



# Patterns of weed co-occurrence at the field and landscape level

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## Keywords

Aggregation; Competition; Environmental heterogeneity; Segregation; Spatial scale

## Nomenclature

Hanf (1982), Jauzein (1995) and Marmarot et al. (1997)

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## Introduction

Understanding the factors underpinning the co-existence of species in natural communities in order to identify general assembly rules remains a fundamental question in ecology (Wilson 2011). During the last decades, the existence of such assembly rules has been largely debated among ecologists (Diamond 1975; Connor & Simberloff 1979; Gotelli 1999; Grime 2006; Wilson 2007). Recent meta-analyses conducted on a large array of natural communities showed that non-random assemblage of species is not rare (Gotelli & McCabe 2002; Ulrich & Gotelli 2010). The results indicated that species co-occurrence estimated by C-score (Stone & Roberts 1990) was in general less than expected by chance, i.e. that natural communities were often segregated. Plant communities were not well represented in the meta-analysis but appeared to follow the general pattern of species

## Abstract

**Question:** Are patterns of weed co-occurrence structured or random? Do these patterns differ at the field and landscape scales? Are co-occurrence patterns related to the effect of environmental filters and/or competition?

**Location:** France.

**Methods:** Weed communities were surveyed in 3008 4-m<sup>2</sup> plots, i.e. 32 plots per field in 94 winter-wheat fields located in the same landscape. We estimated patterns of species co-occurrence (C-score) at the field and landscape level. Additional characteristics of weed communities (degree of habitat specialization, competitive ability) and sampled fields (within-field and among-fields environmental heterogeneity) were used to interpret observed co-occurrence patterns at both scales.

**Results:** Non-randomness was detected in <20% of the fields; these fields were characterized by higher within-field environmental heterogeneity and contained a higher proportion of competitive species. This subset of fields partly drove the pattern of co-occurrence of weed species at the landscape scale. After removing this effect, specialist species were found to be aggregated and species that had an intermediate degree of habitat specialization were segregated, despite the lack of marked environmental gradients across the studied landscape.

**Conclusions:** Patterns of weed co-occurrence differed at the field and landscape scales. Weeds co-occurred mostly randomly within fields but were in some instances segregated as a result of environmental heterogeneity and possibly weed–weed competition. At the landscape scale, aggregation of specialist species and segregation of intermediate species are likely to result from variations in crop management among the sampled fields.

segregation (Gotelli & McCabe 2002). Later studies showed that plant communities could be segregated (Verheyen et al. 2003; Ribichich 2005; Reitalu et al. 2008), aggregated (Franzén 2004; Dullinger et al. 2007; Aragon & Woodcock 2010) or even randomly distributed (Burns 2007).

Segregation can result from species sorting via interspecific competition for limited resources (Diamond 1975) or species sorting by environmental filtering, where species that are not adapted to specific environmental conditions cannot occur (Verheyen et al. 2003; Sanders et al. 2007), while aggregation is often interpreted as facilitation in a context of high environmental severity (Dullinger et al. 2007). Segregation can also result from ecological drift (Ulrich 2004) or from spatial autocorrelation (Hausdorf & Henning 2007). The effect of the forces at play has been shown to be contingent on the spatial scale, i.e. the extent and grain at which species co-occurrence patterns are

being analysed (Levin 1992). For example, some coral reef fish communities were shown to be organized through competition at large scales and randomly distributed at finer scales (Anderson et al. 1981; Sale & Williams 1982), while some forests and communities were shown to be structured by environmental filters at larger scales and randomly distributed at finer scales (Gotelli & Ellison 2002; Sanders et al. 2007). In grassland plant communities, segregation at local scale appears driven by species interactions, while larger-scale structuring results from environmental filtering (Reitalu et al. 2008). Conversely, the effect of environmental severity on aggregation in alpine plant communities appeared more pronounced at finer scales than larger scales (Dullinger et al. 2007).

Most research on assembly rules has been directed at natural communities, and few studies have investigated filters shaping weed communities (but see Fried et al. 2009; Smith et al. 2009; Storkey et al. 2010; Gunton et al. 2011), probably because weed research has until recently mostly focused on understanding the biology and control of individual weeds infesting crops. Yet, the community assembly framework is applicable to highly managed agricultural systems. These simple and highly controlled systems could in fact be perfect testing grounds where assembly rules could be easier to elicit than in natural systems (Booth & Swanton 2002). In addition, community-level approaches provide a necessary holistic framework for understanding why weeds occur where they do, or how they interact in communities (Booth et al. 2003). Current knowledge in weed ecology does not allow clear predictions to be made as to species co-occurrence patterns. Some of the features shared by weed species militate for a random structure in communities. Indeed, most weeds are annual and produce large amounts of seed that can survive for long periods in the soil (Baker 1974), so that their expression is rather transient and unpredictable in cultivated fields. Yet, weed species do not make up a homogeneous group in terms of ecological requirements and species attributes (Lososova et al. 2008; Storkey et al. 2010); they also differ in terms of niche breadth and can be ranked along a specialist–generalist gradient (Fried et al. 2010). As a result, weeds can exhibit contrasted responses to soil properties, climate and agricultural practices (Hallgren et al. 1999; Fried et al. 2008), although variations in communities due to environmental gradients can be very low in some instances (Lososova et al. 2004). Finally, although studies have so far focused on crop–weed competition (Zimdahl 2004), it is possible that competition between weed species for light, nutrients and water could occur, at least during the seedling stage where densities of more than 1000 individuals·m<sup>-2</sup> can be observed. This could potentially result in some sort of competitive exclusion in weed communities.

