



---

Beta Diversity at Different Spatial Scales: Plant Communities in Organic and Conventional Agriculture

Author(s): Doreen Gabriel, Indra Roschewitz, Teja Tscharntke and Carsten Thies

Source: *Ecological Applications*, Vol. 16, No. 5 (Oct., 2006), pp. 2011-2021

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/40061770>

Accessed: 13/05/2014 13:23

---

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



*Ecological Society of America* is collaborating with JSTOR to digitize, preserve and extend access to *Ecological Applications*.

<http://www.jstor.org>

## BETA DIVERSITY AT DIFFERENT SPATIAL SCALES: PLANT COMMUNITIES IN ORGANIC AND CONVENTIONAL AGRICULTURE

DOREEN GABRIEL,<sup>1</sup> INDRA ROSCHEWITZ, TEJA TSCHARNTKE, AND CARSTEN THIES

*Agroecology, University of Göttingen, Waldweg 26, 37073 Göttingen, Germany*

**Abstract.** Biodiversity studies that guide agricultural subsidy policy have generally compared farming systems at a single spatial scale: the field. However, diversity patterns vary across spatial scales. Here, we examined the effects of farming system (organic vs. conventional) and position in the field (edge vs. center) on plant species richness in wheat fields at three spatial scales. We quantified  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversity at the microscale in 800 plots, at the mesoscale in 40 fields, and at the macroscale in three regions using the additive partitioning approach, and evaluated the relative contribution of  $\beta$ -diversity at each spatial scale to total observed species richness. We found that  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversity were higher in organic than conventional fields and higher at the field edge than in the field center at all spatial scales. In both farming systems,  $\beta$ -diversity at the meso- and macroscale explained most of the overall species richness (up to 37% and 25%, respectively), indicating considerable differences in community composition among fields and regions due to environmental heterogeneity. The spatial scale at which  $\beta$ -diversity contributed the most to overall species richness differed between rare and common species. Total richness of rare species (present in  $\leq 5\%$  of total samples) was mainly explained by differences in community composition at the meso- and macroscale (up to 27% and 48%, respectively), but only in organic fields. Total richness of common species (present in  $\geq 25\%$  of total samples) was explained by differences in community composition at the micro- and mesoscale (up to 29% and 47%, respectively), i.e., among plots and fields, independent of farming system. Our results show that organic farming made the greatest contribution to total species richness at the meso (among fields) and macro (among regions) scale due to environmental heterogeneity. Hence, agri-environment schemes should exploit this large-scale contribution of  $\beta$ -diversity by tailoring schemes at regional scales to maximize dissimilarity between conservation areas using geographic information systems rather than focusing entirely at the classical local-field scale, which is the current practice.

**Key words:** arable weeds; field edge; gamma diversity; landscape; mass effect; mixed effect models; organic farming; spatial scale; species richness.

### INTRODUCTION

During the last decades, increasing agricultural intensification in Europe has led to a decrease in species richness and a change in species composition of arable weeds (i.e., non-cultivated wild plants cohabiting the fields with crops; Albrecht 1995, Andreasen et al. 1996, Sutcliffe and Kay 2000, Robinson and Sutherland 2002). At the field and farm scale, improvements in crop management techniques involving the use of herbicides and mechanical weed control, increases in fertilizer usage, simplification of crop rotations, and improvements in seed-cleaning techniques have been responsible for the loss of annual forbs and other taxa in agroecosystems (Firbank 1988, Albrecht 1995, McLaughlin and Mineau 1995, Sotherton 1998, Stoate et al. 2001, Benton et al. 2003). At the landscape scale, farm enlargement and specialization on a narrow range

of arable crops, abandonment of areas with marginal crop yields, and land consolidation has led to large uniformly cropped areas and a decrease in spatial heterogeneity (Robinson and Sutherland 2002, Benton et al. 2003). Arable weeds, as important components of biodiversity in agroecosystems (Marshall et al. 2003), belong to the most endangered plant communities in Germany (Hofmeister and Garve 1998), with roughly one third of the 250–300 arable weed species recorded on the German Red Data List of endangered species (Eggers 1987).

To counteract the decline of biodiversity in agroecosystems, strategies on agri-environmental schemes classically focus on the improvement of local habitat conditions by implementing conservation headlands, i.e., flowering plant strips in the field margin or in the field edge without nitrogen fertilization and herbicide applications (Kleijn and Vandervoort 1997), reducing agrochemical applications, or promoting organic farming (Kleijn and Sutherland 2003). It has been suggested that organic farming enhances biodiversity in agroecosystems (van Elsen 2000, Hole et al. 2005). Positive

Manuscript received 8 September 2005; revised 9 December 2005; accepted 20 January 2006.

<sup>1</sup> E-mail: D.Gabriel@leeds.ac.uk

effects on species richness and composition of arable weeds from organic farming relative to conventional farming have been reported in several studies (Moreby et al. 1994, Hald 1999a, Menalled et al. 2001, Hyvönen et al. 2003, Bengtsson et al. 2005). However, most of this research has focused on only one spatial scale, i.e., plots or fields (see Hole et al. 2005). Such single-scale studies identify only a subset of diversity that may lead to fragmentary results. For example, several high-diversity fields all harboring similar species may collectively be less diverse than comparatively low-diversity fields harboring different species. A multi-scale approach makes it possible to identify the spatial scale at which each farming system contributes most to overall arable weed diversity, i.e., where the highest turnover occurs, and, therefore, the appropriate scale at which the management for conservation (e.g., agri-environment schemes) should be designed.

The additive partitioning approach is a useful tool for quantifying diversity components across multiple spatial scales (Allan 1975, Lande 1996, Wagner et al. 2000, Gering et al. 2003). Total species richness ( $\gamma$ -diversity) found in a given location can be partitioned into  $\alpha$ -diversity (the mean number of species that occur in a sampling unit = within-community diversity) and  $\beta$ -diversity (between community diversity;  $\beta = \gamma - \alpha$ ).  $\alpha$ - and  $\beta$ -diversity can be compared because their units of measurement are the same. Therefore, partitioning can be applied at any spatial scale (Veech et al. 2002). Additive partitioning of diversity was applied in a spatial context by Wagner et al. (2000) and Fournier and Loreau (2001) for plants and carabid beetles of different habitat types in agricultural landscapes. It has also been used for arboreal beetles and forest Lepidoptera (Gering et al. 2003, Summerville et al. 2003), and for butterfly and bird diversity in canyons and mountain ranges (Fleishman et al. 2003).

In general, species richness and composition of arable weeds are related to local abiotic conditions like soil properties (Dale et al. 1992) and farming practices differing in herbicide use, mechanical weed control, tillage systems, and nitrogen fertilizer input (Pyšek and Lepš 1991, McCloskey et al. 1996, Andersson and Milberg 1998, Hyvönen and Salonen 2002). As a consequence, many plant species occur predominantly at the field edge, where management practices are less intensive (Marshall 1989, Wilson and Aebischer 1995, Hald 1999a). The structural complexity of the surrounding landscape, e.g., the amount of ruderal land cover, and the regional species pool is regarded to influence local diversity (Ricklefs 1987, Zobel 1997, Booth and Swanton 2002, Gabriel et al. 2005), and effects of landscape complexity might interfere with effects of farming system (Bengtsson et al. 2005, Hole et al. 2005, Roschewitz et al. 2005). However, the impacts of spatial variability have received little attention in weed ecology as yet.

