

# The effects of landscape complexity on arable weed species diversity in organic and conventional farming

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## Summary

1. There is growing concern about declining species diversity in agro-ecosystems caused by agricultural intensification at the field and landscape scales. Species diversity of arable weeds is classically related to local abiotic factors and resource conditions. It is believed to be enhanced by organic farming but the surrounding landscape may also be important.

2. This study assessed the ruderal vegetation, seed bank and seed rain in 24 winter wheat fields to examine the relative importance of organic vs. conventional farming and landscape complexity for weed species diversity. Diversity was partitioned into its additive components: alpha, beta and gamma diversity. Percentage arable land in a circular landscape sector of 1-km radius around each study site was used as an indicator of landscape complexity.

3. Weed species diversity in the vegetation, seed rain and seed bank was higher in organic than in conventional fields. Increasing landscape complexity enhanced species diversity more strongly in the vegetation of conventional than organic fields, to the extent that diversity was similar in both farming systems when the landscape was complex. Species diversity of the seed bank was increased by landscape complexity irrespective of farming system.

4. Overall diversity was largely determined by the high heterogeneity between and within the fields (beta diversity). Only in very few cases could higher weed species diversity in complex landscapes and/or organic farming be related to species dependence on landscape or farming system.

5. *Synthesis and applications.* Local weed species diversity was influenced by both landscape complexity and farming system. Species diversity under organic farming systems was clearly higher in simple landscapes. Conventional vegetation reached similar diversity levels when the surrounding landscape was complex through the presence of refugia for weed populations. Consequently, agri-environment schemes designed to preserve and enhance biodiversity should not only consider the management of single fields but also of the surrounding landscape.

*Key-words:* additive partitioning, beta diversity, biodiversity, conservation, seed bank, seed rain, winter wheat

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## Introduction

Species richness in agro-ecosystems has dramatically declined during the last decades, mainly as a result of

the intensification of land-use practices (Krebs *et al.* 1999; Tilman *et al.* 2002). On the one hand, intensification has occurred at the field scale through the increased use of pesticides and mineral fertilizers. On the other hand, intensification has also occurred at the landscape scale because of the aggregation of intensively managed arable fields together with land consolidation that has resulted in a transformation of formerly complex landscapes with relatively high

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proportions of (semi)natural habitats to simple landscapes dominated by arable fields.

Organic farming is expected to maintain higher species richness than conventional management as pesticides are not applied in this farming system. Species richness of the above-ground vegetation (Moreby *et al.* 1994; Hald 1999; Menalled, Gross & Hammond 2001; Hyvönen *et al.* 2003), the seed bank (Menalled, Gross & Hammond 2001) and several groups of arthropods (Letourneau & Goldstein 2001; Hutton & Giller 2003) have been reported to be higher in organic/extensive farming systems than on conventional farms. However, several studies have found no effects of farming system on species richness of plants (Weibull, Östman & Granqvist 2003) or arthropods (Kleijn *et al.* 2001; Weibull, Östman & Granqvist 2003).

Arable fields in complex landscapes should support higher species richness than in simple landscapes as complex landscapes provide alternative habitats and sources for recolonization of fields. The relationship between local species richness and landscape context has been addressed for several groups of arthropods (Menalled *et al.* 1999; Krauss, Steffan-Dewenter & Tscharrntke 2003; Schmidt *et al.* 2005) but only Weibull, Östman & Granqvist (2003) and Krauss *et al.* (2004) have investigated this relationship for plants in agricultural landscapes. However, they did not detect an effect of landscape context on plant species richness. Holl & Crone (2004) found only weak importance of landscape-scale variables for the diversity of native riparian understorey plants. Nevertheless, the species diversity of weeds in annual crop fields should depend on both local management and surrounding landscape. Weeds are a highly dynamic group adapted to a frequently disturbed habitat, relying on their seed bank as well as on immigration of seeds through the seed rain from surrounding habitats. Therefore weed species diversity in conventional fields should particularly benefit from landscape complexity as these are more frequently disturbed (e.g. by herbicide use) than organic fields. Knowledge of these relationships is crucial for a better understanding of weed species diversity patterns and should be helpful for future conservation management decisions. However, to our knowledge, this is the first study to analyse how species diversity of arable weeds in the vegetation, seed rain and seed bank responds to the surrounding landscape in organic and conventional fields. In addition, the contribution of the heterogeneity in community composition between weed samples, within and between fields, to field and regional diversity is little known. The concept of additive partitioning of species (Allan 1975; Lande 1996) addresses this problem by dividing total diversity of a given number of samples (gamma diversity) into the additive components alpha (mean diversity) and beta (between sample heterogeneity), thereby allowing species diversity at several spatial scales to be scaled up to whole regions (Wagner, Wildi & Ewald 2000; Gering & Crist 2002; Crist *et al.* 2003; Gering, Crist & Veech 2003).