In this paper, we assess the patterns of co-occurrence of arable weeds using C-score at two nested spatial resolutions: the field scale (i.e. a set of 32 plots of a few square metres located within a single field) and the landscape scale (i.e. a set of 94 fields grown with the same crop type within a small region). Additional characteristics of weed communities (degree of habitat specialization, competitive ability, similarity of niche in species pairs contributing to segregation within communities) and sampled fields (within- and among-field environmental heterogeneity) are used to interpret observed co-occurrence patterns at both scales.

## Methods

### Study area and vegetation sampling

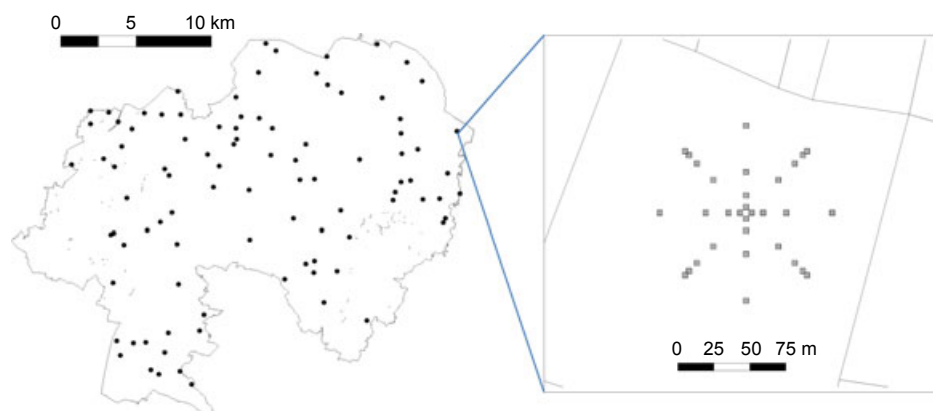
The study was carried out in an intensively managed agricultural landscape (ca. 400 km<sup>2</sup>) located in central-western France (south of the Département des Deux Sèvres, 46°11'N, 0°28'W; Fig. 1a). This area includes 18 000 fields that are devoted mainly to autumn-sown cereal production, i.e. winter wheat and winter barley (ca. 70%); other well-represented crop types were winter oilseed rape, sunflower and a few perennial crops. The geographical extent of the study is large enough to allow the existence of environmental gradients but small enough to avoid the sampling of different regional or biogeographical species pools (Fried et al. 2008). To avoid obvious differences in weed distribution due to different crop type, we focused our weed sampling on a single crop type, winter wheat. Sowing dates and the set of herbicides used were homogeneous enough within the study area to consider winter wheat as a single habitat type for arable weeds.

### Weed sampling and classification

Weed occurrence was recorded in March 2006 in 94 winter wheat fields randomly scattered across the study area (Fig. 1a). At the centre of each sampled field, we positioned a star-shaped array of 32 plots of 2 × 2 m (Fig. 1b). The occurrence of individual weed species was recorded along the eight arms of the star, each arm having four 4-m<sup>2</sup> plots located at 4, 12, 38 and 60 m from the centre of the star.

### Assessing species co-occurrence

Species data were organized as a presence–absence matrix for each scale, where each row of the matrix was a different species and each column was a different site. The C-score (Stone & Roberts 1990) was used as an overall measure of species segregation and quantifies the average number for each unique species pair of 'checkerboard units' in the presence–absence matrix. As matrix sample sizes varied for the two scales, we standardized the



**Fig. 1.** Nested weed sampling design. Weeds were recorded in 94 fields scattered over the study area and within each field in 32 plots (2 × 2 m).

differences between observed and simulated indices for each plot as: (observed index – mean of simulated indices)/standard deviation of simulated indices. This gives a standardized effect size (SES) measure of deviation from randomness that is centred around zero. A negative SES value for the C-score indicates aggregation, while a positive SES value indicates segregation, concordant with deterministic processes structuring the community (Gotelli & McCabe 2002). Detailed descriptions of statistical properties and performance of this metric can be found in Gotelli (2000) and Gotelli & Rohde (2002).

Significance for the observed C-score was tested by comparison with simulated distributions using null models (Gotelli & Graves 1996). We used a ‘fixed–fixed’ algorithm (Gotelli & Ellison 2002) to take into account both the frequency of occurrence of species in the array of plots and differences in species richness per sample unit, making it well suited to data recorded across heterogeneous environments (Rooney 2008). We used the sequential swap algorithm, in which the original matrix is shuffled through repeated swapping of random submatrices (Stone & Roberts 1990), to generate 50 000 new matrices on which we calculated 50 000 simulated C-scores using the Ecosim software v. 7.0 (Kitchener, ON, CA, USA).

For the fine scale analysis, we considered all surveyed plots within each field ( $n = 32$ ) and repeated the analysis for the 94 fields (94 field-level C-score SES values). For the large-scale analysis, we pooled species occurrence per field and compared all the 94 fields (one landscape-level C-score SES value).