Here, we analyzed the contribution of farming system (organic vs. conventional) and position in the field (edge vs. center) to plant species richness in wheat fields at three spatial scales. We quantified species richness at a microscale from 800 plots within 40 fields, at a mesoscale from 40 fields within three regions, and at a macroscale from three regions by partitioning the number of species into the additive components  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversity. We examined whether (1)  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversity of arable weeds is higher in field edges, organic fields, and structurally complex landscapes, and (2) any patterns differ between rare and common species. In addition, we evaluated the relative contribution of  $\beta$ -diversity at the micro, meso, and macroscale to overall species richness and to the richness of rare and common species to identify the most appropriate scale for effective conservation management.

## METHODS

### *Study sites and sampling design*

The study was conducted in three agricultural regions in Germany: Soester Boerde, North Rhine-Westphalia (51°35'00" N, 008°07'00" E); Leine Bergland, Lower Saxony (51°32'00" N, 009°56'00" E); and Lahn-Dill Bergland, Hesse (50°49'00" N, 008°46'00" E) (Fig. 1a). The regions covered 620 km<sup>2</sup>, 670 km<sup>2</sup>, and 1000 km<sup>2</sup> (respectively) at a distance of 100 km to 130 km from each other. Mean annual temperature and mean annual precipitation in the study regions were, respectively, 9.3°C and 764 mm in the Soester Boerde, 8.7°C and 645 mm in the Leine Bergland, and 9.4°C and 745 mm in the Lahn-Dill Bergland. The mean elevation of study sites within each region was as follows: Soester Boerde, 170 m (min = 70 m, max = 320 m); Leine Bergland, 214 m (min = 155 m, max = 295 m); and Lahn-Dill Bergland, 273 m (min = 172 m, max = 496 m). We selected seven circular landscape sectors (2 km diameter) in the Soester Boerde and Lahn-Dill Bergland regions, and six landscape sectors in the Leine Bergland region. These landscape sectors differed in their structural complexity, varying from structurally simple landscapes with a high percentage of arable land, to complex landscapes with a low percentage of arable land and a large proportion of semi-natural land cover and land use types, such as grasslands, hedges, fallows, and margins (Fig. 1b). In the center of each landscape, a pair of one organic and one conventional winter wheat field (*Triticum aestivum* L.) was selected. The matched fields were in close proximity to ensure similar abiotic conditions. Around each focal field, habitat and land use types were surveyed within a radius of 1 km and mapped by field inspections on the basis of official topographical maps (DGK 5, Deutsche Grundkarte, Landesvermessung und Geobasisinformation Lower Saxony, Germany; 1:5000) using the GIS ArcView 3.2 (ESRI 1999). We used the percentage of arable land surrounding each study site as a simple measure of landscape complexity because of its close correlation with other landscape

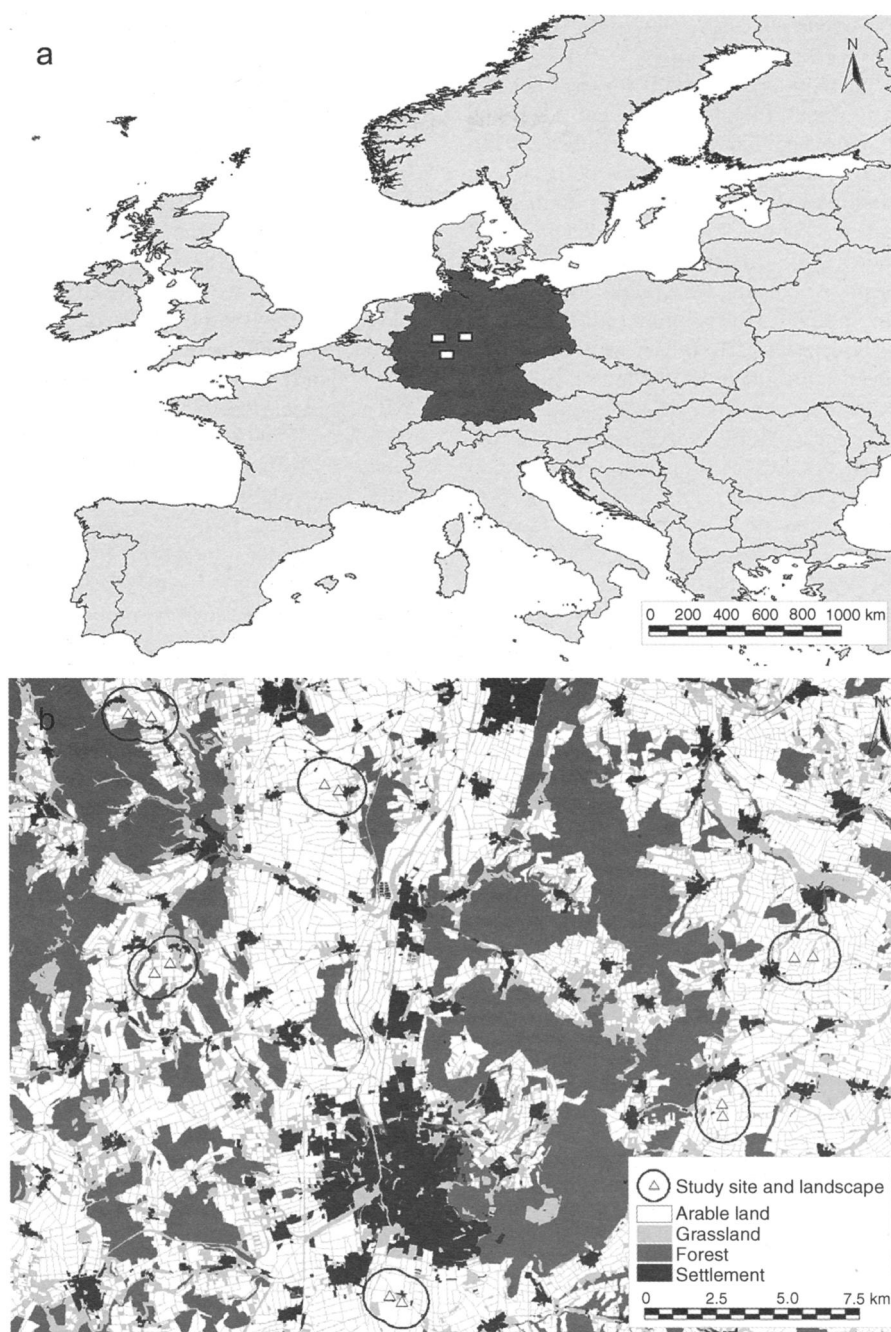


FIG. 1. (a) Overview of the location of the three study regions in Germany (data obtained from ArcView 3.2, ESRI 1999). (b) Example of the landscape gradient approach within the Leine Bergland region, illustrating the paired wheat fields surrounded by landscapes of different complexity (data obtained from ATKIS; digital landscape model 25/1, Landesvermessung und Geobasisinformation, Hannover, Germany, 1991–1996).

metrics such as habitat type diversity (Shannon diversity;  $P < 0.001$ ,  $R = -0.95$ ,  $N = 40$ ) and the perimeter : area ratio ( $P < 0.001$ ,  $R = -0.64$ ,  $N = 40$ ) (see also Gabriel et al. 2005). The mean percentage of arable land  $\pm$  SD within 1 km around the study sites was as follows: Soester Boerde,  $64\% \pm 12.1\%$  (minimum = 42%, maximum = 86%); Leine Bergland,  $68\% \pm 15.8\%$

(min. = 40%, max. = 85%); and Lahn-Dill Bergland,  $47\% \pm 21.5\%$  (min. = 17%, max. = 85%).