In this study, we used this concept to characterize the diversity of arable weeds at two spatial scales. At the regional scale, gamma diversity was the overall number of species found in our study region. Alpha diversity was the average number of species in the individual studied fields within the region, and beta diversity accounted for the within-region heterogeneity (average number of species not found in a field). At the field scale, gamma diversity was the overall number of species found in the samples of one field. Alpha diversity was the average number of species found in the samples of one field, and beta diversity accounted for the within-field heterogeneity (average number of species not found in a sample). At both scales, the relative beta diversity (the percentage of beta contributing to gamma) was also calculated. We analysed the relative importance of local management (organic vs. conventional) and landscape complexity (gradient from simple to complex) on species diversity of arable weeds in the vegetation, seed rain and seed bank (at the field scale) of 24 winter wheat fields.

We hypothesized that the field-scale alpha, beta and gamma diversities of weeds should be higher in organic than in conventional fields and in complex than in simple landscapes, and we tested the idea that landscape complexity may compensate for the reduced diversity in conventional fields. In contrast, the relative within-field heterogeneity, beta (%) was expected to be higher in conventional fields, because these fields should have a low alpha diversity and, consequently, the relative contribution of beta to gamma diversity should be high. In particular, we expected that several species (e.g. threatened species of the Red List of Lower Saxony, Germany; Garve & Letschert 1991; Garve 1993; Korneck, Schnittler & Vollmer 1996) that are more susceptible to disturbances than common species would particularly profit from organic farming and/or from a certain degree of landscape complexity (Korneck & Sukopp 1988; Jedicke 1997; Hofmeister & Garve 1998).

## Methods

### STUDY AREA AND ANALYSIS OF LANDSCAPE COMPLEXITY

The study was conducted in 2002 in 12 agricultural landscapes around the city of Göttingen, north Germany. This area covers approximately 1350 km<sup>2</sup> and is dominated by an arable land–grassland mosaic covering about 75% of the region, while the remaining area is characterized by patchily distributed fragments of near-natural and semi-natural habitats such as forests, fallows, field margins and hedgerows. We selected the 12 landscapes along a gradient of landscape complexity ranging from very simple landscapes with a high percentage of arable land (*c.* 95%) to complex landscapes with a lower percentage of arable land (*c.* 30%). These complex landscapes exhibited large areas of non-crop habitats such as field margins, fallows, grassland and garden

land, which should be potential weed habitats. All landscapes were at least 3 km (from centre to centre) away from each other. In the centre of each landscape we selected as study sites a pair of one conventional and one organic (according to European Union Regulation 2092/91/EEC) winter wheat field located close to each other (< 400 m). The organic fields had been under organic management for at least 7 years.

Landscape complexity was measured around each studied field in a circular landscape sector of 1 km radius. Official digital thematic maps (ATKIS, Digitales Landschaftsmodell 25/1; Landesvermessung & Geobasisinformation, Hannover, Germany, 1991–96) and the geographical information system ArcView 3.1 (ESRI Geoinformatik GmbH, Hannover, Germany) were used to determine the area of arable land, perennial grassland, forests, hedgerows, garden land and settlement in each landscape sector. The percentage of arable land per landscape was considered an indicator for landscape complexity because it is related to other important landscape metrics such as habitat type, Shannon–Wiener diversity ( $F = 124.12$ ,  $P < 0.001$ ,  $R = -0.80$ ) and perimeter-to-area ratio ( $F = 61.28$ ,  $P < 0.001$ ,  $R = -0.69$ ). In the studied landscapes, arable land was the predominant land-use type, covering  $63 \pm 22\%$  of the total area (arithmetic mean  $\pm$  SD, minimum 30%, maximum 95%). The mean size of the study fields was  $3.5 \pm 1.7$  ha (arithmetic mean  $\pm$  SD) and was neither related to landscape complexity (linear regression  $R = 0.29$ ,  $P = 0.17$ ) nor to farming system (paired  $t$ -test,  $t = 1.3$ ,  $P = 0.21$ ). All fields were bordered by old grassy margins that were 1–3 m wide and mowed once a year. The majority of adjacent crops for both field types were conventional winter cereals. In organic fields, winter wheat was grown after a mixture of clover and grass, while the preceding crops of conventional winter wheat were mostly winter wheat and oilseed rape.

