Spatial patterns of weeds along a gradient of landscape complexity

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Abstract

Processes that drive spatial patterning among plant species are of ongoing interest, mostly because these patterns have implications for the structure and function of plant communities. We investigated the spatial strategies of weeds focusing on how spatial patterns of weeds are mediated by agricultural landscape complexity and species life-history attributes. We quantified the spatial distribution of 110 weed species using data collected in ten landscapes in central western France along a gradient of landscape complexity, from structurally complex (numerous small fields) to structurally simple (few large fields). We then related differences observed in species' distribution patterns to ecological attributes of species for resource exploitation and dispersion. Our study reveals that weeds were spatially aggregated at the landscape scale. Their spatial patterns are related to the frequency of occurrence of weeds but surprisingly not directly to the seed dispersal type, nor to the degree of habitat specialization. We show that landscape complexity had no direct effect on the spatial patterning of weeds but through interactions with species attributes. Our results point to the importance of interactions between landscape complexity and species attributes in the spatial patterning of weed species even in intensively managed fields. These patterns appear to be a consequence of the spatial arrangement of landscape elements as well as the result of landscape filtering on species attributes.

Zusammenfassung

Prozesse, die das räumliche Muster von Pflanzenarten steuern, sind von anhaltendem Interesse, insbesondere, weil diese Muster Weiterungen für die Struktur und Funktion von Pflanzengesellschaften haben. Wir untersuchten die räumlichen Strategien von Unkräutern, wobei wir uns darauf konzentrierten, wie die räumlichen Muster der Unkräuter durch die Komplexität der Agrarlandschaft und die ökologischen Merkmale der Arten vermittelt werden. Wir quantifizierten die räumliche Verteilung von 110 Unkrautarten nach Daten, die in zehn Landschaften im zentral-westlichen Frankreich entlang eines Komplexitätsgradienten (komplex, mit vielen kleinen Feldern – einfach, mit wenigen großen Feldern) erhoben worden waren. Wir setzten dann die beobachteten Unterschiede zwischen den Verbreitungsmustern der Arten zu den ökologischen Merkmalen der Arten (hinsichtlich Ressourcennutzung und Ausbreitung) in Beziehung.

Unsere Untersuchung zeigt, dass die Unkräuter auf der Landschaftsskala räumlich aggregiert waren. Ihre räumlichen Muster waren mit der Häufigkeit des Auftretens verbunden, überraschenderweise aber nicht direkt mit Art der Samenausbreitung und auch nicht mit dem Grad der Habitatspezialisierung. Wir zeigen, dass die Komplexität der Landschaft keinen direkten Effekt

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auf die räumlichen Muster der Unkräuter hatte, wohl aber durch die Interaktion mit ökologischen Eigenschaften der Arten. Unsere Ergebnisse weisen auf die Bedeutung dieser Interaktionen hin – auch bei intensiv bewirtschafteten Feldern. Diese Muster scheinen sowohl eine Konsequenz der räumlichen Anordnung von Landschaftselementen zu sein als auch das Ergebnis des Filterns von Pflanzenmerkmalen durch die Landschaft.

Introduction

A major current issue in ecology concerns the identification and the explanation of the spatial pattern in ecological communities (Wiens 1989; Liebhold & Gurevitch 2002). Spatial patterns can result from a combination of processes acting at different scales. At fine spatial scales, many processes underlying population dynamics such as growth, mortality or competition operate between neighbouring individuals, and result in spatial autocorrelation (Dormann et al. 2007). At medium scales, dispersal distance to or from a reservoir affect population distributions among sites. Large scale environmental factors that influence species distribution are themselves spatially structured and induce spatial dependencies in species distributions (Legendre 1993). Within communities, the response of individual species has been shown to be mediated by a number of life-history attributes, such as dispersal ability (Butaye, Jacquemyn, Honnay, & Hermy 2001) or degree of habitat specialization (Devictor, Julliard, & Jiguet 2008; Liira et al. 2008). As a result, communities are assemblages of species with different spatial strategies (Tscharntke & Brandl 2004). Yet, we lack a general understanding of how species attributes and the inherent spatial heterogeneity of the environment create spatial patterns of species at different spatial scales.