Organic fields were managed according to European Union Regulation 2092/91/EEC, which prohibits the use of synthetic fertilizers and pesticides. The mean time since conversion to organic farming was  $11.6 \pm 5.9$  years and varied between 2 years and 24 years. Species



richness of arable weeds was not related to the time since conversion ( $P = 1$ ,  $R = 0.0$ ,  $N = 20$ ).

Local soil chemistry was analyzed from each field by taking 16 soil samples at a depth of 0–30 cm. Sampling was carried out after wheat harvest in September 2003 to ensure representativeness that might have been lacking during vegetation period due to different timings in fertilizer applications. Samples were analyzed for total soil nitrogen and organic carbon using a C/N analyzer (LECO, St. Joseph, Michigan, USA), and soil pH was measured in 0.01 mol/L  $\text{CaCl}_2$  solution. All fields were on loamy soils. Soil parameters (given as mean  $\pm$  SD) were total nitrogen (percentage in dry mass),  $0.14\% \pm 0.033\%$  (min. = 0.10%, max. = 0.23%); organic carbon (percentage in dry mass),  $1.4\% \pm 0.32\%$  (min. = 1.0%, max. = 2.3%); C:N ratio  $10.2 \pm 0.71$  (min. = 8.6, max. = 12.3); and pH  $6.2 \pm 0.52$  (min. = 4.8, max. = 7.0). Soil parameters did not differ significantly between farming systems and regions (all  $P$  values  $> 0.05$ ).

At the end of May 2003, herb and grass species in each field were recorded using two 95-m transects parallel to the machine track. Each transect consisted of 10 plots ( $5 \times 1$  m) at intervals of 5 m. One transect followed the field edge adjacent to a field margin and one transect was 30–50 m away from the edge transect located in the field center.

#### *Additive partitioning of species richness*

At three spatial scales, we partitioned the total observed species richness (i.e., the number of species) into scale-specific diversity components for each treatment factor (edge/organic, edge/conventional, center/organic, center/conventional) using the additive partitioning approach  $\alpha + \beta = \gamma$  (Allan 1975, Lande 1996, Wagner et al. 2000, Gering et al. 2003). The sampling unit at the smallest scale (microscale) was represented by the plots within a field (field = edge or center transect), the medium scale (mesoscale) by the fields within a region, and the largest scale (macroscale) by three regions (Fig. 2). The  $\alpha$ -diversity (within-unit diversity) was the mean number of species found in a sampling unit (e.g., per plot in a field, per field in a region, or per region),  $\gamma$ -diversity (total species diversity) was the number of species found in the pooled sampling unit (e.g., in all plots per field, in all fields per region, or in all regions), and  $\beta$ -diversity (between-unit diversity) was the mean number of species found among the sampling units ( $\beta = \gamma - \alpha$ ). Mean  $\gamma$ -diversity at a given scale (e.g., microscale) is equivalent to mean  $\alpha$ -diversity at the next larger scale (e.g., mesoscale). Thus, total diversity at one scale results from the diversity of the next lower scale plus between-unit diversity ( $\beta$ -diversity). Therefore, the total observed diversity is the sum of  $\alpha$ - and  $\beta$ -diversity at the microscale plus  $\beta$ -diversity at the meso and macroscale.

Additionally, we repeated the complete procedure for a comparison of rare and common plant species. Species that occurred in  $\leq 5\%$  of 80 sampling units at the microscale were defined as rare species (present in  $\leq 4$  of

80 transects), and species that occurred in at least 25% of sampling units were defined as common species (present in  $\geq 20$  of 80 transects).

#### *Statistics*

The variability of  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversity was analyzed using mixed-effect models (Pinheiro and Bates 2000), which account for nonindependent errors that may occur due to the hierarchically nested sampling design. At the microscale, we tested the effect of position in the field (edge/center), farming system (organic/conventional), and region (Soester Boerde/Leine Bergland/Lahn-Dill Bergland) as categorical factors, landscape complexity (percentage arable land) as a continuous variable, and first-order interaction on  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversity by including the field pairs as random factor. At the mesoscale, we tested the effect of position in the field (edge/center), farming system (organic/conventional), and first-order interactions by grouping the regions. In a second analysis at the mesoscale, we tested the effect of the region on diversity components by grouping the treatment factors. Models were simplified by removing nonsignificant interactions ( $P > 0.05$ , first step) and nonsignificant factors (second step). Nonsignificant factors that figured in significant interactions were not removed (Crawley 2002). Statistical analysis was carried out using R (R Development Core Team 2004). Percentage values of arable land were arcsine square-root transformed (Sokal and Rohlf 1995).

#### *Pre-analyses*

Spatial autocorrelation in species composition was tested in a pre-analysis using the Mantel test (Legendre and Legendre 1998) to relate the floristic similarity between sites to geographic distance between sites. The complement of the Jaccard index (Southwood and Henderson 2000) was used as a measure of floristic distance. Mantel tests (based on Spearman correlations, 1000 permutations) were performed for all sites in three regions and for each region separately, but no spatial autocorrelation effect was found (for all sites,  $P = 0.431$ ,  $R = 0.01$ ,  $N = 40$ ; for Soester Boerde,  $P = 0.239$ ,  $R = 0.07$ ,  $N = 14$ ; for Leine Bergland,  $P = 0.871$ ,  $R = -0.13$ ,  $N = 12$ ; and for Lahn-Dill Bergland,  $P = 0.653$ ,  $R = -0.08$ ,  $N = 14$ ).

As local conditions are often considered to influence plant species richness, a multiple regression model (stepwise forward selection) was used to test the effects of local soil chemistry (total nitrogen, organic carbon, C:N ratio, and pH value), geographical coordinates  $x$  and  $y$ , including the seven terms of a cubic trend surface ( $x^2$ ,  $xy$ ,  $y^2$ ,  $x^3$ ,  $x^2y$ ,  $xy^2$ ,  $y^3$ ; Borcard et al. 1992), and elevation on species richness of arable weeds. No factor entered the model ( $P > 0.2$ ,  $R = 0.18$ ,  $N = 40$ ), indicating neither an association between soil chemistry and patterns of plant species richness, nor a predictable spatial pattern of species richness.

