

Alpha and beta diversity of arthropods and plants in organically and conventionally managed wheat fields

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Summary

1. Most studies in applied ecology use measures of α -diversity measures, i.e. the mean diversity on a site, to compare biodiversity effects of different management schemes. The total or α -diversity within a region, however, need not be correlated with the mean α -diversity within any site of the region. Thus, analyses of α -diversity alone may misrepresent the contributions of other diversity components (β) to total diversity (γ).
2. We apply a biodiversity-partitioning approach to species richness from a comparison between paired organic and conventional wheat fields in 21 sites from three regions in Germany, where we recorded plants, bees, carabids, staphylinids and spiders in the centre and edge of the fields.
3. Relative values of α - and β -diversity depended on taxon. Both between-site and between-region β -diversity were very high (in total 60–85%). α -Diversity and between-site β -diversity was larger on the edge than in the centre of fields for all taxa.
4. α -Diversity, between-site β -diversity of plants and bees and between-region β -diversity of bees were higher in organic than in conventional fields, providing local as well as larger-scale species richness benefits. α -Diversity did not differ between management types for the epigeic arthropods. Lower between-site β -diversity was found for spiders in organic fields than in conventional fields, resulting in higher total species richness in conventionally managed wheat.
5. Similarity in composition of landscapes surrounding the study fields was correlated with similarity in species composition for epigeic arthropods in conventional fields. For this group of organisms the variability of landscapes in the sample contributed to increasing β -diversity.
6. *Synthesis and applications.* β -Diversity accounts for the major part of species richness in agro-ecosystems. Implementing an agri-environment scheme such as organic agriculture may result in either an additional increase of total diversity, as could be shown for plants and bees, or in a decrease in total diversity as was the case for the spiders. Therefore, β -diversity needs to be included in the evaluation of different management schemes for conservation. For plant and bees it is recommended to implement agri-environment schemes in contrasting landscapes and in different regions to maximize total species richness benefits.

Key-words: agro-ecosystems, arthropods, diversity, landscape context, organic farming

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Introduction

The decline of biodiversity in agricultural landscapes is of increasing concern (Matson *et al.* 1997; Krebs *et al.* 1999), and alternative management forms such as conversion to organic farming are often considered to be a step towards reversing this trend (e.g. Soil Association 2000). However, studies assessing the effectiveness of organic agriculture in conserving biodiversity have been plagued by methodological shortcomings such as lack of replication (Bengtsson, Ahnström & Weibull 2005; Hole *et al.* 2005). In addition, even when they include measures of landscape composition as an additional explanatory variable, these studies address plot scale diversity exclusively. Ecologists are aware, however, that plot scale diversity is but one component of total diversity (Whittaker 1977; Veech *et al.* 2002; Legendre, Borcard & Peres-Neto 2005). In an additive partitioning approach of biodiversity, diversity components consist of: (1) α -diversity, which is the average diversity within a plot, (2) γ -diversity, which is the total diversity across plots and (3) β -diversity, the difference between γ (total) diversity and α (local), which is a measure of the variation of species composition between plots. High β -diversity values indicate large differences between plots in the identity of species encountered.

The partitioning of diversity is of interest for several reasons. It is viewed as a useful tool for analysing the spatial patterns of diversity and has been used recently to reveal or reformulate macro-ecological diversity patterns (Blackburn & Gaston 1996; Novotny & Weiblen 2005) and to study the effect of spatial grain on the measurement of biodiversity (Arita & Rodriguez 2002; Koleff, Gaston & Lennon 2003). From a more applied perspective, Gering, Crist & Veech (2003) have pointed out that knowledge about the spatial components of diversity of a community of interest may help in selecting the appropriate spatial scale for species conservation. We suggest that it is important to use spatial partitioning of diversity to compare species richness on farmland with different management schemes because processes determining total species richness operate at several spatial scales, and cannot be captured with α -diversity analyses alone (Weiher & Howe 2003). For instance, in hypothetical scenarios, even though α -diversity may be higher on average in sites with a particular management scheme compared to the control, a reduced heterogeneity in habitat characteristics between sites due to the management schemes may, in fact, decrease total diversity within the pool of sites (Fig. 1a), which may be counterproductive in attaining higher levels of species richness. Such effects have been found by Tylianakis, Klein & Tscharrntke (2006) through temporal partitioning of diversity data. On the other hand, if heterogeneity between sites is increased by management, then it may well be that an increase in β -diversity complements the increase in α -diversity, leading to hidden benefits at larger scales (Fig. 1b). When α -diversity