Understanding of the factors that drive the spatial distribution of arable weeds in agro-ecosystems is of fundamental applied importance since weeds can potentially cause severe crop yield losses. Integrating a spatial component into weed studies is crucial for predicting rates of weed invasion (Smolik et al. 2010) and developing weed management strategies at the field (Wallinga, Groeneveld, & Lotz 1998) or landscape scales (Dauer, Luschei, & Mortensen 2009). Furthermore, the importance of weeds in maintaining biodiversity has been recognized. Weeds are the base of agroecosystem food chains (Marshall et al. 2003) and a better understanding of the spatial distribution of plant resources is crucial as it has a strong impact on the intensity and stability of plant–animal interactions (Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies 2005). The spatial distribution of arable weeds has so far mostly been explored at the within-field scale. Weeds are usually distributed in patches (Cardina, Johnson, & Sparrow 1997; Izquierdo, Blanco-Moreno, Chamorro, González-Andújar, & Sans 2009), partly in response to within-field spatial variations in the environment and crop management. At larger spatial scales, one can hypothesize that weed communities are spatially structured because of the existence of (i) short-distance propagule movements, e.g. between the field and its boundaries (Poggio, Chaneton, & Ghersa 2010; Cordeau, Reboud, & Chauvel 2011) and (ii) long-distance weed dispersal whether natural (Dauer, Mortensen, & Vangessel 2007) or anthropogenic (Garnier, Pivard, & Lecomte 2008). The intensity of such dispersal events depends on landscape patterns, i.e. spatial arrangement of crops and their margins and the spatial distribution of linear networks across the whole landscape (Tscharntke et al. 2005). The effect of landscape heterogeneity on weed species richness has been recently assessed (Gabriel, Thies, & Tscharntke 2005; Gaba, Chauvel, Dessaint, Bretagnolle, & Petit 2010; Poggio et al. 2010). Yet, it is unclear how such landscape context affects the degree of spatial structuring of weed communities across a landscape. In addition, as weed species differ in terms of their occurrence, dispersal type (Benvenuti 2007) and degree of specialization to crops (Fried, Petit, & Reboud 2010), one could expect the coexistence of different spatial strategies within weed communities.

The aim of this study was to determine the relative effects of landscape complexity and species life-attributes on the spatial distribution of weeds. We quantified spatial patterns of weed communities using regular 50 m grids on ten 1 km × 1 km landscapes varying in their degree of complexity. Our hypotheses are summarized in Fig. 1. First, we address the following question: Can we identify different spatial patterns within weed communities (Fig. 1a)? Specifically, we tested for the presence of spatial structure in weeds at the landscape scale using Moran's I correlograms. Second, we assess whether spatial patterns in species distributions vary according to species life attributes (Fig. 1b). Specifically, we expect anemochorous and zoochorous species to be less constrained by dispersal events and hence more evenly distributed across suitable habitat patches at the landscape level (leading to weak spatial autocorrelation) than poorer dispersers (i.e. barochorous species). We expect generalist species to be more evenly distributed than specialist species across a landscape, as generalist species may supplement their resources using more than one habitat (Dunning, Danielson, & Pulliam 1992). Third, we investigate how landscape complexity affects the spatial strategies of weed species. On the one hand, we examined changes in the degree of spatial structuring for weed species according to edge density and Shannon habitat diversity (Fig. 1c). On the other hand, we hypothesize that landscape complexity may influence weed composition through filtering some life-attributes
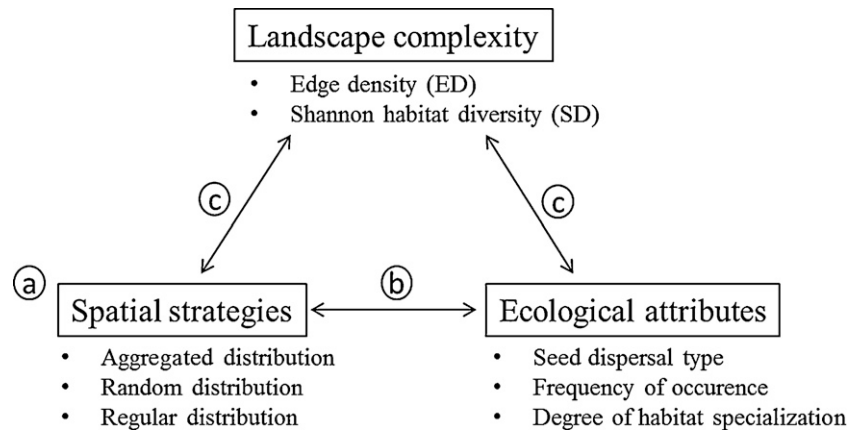
Fig. 1. Diagram summarizing our hypotheses. We first investigate the spatial patterns of weeds species (a). Weeds can exhibit either aggregated, random or regular spatial patterns. We hypothesize that spatial patterns could be related to ecological attributes of weeds (b), in particular seed dispersal type, frequency of occurrence and degree of habitat specialization. We hypothesize that landscape complexity exerts a direct influence on the spatial patterns of weeds or an indirect effect filtering weeds species through their ecological attributes (c). So, we would expect changes in those ecological attributes according to edge density and/or Shannon habitat diversity.

