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Weed species richness in winter wheat increases with landscape heterogeneity

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ABSTRACT

There is empirical evidence that landscape composition and structure can affect the distribution and long-term dynamics of the organisms that live in it. Weeds are no exception and in this paper, we investigated how weed richness and diversity in 123 winter wheat fields within a small agricultural region were affected by the landscape surrounding each field (radii ranging from 100 to 1000 m) and the field properties such as its size and the preceding crop. Landscape was described by its proportion (cover of spring crops, winter crops, woodland, grassland, set-aside) and its structure (number of fields, number of land use types). Akaïke criterion-based models indicated that variations in weeds were best explained at the 200 m radius. At that scale, hierarchical partitioning shows that the independent contributions of field level and landscape level variables were significant for two variables. Weed richness and weed diversity increased significantly as field size decreased and as the number of fields within 200 m increased. This suggests that weed richness and diversity are higher in landscapes that have a finer grain, probably because these landscapes offer more habitat heterogeneity within cultivated areas and contain more crop edges that can shelter many weed species.

1. Introduction

Among the biota found in agro-ecosystems, arable weed species could play an important role in supporting biological diversity, in particular as food resources of primary importance for birds and insects inhabiting farmland (Wilson et al., 1999; Marshall et al., 2003; Holland et al., 2006; Storkey, 2006). In Europe, there is increasing evidence of a general decline in arable weeds over the last decades (Andreasen et al., 1996; Sutcliffe and Kay, 2000; Preston et al., 2002; Baessler and Klotz, 2006; Hyvonen, 2007; Fried et al., 2009b). As for other taxa found in agro-ecosystems, these declines are likely to result from changes in farming practices, in particular the generalised use of herbicides, and other changes associated with land use intensification and landscape simplification (Benton et al., 2003; Tscharntke et al., 2005; Petit and Firbank, 2006; Petit, 2009).

Factors affecting weed communities' composition and diversity have traditionally been studied at the within-field level as it is generally assumed that the main drivers are the farming practices used within the cultivated field. Indeed, crop type (Hallgren et al., 1999; Fried et al., 2008), the main herbicide families and fertilization regimes associated with specific crop types (Andersson and Milberg, 1998), preceding crop (Fried et al., 2008), crop succession or tillage systems (Mayor and Dessaint, 1998; Cardina et al., 2002) have all been recognized to account for variations in weed communities. Effects of organic versus conventional management have also been reported to modify weed species diversity (Bengtsson et al., 2005; Clough et al., 2007). However, other studies have shown considerable differences in community composition among fields grown with similar crop types in different regions (Gabriel et al., 2006) or within the same landscape (Fried, 2007). The structural complexity of the landscape surrounding fields (i.e. area and spatial arrangement of the surrounding land use types) is also likely to increase arable weed diversity as complex landscapes generally offer more diverse non-crop habitats likely to shelter weed species, e.g. ruderal patches such as road verges, fallow land, vegetation gaps (Roschewitz et al., 2005; Gabriel et al., 2006). In addition, complex landscapes generally present higher perimeter/area ratios and therefore proportionally more margins, which can provide refugia for weed species that are most sensitive to intensive agricultural practices (Fried et al., 2009b). In a more comprehensive study, Gabriel et al. (2005) showed significant effects of three landscape variables (perimeter/area ratio, habitat type diversity and proportion of arable land) on the arable weed diversity in 18 winter wheat fields under comparable herbicide and fertilization treatments. In addition, effects of landscape variables were explored at relatively coarse spatial scale (e.g. the smallest being a circle of 1000 m diameter in Gabriel et al.,2005) and recent work suggests that the weed flora should be influenced by landscape context at a local scale, e.g. within a circle of radius smaller than 500 m (Marshall, 2009).

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The focus of the present paper differs from the studies cited above in two major aspects: (i) all fields were sampled in the same geographical area in order to minimize possible effects of environmental conditions and to a certain extent of agronomic practices and (ii) landscape variable effects were investigated at small and intermediate spatial scales. Here, our goal is to quantify within a single large landscape the potential contribution of spatial, landscape and within-field variables for explaining the large variation in levels of species richness and diversity that is often observed in fields grown with similar crops (Fried et al., 2009a). We addressed two questions: (i) which scale is the most relevant to investigate the effects of landscape mosaic structure and composition on weed richness and diversity and (2) at this scale, what is the amount of variation in weed richness and diversity due to the characteristics of the field where it was sampled, of the landscape context of the focal fields and to spatial autocorrelation.