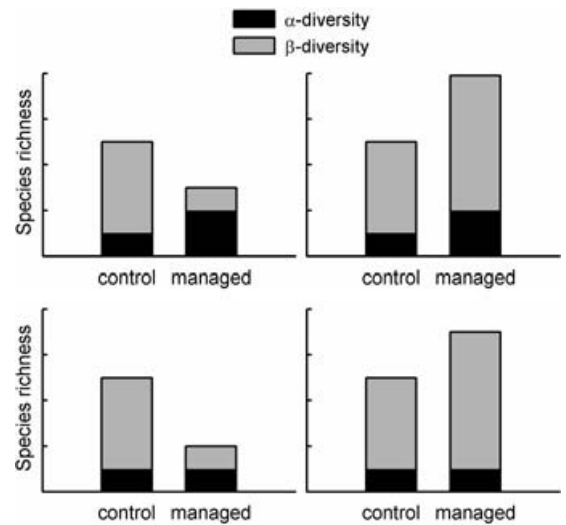


Fig. 1. Four alternative, hypothetical scenarios illustrating the contrasting effects a management scheme may have on species richness at the field scale (α -diversity) and the between-field scale (β -diversity). (a) α increases, but β decreases; (b) α increases, β increases; (c) α unchanged, β decreases; (d) α unchanged, β increases. Note that in (b) and (d), management scheme increases total species richness.

does not differ between managed sites and the control, β -diversity may still lead to higher or lower γ diversity (Fig. 1c,d).

In this study we apply diversity partitioning to a data set resulting from a biodiversity survey conducted in organic and conventional winter wheat fields in three regions of Germany. The main focus of the study, conducted in the framework of the EU-project EASY ('Evaluating current European agri-environment schemes to quantify and improve nature conservation efforts in agricultural landscapes', Kleijn *et al.* 2006), was to reveal whether organic agriculture increases species richness, and if so which species groups profit from the organic management. German organic farmers receive subsidies through the European agri-environment schemes (Grafen & Schramek 2000) which span a whole range of on-farm measures aimed at reducing the negative ecological side-effects of agricultural activity. We sampled 42 fields in 21 sites in three different regions for vascular plants, bees (Hymenoptera: Apiformes), carabid beetles (Coleoptera: Carabidae), staphylinid beetles (Coleoptera: Staphylinidae) and spiders (Aranea). The samples were taken in the centre and at the edge of all fields, as management effects can be expected to differ between the edge and centre of the arable crop.

We used the additive diversity partitioning method (Allan 1975; Lande 1996), such that $\beta = \gamma - \alpha$. This measure of β -diversity is intimately related to Whittaker's multiplicative β (Kiflawi & Spencer 2004). The additive partitioning method is more straightforward and allows direct comparison between α -, β - and γ -diversity, as these components are all expressed in the

same unit. It thus allows the partitioning on an unlimited number of scales (Wagner, Wildi & Ewald 2000). In this study we partitioned the diversity in α -diversity, between-site β -diversity (β_s) and between-region β -diversity (β_R) for each combination of management type and location in field (edge or centre). The results of the diversity partitioning are expected to depend on the scale chosen for the study design, such as the distances between regions and between sites in the different regions (Loreau 2000) as well as sampling efficiency, but this will not affect the validity of the comparisons between habitat types. The research questions we addressed in this study are: (1) how do α , β_s and β_R components of species richness differ between organic and conventional fields, (2) do these components differ between the edge and centre of wheat fields, (3) how does the partitioning of diversity differ between taxa and (4) does the variability in landscape composition and/or local habitat factors affect β -diversity? The effectiveness of organic management in increasing species richness of plants and arthropods, and whether the β -diversity results alter the conclusions one may draw with conventional α -diversity analyses are discussed.