### Detecting the processes underlying the structuring of communities

At a field scale, observed co-occurrence patterns could result either from competitive exclusion and/or environmental heterogeneity within individual fields. In the first

case, one would expect more non-random co-occurrence within fields with a larger proportion of competitive species and/or limited nitrogen, light or water resources. We therefore assessed the competitive ability of communities within each field with three variables: the proportion of competitive species sensu Grime’s strategies, i.e. C, CS and CR strategists (Grime et al. 1988), a mean community value for life form (percentage perennial species) and a mean community value for seed weight (Kühn et al. 2004); two life traits that are relevant proxies for the competitive ability of species (Schamp et al. 2008). Resource limitation in individual fields was estimated with mean field values for the Ellenberg indicators N (soil nitrogen), L (light) and F (soil moisture) (Ellenberg et al. 1992). Although Ellenberg scores derived from plant communities cannot rival direct measures of environmental gradients, such indicators have been widely used as surrogates for environmental conditions in the literature (Smart et al. 2003; Gunton et al. 2011). If within-field environmental heterogeneity is at play, one would expect non-random co-occurrence patterns to occur in fields that are internally environmentally heterogeneous. We therefore estimated within-field environmental heterogeneity by calculating the variations of Ellenberg indicators (N: soil nitrogen, L: light, R: soil reaction/acidity, T: temperature, F: soil moisture) applied to the total pool of species occurring within each field.

In addition, following the approach of Reitalu et al. (2008), we identified the species that contributed most to observed segregation patterns. For each species pair, we computed the average checkerboard units (CUs) in the fields showing significant segregation patterns and where the two species of the pair co-occurred. We then used an ordination approach to compare the position and the amplitude of the ecological niche of the species pairs with the highest CU scores. The ecological niche of individual weed species was estimated using ordination (canonical correspondence analysis, CCA) on a wider national data

set (153 arable weed species over 700 fields) using constraining variables describing soil conditions, climatic conditions, geographical location, cropping practices and field topography (see Fried et al. 2008 for more details). These analyses were performed with the R software v. 2.12.1 (R Development Core Team 2004; R Foundation for Statistical Computing, Vienna, AT, USA) using the libraries *ade4*. If species contributing most to the segregation patterns within fields belong to the same ecological groups, competition may be at play. If, on the other hand, they belong to different ecological groups, species co-occurrence may be explained by environmental heterogeneity.

A Spearman correlation coefficient was computed for each field between its C-score SES value and the characteristics of the weed community and environmental conditions occurring within the field.

At the landscape scale, the overall C-score value of weed communities is likely to result from the effect of environmental gradients across the study area. This hypothesis was tested in two ways. First, weed species were classified according to a generalist/specialist index computed on an independent data set (for details, see Fried et al. 2010). The expectation here is that a potential effect of environmental gradients (soil, climate and cultivation practices) at a landscape scale will be easily detected for specialist species, while the response of generalist species is expected to be weaker. It is important to note that the classification on the generalist/specialist gradient is independent of species occurrence as shown in Fried et al. (2010), i.e. a generalist species can be rare and a specialist can be frequent. Second, we carried out a cluster analysis on field weed species composition in order to identify weed community groups. The Euclidean distances between species coordinates in a CCA multidimensional space was used to conduct a Ward ascendant hierarchy grouping (Ward 1963) on the species composition of each field, so that each pair of fields could be assessed in terms of compositional similarity and therefore in terms of environmental conditions prevailing in the field. We then calculated the landscape-level C-score value by progressively pooling fields that increasingly differed in terms of weed community composition. If a regional environmental gradient is at play in the landscape structuring of weed communities, one would expect the regional C-score value to increase as increasingly different weed communities are added. We tested for spatial autocorrelation among fields in total weed species richness, richness of specialist species, C-score SES values and Ellenberg scores of weed communities (Moran 1948).

## Results

Overall, we recorded 114 arable weed species in the study area. Out of the 114 recorded species, 79 species could be

classified according to Fried et al. (2010): 32 generalist, 23 intermediate and 24 specialist species. The other species were either rare species that were not used in Fried et al. (2010) or were deemed too variable in terms of their specialization index by these authors. Mean species richness of total, specialist, generalist and intermediate weed species at the field and plot scales are presented in Table 1. Figure 2 presents the distribution of species richness and specialist species richness across the 94 sampled fields. The spatial distribution of species richness across the region was clustered (Moran  $I = 0.0509$ ,  $P = 0.00147$ ) but the distribution of specialist species was random (Moran  $I = 0.0187$ ,  $P = 0.12$ ). Field-level species richness was positively correlated with the proportion of specialist species within the field ( $r = 0.395$ ,  $P < 0.01$ ).

### Patterns of species co-occurrence within a field

Over all the 94 fields sampled, C-score mean values for total weed communities, generalist or specialist species were not significant, suggesting that in general within a given field weeds were randomly assembled, regardless of their degree of habitat specialization (Table 2). However, C-score values within individual fields were highly variable across the study area (Fig. 3) although not spatially correlated (Moran  $I = 0.0156$ ,  $P = 0.17$ ). For 20 of the 94 fields sampled, C-score values indicated non-random assemblages, with segregation in 19 cases. Overall, C-score values at the plot level were positively correlated with species richness and the proportion of specialist species, and to a lesser extent with the proportion of competitive species (Table 3). C-score values were, on the other hand, negatively correlated with the Ellenberg-N and Ellenberg-F indicator values (Table 3). No relationship was found with the mean community value for seed weight or proportion of perennial species.