2. Materials and methods

The study was carried out in an intensively managed agricultural landscape (ca. 400 km^2) located in central-western France (south of the Département des Deux Sèvres, 46°11′N, 0°28′W). We detected no overall gradients in the soil, weather and landscape characteristics of the study area. The 18,000 fields in this area are mainly devoted to autumn sown cereal production (ca. 70%) and few perennial crops (*Lolium perenne* L. or *Medicago sativa* L. and *Trifolium pratense* L.). As a result, the typical and most frequent 4-year crop rotation in the area was winter wheat, followed by either winter oilseed rape or sunflower every 2 years.

2.1. Vegetation data

Weed occurrence was recorded in 123 winter wheat fields between March and June in 2006 ($n = 84$ fields) and in 2007 ($n = 39$ fields). Fields were selected based on random sampling of their latitude and longitude. Fields sampled in 2006 and 2007 represented 2.1% and 0.9%, respectively of the fields cultivated with winter wheat in the study area. The average distance between two sampled fields was 1000 m (range 175–2100).

At the centre of each sampled field, we positioned a star-shaped array of 32 plots of 2 m × 2 m. The occurrence of individual weed species was recorded along the eight arms of the star, each arm having four 4 m^2 plots located at 4, 12, 38 and 60 m from the centre of the star. The outermost plot of the array was at least 5 m from any field margin. Thus all samples were performed within the core of the field. Plants were identified and named according to Hanf (1982), Jauzein (1995) and Marmarot et al. (1997), except for a few taxa for which small seedling size and the absence of reproductive parts constrained the identification to genus level. Data recorded in the 32 plots were aggregated in order to estimate species richness and diversity (Shannon index) at the field level. Since we only recorded species presence/absence within individual plots, the frequency of a species in a field ranged from 0 to 32.

2.2. Spatial and landscape predictors

The spatial description of fields and their surrounding landscape was performed using the database of land use on every single agricultural field. This database has been updated yearly since 1995 and classifies land use into 48 types. These land use types comprise built-up areas (3), garden (1), woodland (1), fallow land (1), set-aside (2), tilled bare soil (1), vineyard (1), types of annual crops, i.e. winter crops (11) and spring crops (12), and types of grasslands (15) differing by species sown (*L. perenne*, *M. sativa*, *T. pratense*) and age (1, 2, 3 or more years). The Geographical Information System ArcView 9.2 (ESRI) was used to measure the size of individual fields and to calculate variables describing the composition and structure of the surrounding landscapes. Landscape variables were measured around the centre of each star-shaped array at five spatial scales (i.e. circular landscape sectors of 100, 200, 300, 500 and 1000 m radius). These distances were chosen in order to explore the effects of landscape variables at local (i.e. field and field margins), intermediate (field, field margins and neighbouring habitats) and larger scales (landscape mosaic).

Eleven explanatory variables (10 quantitative and 1 categorical) were grouped into four categories. The first category was named *Field characteristics* and comprised the size of the sampled fields (FSize) and the crop that preceded winter wheat (PCrop). PCrop classes are winter crop ($n = 51$ fields), spring crop ($n = 48$) or perennial crop and meadow ($n = 24$). The second category described *Spatial autocorrelation*, i.e. the spatial structure within our set of observations, which was explored by including the geographical coordinates of the sampled data, i.e. the latitude (LAT) and the longitude (LONG) of the centre of the star-array. Taking into account spatial autocorrelation is important to avoid confounding effects due to a higher or lower similarity in weed richness (diversity) in neighbouring sites than it would be in a random set (Legendre, 1993). The third category described *Landscape composition* and included five variables that quantified the proportion of the total area within each radius that was used by the following land use types: winter crops (%WC), spring crops (%SC), set-asides and abandoned fields (%SAA), grass (%GR) and woody habitats (%WO). The fourth category described *Landscape structure* and included two variables, i.e. the number of fields within each radius (NField) and the number of different types of land use occurring within each radius (NLUT) out of the 48 land use types described in the database.