Methods

STUDY AREA

We surveyed 42 paired organic and conventional wheat fields in 21 sites in three regions of Germany: seven pairs in the Soester Boerde, seven pairs in the Leine Bergland and seven pairs in the Lahn-Dill Bergland. The Soester Boerde (51°35'00"N; 008°07'00"E) is a rather flat area of Nordrhein-Westfalen known for its very fertile silt-like loess soil and intensive agriculture centred mainly on arable crops such as wheat. The Leine Bergland (51°32'00"N; 009°56'00"E) in Niedersachsen is dominated by arable crops in the flatter parts situated in the valleys, while in the more hilly parts land-use is more diversified. The Lahn-Dill Bergland in Hessen (50°49'00"N; 008°46'00"E) spans a range from homogeneous, arable-dominated to heterogeneous, often afforested areas. Organic and conventional fields within a pair were never more than 600 m apart, and were chosen to be as similar as possible with respect to size and soil conditions. The size of the fields ranged from 1 to 12.5 ha. Field-pairs within regions are between 25 km and 3 km from each other, while the distance between three regions is about 150 km.

ORGANIC FARMING

The organic regulations tend to be specific to the local organic producers associations but are all based on those issued by IFOAM (International Federation of Organic Agriculture Movements). Organic crop production guidelines have been integrated within the EU

legislation since 1991: the regulation (EEC) no. 2092/91 provides a set of minimum production and processing rules which must be followed in order to label a product as 'organic', and specifies an inspection regime which is obligatory for all operators which are involved in placing organic products on the market. Certified organic farmers are not allowed to use synthetic fertilizers or any pesticides, and have to rely on organic manure and strategies such as incorporating 1 or 2 years of clover *Trifolium* sp. in the crop rotation to suppress weeds and increase soil fertility.

SAMPLING

Plants

At the end of May 2003, herb and grass species in each field were recorded using two 95-m parallel transects. Each transect consisted of 10 plots (5 × 1 m) at intervals of 5 m. One transect followed the field edge and one was located in the field centre. One conventional field that had previously been managed organically was omitted from the plant analyses together with the organic field with which it was paired as seed bank effects were still apparent.

Bees

Bees (Apiformes) were caught by sweep-netting at four dates between May and July along 95-m long and 1-m wide transects in the field centre and the field edge for 15 min per transect and date. All bees were collected and brought to the laboratory for identification. Fields of a pair were sampled directly after one another, between 10 : 00 h and 18 : 00 h, in appropriate weather conditions (low wind speeds, temperature > 18 °C, cloud cover < 30%). The number of bee species is the total number caught within the study period.

Spiders, carabids and staphylinids

Two pitfall traps (11 cm diameter) were placed in the centre (distance from edge: 50 ± 15 m) and two at the edge (between the first and the second wheat row) of each field, and opened for three 2-week sampling periods during spring and early summer (1–15, 15–28 May; 11–26 June, ±2 days depending on the region). The distance between traps was 5–6 m. The decision of when to start trapping in each region was based on a phenological indicator: the traps were opened 1 week after the beginning of the mass flowering of *Taraxacum officinale* L. This sampling scheme was designed following Duelli (1997). The trapping fluid was ethylene glycol diluted with water (1/3 v/v) (Schmidt *et al.* 2006). Spiders and staphylinids were identified from all samples, carabids only from the first and third sampling period due to the extremely large number of individuals per sample. Samples were pooled over the season for analysis.