Local abiotic factors, such as soil quality, and factors of land-use intensity, such as nitrogen fertilization and herbicide use, are known to be important determinants of local arable weed species diversity (Grime 1979; Tilman 1982; Ellenberg 1988; Hyvönen & Salonen 2002; Gerowitt 2003). For our study, we selected exclusively loamy soils. Therefore, the variability of local soil characteristics was low. However, in a pre-analysis (linear regressions), we tested whether several soil and land-use characteristics were correlated with landscape complexity or weed species diversity. Therefore, one soil sample per field, consisting of 16 randomly taken subsamples from the top 30 cm, was analysed. Data on land use were based on interviewing the farmers. Soil characteristics (total nitrogen contents, organic carbon contents, ratio of organic carbon to total nitrogen, pH value) in conventional as well as organic fields were unrelated to percentage arable land in the landscape ( $R = -0.39$ – $0.18$ , all  $P > 0.2$ ). Additionally, these soil characteristics were not related with any component of weed species diversity (i.e. alpha, beta and gamma

diversities, all  $P$ -values from linear regressions  $> 0.2$ ). The number of herbicide applications in conventional fields was 1–3 year<sup>-1</sup> and were neither related to percentage arable land ( $R = -0.01$ ,  $P = 0.99$ ) nor to weed species diversity (e.g. gamma diversity,  $R = -0.01$ ,  $P = 0.98$ ). In contrast to expectations (Roschewitz, Thies & Tschardt 2005), mineral nitrogen fertilizers (kg N ha<sup>-1</sup>) applied in conventional fields even tended to decrease with increasing percentage arable land ( $R = -0.58$ ,  $P = 0.05$ ), but they did not influence weed species diversity (e.g. gamma diversity,  $R = 0.43$ ,  $P = 0.17$ ).

#### QUANTIFICATION OF ARABLE WEED SPECIES DIVERSITY

##### *Vegetation*

The diversity and abundance of weeds were recorded three times during the growing season. The first sample date was at the beginning of April to record the initial state of the weeds in spring. This was before herbicides were applied in the conventional fields (all conventional farmers used herbicides against broad-leaved species and grasses). The second sampling was conducted in the second half of May and the third in the middle of July. Sampling in all periods was conducted within 1 week. All broad-leaf and grass species and their percentage cover were recorded in four  $3 \times 10$ -m plots per field using the nomenclature of plant names of Wisskirchen & Haeupler (1998); tree seedlings were not considered. Two plots were situated in the centre of the field (approximately 30 m apart from any edge as well as 30 m from each other) and two plots at the field edge (0–3 m apart from the first drill row and 30 m from each other). The location of the vegetation plots was the same for all three sampling sessions. Species numbers per plot were summed and percentage cover was averaged for the three sample dates.

##### *Germinable seed rain*

Germinable seed rain was measured from the beginning of April until the middle of July, which is the time when the seeds of most central European weeds are produced and dispersed (Kästner, Jäger & Schubert 2001). To catch and hold the seeds, eight plastic boxes were used, measuring  $50 \times 32 \times 6$  cm and filled with seedless garden soil. Four of the boxes were buried in the centre of the fields (30 m from the edge), and four at the field edge (1–1.5 m from the first drill row). The boxes were arranged in pairs, with a distance of 50 cm to each other; the distance between the two pairs was 25 m. The box pairs were placed close to and between the vegetation plots. The garden soil was watered regularly, depending on weather conditions. Once a month all germinated plants were identified to species, counted and removed from the boxes. In the middle of July, before the wheat harvest, all boxes were removed

from the fields and brought into the greenhouse, where all germinated plants were identified, counted and removed monthly for another 10 months. To initiate germination of seeds requiring stratification, we induced a 3-week frost period during the winter. Species numbers per box pair were summed for the 14 sample dates. This experiment was conducted in all fields but one organic field was omitted because of destroyed boxes.

#### *Germinable seed bank*

To measure the germinable weed seed bank, we collected four samples of the soil of each winter wheat field at the beginning of September, after the wheat harvest. Each sample consisted of eight subsamples randomly taken from a plot of 20 m<sup>2</sup>. Two plots were located in the field centre and two at the edge, analogous to the seed rain experiment. The subsamples were taken from the top 25 cm of the soil with the help of a spade. Most weeds are known to germinate and emerge from the first centimetres of soil (Buhler 1995). However, 25 cm was chosen in order to include all seeds that potentially could germinate in the next few years, as annual ploughing is normally conducted to this depth in this region (I. Roschewitz, unpublished data). The eight subsamples were mixed and put into a plastic box (similar to the boxes in the seed rain experiment). The boxes were brought into the greenhouse, where all germinated plants were recorded monthly for 14 months. The samples were kept under the same conditions as the seed rain samples. Species numbers per box were summed for the 14 sample dates.