Adequacy of sampling effort was validated by calculating species accumulation curves and the In-

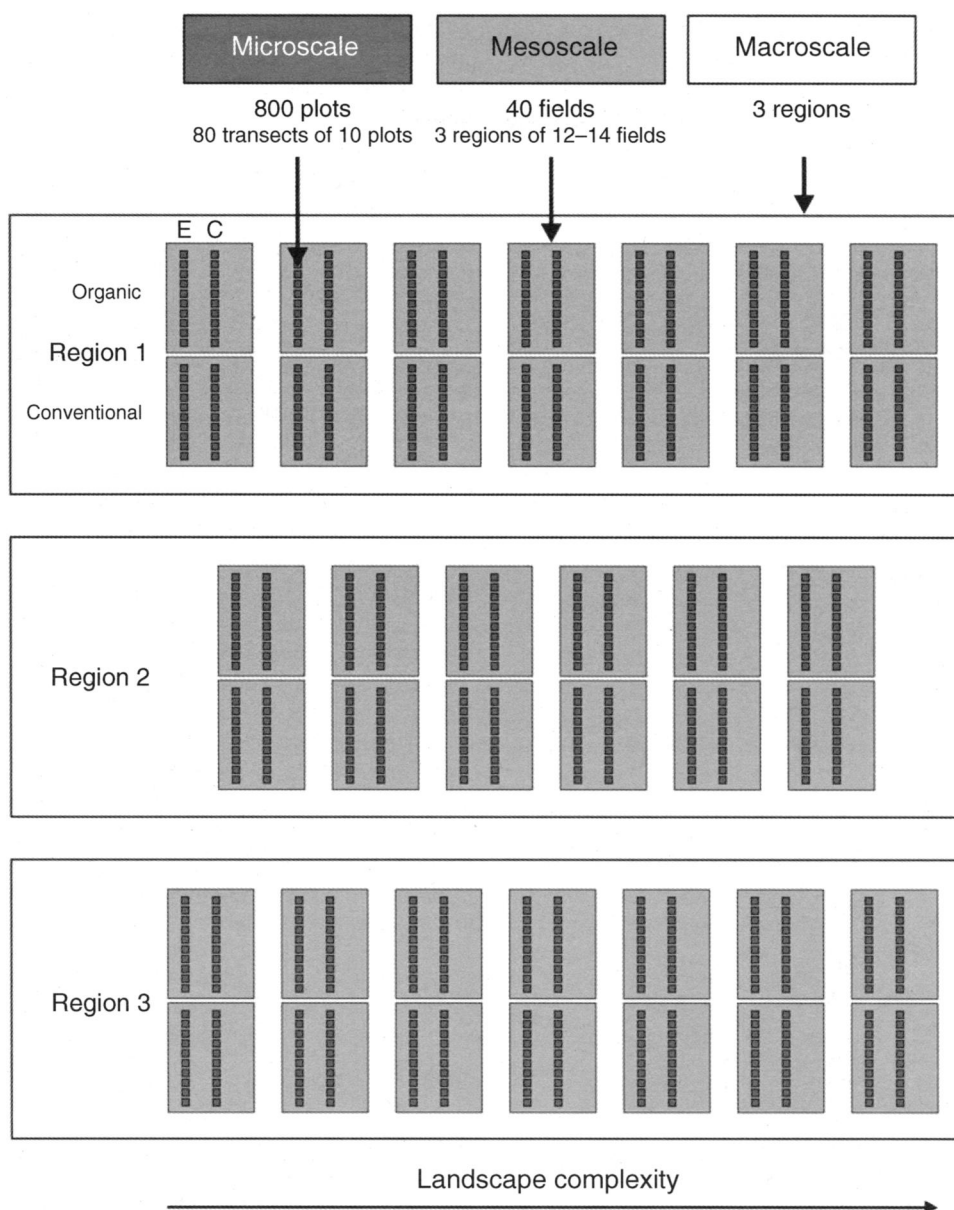


FIG. 2. Hierarchical sampling design used to record plant species at three spatial scales: 800 plots within 80 transects (40 edge transects [E] + 40 center transects [C]) were nested within 40 fields, and 40 fields (20 organic + 20 conventional) were nested within three regions. The arrow at the bottom indicates the gradient in landscape complexity surrounding the fields. Regions are: 1, Soester Boerde; 2, Leine Bergland; 3, Lahn-Dill Bergland.

cidence-based Coverage Estimator (ICE) using EstimateS, Version 5 (Colwell 1997) with 500 randomizations. The degree of species saturation was indicated by the percentage of observed species relative to the estimated species richness. We used sampling units at the microscale (i.e., pooled transect plots) to avoid pseudo-replication. The degree of species saturation was 91.8% for all samples, 86.1% for field edges in organic fields, 83.5% for centers in organic fields, 83.4% for edges in conventional fields, and 78.2% for centers in conven-

tional fields. These results indicated that sample size and sampling effort were sufficient.

## RESULTS

### *Additive partitioning of arable weed species*

In total, 110 plant species from 28 families were recorded, of which 89 were herbaceous and 21 were graminaceous species (for species list see Appendix). The  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversities were higher in organic than in conventional fields and higher in field edges than in field

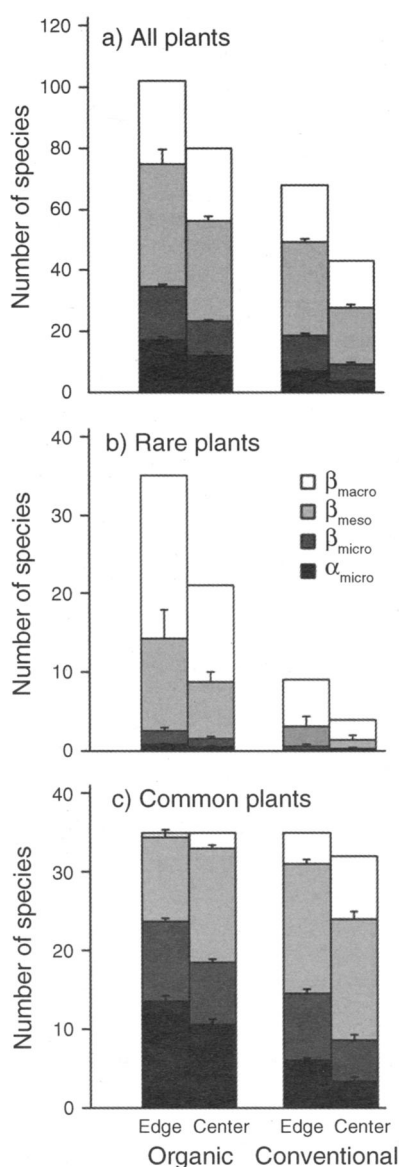


FIG. 3. Mean  $\alpha$ - and  $\beta$ -diversity components ( $\pm$ SE) of (a) all, (b) rare, and (c) common plant species at three spatial scales (micro-, meso-, and macroscale) in the edges and centers of organic and conventional fields. See also Table 1.

centers at all three spatial scales (micro-, meso-, and macroscale; Fig. 3a). The contribution of each treatment factor to the total observed species richness of 110 species varied considerably (see  $\gamma$ -diversity at the macroscale; Table 1). Of the total observed species richness, 93% was found in the edges of organic fields, 73% in the centers of organic fields, 62% in the edges of conventional fields, and only 39% in the centers of conventional fields. Thereby,  $\beta$ -diversity among organic fields at the meso and macroscale made the greatest contribution to the observed overall species richness (Table 1). The variability of diversity components was mainly explained by the farming system and the position

in the field (Tables 2 and 3). In addition, at the microscale,  $\beta$ -diversity increased with increasing landscape complexity (i.e., decreasing percentage of arable land in the surrounding landscape). At the mesoscale,  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversity differed between regions, being highest in the Lahn-Dill Bergland and decreasing to Leine Bergland and Soester Boerde (all  $P$  values  $< 0.01$ ).