2.3. Data analysis

First, the potential effect of weather conditions in 2006 and 2007 on weed species richness and diversity was tested using a Wilcoxon rank sum test. No significant effects were found on weed richness ($W = 1657.5$, p-value = 0.9177) or on weed diversity ($W = 1589$, p-value = 0.7795). Therefore, data sampled in 2006 and 2007 were pooled for the rest of the analysis.

Second, the spatial scale at which the variables describing landscape composition and structure had the highest impact on species richness and diversity was assessed. We compared the fits of five models (using Generalized Linear Model (GLM) with Poisson error distribution for weed richness and Gaussian error distribution for weed diversity) that included the variables describing Field characteristics, Spatial autocorrelation and the values of the variables within the categories Landscape composition and Landscape structure in circles of radius 100, 200, 300, 500 and 1000 m (Table 1). The fits of these five models were compared using the Akaïke Information Criterion (AIC). The model, i.e. the scale, with the smallest AIC value gives the best fit among the given models.

Third, the total variation explained by the models was estimated using variance partitioning by partial redundancy analysis (Ter Braak, 1998) because of the collinearity between variables. A hierarchical partitioning analysis was then conducted in order to compute the independent contributions of the variables within the four categories Field characteristics, Spatial autocorrelation, Landscape composition and Landscape structure. The significance of the independent effect of each variable was determined by a randomization approach ($n = 1000$) which yields Z-scores (Mac Nally and Walsh, 2004). Statistical significance was based on an upper confidence limit of 0.95.

Finally, the relationships (positive or negative) of richness and of diversity to each explanatory variable were explored by studying residuals of the models with the smallest AIC for both weed richness and diversity in which three of the four categories of variables were controlled (Leprieur et al., 2008). For example, to test the effect of Field characteristics, we analysed the form of the relationship between each variable of this category (FSize and PCrop) and the residuals from a GLM with a Poisson error function for weed richness and a GLM with Gaussian error for weed diversity. In both of these models, species richness and diversity were explained by using all the other variables for the selected scale as predictor variables. The same procedure was applied for testing Spatial autocorrelation, Landscape composition and Landscape structure effects, i.e. by testing the form and the sign of the relationship of each Spatial autocorrelation variable (or each Landscape composition or Landscape structure variable, respectively) with the residuals of models explaining species richness (diversity) using the three other categories of explanatory variables.

Statistical analyses were performed with the packages 'hier.part' (Walsh and Mac Nally, 2009) and 'vegan' (Oksanen et al., 2009) of the software R (R Development Core Team, 2008).

3. Results

In total, 135 weed species (from 31 families and 93 genera) were observed. Mean species richness per field was 17.85 species (range 5–47). Mean species diversity was 3.31 (range 1.01–4.99). Sample accumulation curves revealed a high heterogeneity in weed richness among the sampled winter wheat fields, e.g. to observe 80% of the weed species found in the landscape required a sample size of fifty individual fields (Fig. 1). Four species (*Fallopia convolvulus* Löve, *Veronica hederifolia* L., *Polygonum aviculare* L., *Veronica persica* Poir.), known to be ubiquitous, were observed in ca. 90% of the sampled fields. Weed communities were dominated by dicotyledonous plants (89%). Most of the species were winter-germinating weeds (43%) and only 16% were spring weeds.

3.1. Characteristics of the sampled fields

FSize varied greatly across the 123 winter wheat fields sampled (median = 3.63 ha, range 1.03–17.54). Values for Landscape composition and Landscape structure variables at each of the five radii are provided in Table 1. Differences in landscape composition were also observed between the five radii. All the groups of land use type describing landscape composition occurred in the neighbourhoods of the 123 sampled fields. Winter crops, spring crops and grasslands were predominant whatever the radius, whereas set-aside, abandoned land and woodland were more scarcely represented in the neighbourhood of the 123 sampled fields, especially for low radius values. The variable %WC decreased as the length of the radius increased whereas the proportion of the other four variables increased. The proportion of land covered by each of the five land use types was highly variable whatever the radius, indicating a certain degree of landscape heterogeneity across the study area. In terms of landscape structure, for 50% of the sampled fields, NField ranged from a value of four fields at the 100 m radius to 131 fields at the 1000 m radius. The highest increase was observed when moving from the 300 to the 500 m radius. A similar pattern was observed with NLUT which ranged from three different types of