#### ADDITIVE PARTITIONING OF WEED SPECIES DIVERSITY

The total regional diversity can be seen as the sum of alpha diversity (mean diversity within the sampling units) and beta diversity (difference in diversity between the sampling units) (Allan 1975; Lande 1996). This relationship is not only valid for regional diversity but also for smaller scale diversity (Wagner, Wildi & Ewald 2000). Thus, it is possible to partition species diversity in a region additively into scale-specific components. In our study, we partitioned species richness at two spatial scales, the regional and the field scale.

To describe the overall regional weed species diversity of the winter wheat fields (gamma diversity), we first calculated diversity of all species found at the regional scale (vegetation, seed rain and seed bank). The alpha diversity of the region was calculated as the mean number of species of all 24 wheat fields, as well as separately for 12 organic and 12 conventional fields. The gamma diversity of the region was calculated as the total species number of all 24 fields, and separately for 12 organic and 12 conventional fields. The beta diversity of the region (between-field diversity) was calculated by subtracting  $\alpha$  from  $\gamma$ .

In all three studies (vegetation, seed rain and seed bank) the number of weed species was recorded for four plots per field, which allowed us to assess the within-field heterogeneity. The gamma diversity of a field ( $\gamma_f$ ) was calculated as the total number of species per field. The alpha diversity ( $\alpha_f$ ) was calculated as the mean number of species of the four plots per field. The beta diversity of a field ( $\beta_f$ , between-plot diversity) was generated by subtracting  $\alpha_f$  from  $\gamma_f$ , and represented a measure of within-field heterogeneity. As species numbers were generally lower in conventional than in organic fields, we additionally calculated a relative beta diversity ( $\beta^{\%} = \beta/\gamma \times 100$ ) at the regional as well as field level. This measure can be seen as the opposite of Lande's (1996) measure of community similarity, which was calculated as  $\phi_D = 1 - D_{\text{among}}/D_T$  (in our terminology  $1 - \alpha/\gamma$ ).

#### STATISTICAL ANALYSIS

Mixed effect models (Pinheiro & Bates 2000) with stepwise backwards selection were used to analyse the effects of farming system, landscape complexity and first-order interaction on the alpha, beta and gamma diversity of arable weeds at the field scale, and on the number of species registered in the Red List of threatened plant species of Lower Saxony, Germany (Garve & Letschert 1991; Garve 1993; Korneck, Schnittler & Vollmer 1996). By blocking field pairs (organic-conventional), these models accounted for non-independent errors. Multiple logistic regressions (with stepwise backwards selection) were used to examine which plant species were affected by landscape complexity and/or farming system. Therefore, the presence-absence of each species occurring in at least four fields (pooled for vegetation, seed rain and seed bank) was related to the percentage of arable land and farming system. Statistical analyses were carried out using R (R Development Core Team 2004) and Statgraphics Plus 5.1 (Statistical Graphics Corp. 2001). Logarithmic transformation of the variables was used to achieve normality of the residuals, and arcsine-square root transformation for the percentages (Sokal & Rohlf 1995). In the text and tables arithmetic means  $\pm$  SD from original values are given.

## Results

### OVERVIEW

In total, we found a gamma diversity in the region of 153 weed species, of which 135 were broad-leaves and 18 were grasses (see the Appendix). In conventionally managed fields 104 species were recorded (86 broad-leaves and 18 grasses), and in organically managed fields 142 species were recorded (126 broad-leaves, 16 grasses). The average percentage vegetation cover and numbers of seedlings germinated from the seed rain and seed bank are shown in Table 1. Eleven weed

**Table 1.** Percentage cover of weeds in the vegetation, numbers of seedlings  $m^{-2}$  ground in the seed rain, and numbers of seedlings  $m^{-2}$  ground in 0–25 cm depth in the seed bank. Medians, minima and maxima are given for 12 organic and 12 conventional winter wheat fields (seed rain: 11 organic fields)

	Median		Minimum		Maximum	
	Organic	Conventional	Organic	Conventional	Organic	Conventional
Vegetation (% cover)						
Broad-leaves	10.6	1.3	4.0	0.2	28.6	11.7
Grasses	3.9	1.6	1.1	0.5	10.3	28.3
Seed rain (seedlings $m^{-2}$ )						
Broad-leaves	2332	1779	1210	402	8996	3578
Grasses	2300	1955	164	222	65 148	36 566
Seed bank (seedlings $m^{-2}$ in 0–25 cm)						
Broad-leaves	8093	2343	2015	968	23 007	7414
Grasses	2187	1371	242	445	9757	64 046