The 20 fields within which we detected non-random assemblages were characterized by significantly higher within-field variation in Ellenberg scores (Table 4a) but

**Table 1.** Species richness for the total weed community ( $n = 114$  species) and for generalist ( $n = 32$ ), intermediate ( $n = 23$ ) and specialist species ( $n = 24$ ) at the field and at the plot scale.

	Mean (SD)	Min	Max
Field scale (3008 plots)			
Total weeds	4.1 (2.3)	0	9
Generalists	2.0 (1.5)	0	9
Intermediate	1.1 (0.9)	0	5
Specialists	0.2 (0.59)	0	4
Landscape scale (94 fields)			
Total weeds	17.9 (7.3)	5	36
Generalists	9.3 (3.6)	1	16
Intermediate	3.6 (1.7)	0	8
Specialists	1.4 (1.6)	0	8

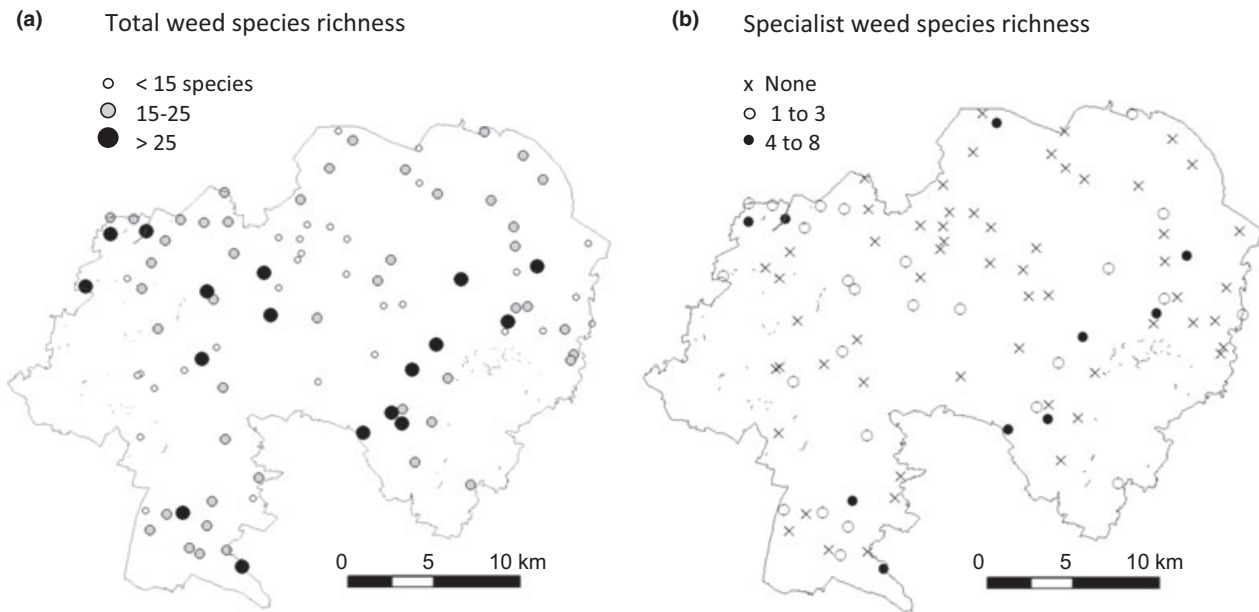


Fig. 2. Distribution of (a) Total weed richness and (b) Specialist weed richness across the 94 sampled fields.

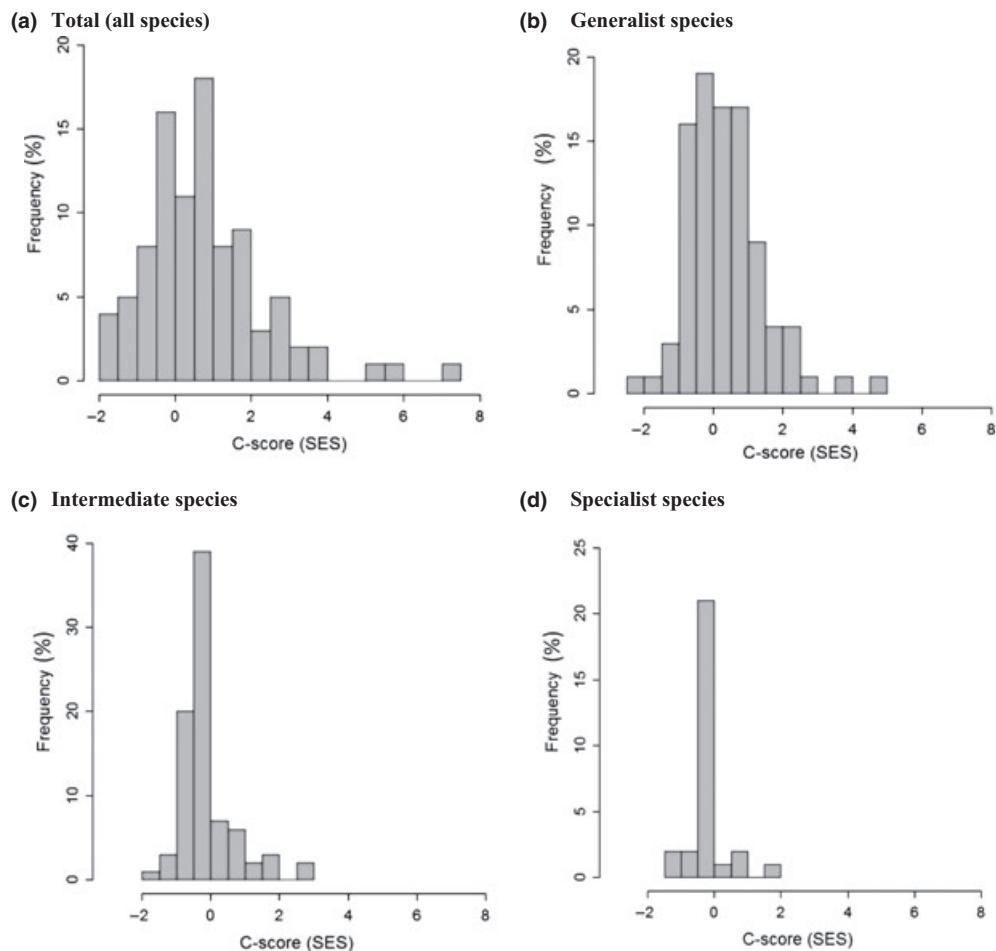
**Table 2.** Standardized effect sizes (SES) and *P*-values for C-score at the two scales for the total weed community (*n* = 114 species) and for generalist (*n* = 32), intermediate (*n* = 23) and specialist species (*n* = 24). At the field scale, SES values are mean values and SE within brackets (94 fields). At the landscape scale, SES values are presented for the total data set, for the fields within which communities are structured and for the fields within which communities are non-structured assemblages. Significant values are in bold.