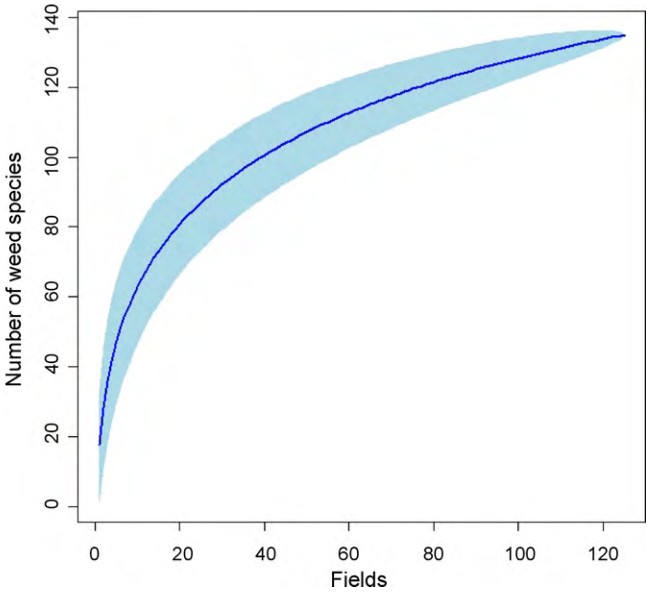

Fig. 1. Species accumulation curve generated for weed species in the 123 sampled fields sampled in 2006 and 2007. The curve was fitted with a saturating function to estimate total species richness for each field. The blue line represents the mean species accumulation, and the blue area, its standard deviation based on random permutations of the data using sub-sampling without replacement (Gotelli and Colwell, 2001; R library vegan). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Table 1

Occurrence of land use types, median (min–max) for the percentage cover of land use types, NField and NLUT at the five radii around sampled fields. Goodness of fit of models (AIC) explaining weed richness and weed diversity according to the radius at which landscape composition and structure variables were estimated.

	Radius 100 m	Radius 200 m	Radius 300 m	Radius 500 m	Radius 1000 m
Landscape composition					
# Occurrence winter crops	123	123	123	123	123
% Cover winter crops (%WC)	95.5 (28.2–100)	73.1 (13.4–100)	61.6 (8.9–99.5)	57.6 (15.3–90.3)	56.5 (23.1–75.8)
# Occurrence spring crops	33	88	107	120	123
% Cover spring crops (%SC)	0 (0–42.5)	6.4 (0–58.8)	12.1 (0–62.3)	15.4 (0–54.6)	17.6 (4.7–55.9)
# Occurrence grassland	51	102	104	118	123
% Cover grassland (%GR)	0 (0–63.1)	9.2 (0–47.8)	11.6 (0–55.9)	13.8 (0–49.1)	15.4 (1.5–44.7)
# Occurrence set-aside & abandoned	9	18	28	51	91
% Cover set-aside & abandoned (%SAA)	0 (0–10.8)	0 (0–20.9)	0 (0–19.8)	0 (0–11.6)	0.4 (0–7.3)
# Occurrence woodland	13	30	38	62	110
% Cover woodland (%WO)	0 (0–28.5)	0 (0–32.4)	0 (0–35.3)	0.1 (0–33.6)	1.3 (0–17.7)
Landscape structure					
Number of fields (NField)	4.0 (1–20)	11.4 (5–31.8)	14.7 (3.2–38.7)	40.99 (19.0–84.0)	131.2 (66.3–231.5)
Number of land use types (NLUT)	3.0 (1–9)	5.0 (1.7–17)	9.4 (3.4–36.7)	11.4 (5.9–25.1)	17.0 (9.3–30.4)
AIC models					
Weed species richness	940.8	913.9	941.1	941.3	953.3
Weed species diversity	268.6	259.7	271.7	269.5	272.9

Table 2
Independent and joint contributions (% of total variance explained) of variables in the models developed for (a) weed richness and (b) weed diversity. Significant contributions ($p < 0.05$) are in bold.