#### Additive partitioning of rare and common species

Forty-three species (35 herbs and 8 grasses) were rare. Differences between organic and conventional fields were markedly larger for rare species compared with all species combined (Fig. 3b vs. 3a). The contribution of each treatment factor to total rare species richness was 81% in organic fields at the edge, 49% in organic fields in the center; 21% in conventional fields at the edge; and only 9% in conventional fields in the center. Total richness of rare species was mainly explained by  $\beta$ -diversity among organic fields at the meso and macroscale (Table 1). At all spatial scales, diversity components of rare species were higher in organic than in conventional fields (Tables 2 and 3, Fig. 3b). At the microscale,  $\beta$ - and  $\gamma$ -diversity of rare species were also higher at the field edge than in the field center.

Thirty-five species (30 herbs and 5 grasses) were common. Patterns of diversity components of common species varied strongly compared with all or rare species (Fig. 3c vs. 3a and b). The relative contribution to total common species richness was 100% in organic fields (both center and edge), as well as in conventional fields at the edge, and 92% in conventional fields in the center.

TABLE 1. Relative contribution (%) of  $\alpha$ -diversity at the microscale,  $\beta$ -diversity at the micro-, meso-, and macroscale, and  $\gamma$ -diversity at the macroscale to total observed species richness of all 110 plant species, 43 rare species, and 35 common species in the edges and centers of organic and conventional fields.

Diversity	Organic		Conventional	
	Edge	Center	Edge	Center
<b>All species</b>				
$\alpha_{\text{micro}}$	15.5	11.0	6.4	3.2
+ $\beta_{\text{micro}}$	15.8	10.1	10.5	5.2
+ $\beta_{\text{meso}}$	36.6	30.1	27.9	16.8
+ $\beta_{\text{macro}}$	24.8	21.5	17.0	13.9
= $\gamma_{\text{macro}}$	92.7	72.7	61.8	39.1
<b>Rare species</b>				
$\alpha_{\text{micro}}$	1.8	1.2	0.2	0.2
+ $\beta_{\text{micro}}$	4.2	2.5	1.2	0.5
+ $\beta_{\text{meso}}$	27.0	16.5	5.8	2.6
+ $\beta_{\text{macro}}$	48.4	28.6	13.7	6.0
= $\gamma_{\text{macro}}$	81.4	48.8	20.9	9.3
<b>Common species</b>				
$\alpha_{\text{micro}}$	38.6	30.0	17.1	9.7
+ $\beta_{\text{micro}}$	29.1	22.9	24.3	14.9
+ $\beta_{\text{meso}}$	30.3	41.4	47.1	44.0
+ $\beta_{\text{macro}}$	2.0	5.7	11.4	22.8
= $\gamma_{\text{macro}}$	100.0	100.00	100.0	91.4

Note: See Fig. 3.

TABLE 2. *F* values and level of significance of mixed-effect models testing the effects of position in the field (edge vs. center), farming system (organic vs. conventional), region (Soester Boerde/Leine Bergland/Lahn-Dill Bergland, Germany), and landscape complexity (percentage of arable land) for  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversity of plant species at the microscale ( $n = 80$ ).

Source of variation	$\alpha$		$\beta$		$\gamma$	
	df	<i>F</i>	df	<i>F</i>	df	<i>F</i>
All species						
Edge vs. center	1, 58	31.6***	1, 57	80.2***	1, 58	65.9***
Organic vs. conventional	1, 58	156.0***	1, 57	67.5***	1, 58	139.7***
Region		NS		NS		NS
Arable land (%)		NS	1, 57	7.6**		NS
Rare species						
Edge vs. center		NS	1, 58	4.7*	1, 58	5.2*
Organic vs. conventional	1, 59	25.1***	1, 58	25.7***	1, 58	30.8***
Region		NS		NS		NS
Arable land (%)		NS		NS		NS
Common species						
Edge vs. center	1, 58	27.0***	1, 58	24.3***	1, 57	42.5***
Organic vs. conventional	1, 58	178.4***	1, 58	16.6***	1, 57	126.5***
Region	2, 17	4.8*		NS	2, 17	4.2*
Arable land (%)		NS		NS	1, 57	5.1*

Note: First-order interactions were not significant.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

Total richness of common species was mainly explained by diversity components at micro and mesoscale (Table 1). One important deviation from the general patterns of all and rare species is that, at the meso and macroscale,  $\beta$ -diversity of common species was higher in conventional fields than in organic fields (Table 3, Fig. 3c). The  $\beta$ -diversity at the mesoscale was highest at the edge in conventional fields and lowest at the edge of organic fields. For  $\gamma$ -diversity, an interaction showed stronger differences between edges and centers in conventional fields than in organic fields. At the microscale,  $\alpha$ - and  $\gamma$ -diversity were higher in the Lahn-Dill Bergland than in the Soester Boerde, and  $\gamma$ -diversity increased with increasing landscape complexity (i.e., decreasing percentage of arable land in the surrounding landscape). At the mesoscale,  $\alpha$ -diversity differed between regions, being highest in the Lahn-Dill Bergland and decreased

to the Leine Bergland and to the Soester Boerde ( $P < 0.05$ ).

#### DISCUSSION

Analyses of diversity patterns of arable weeds in field edges and centers of organic and conventional fields at multiple spatial scales (plots, fields, regions) showed that organic farming and field edges contributed most to  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversity. Our finding that 93% of the total observed species richness of 110 plant species were found in the edges of organic fields, 73% in the centers of organic fields, 62% in the edges of conventional fields, and only 39% in the centers of conventional fields, underlines the importance of organic farming and field edges for regional diversity. However, in both farming systems, the relative contribution to the total observed species richness was mainly determined by  $\beta$ -diversity at

TABLE 3. *F* values and level of significance of mixed-effect models testing the effects of position in the field (edge vs. center), farming system (organic vs. conventional), and first-order interaction for  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversity of plant species at the mesoscale ( $n = 12$ ).