	C-score	
	SES	<i>P</i>
Field scale		
Total weeds	0.769 (0.164)	0.291
Generalists	0.343 (0.113)	0.314
Intermediate	-0.060 (0.083)	0.574
Specialists	-0.024 (0.092)	0.799
Landscape scale		
1. All fields ( <i>n</i> <sub>fields</sub> = 94)		
Total weeds	<b>2.851</b>	<b>0.003</b>
Generalists	-0.099	0.483
Intermediate	<b>1.917</b>	<b>0.033</b>
Specialists	- <b>1.889</b>	<b>0.014</b>
2. Fields within which communities are structured ( <i>n</i> <sub>fields</sub> = 20)		
Total weeds	<b>2.491</b>	<b>0.012</b>
Generalists	-0.047	0.495
Intermediate	-0.572	0.704
Specialists	-1.198	0.093
3. Fields within which communities are not structured ( <i>n</i> <sub>fields</sub> = 74)		
Total weeds	0.207	0.388
Generalists	-0.256	0.577
Intermediate	<b>2.469</b>	<b>0.014</b>
Specialists	- <b>1.930</b>	<b>0.014</b>

did not stand out as fields where mean environmental conditions were atypical of the region (Table 4b). They also had significantly higher species richness (23.6) than the remaining 74 fields (16.4, Wilcoxon test, *P* < 0.001) and higher proportion of specialists (2.80 against 1.08) (Wilcoxon test, *P* < 0.001). The species pair *Lamium purpureum*–*Mercurialis annua* had the maximum CU score within the fields (Table 5). Nine out of the ten species pairs that contributed the most to the segregation patterns at the field scale belonged to different ecological groups, as identified by CCA (Table 5, Figs 4, 5) with distinct or only partially overlapping ecological niches.

**Patterns of species co-occurrence at the landscape scale**

The landscape-level C-score value indicated segregation among weed communities (Table 2). The assemblage of generalist species was random, intermediate species were segregated (positive C-Score) and specialist species were aggregated (negative C-score). As 20 of the 94 fields exhibited non-random co-occurrence patterns, we excluded them in order to avoid any effect of within-field structuring on the assessment of landscape-scale species co-occurrence patterns. This analysis shows that total weed communities and generalist species were randomly assembled, while we could still detect the segregation of intermediate species and the aggregation of specialist species. Conversely, an analysis of landscape-scale co-occurrence patterns that included only the 20 fields indicated segregation for total weed communities, with no differential effect



**Fig. 3.** Distribution of C-score Standardized Effect Sizes (SES) at the field scale. Scores significantly differing from the null model have a value that is  $>2$  or a value that is  $<-2$ .

**Table 3.** Spearman rank correlations ( $r_s$ ) and associated  $P$ -value between the C-score standardized effect sizes (SES) at the plot level and characteristics of weed communities and potential resource limitation in the plots. (a) For all 94 surveyed fields ( $n = 3008$  plots) and (b) for the 74 fields with non-significant C-score values ( $n = 2368$  plots). Significant values are in bold.

	(a) 94 fields		(b) 74 fields with non-significant C-scores	
	$r_s$ with C-score SES	$P$ -value	$r_s$ with C-Score SES	$P$ -value
Species richness	<b>0.430</b>	<b>&lt;0.001</b>	0.226	0.053
% Specialist species	<b>0.314</b>	<b>0.002</b>	0.140	0.235
% Competitive species	<b>0.245</b>	<b>0.017</b>	<b>0.256</b>	<b>0.028</b>
% Perennial species	0.120	0.250	0.020	0.867
Seed weight	-0.077	0.459	-0.117	0.321
Ellenberg-N (soil nitrogen)	<b>-0.225</b>	<b>0.029</b>	-0.140	0.233
Ellenberg-F (soil moisture)	<b>-0.238</b>	<b>0.021</b>	<b>-0.237</b>	<b>0.042</b>
Ellenberg-L (light)	-0.061	0.558	-0.088	0.455

**Table 4.** Comparison of the mean variance (a) and mean value (b) in Ellenberg indicators for fields exhibiting significant C-score standardized effect sizes (SES) ( $n = 20$  fields) and those with no apparent community structuring ( $n = 74$ ).