which would probably result in different distribution patterns (Fig. 1c).

Methods

Study area

The study was carried out in an intensively managed agricultural region (450 km^2) located in central-western France (zone Atelier "Plaine and Val de Sèvres", 46°11′N, 0°28′W). This area contains 18,000 fields mainly devoted to autumn-sown cereal production (50%) and few perennial crops (*Lolium perenne* L., *Medicago sativa* L. and *Trifolium pratense* L.). The typical four-year crop rotation in the area is winter wheat, followed by either winter oil seed rape or sunflower every two years. Within the northern part of the area, we selected 10 landscapes of 1 km × 1 km which represented a gradient of landscape complexity ranging from simple landscapes with few large fields to structurally complex landscapes with numerous smaller fields (Fig. 2). The soil texture (calcareous loamy-clay soil) was similar for the 10 areas.

Weed sampling and plant characteristics

In each 1 km^2 landscape, the arable flora was recorded between March and June 2008 in 2 m × 2 m plots located at each node of a regular 50 m grid. There were 400 plots per landscape and an overall total of 4000 plots distributed in 230 fields. Plants were identified and named according to Jauzein (1995) except for a few taxa for which small seedling size and the absence of reproductive parts constrained the identification to genus level (*Carduus* spp., *Lactuca* spp., *Setaria*

spp., *Torilis* spp. and *Valerianella* spp.) or were not identified at the level species for simplification (*Lolium* sp.). Overall, 151 arable weed species were recorded. After eliminating the rarest species, i.e. those occurring in fewer than three plots per landscape, the species data set was composed of 110 weed species.

Fig. 2. Location of the 10 landscapes (1 km^2) selected in the studied area (Chizé, France). Two landscapes illustrate the extremes of the complexity gradient, from structurally simple landscape (few large fields) to structurally complex (numerous small fields). For details on landscape characteristics, see Table 1.

Table 1. Characteristics of the ten landscapes studied sorted by landscape complexity (Shannon habitat diversity).

Landscape	Total area (ha)	#Fields	Mean field size (ha)	Mean field length (m)	Mean field width (m)	SD	ED	S
E	144.16	17	8.48	392.8	303.4	0.86	123.48	63
C	132.16	14	9.44	566.9	286.9	1.02	143.50	63
D	181.85	19	9.57	543.7	312.6	1.22	140.56	60
J	140.89	33	4.27	383.1	188.8	1.54	224.16	67
A	128.75	40	3.22	318.9	169.2	1.57	248.75	61
G	124.98	26	4.81	396.4	203.3	1.64	202.62	64
I	150.66	47	3.21	290.7	192.8	1.71	239.20	59
H	157.77	32	4.93	387.5	206.2	1.82	197.86	65
B	152.76	14	10.91	616.2	315.6	1.87	134.83	58
F	168.46	23	7.32	433.2	300.1	1.94	156.73	72
Mean	148.25	26.50	6.62	432.94	247.89	1.52	181.17	63.20
Std dev	17.97	11.29	2.87	107.77	60.14	0.37	46.74	4.16

SD, Shannon habitat diversity; ED, edge density (m/ha); S, weed species richness.