**Table 2.** The alpha ( $\alpha_f$ ), beta ( $\beta_f$ ), relative beta ( $\beta\%_f$ ), gamma ( $\gamma_f$ ) and Red List species diversity of weeds at the field scale: data from vegetation, seed rain and seed bank mappings. Means  $\pm$  SD, minima and maxima are given for 12 organic and 12 conventional winter wheat fields (seed rain: 11 organic fields)

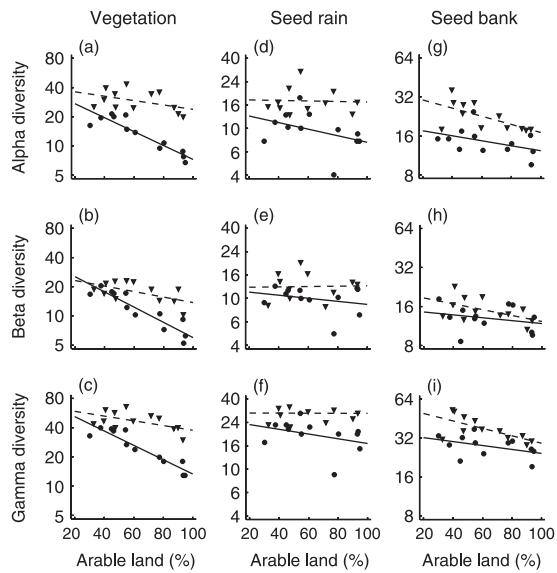
	Mean $\pm$ SD		Minimum		Maximum	
	Organic	Conventional	Organic	Conventional	Organic	Conventional
Vegetation						
$\alpha_f$	29.7 $\pm$ 7.4	14.2 $\pm$ 5.4	19.8	6.8	43.0	21.3
$\beta_f$	18.1 $\pm$ 4.0	12.5 $\pm$ 5.1	10.3	5.3	23.0	20.5
$\beta\%_f$ (%)	38.0 $\pm$ 5.4	46.6 $\pm$ 4.2	29.0	40.3	47.9	52.5
$\gamma_f$	47.8 $\pm$ 10.2	26.7 $\pm$ 10.4	30.0	13.0	66.0	40.0
Red List species	1.4 $\pm$ 1.8	0.8 $\pm$ 0.9	0.0	0.0	6.0	2.0
Seed rain						
$\alpha_f$	17.7 $\pm$ 5.2	10.2 $\pm$ 3.6	13.0	4.0	30.8	18.3
$\beta_f$	13.1 $\pm$ 3.6	10.3 $\pm$ 2.3	8.5	5.0	20.3	12.8
$\beta\%_f$ (%)	42.6 $\pm$ 6.9	51.0 $\pm$ 6.3	34.0	39.2	52.4	61.3
$\gamma_f$	30.8 $\pm$ 7.6	20.4 $\pm$ 5.2	23.0	9.0	51.0	30.0
Red List species	1.0 $\pm$ 1.2	0.4 $\pm$ 0.8	0.0	0.0	3.0	2.0
Seed bank						
$\alpha_f$	22.8 $\pm$ 6.0	14.6 $\pm$ 3.7	17.5	9.5	35.8	24.3
$\beta_f$	15.1 $\pm$ 3.4	13.1 $\pm$ 2.9	10.5	8.5	22.5	18.0
$\beta\%_f$ (%)	40.1 $\pm$ 5.5	47.3 $\pm$ 6.9	31.3	34.5	50.7	56.9
$\gamma_f$	31.8 $\pm$ 8.2	21.6 $\pm$ 5.6	23.0	14.0	46.0	31.0
Red List species	1.9 $\pm$ 2.1	1.00 $\pm$ 0.7	0.0	0.0	6.0	2.0

species were detected in conventional, but not in organic fields, and 49 species only in organic fields. Most of these species were detected in one or two fields only, indicating a high variability in local occurrence. In total, 31 weed species were only found established in crop fields, 10 species only in the seed rain, and 24 species only in the seed bank. Overall, 58 species appeared in the vegetation, the seed rain and the seed bank. As many as 23 species were registered in the Red List of threatened plant species of Lower Saxony, of which 21 species were found in organic and 10 in conventional fields (see the Appendix). Alpha diversity at the regional scale (mean diversity per field) was 53.1 species (conventional 43.7, organic 62.6). Beta diversity (between-field diversity) was 99.9 species (conventional 60.3, organic 79.4). Hence, relative beta diversity was 65.3% (conventional 58.0%, organic 55.9%). The species diversity

and numbers of Red List species at the field scale are outlined in Table 2, separated for vegetation, seed rain and seed bank. Diversity varied considerably between the two farming systems and the 12 landscapes.

