & Navas, M.-L. 2012. A trait-based approach to comparative functional plant ecology: concepts, methods and applications for agroecology. A review. *Agronomy for Sustainable Development* 32: 365–399.

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., (…) & Toussaint, J.-P. 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85: 2630–2637.

Gunton, R.M., Petit, S. & Gaba, S. 2011. Functional traits relating arable weed communities to crop characteristics. *Journal of Vegetation Science* 22: 541–550.

Hallgren, E.M., Palmer, W. & Milberg, P. 1999. Data diving with cross-validation: and investigation of broad-scale gradient in Swedish weed communities. *Journal of Ecology* 87: 1037–1051.

Hill, M.O. 1973. Diversity and evenness: a unifying notation and its consequence. *Ecology* 54: 427–432.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* 6: 65–70.

Hubbell, S.P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ, US.

Jung, V., Violle, C., Mondy, C., Hoffmann, L. & Muller, S. 2010. Intraspecific variability and trait-based community assembly. *Journal of Ecology* 98: 1134–1140.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., van Groenendael, J.M., Klimeš, L., (…) & Peco, B. 2008. The LEDA Traitbase: a database of life history traits of the Northwest European flora. *Journal of Ecology* 96: 1266–1274.

Laliberté, E. & Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91: 299–305.

Legendre, P. & Legendre, L. 1998. *Numerical ecology*. Elsevier Scientific, Oxford, UK.

Leibold, M.A. & McPeek, M.A. 2006. Coexistence of the niche and neutral perspectives in community ecology. *Ecology* 87: 1399–1410.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., (…) & Gonzalez, A. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7: 601–613.

Moles, A.T. & Westoby, M. 2006. Seed size and plant strategy across the whole life cycle. *Oikos* 113: 91–105.

Mouchet, M., Villéger, S., Mason, N.W. & Mouillot, D. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology* 24: 867–876.

Pakeman, R.J. 2013. Intra-specific leaf trait variation: management and fertility matter more than the climate at continental scales. *Folia Geobotanica* 48: 255–371.

Perronne, R., Gaba, S., Cadet, E. & Le Corre, V. 2014. The interspecific and intraspecific variation of functional traits in weeds: diversified ecological strategies within arable fields. Acta Botanica Gallica. *Botany Letters* 161: 243–252.

Petit, S., Alignier, A., Colbach, N., Joannon, A., Le Cœur, D. & Thenail, C. 2013. Weed dispersal by farming at various spatial scales. A review. *Agronomy for Sustainable Development* 33: 205–217.

Poggio, S.L., Chaneton, E.J. & Ghersa, C.M. 2010. Landscape complexity differentially affects alpha, beta, and gamma diversities of plants occurring in fencerows and crop fields. *Biological Conservation* 143: 2477–2486.

Siefert, A. 2012. Incorporating intraspecific variation in tests of trait-based community assembly. *Oecologia* 170: 767–775.

Smith, R.G. 2006. Timing of tillage is an important filter on the assembly of weed communities. *Weed Science* 54: 705–712.

Smith, V., Bohan, D.A., Clark, S.J., Haughton, A.J., Bell, J.R. & Heard, M.S. 2008. Weed and invertebrate community compositions in arable farmland. *Arthropod-Plant Interactions* 2: 21–30.

Spasojevic, M.J. & Suding, K.N. 2012. Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *Journal of Ecology* 100: 652–661.

Storkey, J.S. 2005. Modelling assimilation rates of 14 temperate arable weed species as a function of the environment and leaf traits. *Weed Research* 45: 361–370.

Storkey, J., Moss, S.R. & Cussans, J.W. 2010. Using assembly theory to explain changes in a weed flora in response to agricultural intensification. *Weed Science* 58: 39–46.

Stubbs, W.J. & Wilson, J.B. 2004. Evidence for limiting similarity in a sand dune community. *Journal of Ecology* 92: 557–567.

Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences of the United States of America* 101: 10854–10861.

Tokeshi, M. 1986. Resource utilization, overlap and temporal community dynamics: a null model analysis of an epiphytic chironomid community. *Journal of Animal Ecology* 55: 491–506.

Westoby, M. 1998. A leaf–height–seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199: 213–227.

Winegardner, A.K., Jones, B.K., Ng, I.S.Y., Siqueira, T. & Cottenie, K. 2012. The terminology of metacommunity ecology. *Trends in Ecology & Evolution* 27: 253–254.

World Reference Base for Soil Resources. 1998. World Soil Resources Reports, No. 84. FAO–ISRIC–ISSS, Rome, IT.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Linear model analyses on functional metrics CWM and FDis for the chosen traits.
Appendix S2. Pair-wise comparisons of the compositional dissimilarity between crop types.