Recorded weed species were characterized for their frequency of occurrence overall and within the landscape, and for two life-history attributes. A species with an occurrence frequency lower than 2% in a landscape (respectively higher than 10%) was considered as *rare* (respectively *frequent*). Seed dispersal strategy was extracted from the trait database Baseflor (Julve 1998) corrected by expert knowledge when required. We distinguished three classes: *Anemochorous* species, *Barochorous* species and species with *other* seed dispersal type (endo- and epizoochorous, myrmecochorous and hydrochorous species). Information on the degree of habitat specialization of weed species was extracted from Fried et al. (2010). Fried et al. (2010) attributed Is (degree of habitat specialization) values to 152 weed species, based upon six indices representing different measures of species niche breadth, from the most specialized (high value of Is) to the most ubiquitous (low value of Is) and classified those as either *Generalist* (Is < 54), *Intermediate* or *Specialist* (Is > 92). Is value and associated classes were available for 76 species of the 110 species surveyed in the present study.

Landscape metrics

The 10 landscapes had a mean field size of 6.62 ha and on average 3.04% area cover (range 0.34–10.34) of non-cropped habitats (grazed permanent grasslands, field margins, woodlands, urban zones) (Table 1). Landscape complexity was assessed with two metrics, as preliminary analyses showed strong correlations with other candidate metrics (see Appendix A: Table 1). We used the edge density (ED) (i.e. total length of all edges of patches/total landscape area) as an indicator of landscape configuration and the Shannon habitat diversity (HD) as an indicator of landscape composition. HD was calculated including all landcover types (see Appendix A: Table 2) found in the 10 landscapes

($n = 24$). ED varied from 123.5 to 248.8 m/ha and HD varied from 0.86 to 1.94 (Table 1). ED and HD were not significantly correlated (Spearman rank correlation test, rho = 0.42, $p = 0.224$) (see Appendix A: Table 1). Analyses were performed using ArcGis 9.1 (ESRI Inc., Redlands, CA, USA).

Data analysis

Relationship between landscape complexity and life-history attributes

To assess whether landscape complexity acted as a filter on weed communities, the representation of the different life-history attributes in the 10 landscapes was correlated to landscape metrics using Spearman rank correlation tests.

Spatial patterns of weed species

The degree of spatial autocorrelation in single species weed abundance across each landscape was assessed by processing correlograms based upon Moran's statistic *I* (Moran 1948). We calculated the Moran's *I* values for 20 regular inter-sample distances (lags) of 50 m. The statistical significance was tested with 999 Monte Carlo permutations against the null hypothesis for each distance class separately (see Legendre & Legendre 1998). A significant positive value indicates an aggregated pattern (positive autocorrelation), a significant negative value indicates a regular spatial pattern (negative autocorrelation) whereas non-significant values indicate a random distribution. Two metrics were retained for analysis as quantitative metrics of the autocorrelation decay: the Moran's *I* value at lag 1 considered as the intercept of the autocorrelation decay and the Moran's *I* value at lag 6, as a proxy of the slope of the autocorrelation decay. We chose the lag 6 because it corresponded to the maximum distance up to which positive autocorrelation was observed in weed communities (see Appendix A: Fig. 1).

Table 2. Proportion of species according to their seed dispersal type and degree of habitat specialization (Is) in each of the ten landscapes.