#### RELATIVE INFLUENCE OF FARMING SYSTEM AND LANDSCAPE COMPLEXITY ON WEED SPECIES DIVERSITY

In the vegetation, weed alpha, beta and gamma diversities responded similarly to farming system and landscape complexity (= percentage arable land). They were higher in organic than in conventional fields and decreased as the percentage of arable land increased, i.e. they were higher in complex than in simple landscapes. This decrease was very steep in conventional, but not in organic fields, resulting in similar diversities



**Fig. 1.** The field-scale alpha, beta and gamma diversities of weeds in the vegetation (a, b, c), seed rain (d, e, f) and seed bank (g, h, i) in relation to percentage arable land and farming system (organic vs. conventional). Results from mixed effect models (see Table 3). Organic fields, triangles and dashed regression lines; conventional fields, points and solid regression lines.

in the two farming systems in complex landscapes and higher diversities in organic fields in simple landscapes (Fig. 1a–c and Table 3). In the seed rain, all three measures of weed diversity were higher in organic than in conventional fields and not related to percentage arable land (Fig. 1d–f and Table 3). In the seed bank, weed alpha and gamma diversities were significantly higher in organic than in conventional fields. Additionally, alpha and gamma diversities decreased with increasing percentage of arable land, irrespective of farming system (Fig. 1g,i and Table 3). For beta diversity, no significant model could be found (Fig. 1h and Table 3). In all three studies, the relative within-field heterogeneity (beta %) of weeds was significantly higher in conventional than in organic fields (vegetation  $F = 27.0$ ,  $P < 0.001$ ; seed rain  $F = 7.6$ ,  $P < 0.05$ ; seed bank  $F = 8.9$ ,  $P < 0.05$ ) and not related to landscape complexity.

When alpha, beta, gamma and relative beta diversities were partitioned for broad-leaves and grasses, it became clear that the above described patterns were mainly determined by the broad-leaves (Table 3). Although alpha diversity of grasses in the vegetation increased with decreasing percentage arable land and was higher in organic than in conventional fields, there was no significant interaction between percentage arable land and farming system. Beta and gamma diversities of grasses in the vegetation also increased with decreasing percentage arable land but irrespective of farming system. Only the alpha and gamma diversities of grasses in the seed rain showed the same pattern as all weeds (higher in organic than in conventional fields). No significant models for the diversity of

**Table 3.** The alpha ( $\alpha_f$ ), beta ( $\beta_f$ ) and gamma ( $\gamma_f$ ) diversities of weeds (field scale) in the vegetation, seed rain and seed bank in relation to farming system and landscape complexity.  $F$ -values and levels of significance ( $*P < 0.05$ ,  $**P < 0.01$ ,  $***P < 0.001$ ) from mixed effect models,  $n = 24$  wheat fields (seed rain:  $n = 22$  fields)

	Vegetation	Seed rain	Seed bank
<b>All weeds</b>			
$\alpha_f$			
A: arable land (%)	35.0***	NS	9.0*
B: farming system	128.5***	24.5***	31.4***
A $\times$ B	13.5**	NS	NS
$\beta_f$			
A: arable land (%)	39.3***	NS	NS
B: farming system	29.8***	5.2*	NS
A $\times$ B	9.4*	NS	NS
$\gamma_f$			
A: arable land (%)	46.6***	NS	10.3**
B: farming system	98.3***	19.3**	18.4**
A $\times$ B	15.1**	NS	NS
<b>Broad-leaves</b>			
$\alpha_f$			
A: arable land (%)	40.9***	NS	8.5*
B: farming system	150.5***	19.9**	34.8***
A $\times$ B	18.5***	NS	NS
$\beta_f$			
A: arable land (%)	34.3***	NS	NS
B: farming system	29.9***	NS	NS
A $\times$ B	12.5**	NS	NS
$\gamma_f$			
A: arable land (%)	45.5***	NS	6.5*
B: farming system	107.8***	18.6**	16.3**
A $\times$ B	19.5**	NS	NS
<b>Grasses</b>			
$\alpha_f$			
A: arable land (%)	7.6*	NS	NS
B: farming system	8.3*	10.9**	NS
A $\times$ B	NS	NS	NS
$\beta_f$			
A: arable land (%)	6.5*	NS	NS
B: farming system	NS	NS	NS
A $\times$ B	NS	NS	NS
$\gamma_f$			
A: arable land (%)	10.6**	NS	NS
B: farming system	NS	10.4**	NS
A $\times$ B	NS	NS	NS

grasses could be found for beta diversity in the seed rain, relative beta diversity in all three studies, and all diversity components in the seed bank (for statistics see Table 3).