DATA ANALYSIS

Diversity partitioning

The total observed diversity γ_{obs} , for each management type and location in field combination, can be partitioned as:

$$\gamma_{\text{obs}} = \alpha + \beta_{\text{S}} + \beta_{\text{R}}$$

where α is the mean α -diversity per site, β_{S} is the between-site β -diversity, β_{R} the mean between-region β -diversity. These values can be obtained as follows:

$$\alpha = \frac{1}{n} \sum_{ij} \alpha_{ij}$$

$$\beta_{\text{S}} = \frac{1}{n} \sum_{ij} (\gamma_i - \alpha_{ij})$$

$$\beta_{\text{R}} = \frac{1}{N} \sum_i (\gamma_{\text{obs}} - \gamma_i)$$

where n is the number of regions ($n = 3$), i the identifier for region (i from 1 to 3), n the total number of sites (21) and j the identifier for sites within region (j from 1 to 7). For each region i , γ_i is the total regional diversity.

Statistical models and hypothesis tests for α - and β -diversity

We used a split-plot ANOVA to test the effect of management (organic vs. conventional) and location in field (edge vs. centre) on the α -, β_{S} - and β_{R} -diversity of each taxonomic species examined. Site was used as a blocking factor, as fields within pairs and locations within fields are not independent. Mean values for each 'site' in each region were used for the two way ANOVA of diversity β_{R} analysis. Non-significant interactions were removed from the models. Normality of the distribution of the raw dependent variables was confirmed using QQ-plots. Analyses were performed using R (R Development Core Team 2006).

Landscape context, local habitat characteristics and β -diversity

Whether similarity in species composition was related to similarity in landscape context was investigated by correlating Bray–Curtis similarity matrices for the species (presence/absence) with a similarity matrix for landscape metrics. The Mantel test with Pearson's product–moment correlation was used, with P -values being based on 1000 run permutation of rows and columns of the species composition matrices. Landscape metrics were: total number of patches, total edge length and percentage cover of arable land, grassland, settlements, forest and set-aside, measured in a 1000-m radius around each field. Separate analyses were conducted for all management type and location in field

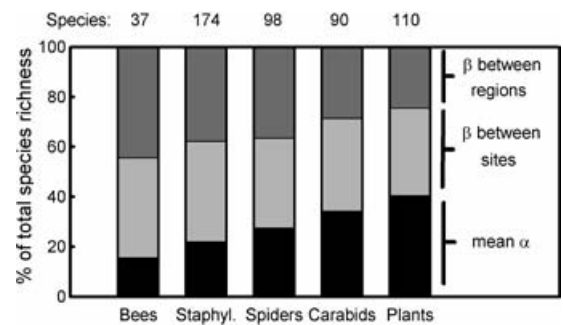


Fig. 2. Relative contributions of mean α -diversity, between-site and between-region β -diversity scales to species richness of plants and arthropods found in German wheat fields.

combinations. A similar analysis was conducted to test whether similarity in species composition could be correlated to similarity in local habitat characteristics (soil: percentage N, percentage C, pH, percentage Mg, percentage P; vegetation: percentage of bare ground, wheat cover; management: kg N fertilizer applied, number of insecticide applications, number of herbicide applications, number of comb-harrow treatments; wheat yield). Analyses were conducted using R (R Development Core Team 2006) and the *vegan* package for R (version 1.6.9; Oksanen 2005).

Results

SPATIAL PARTITIONING OF DIVERSITY IN DIFFERENT TAXA

Our samples contained 1507 bees from 37 species, 24 759 spiders from 98 species, 37 322 carabids from 90 species and 10 693 staphylinids from 174 species; 110 species of plants were recorded.

Mean α -diversity was between 18% and 40% of observed total diversity (γ_{obs}), depending on the taxon (Fig. 2). β -Diversity thus accounted for the bulk of total species richness. Relative α -diversity was highest for the plants (40%), followed by carabids (34%), spiders (27%), staphylinids (22%) and finally bees (16%). β -Diversity is divided roughly equally among between-site β_{S} and between-region β_{R} .