Landscape	% anemochorous	% barochorous	% zoochorous	Mean Is	% generalist	% intermediate	% specialist
A	16.39	68.85	14.75	51.22	58.33	37.50	4.17
B	10.34	72.41	17.24	58.50	58.70	26.09	15.22
C	12.70	71.43	15.87	54.04	55.77	34.62	9.62
D	11.67	75.00	13.33	54.69	54.00	36.00	10.00
E	15.87	68.25	15.87	49.22	62.50	31.25	6.25
F	16.67	68.06	15.28	55.07	47.17	43.40	9.43
G	14.06	70.31	15.63	56.01	47.27	43.64	9.09
H	15.38	69.23	15.38	53.92	55.10	36.73	8.16
I	15.25	69.49	15.25	53.23	58.70	30.43	10.87
J	13.43	70.15	16.42	55.34	51.92	38.46	9.62
Mean	14.18	70.32	15.50	54.12	54.95	35.81	9.24
Std dev	2.12	2.13	1.03	2.55	5.02	5.53	2.89

Linking weed spatial patterns to life-history attributes and landscape complexity

The effects of life-history attributes (seed dispersal type, degree of habitat specialization (Is) and weed occurrence) and landscape (ED and HD), and the two-way interactions of these predictor variables on Moran's I values at lag 1 and 6 were analyzed using two linear mixed-effects models (LMMs). The factors landscape ($n = 10$), genus ($n = 89$) and family ($n = 32$) were included as random effects. Models were fitted by maximum likelihood (ML) and their suitability was assessed by checking normality and randomness of residuals. Significance of terms in each model was assessed by calculating the F- and p-values of ANOVA type III error tests.

Statistical analyses were carried out using packages ade4, nlme for mixed models and spdep in R 2.12.1 (R Development Core Team 2010).

Results

In total, 110 plant species from 89 genera and 31 families were recorded. Mean species richness per landscape was 63.2 species, ranging from 58 to 72 species per landscape (Table 1). Across the 10 landscapes, we detected no significant correlation between species richness per landscape and the edge density (Spearman correlation test rho = 0.15, $p = 0.663$) or the Shannon habitat diversity (rho = 0.21, $p = 0.566$) of the different landscapes.

Within a landscape, the proportion of rare species was on average $35.4 \pm 6.7\%$ and that of frequent species $20.6 \pm 6.1\%$. On average, $70.3 \pm 2.2\%$ of species were barochorous, $14.2 \pm 2.1\%$ were anemochorous and $15.5 \pm 1.0\%$ showed another type of seed dispersal. The proportion of generalist species was on average $54.9 \pm 5.0\%$ and that of specialist species $9.2 \pm 2.9\%$ (Table 2).

Relationship between species life-attributes and landscape complexity

The proportions of anemochorous, barochorous and of species with other seed dispersal type among landscapes were not significantly related to landscape metrics. Similarly, the proportions of generalist, intermediate and specialist species, and the mean specialization index of weed species were not related to landscape metrics (Table 3).

Spatial patterns of weed species

The proportion of aggregated species was found to decline as the inter-sample distance increased (Fig. 3). Inversely, the proportion of random and regular species increased as the
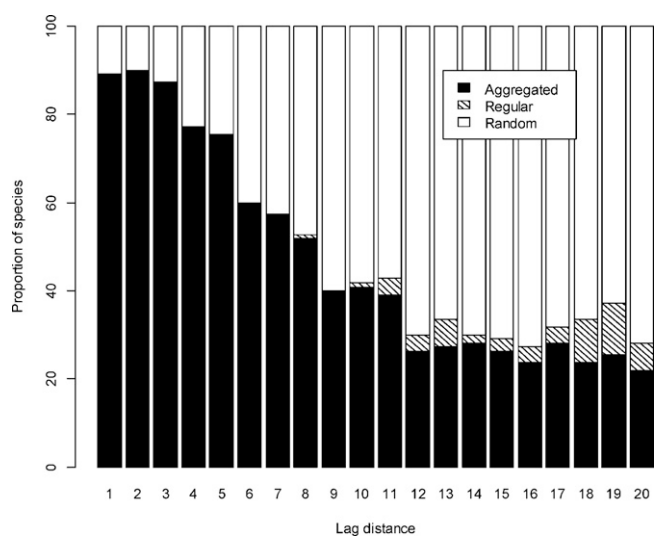

Fig. 3. Proportion of aggregated, regular and random species in each distance class (1 lag = 50 m). Spatial patterns of the 110 weed species were determined using Moran's correlograms performed on all plots ($n = 4000$).