#### SINGLE SPECIES

Many species were abundant either in only very few or in nearly all fields. However, when summed across vegetation, seed rain and seed bank, 64 out of 153 species were suitable for logistic regressions, i.e. they were present or absent in at least four fields (see the Appendix). Only four of these species could be related to the percentage of arable land: *Poa pratense* L. occurred with 75% probability when the percentage arable land

was lower than 34.7% [ $P < 0.01$ ; percentage of deviance explained by the model (similar to  $R^2$ ) = 39.2%], *Euphorbia helioscopia* L. when arable land cover was lower than 33.2% ( $P < 0.01$ , 26.0%), and *Lamium amplexicaule* L. when arable land cover was lower than 54.0% ( $P < 0.05$ , 17.4%). *Taraxacum officinale* Weber occurred when arable land cover was lower than 83.7% in organic fields and 66.6% in conventional fields ( $P_{\text{arable land}} < 0.001$ ,  $P_{\text{farming system}} < 0.05$ ,  $P_{\text{model}} < 0.001$ ; 84.4%). Another eight species [*Cerastium dubium* (Bastard) Guépin, *Equisetum arvensis* L., *Medicago sativa* L., *Potentilla reptans* L., *Trifolium pratense* L., *Tussilago farfara* L., *Vicia cracca* L. and *Vicia faba* L.] were significantly more likely to be present in organic farming, irrespective of landscape complexity ( $P$ -values ranging from  $< 0.05$  to  $< 0.001$ ; percentage deviance explained by the models ranged from 20.0% to 57.5%). Independent of farming system, the number of Red List species per field in the vegetation decreased significantly when the percentage arable land cover increased (mixed effect models  $F = 7.4$ ,  $P < 0.05$ ).

## Discussion

In this study, local management (organic vs. conventional) and complexity of the surrounding landscape had an influence on alpha, beta and gamma diversities of weeds in 24 winter wheat fields. The arable weed gamma diversity in the whole study region was 153 species. This overall diversity was strongly determined by the heterogeneity between the fields, as beta diversity made up *c.* 65%. Similarly, Wagner, Wildi & Ewald (2000) described low within-field diversity and large between-field diversity in arable fields and attributed this to crop variability. In our study, the crop species was the same in all analysed fields, which underlines the high variability of weed community structure in the region.

At the field scale, the gamma diversity of weeds in the vegetation was higher in organic than in conventional fields, a finding consistent with the results of other studies (Moreby *et al.* 1994; Hald 1999; Hyvönen *et al.* 2003). However, our results showed that this was particularly valid in fields located in simple landscapes with a high percentage of arable land, as gamma diversity in conventional fields was strongly positively affected by landscape complexity, which resulted in nearly similar gamma diversities in organic and conventional fields when landscapes were complex with high percentages of non-crop areas. Gamma diversity of organic fields was only weakly related to landscape complexity, suggesting organic fields to be more or less self-sufficient ecosystems, not depending on species immigration from surrounding habitats in complex landscapes. Plant diversity of organic and conventional farms in Sweden showed a similar tendency: in conventional pastures and field margins, diversity tended to increase more steeply with increasing perimeter-to-area ratio than in organic pastures and field margins

(Weibull, Östman & Granqvist 2003). Alpha and beta diversities revealed a similar pattern to gamma diversity.

In contrast to broad-leaf diversity, the gamma and beta diversities of grasses in the vegetation did not differ between the farming systems, but were also negatively related with the percentage of arable land. The number of grass species was generally much lower than that of broad-leaves (in the whole study only 18 grass species were found), which may partly explain why the observed differences between organic and conventional fields in broad-leaf diversity could not generally be found for grasses. As all conventional farmers applied herbicides, broad-leaf species may have been more affected by the applications than grasses, as suggested by Hole *et al.* (2005).

The reasons for the high importance of landscape complexity for the local weed species diversity, especially in conventional fields, might reflect species entering the fields through the seed rain. Unexpectedly, species diversity in the seed rain appeared to be mainly determined by the local vegetation, as it was higher in organic than in conventional fields and not related to percentage arable land. Many seeds appeared to come from the fields themselves, but not from the landscape. This is supported by several studies showing that seeds of many arable weeds are dispersed only a few metres (Rew, Froud-Williams & Boatman 1996; Bischoff & Mahn 2000). However, Fig. 1 shows a trend that, in complex landscapes, diversity was high in both organic and conventional fields, whereas it decreased with increasing percentage of arable land only in conventional fields. Most of the weed species occurring in the seed rain, but not in the vegetation and seed bank (see the Appendix), should be relatively good dispersers because they are either wind or animal dispersed (Kästner, Jäger & Schubert 2001). Their seeds should have had the potential to reach an arable field from the surrounding habitats, which should provide a higher species pool in complex than in simple landscapes.