	200 m		
	Independent contribution	Joint contribution	Total
(*a*) *Weed richness*			
Field characteristics			
Fsize	**6.45%**	12.60%	19.05%
Pcrop	1.76%	0.83%	2.59%
Landscape composition			
WO	1.94%	1.86%	3.80%
WC	1.18%	−1.18%	0.00%
SC	3.69%	4.68%	8.37%
SAA	1.35%	−0.43%	0.92%
GR	1.41%	1.36%	2.77%
Landscape structure			
NFIELD	**9.74%**	19.25%	28.98%
NLUT	**5.08%**	11.42%	16.50%
Spatial autocorrelation			
YLAT	2.61%	3.88%	6.50%
XLONG	3.82%	6.71%	10.53%
(*b*) *Weed diversity*			
Field characteristics			
Fsize	**5.71%**	11.58%	17.29%
Pcrop	0.70%	−0.69%	0.01%
Landscape composition			
WO	2.79%	3.34%	6.14%
WC	0.97%	−0.87%	0.10%
SC	1.89%	1.23%	3.11%
SAA	2.57%	1.06%	3.63%
GR	0.89%	−0.07%	0.82%
Landscape structure			
NFIELD	**11.10%**	20.86%	31.96%
NLUT	4.31%	8.98%	13.28%
Spatial autocorrelation			
YLAT	4.94%	7.12%	12.07%
XLONG	4.27%	7.32%	11.59%

Table 3
Spearman rank correlation between residuals of models for weed richness and weed diversity and model variables of the four categories after controlling the effect of the variables of the three other categories.

	Weed richness	Weed diversity
Field characteristics		
FSize	−0.1626	−0.1949
PCrop	n/a	n/a
Landscape composition		
%WO	−0.0315	0.0024
%WC	0.1063	0.0770
%SC	−0.1076	−0.1021
%SAA	−0.0979	−0.1301
%GR	0.0426	0.0228
Landscape structure		
NField	0.2019	0.2433
NLUT	0.1264	0.1205
Spatial autocorrelation		
LAT	−0.0207	−0.0971
LONG	−0.0427	−0.0515

land use at the 100 m radius to 17 types at the 1000 m radius, the highest increase in NLUT being observed between the 200 and the 300 m radii.

3.2. Factors affecting weed species richness

The goodness of fit for the five 'scale' models (Table 1) was lowest at the 1000 m radius (AIC = 953.3) and highest at the 200 m radius (AIC = 913.9). At the 200 m radius the global model explained 18.9% of the variation observed in weed richness. The sum of the independent contributions of all the variables, i.e. 39.02% of the explained variance, was lower than the sum of the joint effects, i.e. 61.98% of the explained variance (Table 2a). This was mostly the result of high joint contributions of Landscape structure (30.7%) and Field characteristics (13.4%), while Landscape composition, with five variables, had a lower joint contribution (6.3%).

Table 2a shows the independent and joint effects of all variables at 200 m. Field characteristics had an overall contribution of 21.6% with a significant independent contribution of FSize, which was negatively correlated with weed richness (Table 3). Spatial autocorrelation (LAT and LONG) accounted for 17.0% of the explained variation in weed richness (6.4% independent and 10.6% joint) and were negatively correlated with weed richness (Table 3). Landscape structure (NField and NLUT) had significant independent contributions and a high positive joint contribution to explaining the variation in weed richness. Spearman rank correlations showed positive effects of NField and NLUT on weed richness (Table 3). The independent contribution of Landscape composition was higher than its joint contribution (9.6% independent and 6.3% joint). Among the variables, %SC had the highest independent contribution to explaining weed richness variability and %WC the smallest. Two variables (%WC and %SAA) had negative joint effects indicating antagonistic interactions with the other variables. The relationships between weed richness and each of the explanatory variables of the Landscape composition varied: some of the variables (%SC, %WO and %SAA) were negatively correlated while %GR and %WC were positively correlated to weed richness.

The overall contributions of Field characteristics and Spatial autocorrelation were not affected by the scale at which the landscape variables were computed (Fig. 2a) and FSize had a significant effect on weed richness (data not shown). Conversely, the part of the variation explained by landscape variables highly varied between scales. The part of variance explained by landscapes variables in particularly Landscape structure was the highest at 200 m and the smallest at 100 and 1000 m. Landscape composition had the highest contribution in explaining weed richness variability at, in decreasing order, 100, 200 and 1000 m.

3.3. Factors affecting weed species diversity

The lowest goodness of fit for the five 'scale' models was at the 1000 m radius (AIC = 272.8) and the highest at the 200 m radius (AIC = 259.7). The global model testing the eleven explanatory variables explained 17.8% of the variation in weed diversity, 59.9% of which was attributed to joint contributions of variables rather than to independent effects (Table 2b).