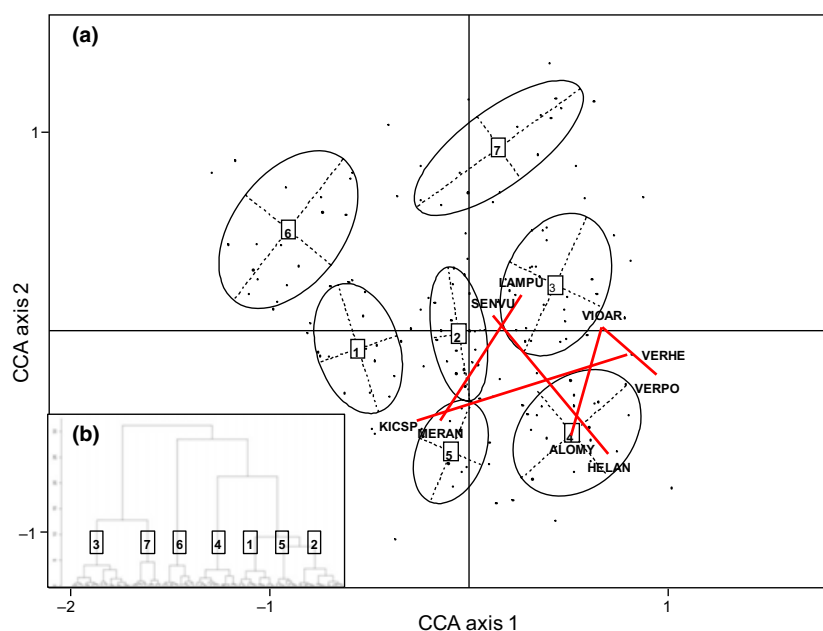
	Fields with significant C-score SES values ( $n = 20$ )	Fields with non-significant C-score SES values ( $n = 74$ )	Wilcoxon Test $P$
(a) Mean variance in the field			
Ellenberg-L (light)	0.064	0.037	$<0.001$
Ellenberg-R (soil reaction)	0.065	0.026	$<0.05$
Ellenberg-T (temperature)	0.032	0.018	$<0.002$
Ellenberg-F (soil moisture)	0.089	0.053	$<0.05$
Ellenberg-N (soil nitrogen)	0.165	0.083	$<0.001$
(b) Mean value for the whole field			
Ellenberg-L (light)	6.64	6.63	0.477
Ellenberg-R (soil reaction)	6.81	6.85	0.674
Ellenberg-T (temperature)	5.91	5.87	0.533
Ellenberg-F (soil moisture)	4.73	4.80	0.256
Ellenberg-N (soil nitrogen)	6.32	6.45	0.105

**Table 5.** The ten species pairs giving the ten highest mean checkerboard unit (CU) values showing species segregation within fields. The mean CU, standard deviation (SD) and the number of replicates where the species pair is found ( $n$ ) are given. Growth form and ecological group within each pair are also presented. The numbering of ecological groups refers to the ordination plot (CCA analysis).

Species pairs	Mean CU	SD	$n^*$	Growth forms	Ecological group
<i>Lamium purpureum</i> – <i>Mercurialis annua</i>	67	18.4	4	T & sT	3–5
<i>Veronica polita</i> – <i>Viola arvensis</i>	57.75	28.0	4	wT	4–3
<i>Helianthus annuus</i> (volunteer)– <i>Senecio vulgaris</i>	55	42.5	4	T	4–3
<i>Kickxia spuria</i> – <i>Veronica hederifolia</i>	55	0	6	sT & wT	5–4
<i>Alopecurus myosuroides</i> – <i>Viola arvensis</i>	52.33	21.7	3	wT	4–3
<i>Helianthus annuus</i> (volunteer)– <i>Veronica hederifolia</i>	50	13.1	3	T & wT	4–4
<i>Geranium dissectum</i> – <i>Fallopia convolvulus</i>	48	36.4	4	wT & sT	3–5
<i>Lamium purpureum</i> – <i>Veronica hederifolia</i>	47.5	31.0	4	T & wT	3–4
<i>Convolvulus arvensis</i> – <i>Veronica hederifolia</i>	47	24.1	7	G & wT	1–4
<i>Helianthus annuus</i> (volunteer)– <i>Solanum nigrum</i>	46.33	40.0	3	T & sT	4–1

\*Species that co-occurred in fewer than three fields (on a total of 19 fields) where excluded from the analysis.

T, therophyte; G, geophyte; w, winter-germinating; s, spring-germinating.



**Fig. 4.** Position of the five species pairs (represented by a line) that contributed the most to the segregation pattern in the CCA ordination plot. The numbers in the ellipses correspond to the ecological groups highlighted in by the Ward Hierarchical Ascending grouping. LAMPU, *Lamium purpureum*; SENVU, *Senecio vulgaris*; VIOAR, *Viola arvensis*; VERHE, *Veronica hederifolia*; VERPO, *Veronica polita*; KICSP, *Kickxia spuria*; MERAN, *Mercurialis annua*; ALOMY, *Alopecurus myosuroides*; HELAN, *Helianthus annuus*.

in relation to the degree of habitat specialization of weed species.