The gamma and alpha diversities in the seed bank were generally higher in organic than in conventional fields. Long-term effects of farming systems on weed species richness were also shown by Menalled, Gross & Hammond (2001). Additionally, weed species diversity decreased with increasing percentage of arable land but, in contrast to the diversity of the vegetation, the surrounding landscape affected both organic and conventional fields similarly. So, landscape complexity did not seem to determine the weed species diversity of organic fields immediately (i.e. in the vegetation) but revealed the potential to do so in the following years, expressed via the more diverse germinable seed bank in complex landscapes.

In contrast to the absolute beta diversities, the relative beta diversities of weeds in the vegetation, seed rain and seed bank were higher in conventional than in organic fields, irrespective of landscape complexity. This shows the particular importance of species

heterogeneity within a field for the gamma diversity of conventional fields, as the mean (alpha) diversity within a field was comparatively low. Heterogeneity in conventional fields may be the result of less intensive herbicide spraying and fertilization at the field edges. Wilson & Aebischer (1995) showed that several weed species in conventional fields declined with increasing distance from the field edges, and Hald (1999) found a gradient in species density from edge to centre in conventional, but not organic, fields.

The number of Red List species in the vegetation was shown to be higher in complex than in simple landscapes, indicating a high importance of alternative habitats in the surrounding landscape for these species. However, numbers of species did not differ between organic and conventional fields. Thus, our study only partly supports the general opinion that the decline of particular species is caused by intensive agricultural practices at the field scale and the simplification of landscape complexity (Korneck & Sukopp 1988; Jedicke 1997; Hofmeister & Garve 1998). The unexpectedly similar numbers of Red List species in organic and conventional farming may result from a gradual decrease in the land-use intensity of conventional fields, which seemed to be irrespective of landscape complexity (see the Methods). For example, the fertilizer consumption in Germany decreased from c. 3 million t (1991) to c. 2.6 million t (2001) and herbicide consumption from c. 18 000 t (1991) to c. 15 000 t (2001) (Food and Agriculture Organization of the United Nations 2001). However, out of the 23 Red List species 21 were found in organic fields and only half (10 species) in conventional fields.

The results of multiple logistic regressions showed that only very few single species depended on landscape complexity and/or organic farming. Thus, higher species numbers found in complex landscapes and in organic farming cannot only be attributed to single species depending on such landscapes and/or organic farming. Which particular species have contributed to higher species numbers in complex landscapes is more likely to be a matter of chance. This might suggest mass effect (Shmida & Wilson 1985; Auerbach & Shmida 1987; Palmer 1992), which explains high local species richness with continuous immigration from nearby but dissimilar habitats. One characteristic of many arable weed species is their ability to quickly colonize and survive in ruderal and disturbed habitats. Thus, the probability that many species randomly immigrate into a field is obviously greater when the proportion of alternative habitats in the landscape is increased. Eight species could be shown to depend on organic farming. These species were hemicryptophytes or geophytes and some of them were legumes, which may have profited from diverse crop rotations including perennial crops for green manure. Legumes should be more competitive in organic than in conventional fields because of the absent mineral nitrogen input.

Our results have implications for the future management of both arable fields and landscape complexity to conserve species diversity of arable weeds, which are important components of the biodiversity in agricultural landscapes (Marshall *et al.* 2003). Organic farming generally promoted species diversity of arable weeds and the surrounding landscape was important for the seed bank. In conventional fields, species diversity strongly increased with increasing landscape complexity, thereby generating nearly similar diversity levels as in organic fields when the surrounding landscape was complex. Hence, organic farming contributed most effectively to weed species diversity in simple agricultural landscapes. Therefore, the conversion of conventional to organic farming should be supported in these areas, especially where it will be particularly effective. This is in contrast to the present uptake of agri-environment schemes, which is highest in areas where biodiversity is already relatively high and lowest where biodiversity is low (Kleijn & Sutherland 2003). Promoting non-crop habitats in agricultural landscapes as refugia for weed species appears to be of particular importance for landscape management, especially when organically managed fields are rare. Moreover, differences in species composition (beta diversity) have been shown to be very large within fields (particularly in conventional farming) and between fields, thereby making an important contribution to overall diversity (gamma diversity) at the field and regional scales. Future management policies should therefore take into account the heterogeneity in community composition at different spatial scales.

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### Supplementary material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JPE/JPE1072/JPE1072sm.htm>.

**Appendix.** Abundance and conservation status of weed species in the vegetation, seed rain, and seed bank of 12 organic and 12 conventional winter wheat fields.

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