EFFECTS OF ORGANIC MANAGEMENT ON α - AND β -DIVERSITY

The results for the hypothesis tests comparing α - and β -diversity are shown in Tables 1, 2 and 3 and Fig. 3. α -Diversity was significantly higher in organic fields than in the conventional fields for both plants and bees (Table 1). β -Diversity between sites β_{S} of bees and plants was higher in organically managed fields compared to conventionally managed fields (Table 2). β_{S} was higher for spiders in conventional fields. For carabids, β_{S} was higher at the edge of conventional fields than at the edge of organic fields, but the pattern

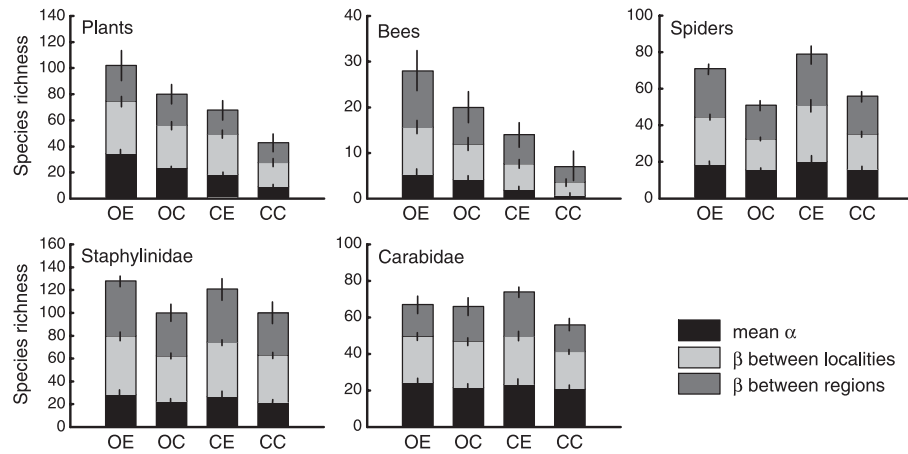


Fig. 3. α - β - (between-field and between-region) and γ_{obs} -diversity values for the species richness of plant and arthropod groups recorded in the edge and centre of organic and conventional fields in three regions of Germany; treatment combinations are: OE = organic-edge; OC = organic-centre; CE = conventional-edge; CC = conventional-centre; Error bars are ± 2 SE of the means.

Table 1. Effect of management (O = organic, C = conventional) and location in field (E = edge, C = centre) on α -diversity of different taxa in German wheat fields (mixed-model ANOVA with fields nested in site). Interactions were not significant. Significance levels: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; NS: $P > 0.10$. Denominator degrees of freedom (d.f.) are given

| | Variable | d.f. | F-value | Direction of effect |
|--------------|-------------------|------|-----------|---------------------|
| Plants | Management | 19 | 139.48*** | O > C |
| | Location in field | 39 | 65.93*** | E > C |
| Bees | Management | 20 | 32.16*** | O > C |
| | Location in field | 40 | 9.69** | E > C |
| Spiders | Management | 20 | 2.05 NS | |
| | Location in field | 41 | 26.04*** | E > C |
| Carabids | Management | 20 | 1.04 NS | |
| | Location in field | 41 | 18.66*** | E > C |
| Staphylinids | Management | 20 | 0.91 NS | |
| | Location in field | 41 | 16.97*** | E > C |