Table 3. Spearman correlations (rho) between landscape metrics and the representation of life-history attributes.

	Edge density		Shannon habitat diversity	
	rho	*p*	rho	*p*
Seed dispersal type				
% anemochorous	0.3454	0.3305	0.1878	0.6076
% barochorous	−0.2363	0.5139	−0.1878	0.6076
% other	−0.3769	0.2830	−0.0486	0.8939
Degree of specialization (*N* = 76)				
Is (mean)	−0.1272	0.7329	0.4303	0.2180
% generalist	−0.2431	0.4984	−0.2857	0.4236
% intermediate	0.4424	0.2042	0.1393	0.7072
% specialist	−0.2006	0.5784	0.2249	0.5321

inter-sample distance increased. At 50 m inter-sample distances (lag 1), 89% of weed species exhibited an aggregated pattern and 11% a random one. At lag 6 (*c.* 300 m), 60% of species exhibited an aggregated pattern and 40% a random one. Beyond lag 11, the proportion of aggregated and random species was relatively constant, nearing 25% and 70%, respectively.

Linking weed spatial patterns to species life-attributes and landscape complexity

Analysis of the fixed effects showed that only the frequency of occurrence of weeds had a significant direct effect on Moran's *I* values at lag 1 and lag 6 (Table 4 and Fig. 4). Frequent weed species exhibited higher spatial autocorrelation than rare ones. Although seed dispersal type had no
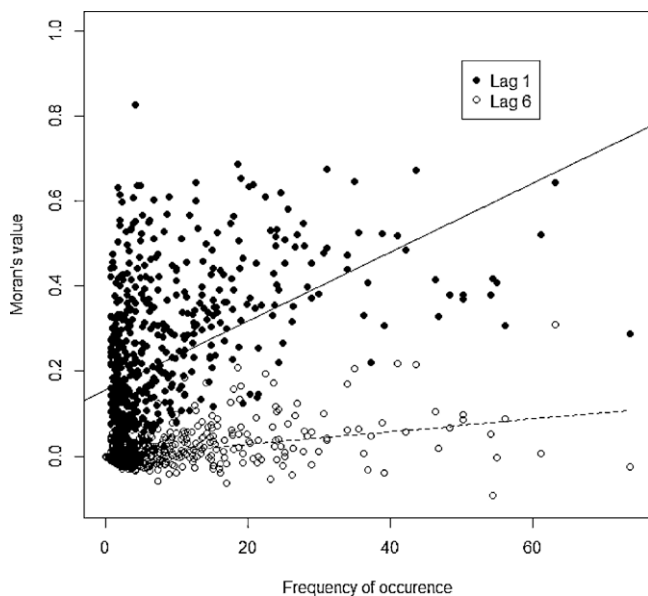

Fig. 4. Relationship between frequency of occurrence of weeds and their Moran's values for the lag 1 and the lag 6. Linear trend lines were drawn.

significant direct effect on Moran's *I* values at both lags, we found evidence of its effect through interaction with the frequency of occurrence of weeds. The relationship between the Moran's values and the frequency of occurrence grew more slowly for barochorous species than for other dispersal types. Landscape complexity (SD and ED) had no significant direct effects on Moran's *I* values but we detected significant interactions with frequency of occurrence at both lags, and with seed dispersal type at lag 6 (Table 4). Frequent species showed different spatial patterns according to landscape complexity whereas rare species were insensitive.

For the individual weed species, we found five species at lag 1 showing a significant decline in their Moran's *I* values as landscape complexity increased (*Daucus carota* L., *Euphorbia helioscopia* L., *Geranium rotundifolium* L., *Lolium* sp., *M. sativa* L.) whereas only one species exhibited an increase (*Veronica persica* Poiret). At lag 6, five species (*Cerastium glomeratum* Thuill., *Linum usitatissimum* L., *Oilseed rape regrowth*, *Picris echioides* L., *Setaria pumila* (Poiret) Roemer and Shultes), presented a significant and negative correlation between their Moran's *I* values and landscape complexity metrics whereas one species showed a positive correlation (*Adonis annua* L.).