Field characteristics had an overall contribution of 17.3% with a significant effect of FSize, although this was around two-fold lower than the contribution of NField. Spearman rank correlation with weed diversity was negative for FSize (Table 3). PCrop had a negative joint effect indicating antagonistic interactions with other variables. Spatial autocorrelation contributed highly to explaining the variation of weed diversity, with an overall contribution of 23.7% (9.2% independent and 14.5% joint). LAT had a significant independent contribution. Spearman rank correlations showed negative effects of both LAT and LONG on weed diversity (Table 3). As shown above for species richness, Landscape structure had the highest overall contribution (45.2%) with 15.4% of independent and 29.8% of joint contributions, mostly as a result of the significant independent contribution of NField. Spearman rank correlations revealed positive correlations between the two variables describing landscape structure (NField and NLUT) and weed diversity (Table 3). The con-

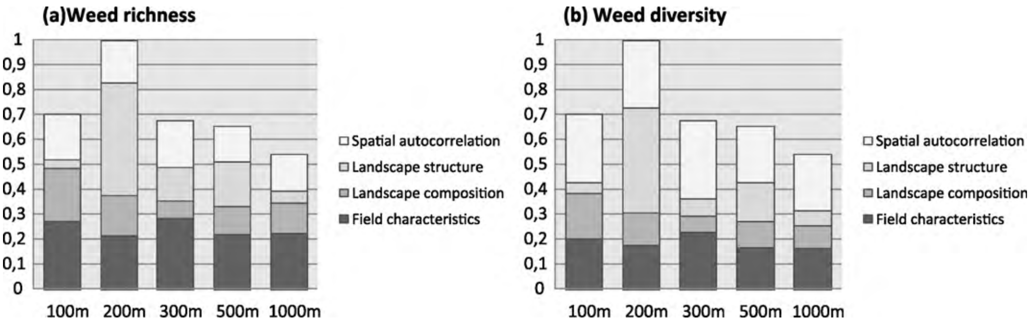

Fig. 2. Amount of variations of the weed richness (a) and diversity (b) explained by the four categories at each scale relative to the total percentage of variance explained by the variables. The percentage of variance explained at each scale has been scaled by the highest percentage explained, i.e. by the percentage of total variance explained when the landscape variables were computed at 200 m.

tribution of the variables of Landscape composition was the lowest (13.8%). %WC was the only variable which had a negative joint effect, indicating antagonistic interactions with other variables. The relationship between weed diversity and each of the explanatory variables of this group showed similar results as for weed richness for %WC, %SC, %SAA and %GR, but different for %WO, which was negatively correlated with weed richness and positively correlated with weed diversity (Table 3). Moreover the quantitative contribution of each of the variables was different. %WO had the highest overall contribution to explaining variation in weed diversity (%SC for weed richness) and %WC and %GR the smallest (Table 2).

The overall contribution of Field characteristics was not affected by the scale at which the landscape variables were computed (Fig. 2b) and FSize had a significant effect on weed diversity (data not shown). Conversely, the overall contributions of Spatial autocorrelation and Landscape structure highly varied between scales. Spatial autocorrelation explained an important part of the variation in weed diversity at 100 and 300 m. The highest part of variance explained by Landscape structure was observed at 200 m and the smallest at 100 and 1000 m. Landscape composition had the highest contribution in explaining weed richness variability in decreasing order, 100, 200 and 500 m.