Table 2. Effect of management (O = organic, C = conventional) and location in field (E = edge, C = centre) on between-site β -diversity of different taxa in German wheat fields (mixed-model ANOVA with fields nested in site). Interactions shown when significant. Significance levels: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; NS: $P > 0.10$. Denominator degrees of freedom (d.f.) are given

| | Variable | d.f. | F | Direction of effect |
|--------------|-------------------|------|-----------|---------------------|
| Plants | Management | 19 | 77.56*** | O > C |
| | Location in field | 39 | 49.26*** | E > C |
| Bees | Management | 20 | 56.06*** | O > C |
| | Location in field | 41 | 35.05*** | E > C |
| Spiders | Management | 20 | 22.12*** | O < C |
| | Location in field | 41 | 174.78*** | E > C |
| Carabids | Management | 20 | 5.75 NS | |
| | Location in field | 40 | 9.42** | |
| | Interaction | 40 | 11.16* | CE > CC |
| Staphylinids | Management | 20 | 0.74 NS | |
| | Location in field | 41 | 31.12*** | E > C |

was the reverse in the centre of the fields. No significant effects of management could be found on β_S of staphylinids. At the regional scale, β_R was higher in organic fields than in conventional fields for bees. In addition, β_R , like β_S , was higher at the edge of conventional fields than at the edge of organic fields, while the opposite was found to be the case in the centre of the fields (Table 2).

EFFECTS OF LOCATION IN FIELD ON α - AND β -DIVERSITY

The effect of location in field on α -, β_S - and β_R -diversity can be found in Tables 1, 2 and 3 and Fig. 3. α -Diversity of all groups was higher in the edge than at the centre of the fields. The same was true for β_S of all groups except carabids, where this was the case only in conventional fields, not in organic fields. The β_R -diversity patterns were less clear; β_R was higher for staphylinids in the edge than in the centre of fields. A similar trend could be found for bees and plants, but this was not significant ($P > 0.05$); β_R was higher in the edge than in the centre of organic fields than conventional fields, with the pattern being reversed in organic fields.

EFFECTS OF LANDSCAPE CONTEXT AND LOCAL HABITAT CHARACTERISTICS ON SPECIES COMPOSITION

Species composition was more similar in fields surrounded by a similar landscape for some species groups in some management type and location in field combinations (Table 4). Landscape was correlated with the species composition of spider, staphylinid and carabid communities ($P < 0.10$) in both edges and centres of conventional fields. In organically managed fields, the species composition of staphylinid communities was correlated with landscape composition at the centre of the fields.

Table 3. Effect of management (O = organic, C = conventional) and location in field (E = edge, C = centre) on between-region β -diversity of different taxa in German wheat fields (ANOVA). Interactions shown when significant. Significance levels: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; NS: $P > 0.10$. Denominator degrees of freedom (d.f.) are given

| | Variable | d.f. | <i>F</i> | Direction of effect |
|--------------|-------------------|------|----------|---------------------|
| Plants | Management | 9 | 0.72 NS | |
| | Location in field | 9 | 4.22 NS | |
| Bees | Management | 9 | 9.44* | O > C |
| | Location in field | 9 | 4.46 NS | |
| Spiders | Management | 9 | 0.64 NS | |
| | Location in field | 9 | 9.43* | E > C |
| Carabids | Management | 8 | 3.84 NS | |
| | Location in field | 8 | 0.43 NS | |
| | Interaction | 8 | 7.71* | CE > CC |
| Staphylinids | Management | 9 | 0.05 NS | |
| | Location in field | 9 | 5.90* | E > C |

Table 4. Mantel test *r*-values (Pearson's product-moment correlation) for the correlation between similarity matrices for species composition in wheat fields and similarity matrices for landscape composition surrounding the fields. Separate tests were conducted for each management-type (O = organic, C = conventional) and location in field (E = edge, C = centre) combination. Significance levels: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; NS: $P > 0.10$

| | OC | OE | CC | CE |
|--------------|------------|------------|----------|------------|
| Plants | 0.031 NS | < 0.001 NS | 0.016 NS | 0.024 NS |
| Bees | - 0.023 NS | 0.145 NS | 0.029 NS | - 0.057 NS |
| Spiders | 0.220* | - 0.084 NS | 0.160 NS | 0.200* |
| Carabids | 0.174 NS | - 0.024 NS | 0.245* | 0.326** |
| Staphylinids | 0.051 NS | 0.125 NS | 0.386** | 0.336** |

Species composition did not depend on local habitat factors as defined in this study, with the exception of staphylinids in the centre and edge of conventional fields ($P < 0.05$; for all other results $P > 0.10$).