The cluster analysis identified 13 types of weed communities across the 94 fields. Individual fields within which we detected significant C-scores were spread across the 13 types of weed communities. The steady increase of the overall regional C-score as the 13 groups of weed communities identified with the classification were progressively pooled, confirms the role of the 20 fields in the regional structuring of communities (Fig. 6). When excluding the 20 fields from the pooling process, the overall C-score remained low, suggesting a lack of marked environmental gradient across the

landscape. This is confirmed by a relatively limited degree of spatial autocorrelation in the environmental conditions prevailing in fields, measured through the weed community Ellenberg scores N (soil nitrogen) (Moran  $I = 0.033$ ,  $P = 0.03$ ), F (soil moisture) (Moran  $I = 0.041$ ,  $P = 0.02$ ) and L (light) (Moran  $I = 0.04$ ,  $P = 0.02$ ).

## Discussion

### Patterns of weed co-occurrence at the field scale

Within 74 of the 94 fields sampled, we did not detect significant patterns of weed species co-occurrence and this pattern

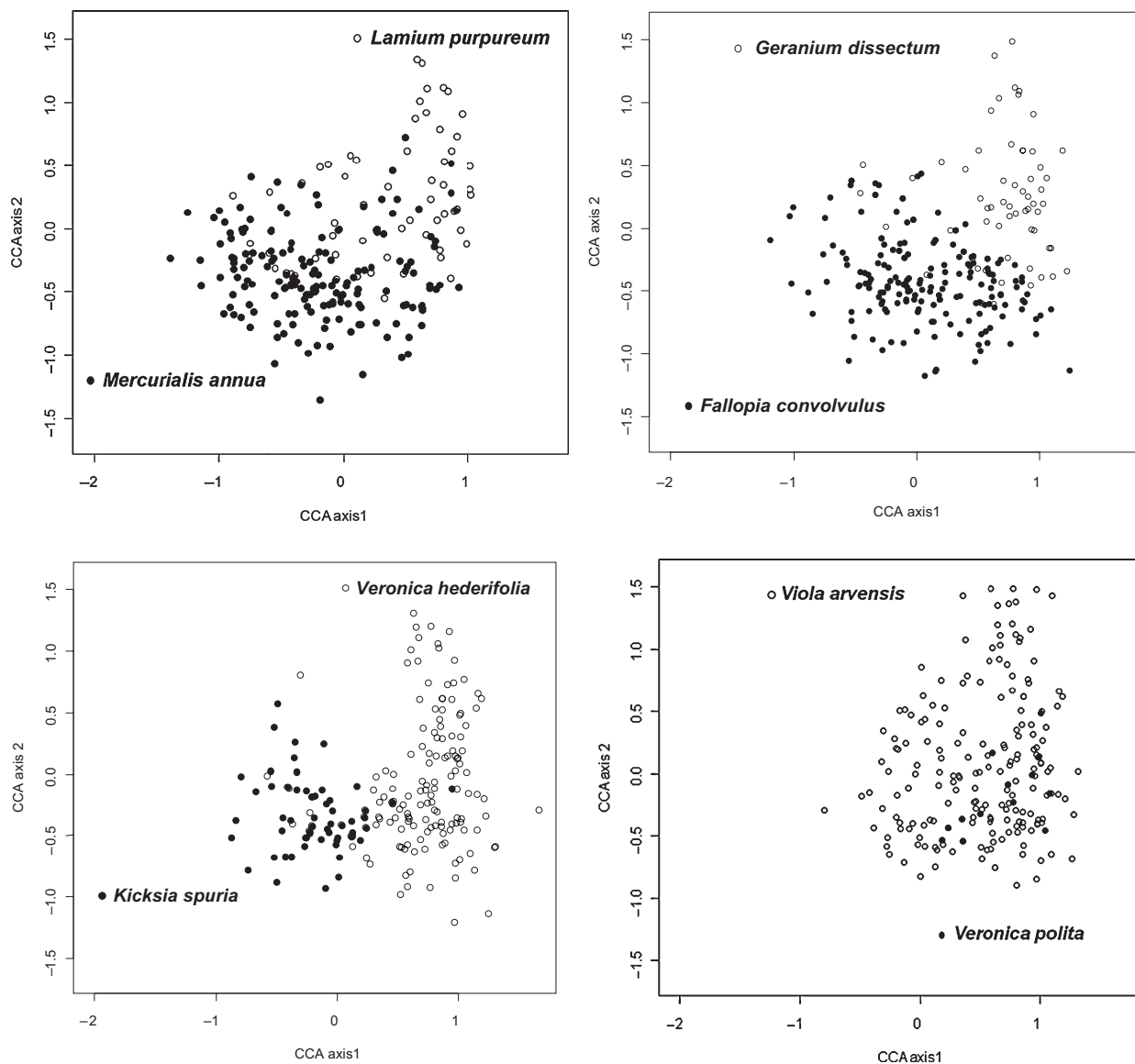
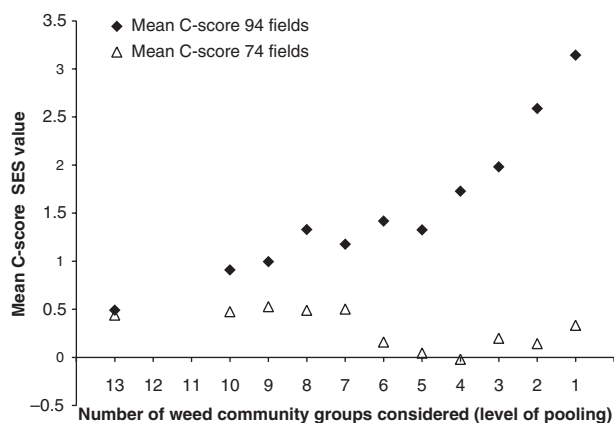