Source of variation	$\alpha$		$\beta$		$\gamma$	
	df	<i>F</i>	df	<i>F</i>	df	<i>F</i>
All species						
Edge vs. center	1, 7	245.1***	1, 7	26.0**	1, 7	106.3***
Organic vs. conventional	1, 7	514.7***	1, 7	40.2***	1, 7	193.8***
Rare species						
Edge vs. center		NS		NS		NS
Organic vs. conventional	1, 8	24.8**	1, 8	17.4**	1, 8	18.6**
Common species						
Edge vs. center	1, 7	88.4***	1, 6	3.2	1, 6	20.2**
Organic vs. conventional	1, 7	261.0***	1, 6	19.3**	1, 6	44.2***
Edge/center $\times$ organic/conventional		NS	1, 6	10.7*	1, 6	9.3*

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .



the mesoscale (fields) and macroscale (regions), indicating considerable differences in species composition among fields and regions.

#### *Determinants of $\alpha$ -, $\beta$ -, and $\gamma$ -diversity*

At the microscale, differences between organic and conventional fields were most pronounced;  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversity were more than twice as high in organic fields. The lack of herbicides and mineral fertilizers in organic farming, as well as the greater variability in crop rotations including spring cropping is known to favor species rich plant communities (Moreby et al. 1994, Hald 1999a, b). Higher plant diversity in field edges compared to field centers supports the findings of Marshall (1989) and Wilson and Aebischer (1995), and may be related to a range of direct and indirect effects (Murcia 1995). First, a reduced intensity of herbicide application or mechanical weed control associated with reduced nitrogen fertilization and increased light supply due to lower crop cover may allow more typical herbaceous arable weed species to establish from the seed bank and survive at the field edge (Kleijn and Vandervoort 1997). In our study, strong edge-center differences in frequency of occurrence were observed for *Euphorbia platyphyllos* L., *Geranium dissectum* L., and *Arabidopsis thaliana* (L.) Heynh. in both farming systems and for *Aphanes arvensis* L., *Galeopsis tetrahit* L., and *Veronica persica* Poir. in conventional fields (see Appendix). Second, neighborhood effects due to immigrating species from adjacent field margins might have lead to an increase in  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversity at the field edge. Marshall and Arnold (1995) found that field margins and crop fields had 25% of species in common. In our study, a major proportion of plant species that occurred predominately at the field edge were ruderal or grassland species like the grasses *Dactylis glomerata* L. s. str., *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl and C. Presl, *Poa pratensis* L. s. str., and the herbs *Plantago major* L. s. str., *Potentilla anserina* L., and *Sisymbrium officinale* (L.) Scop. (see Appendix). It is likely that these species originate from the field boundary (Marshall 1989). Consequently, the increased diversity at field edges in organic and conventional fields might result from an ecotone effect harboring an intermixed subset of the adjacent communities (Forman 1995). Increased diversity at the field edge was found in both farming systems, contradicting the results of Hald (1999a), who found a decrease in the number of plant species from the crop margin to the mid-field in conventional but not in organic fields. In addition,  $\beta$ -diversity of all species and  $\gamma$ -diversity of common species increased with increasing landscape complexity (i.e., decreasing percentage of arable land in the surrounding landscape). We assume that local abiotic conditions within fields in complex landscapes are more variable than in simple landscapes with large, homogeneous fields, promoting heterogeneity in plant communities. Furthermore, complex landscapes (characterized by high habitat type diversity and

high perimeter:area ratio; Gabriel et al. 2005) provide many disturbed habitats for annual and ruderal plant populations like road verges, fallow land, and dry grassland, which may enhance the probability of invasion from the surrounding landscape to the local field (analogous to the mass effect of Shmida and Wilson, 1985). However, effects of landscape complexity on plant species richness in arable fields were weaker than the effects of farming system and position in the field.

At the mesoscale,  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversity differed between regions and were highest in the Lahn-Dill Bergland. Of the three regions, Lahn-Dill Bergland had the largest gradient in landscape complexity (17–85% arable land), the highest amplitude in elevation (172–496 m), and the largest area ( $\sim 1000$  km<sup>2</sup>).

#### *$\beta$ -diversity at different spatial scales*

Comparing  $\beta$ -diversity at different spatial scales revealed that total observed species richness was mainly explained by  $\beta$ -diversity at the mesoscale (up to 37%) and the macroscale (up to 25%), and to a lesser extent by  $\beta$ -diversity at the microscale (up to 16%).

The  $\beta$ -diversity at each scale was the result of environmental heterogeneity in space, time, and/or resources and niche differences among species (Loreau 2000). Environmental heterogeneity may occur from small scales up to large scales. For example, plots (within fields) may vary in soil properties, surface topography, and microclimate. Fields and regions may vary even more in soil type, soil pH, water regime, elevation, and/or climate, and they differ in landscape context, including various habitat and land use types and different species pools. It is suggested that these factors influence local assemblages and composition of arable weed communities and increase heterogeneity in plant communities among plots, fields, and regions, i.e.,  $\beta$ -diversity (Loreau 2000, Booth and Swanton 2002, Walter et al. 2002, Kneitel and Chase 2004, Lososová et al. 2004, Pyšek et al. 2005).

Beta-diversity of plant communities may be lowered by dispersal between spatial units that acts as a homogenizing force (Shmida and Wilson 1985, Loreau 2000). Thereby, dispersal processes operate at different spatial scales (Marshall and Hopkins 1990). At the microscale, short-distance dispersal causes the majority of seeds to be deposited  $< 5$  m away from a parent plant, either by seed rain (Harper 1977, Cousens and Mortimer 1995, Bischoff 2005) or by post-dispersal events such as soil cultivation (Rew and Cussans 1997, Marshall and Brain 1999). At the meso and macroscale, less frequent events such as long-distance dispersal by machinery, animals (mainly vertebrates), and wind may occur (Harper 1977, Marshall and Hopkins 1990, Cousens and Mortimer 1995). Dispersal is irrefutably important for population persistence (Nathan and Muller-Landau 2000, Bullock et al. 2002), but in our study, dispersal obviously did not have a homogenizing effect. Dispersal

among fields and regions may have played a minor role relative to environmental factors, as field pairs were widely distributed within a region and plant communities were not spatially autocorrelated, i.e., the similarity of plant communities did not decrease with increasing distance. Thus, the interplay between environmental heterogeneity and dispersal processes influencing local and regional plant community patterns has to be considered.

#### *Rare and common species*

The spatial scale at which  $\beta$ -diversity made the greatest contribution to total observed species richness differed between rare and common species. Total richness of rare species was mainly explained by  $\beta$ -diversity at the meso and macroscale, whereas richness of common species was mainly explained by diversity components at the micro and mesoscale. In principle, these patterns correspond with the findings of Gering et al. (2003) from arboreal beetle diversity suggesting that rare species are encountered more frequently at the largest scale. But arable weed patterns differed between farming systems. In our study, richness of rare species was mostly explained by  $\beta$ -diversity in organic fields at the meso and macroscale, suggesting a high variability in community composition but only in organic fields. In contrast, the majority of common species were found in organic fields at the microscale, where  $\alpha$ - and  $\beta$ -diversity together explained up to 68% of the total richness of common species. However, in conventional fields,  $\alpha$ -diversity at the microscale was relatively low. Hence,  $\beta$ -diversity at the micro and mesoscale was more important, explaining up to 71% of total richness of common species.