Discussion

This study aimed at assessing spatial patterns in weeds at the landscape level and at shedding light on the processes underlying such patterns. We showed that spatial patterns of weeds were directly related to the frequency of occurrence of weeds but also to seed dispersal types and landscape complexity through interactions.

Spatial patterns of weeds

We demonstrate here spatial aggregation of weed species at the landscape scale. Spatial aggregation has often been

Table 4. Summary of linear mixed effect models (LMMs) to analyze effects of life-history attributes of weeds (seed dispersal type, degree of specialization and frequency of occurrence) and landscape complexity (Shannon habitat diversity and edge density) and their two-way interactions on Moran's *I* values at lag 1 and lag 6. Degree of freedom (df), *F*- and *p*-value (*p*) from ANOVA type III error tests are given. Bold values indicate significant results.

	Lag 1			Lag 6		
	df	*F*-value	*p*	df	*F*-value	*p*
Seed dispersal type	2, 410	0.3504	0.7046	2, 410	2.3003	0.1015
Degree of specialization (Is)	1, 63	0.0446	0.8333	1, 63	0.0638	0.8013
Frequency of occurrence	1, 63	4.3057	**0.0421**	1, 63	25.2354	**<0.0001**
Shannon habitat diversity (SD)	1, 6	0.6434	0.4531	1, 6	1.0007	0.3557
Edge density (ED)	1, 6	0.1453	0.7161	1, 6	5.9007	0.0512
Seed dispersal × Is	2, 63	1.0040	0.3720	2, 63	0.1342	0.8746
Seed dispersal × frequency	2, 63	6.9748	**0.0018**	2, 63	3.7723	**0.0284**
Is × frequency	1, 63	0.0563	0.8131	1, 63	0.6943	0.4078
Seed dispersal × SD	2, 410	0.2354	0.7903	2, 410	3.3283	**0.0368**
Is × SD	1, 63	2.8114	0.0986	1, 63	0.0096	0.9220
Frequency × SD	1, 63	4.9824	**0.0292**	1, 63	13.3127	**0.0005**
Seed dispersal × ED	2, 410	0.7897	0.4547	2, 410	0.1020	0.9030
Is × ED	1, 63	0.0934	0.7609	1, 63	0.1721	0.6796
Frequency × ED	1, 63	0.0837	0.7733	1, 63	42.6136	**<0.0001**
SD × ED	1, 6	0.0620	0.8116	1, 6	5.9750	0.0502

demonstrated for single weed species at a within-field scale and using fine spatial resolution, i.e. from less than 1 m up to 10 m (Wiles, Oliver, York, Gold, & Wilkerson 1992; Colbach, Forcella, & Johnson 2000; Nordmeyer 2009). Several weed species such as *Cirsium arvense* (L.) Scop. (Donald 1994), *Galium aparine* L. (Wallinga 1995) are spatially aggregated at short distances but also in some instances over quite larger distances, i.e. up to 40 m for *Convolvulus arvensis* L. (Jurado-Expósito, López-Granados, González-Andújar, & García-Torres 2004) and *Avena sterilis* L. (Blanco-Moreno, Chamorro, & Sans 2006). Few studies have considered the spatial autocorrelation of weed species at a coarse scale. Wilson and Brain (1991) demonstrated spatial aggregation for *Alopecurus myosuroides* Hud. using a 36–40 m grid spacing. More recently, Nordmeyer (2009) showed that *Apera spica-venti* L. (P.) Beauv. populations form aggregated spatial patterns within three agricultural fields using a grid of 25 m × 36 m. Using a 50 m grid spacing, we showed positive spatial autocorrelation over long inter-sample distance for numerous weed species, 50% of weed species being aggregated up to 400 m. We cannot exclude that these patterns at large scale were linked to the spatial distribution of fields and their own characteristics. Spatial patterns of weed communities can indeed arise from environmental variables, themselves spatially structured such as soil type, soil pH, water regime (Lososová et al. 2004). Although the study area is relatively homogeneous regarding soil properties, this assumption could not be tested here as we did not have the environmental data for each of the 4000 vegetation plots.