Fig. 5. Examples of CCA ordination plots visualizing the ecological amplitudes of species pairs which gave the highest C-score values.

was valid for both specialist and generalist species. Such general random association of plant species at fine scale has already been demonstrated in grasslands (Franzén 2004). Yet, in the 20 other fields surveyed, we detected a significant segregation within total weed communities. Our analysis indicates that such structuring occurs in fields where environmental heterogeneity is particularly high. This is confirmed by the comparison of the ordination plots of the ten species pairs forming the highest mean checkerboard units, which shows that the segregated species pairs occupy different ecological niches (Fig. 4). An explanation could therefore be that such fields offer a higher number of ecological niches, and as such shelter a higher number of species that are segregated across the 32 plots located in the field.

Other elements seem to indicate a possible effect of weed–weed competition in species co-occurrence patterns within the plots. Among the species pairs that contributed most to the segregation patterns, some use the same ecological niche (*Viola arvensis* and *Veronica polita*; Fig. 5). Finally, C-score values across the 94 fields were also positively correlated with the proportion of competitive species within a field. These competitors can be perennial species with rhizomes or runners (*Cirsium arvense*, *Elytrigia repens*), known for their ability to form dense stands which can probably exclude seedlings of annual species. Such exclusive competition between perennial and annual weed species has been shown in the case of succession in old fields (Kosola & Gross 1999). Finally, the fact that the Ellenberg-





**Fig. 6.** Mean C-score SES values for different levels of plot pooling on the X-axis, from  $x = 13$  (no pooling i.e. 13 distinct weed groups) to  $x = 1$  (all weed groups are pooled). Results are shown for analyses with all the 94 fields and with only the 74 fields where no significant C-score was detected within fields.

N value of the community, which is a good predictor of nitrogen availability, is negatively correlated with C-score SES across the 94 fields could mean that more species can co-occur despite competition in situations where levels of resources are high. Further studies are required to fully investigate the role of weed–weed competition in community structuring. Yet, our results question traditional modelling approaches which account for the competitive effect of the crop upon weeds but rarely for competition between weeds (Holst et al. 2007).

#### Patterns of weed co-occurrence at the landscape scale

At the landscape scale, when excluding the 20 ‘atypical fields’ in our analyses, whilst the general pattern of total weed co-occurrence did not differ from randomness, intermediate and specialist species were structured. The lack of segregation at the regional level and the low spatial autocorrelation in the mean Ellenberg scores of fields could both mean that the environmental gradient (especially soil conditions) was not marked enough in the data set for structuring weed communities. However, for intermediate species, the observed pattern indicated significant species segregation, probably as a result of differences in management practices among fields. Although we have removed the strongest agricultural filter, i.e. the crop type (Fried et al. 2008), there were most likely inherent differences in agricultural practices applied in each field and some of these have direct effect on weed communities, e.g. intensity of weed control, N input (Gabriel et al. 2005; José-Maria et al. 2010) and the preceding crop type, especially in our study area, where weed communities have been shown to shift if perennial crops are included in the rota-

tion (Meiss et al. 2010). These variations are likely to explain the segregation of weed species that have an intermediate specialization index (e.g. *Brassica nigra*, which is mainly related to oilseed rape as a preceding crop and never co-occurs with *Picris echioides*, a pluriannual species favoured by alfalfa as preceding crop). Specialist species, on the other hand, co-occurred more often than expected by chance and indeed our distribution data indicated that 20% of the sampled fields sheltered three to eight specialist species (with for example *Aphanes arvensis*, *Arenaria serpyllifolia*, *Legousia speculum-veneris* and *Petroselinum segetum* all occurring within a single field), while 60% of the sampled fields sheltered none or just one specialist species. Spatial aggregation of rare or specialist species is commonly observed for trees in tropical forests, and this pattern seems often determined by weak dispersal capabilities (Condit et al. 2000; Li et al. 2009). In our case, the clumped distribution of specialist arable weeds is more likely to be associated with favourable local management practices. Several studies have indeed shown that agricultural intensification has resulted in the decline of the most specialist arable weeds (Albrecht 2003; Fried et al. 2010). In addition, the existence of species-rich fields might also be explained by the local landscape context of fields, i.e. in this study area, fields of small size surrounded by small fields have been shown to shelter more weed species (Gaba et al. 2010).

#### Conclusion

Non-randomness in weed species co-occurrence was detected in only a subset of studied sites (20% of the fields) in which segregation patterns could be explained by a high degree of environmental heterogeneity and possibly, to a lesser extent, the expression of weed–weed competition. This subset of fields partly drives the pattern of co-occurrence of weed species at the landscape scale but, in addition, our results show that patterns of weed co-occurrence are strongly dependent on the degree of habitat specialization of individual species. We could not detect significant weed co-occurrence patterns for generalist species across the landscape, while specialist species were aggregated in particular fields, and species that had an intermediate degree of habitat specialization were segregated, i.e. some pairs of species never co-occurred. Given the lack of strong environmental gradients across the study area, the structuring of non-generalist species at the landscape level is probably driven by among-field differences in the intensity of crop and weed management.

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