#### *Conclusions and management implications*

Agriculture, occupying ~40% of total land surface, is one of the predominating land use forms worldwide (Ramankutty and Foley 1999). Sustainability and maintenance of biodiversity in these systems is therefore of great importance (Tilman et al. 2002, Foley et al. 2005). We reemphasize that organic fields have significantly higher plant diversity than conventional fields, a finding that is in accordance with previous studies. Organic farming is therefore supported by current agri-environment schemes and may be an example of reconciliation ecology (Rosenzweig 2003a, b) and a conservation tool for diversification of crop fields. However, current agri-environment schemes are almost exclusively locally oriented by tailoring at the field and farm scale. By contrast, our findings make clear that (1)  $\beta$ -diversity among fields and regions explained most of the total observed species richness in both farming systems, but (2) organic farming, at large spatial scales, also contributes more to regional diversity than conventional farming. Agri-environment schemes should, therefore, consider the large-scale contribution of  $\beta$ -diversity to regional species richness rather than focus

entirely on the local field or farm scale. To optimize limited budgets in conservation management, policy-makers at regional level of government (i.e., the administrative agencies of counties, districts, and/or states) should be advised to select conservation areas of maximum dissimilarity in abiotic and biotic site conditions using digital data and geographic information systems, thereby taking advantage of the existing environmental heterogeneity among fields and regions.

#### ACKNOWLEDGMENTS

We thank Yann Clough, Andrea Holzschuh, Stephanie Domptail, and Tobias Purtauf for study site selection and surveying and mapping the landscapes; and Katja Poveda, Sabine Eber, and Joachim Saborowski for statistical advice. Many thanks to Jens Dauber, Jon Marshall, Erica Fleishman, Tobias Purtauf, Jaan Liira, David Kleijn, Jochen Krauss, and Jason Tylianakis for helpful comments and discussions on this manuscript. D. Gabriel was supported by the Niedersächsische Graduiertenförderung and I. Roschewitz by the German Science Foundation (DFG). The study was part of the EU project QLK5-CT-2002-01495 "EASY" (Evaluating current European agri-environment schemes to quantify and improve nature conservation efforts in agricultural landscapes).

#### LITERATURE CITED

- Albrecht, H. 1995. Changes in the arable weed flora of Germany during the last five decades. Pages 41–48 in *Proceedings of the 9th European Weed Research Society Symposium, Challenges for Weed Science in a Changing Europe*. Budapest, Hungary.
- Allan, J. D. 1975. Components of diversity. *Oecologia* **18**:359–367.
- Andersson, T. N., and P. Milberg. 1998. Weed flora and the relative importance of site, crop, crop rotation, and nitrogen. *Weed Science* **46**:30–38.
- Andreasen, C., H. Stryhn, and J. C. Streibig. 1996. Decline of the flora in Danish arable fields. *Journal of Applied Ecology* **33**:619–626.
- Bengtsson, J., J. Ahnström, and A. C. Weibull. 2005. The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *Journal of Applied Ecology* **42**:261–269.
- Benton, T. G., J. A. Vickery, and J. D. Wilson. 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution* **4**:182–188.
- Bischoff, A. 2005. Analysis of weed dispersal to predict changes of re-colonisation. *Agriculture, Ecosystems and Environment* **106**:377–387.
- Booth, B. D., and C. J. Swanton. 2002. Assembly theory applied to weed communities. *Weed Science* **50**:2–13.
- Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. *Ecology* **73**:1045–1055.
- Bullock, J. M., I. L. Moy, R. F. Pywell, S. J. Coulson, A. M. Nolan, and H. Caswell. 2002. Plant dispersal and colonization processes at local and landscape scales. Pages 279–302 in J. M. Bullock, R. E. Kenward, and R. S. Hails, editors. *Dispersal ecology*. Blackwell Science, Oxford, UK.
- Colwell, R. K. 1997. EstimateS: Statistical estimation of species richness and shared species from samples. Version 5. (<http://viceroy.eeb.uconn.edu/EstimateS>)
- Cousens, R., and M. Mortimer. 1995. *Dynamics of weed populations*. Cambridge University Press, Cambridge, UK.
- Crawley, M. J. 2002. *Statistical computing. An introduction to data analysis using S-Plus*. John Wiley and Sons, Chichester, UK.