The most interesting finding was that within communities, weed species shared different spatial patterns. Although weeds are mostly aggregated within fields, the observation of species exhibiting a consistent random pattern whatever the distance would not be particularly surprising. Rew and Cousens (2001) reported that weed seeds disperse close to their source and in fields mapped using a grid > 5 m, weed aggregation could have been missed. We hypothesize that our grid resolution was too coarse to detect any spatial structure for these species.

For species exhibited an aggregated pattern over large distances, even larger than the field length, we suggest that long dispersal events occur. Agricultural practices are known to strongly impact weed communities modifying their distribution. Tillage implements can move seeds up to 20 m from their source (Rew & Cussans 1997). Weed seeds can also be dispersed longer distances when mature plants are caught on farm machinery, such as spraying equipment and seed drills (Barroso et al. 2006). For example, Johnson, Mortensen, and Gotway (1996) reported elongated patches up to 45 m of *Abutilon theophrasti* Med. in the direction of cropping and machinery movement whereas its maximal maximum natural distance was less than 1.5 m.

Linking weed spatial patterns to species life-attributes and landscape complexity

Although the spatial organization of species depends to a large extent on biotic processes, i.e. regeneration, dispersal

limitation, and competition (Begon, Harper, & Townsend 1986), little work has been done to relate spatial patterns to life history attributes of plants. Recently, Pottier, Marrs, and Bédécarrats (2007) showed a significant relationship between the spatial patterns exhibited by grassland species and their Grime C-S-R strategies. Here, we found that rare species exhibited either a random pattern or an aggregated pattern whereas frequent species were aggregated. Our results were consistent with previous work on weed seeds in the cultivated soil seed bank (Dessaint, Chadoeuf, & Barralis 1991). We also showed that spatial patterns of weeds were not directly related to their generalist/specialist character and more surprisingly not directly to their seed dispersal type. However, we detected an indirect effect of seed dispersal type on spatial patterns through its interaction with the frequency of occurrence. The latter result reveals the need to improve our current understanding of seed dispersal influence. Despite the extensive role believed to be played by seed dispersal in the spatial patterning of weeds, few agronomic surveys on seed movement are available (Benvenuti 2007). From our results, we conclude that the selected life-history attributes, generally assumed as determinants in the spatial patterning of plants, do not play a direct role in structuring weed species in space except for the frequency of occurrence.

The analyses of landscape factors and life-history attributes on Moran's values showed that there is no direct effect of landscape complexity on the spatial patterning of weeds. However, we detected a signal through interactions with life-history attributes. Spatial patterns of rare species remained relatively insensitive to landscape complexity while the spatial aggregation of frequent species tended to increase with landscape complexity. We found a comparable interaction with seed dispersal type, i.e. the spatial distribution of barochorous species appeared less sensitive to landscape complexity than the spatial pattern of zoochorous and anemochorous species. These results suggest that the effect of landscape complexity on weed distribution was mediated by the species life-history attributes. The marginal effect of landscape complexity may be due to the weak landscape complexity gradient range. While most studies on arable weeds summarize landscape complexity to the proportion of non-cropped habitat (i.e. Gabriel et al. 2005), our complexity gradient was reduced to empirical contrasts in field size only and lack of landscapes with extremely high or low proportions of semi-natural habitats. To improve these results, we suggest comparing spatial patterns of weeds along a more contrasted landscape complexity gradient.

Conclusion

In this study, we found that spatial patterns of weeds were mainly related to their frequency of occurrence. Although dispersal limitation has been repeatedly advocated as one of the principal ecological determinants of spatial patterns, we did not detect such direct effect in this study. Landscape did not seem to exert any filtering on weeds through their life-attributes, however, species traits (frequency of occurrence, dispersal type) appear to mediate the effect of landscape complexity on the spatial patterning of weed species through interactions. In order to provide detailed recommendations for weed management and/or conservation at coarse scale, further research is needed on the links between species life attributes, the mechanisms through which species interact with the surrounding mosaic landscape and their consequences for population dynamics.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2012.05.005

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