4. Discussion

Our results indicate that the part of variation in weed richness and diversity explained overall by our four categories of variables is highest when landscape variables are measured at the 200 m radius (Fig. 2). At this scale, factors explaining the largest part of variation are the two variables describing landscape structure. Beyond this scale, the overall part of variation explained is much lessened, mainly because the effect of landscape structure becomes non-significant. This confirms previous results suggesting that landscape variables affecting weeds act at a local scale rather than larger ones (Marshall, 2009). Our study shows that at this local scale, weed species richness and diversity within cultivated fields are enhanced when the local surroundings of the focal field are more heterogeneous. Here, this heterogeneity is not so much linked to the diversity of land use types (although NLUT is significantly positively related to weed richness) but mostly relates to the grain of the landscape, i.e. the number of parcels surrounding the focal field (NField). This partly fits expectations from the mosaic concept (Duelli, 1997), where species number should increase with habitat heterogeneity, i.e. with number of habitat patches per unit area and with habitat variability (number of habitat types per unit area). Natural dispersal in arable weeds is limited and the vast majority of arable weeds have no adaptation for dispersing seeds far from the mother plant (Benvenuti, 2007). It is therefore likely that this local heterogeneity maintains varied sources of propagules in the near vicinity of the sampled fields and ensures that individual weed species can penetrate cultivated fields when the crop type is suitable, even though this is a transient situation because of crop rotation. This is not to say that anthropogenic dispersal, due for example to mechanical machinery during harvesting and soil tillage operations (Wiles and Brodahl, 2004) does not play a role in the observed pattern. Indeed it could be argued that the more fields and crop types there are within a given area, the more farming operations are required, including crop sowing, and therefore the higher the chance of weed seed contamination. However, seed contamination would have a significant effect on the community at the field level only if seeds can pass through agronomical and ecological filters.

In agreement with other studies (Marshall, 2009), no significant relationship was found between weed richness/diversity and variables describing the composition of the surroundings of the winter wheat fields. It is likely that within the landscape unit we have studied, i.e. an area devoted to intensive cereal production, arable weeds occurring in winter wheat would have encountered comparable levels of habitat availability across the landscape. The second issue that could blur a potential effect of landscape composition is the fact that landscape composition changes yearly with crop rotations and we estimated landscape composition for the year when vegetation sampling was done. In contrast, the arable flora expressed within a field in any given year results from a seed bank (Sosnoskie et al., 2006; Koocheki et al., 2009) that has formed over the years within the field and from the potential of the different species to develop under the management applied during the sampling year.

In contrast to the effect of landscape structure, we found a significant effect of FSize that was stable at all scales and indicating that weed species richness and diversity tended to be significantly higher in smaller winter wheat fields. The sampling design ensured that the sampling effort was constant across the 123 fields sampled and that vegetation plots were recorded in the core area of the fields at least 5 m from the field margin regardless of the size of the field. It has been shown that the higher perimeter to area ratio provided by smaller fields is correlated with small-scale landscape complexity and higher species richness for plants as well as invertebrates (Weibull et al., 2003). Moreover, the increase of field size associated with a reduction of linear elements reduces the possibility to retreat for many weed species (Hovd and Skogen, 2005). However, in our study, even though NField had a significant effect on weed richness and diversity (see previous paragraph), it is important to note that FSize was not significantly correlated with the number of fields found at the 200 m scale NField ($r_s = -0.0639$, p-value = 0.4811). Therefore, the negative relationship between FSize and weed richness/diversity may result from processes acting at the field scale. There may be two explanations for this effect. There could be a direct effect where in the case of small fields, vegetation plots tend to be near to more than one field margin and the adjacent crops and therefore could be reached by more of the arable weeds that occur in neighbouring habitats. A second explanation would be that land use history and/or current and past management practices differ between small fields and large fields. A positive trend has been observed across temperate Europe but only a weak one, probably because the analysis was performed without regard to crop type (Herzog et al., 2006). Within a given crop type, however, one could expect that weed control is more efficient in larger fields as they can be managed more intensively due to easier use of agricultural machinery. In these fields, higher disturbances could also have an indirect effect on weed diversity since it has been shown that populations of most plant species are seed limited especially in disturbed microsites (Clark et al., 2007).

Finally, some variables that could have been expected to play a major role in explaining weed richness and diversity patterns did not appear to play a significant role here. Among those, the preceding crop has previously been shown to affect weed assemblages (Fried et al., 2008). Two reasons might explain the lack of relationship in the present study. First, winter wheat is frequently part of a 4-year crop rotation that includes three crops, wheat with winter oilseed rape and sunflower. Therefore most of our sampled fields were cultivated with simple rotations. In such cases, the effect of the preceding crop is less likely to have an important effect on the weed flora than when the field is cultivated with a complex rotation (e.g. Andersson and Milberg, 1998). Second, the remainder of the sampled crops was preceded by a perennial crop or meadow and here the expected effect is more likely to show in the composition of weed communities (e.g. an increase in perennial weeds and a decrease in annual weeds) rather than on weed species richness or diversity. This effect on weed community composition is also likely to be strongly reduced if tillage is carried out between the harvest of the perennial crops and the sowing of winter wheat.

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