- Dale, M. R. T., A. G. Thomas, and E. A. John. 1992. Environmental factors including management practices as correlates of weed community composition in spring seeded crops. *Canadian Journal of Botany* **70**:1931–1939.
- Eggers, T. 1987. Environmental impact of chemical weed control in arable fields in the Federal Republic of Germany. Pages 267–275 in *Proceedings of the Brighton Crop Protection Conference, Weeds 1987*. Lavenham Press, Lavenham, UK.
- ESRI. 1999. ArcView 3.2. ESRI Geoinformatik, Hannover, Germany.
- Firbank, L. G. 1988. Biological flora of the British Isles: *Agrostemma githago* L. *Journal of Ecology* **76**:1232–1246.
- Fleishman, E., C. J. Betrus, and R. B. Blair. 2003. Effects of spatial scale and taxonomic group on partitioning of butterfly and bird diversity in the Great Basin, USA. *Landscape Ecology* **18**:675–685.
- Foley, J. A., et al. 2005. Global consequences of land use. *Science* **309**:570–574.
- Forman, R. T. T. 1995. *Land mosaics: the ecology of landscapes and regions*. Cambridge University Press, Cambridge, UK.
- Fournier, E., and M. Loreau. 2001. Respective roles of recent hedges and forest patch remnants in the maintenance of ground-beetle (Coleoptera: Carabidae) diversity in an agricultural landscape. *Landscape Ecology* **16**:17–32.
- Gabriel, D., C. Thies, and T. Tschamtkke. 2005. Local diversity of arable weeds increases with landscape complexity. *Perspectives in Plant Ecology, Evolution and Systematics* **7**: 85–93.
- Gering, J. C., T. O. Crist, and J. A. Veech. 2003. Additive partitioning of species diversity across multiple spatial scales: implications for regional conservation of biodiversity. *Conservation Biology* **17**:488–499.
- Hald, A. B. 1999a. Weed vegetation (wild flora) of long established organic versus conventional cereal fields in Denmark. *Annals of Applied Biology* **134**:307–314.
- Hald, A. B. 1999b. The impact of changing the season in which cereals are sown on the diversity of the weed flora in rotational fields in Denmark. *Journal of Applied Ecology* **36**: 24–32.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, London, UK.
- Hofmeister, H., and E. Garve. 1998. *Lebensraum Acker*. Second edition. Parey, Berlin, Germany.
- Hole, D. G., A. J. Perkins, J. D. Wilson, I. H. Alexander, P. V. Grice, and A. D. Evans. 2005. Does organic farming benefit biodiversity? *Biological Conservation* **122**:113–130.
- Hyvönen, T., E. Ketola, J. Salonen, H. Jalli, and J. Tianinen. 2003. Weed species diversity and community composition in cropping of spring cereals. *Agriculture, Ecosystems and Environment* **97**:131–149.
- Hyvönen, T., and J. Salonen. 2002. Weed species diversity and community composition in cropping practices at two intensity levels: a six-year experiment. *Plant Ecology* **159**:73–81.
- Kleijn, D., and W. J. Sutherland. 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology* **40**: 947–969.
- Kleijn, D., and L. A. C. Vandervoort. 1997. Conservation headlands for rare arable weeds: the effects of fertilizer application and light penetration on plant growth. *Biological Conservation* **81**:57–67.
- Kneitel, J. M., and J. M. Chase. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters* **7**:69–80.
- Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* **76**:5–13.
- Legendre, P., and L. Legendre. 1998. *Numerical ecology*. Second English Edition, Elsevier, Amsterdam, The Netherlands.
- Loreau, M. 2000. Are communities saturated? On the relationship between alpha, beta and gamma diversity. *Ecology Letters* **3**:73–76.
- Lososová, Z., M. Chytrý, S. Cimalová, Z. Kropáč, Z. Otýpková, P. Pyšek, and L. Tichý. 2004. Weed vegetation of arable land in Central Europe: gradients of diversity and species composition. *Journal of Vegetation Science* **15**:415–422.
- Marshall, E. J. P. 1989. Distribution patterns of plants associated with arable field edges. *Journal of Applied Ecology* **26**:247–257.
- Marshall, E. J. P., and G. M. Arnold. 1995. Factors affecting field weed and field margin flora on a farm in Essex, UK. *Landscape and Urban Planning* **31**:205–216.
- Marshall, E. J. P., and P. Brain. 1999. The horizontal movement of seeds in arable soil by different soil cultivation methods. *Journal of Applied Ecology* **36**:443–454.
- Marshall, E. J. P., V. K. Brown, N. D. Boatman, P. J. W. Lutman, G. R. Squire, and L. K. Ward. 2003. The role of weeds in supporting biological diversity within crop fields. *Weed Research* **43**:77–89.
- Marshall, E. J. P., and A. Hopkins. 1990. Plant species composition and dispersal in agricultural land. Pages 98–116 in R. G. H. Bunce and D. C. Howard, editors. *Species dispersal in agricultural habitats*. Belhaven Press, London, UK.
- McCloskey, M., L. G. Firbank, A. R. Watkinson, and D. J. Webb. 1996. The dynamics of experimental arable weed communities under different management practices. *Journal of Vegetation Science* **7**:799–808.
- McLaughlin, A., and P. Mineau. 1995. The impact of agricultural practices on biodiversity. *Agriculture, Ecosystems and Environment* **55**:201–212.
- Menalled, F. D., K. L. Gross, and M. Hammond. 2001. Weed aboveground and seedbank community responses to agricultural management systems. *Ecological Applications* **11**:1586–1601.
- Moreby, S. J., N. J. Aebischer, S. E. Southway, and N. W. Sotherton. 1994. A comparison of the flora and arthropod fauna of organically and conventionally grown winter-wheat in Southern England. *Annals of Applied Biology* **125**:13–27.
- Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* **10**: 58–62.
- Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* **15**:278–285.
- Pinheiro, J. C., and D. M. Bates. 2000. *Mixed-effect models in S and S-plus*. Springer-Verlag New York, New York, USA.
- Pyšek, P., V. Jarošík, Z. Kropáč, M. Chytrý, J. Wild, and L. Tichý. 2005. Effects of abiotic factors on species richness and cover in Central European weed communities. *Agriculture, Ecosystems and Environment* **109**:1–8.
- Pyšek, P., and J. Lepš. 1991. Response of a weed community to nitrogen-fertilization: a multivariate-analysis. *Journal of Vegetation Science* **2**:237–244.
- R Development Core Team. 2004. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. (<http://www.R-project.org>)
- Ramankutty, N., and J. A. Foley. 1999. Estimating historical changes in global land cover: croplands from 1700 to 1992. *Global Biogeochemical Cycles* **13**:997–1027.
- Rew, L. J., and G. W. Cussans. 1997. Horizontal movement of seeds following tine and plough cultivation: implications for spatial dynamics of weed infestations. *Weed Research* **37**: 247–256.
- Ricklefs, R. E. 1987. Community diversity: relative roles of local, regional processes. *Science* **235**:167–171.
- Robinson, R. A., and W. Sutherland. 2002. Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology* **39**:157–176.

- Roschewitz, I., D. Gabriel, T. Tschardt, and C. Thies. 2005. The effects of landscape complexity on arable weed species diversity in organic and conventional farming. *Journal of Applied Ecology* **42**:873–882.
- Rosenzweig, M. L. 2003a. Reconciliation ecology and the future of species diversity. *Oryx* **37**:194–205.
- Rosenzweig, M. L. 2003b. Win-win ecology: how the earth's species can survive in the midst of human enterprise. Oxford University Press, New York, New York, USA.
- Shmida, A., and M. V. Wilson. 1985. Biological determinants of species diversity. *Journal of Biogeography* **12**:1–20.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry*. Freeman, New York, New York, USA.
- Sotherton, N. W. 1998. Land use changes and the decline of farmland wildlife: an appraisal of the set-aside approach. *Biological Conservation* **83**:259–268.
- Southwood, T. R. E., and P. A. Henderson. 2000. *Ecological methods*. Blackwell Science, Oxford, UK.
- Stoate, C., N. D. Boatman, R. J. Borralho, C. Rio Carvalho, G. R. de Snoo, and P. Eden. 2001. Ecological impacts of arable intensification in Europe. *Journal of Environmental Management* **63**:337–365.
- Summerville, K. S., M. J. Boulware, J. A. Veech, and T. O. Crist. 2003. Spatial variation in species diversity and composition of forest Lepidoptera in eastern deciduous forests of North America. *Conservation Biology* **17**:1045–1057.
- Sutcliffe, O. L., and Q. O. N. Kay. 2000. Changes in the arable flora of central southern England since the 1960s. *Biological Conservation* **93**:1–8.
- Tilman, D., K. G. Cassman, P. A. Matson, R. Naylor, and S. Polasky. 2002. Agricultural sustainability and intensive production practices. *Nature* **418**:671–677.
- van Elsen, T. 2000. Species diversity as a task for organic agriculture in Europe. *Agriculture, Ecosystems and Environment* **77**:101–109.
- Veech, J. A., K. S. Summerville, T. O. Crist, and J. C. Gering. 2002. The additive partitioning of species diversity: recent revival of an old idea. *Oikos* **99**:3–9.
- Wagner, H. H., O. Wildi, and K. C. Ewald. 2000. Additive partitioning of plant species diversity in an agricultural mosaic landscape. *Landscape Ecology* **15**:219–227.
- Walter, A. M., S. Christensen, and S. E. Simmelsgaard. 2002. Spatial correlation between species densities and soil properties. *Weed Research* **42**:26–38.
- Wilson, P. J., and N. J. Aebischer. 1995. The distribution of dicotyledonous weeds in relation to distance from the field edge. *Journal of Applied Ecology* **32**:295–310.
- Zobel, M. 1997. The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology and Evolution* **12**:266–269.

#### APPENDIX

An overview of species and their frequency of occurrence in pooled transects and centers of organic and conventional fields (*Ecological Archives* A016-068-A1).