Discussion

SPATIAL PARTITIONING OF DIVERSITY IN DIFFERENT TAXA

The comparison between taxa of α - and β -diversity contributions to total species richness yielded two important findings. First, β -diversity, both between sites and between regions, accounted for a large part of the total species richness in our set of wheat fields regardless of taxon. Between-region β -diversity most probably reflects differences in species pool. The results for between-site β -diversity are similar to those of two previous studies in which between-field β -diversity has also been shown to be a major contributor to total plant diversity in agricultural landscapes (Wagner, Wildi & Ewald 2000; Roschewitz *et al.* 2005). This seems surprising as the fields, as dense, tilled monocrops, are somewhat homogeneous. In addition, arable fields are not subject to fragmentation, which is one

possible cause of large β -diversity values. Instead, they cover a large part of western and central Europe and are not isolated habitats (FAOSTAT 2005). On the other hand, several studies have shown the large impact that field surroundings may have on species diversity: many species colonize the arable fields from perennial habitats, which are the major source of species richness in agro-ecosystems (Dauber *et al.* 2003; Jeanneret *et al.* 2003; Clough *et al.* 2005; Gabriel, Thies & Tschardtke 2005; Clough, Krues & Tschardtke 2007). Heterogeneity between landscapes can explain the high β -diversity between fields, just as heterogeneity within landscapes can explain the α -diversity at the field level. The significant correlation of similarity matrices for landscape composition with similarity matrices for species composition for epigeic arthropods in conventional wheat fields shows that landscape context is indeed determining the size of the contribution of β -diversity to total species richness for these species groups, although the extent of the contribution of landscape variability may depend on management type.

In addition to landscape effects, differences in habitat characteristics, low dispersal rates and sampling efficiency may contribute to increasing the contribution of β -diversity (Crist & Veech 2006; Chandy, Gibson & Robertson 2006), with differential effects in different species groups. Our analysis of habitat characteristics showed that the species composition of only one group, the staphylinids, was affected by local habitat factors. In addition, this effect was restricted to conventional fields, which is surprising, as the variability between conventional fields is lower than that in organic fields (Y. Clough, unpublished data). One would have expected habitat characteristics to determine species composition to a large extent, especially for sessile organisms such as plants. On the other hand, plots within a certain management type and location in field combination may already be so similar that habitat characteristics are negligible in explaining species composition. Also, despite the inclusion of many factors in the habitat matrix, it cannot be excluded that factors relevant for the organisms studied were omitted.

Dispersal limitation has often been stated to be the main cause for spatial patterns in diversity, but this has previously been considered to be more likely for plants than for mobile organisms, which are able to select their habitat actively and are less limited by available space (Loreau & Mouquet 1999). The effect of dispersal on β -diversity is difficult to test with this data set, given the differences in size and dispersal type (airborne: bees, carabids (part), staphylinids (part), spiders (part), plant seeds; ground dispersers: carabids, staphylinids, spiders). A comparison of the relative contributions of α - and β -diversity to the species richness of winged and unwinged carabids suggested that β -diversity was indeed greater for the more dispersal limited group, the unwinged, but the probable differences in the sampling efficiency between the two groups made conclusions difficult (Y. Clough, unpublished data). A previous study

focusing on very divergent organisms (Fleishman, Betrus & Blair 2003; for birds vs. butterflies) found that dispersal limitation caused a higher contribution of β -diversity to total diversity. In a study of forest Lepidoptera, Summerville *et al.* (2006) did not find any significant effect of body size, used as a surrogate for dispersal ability, on diversity partitioning. Sampling efficiency may also be a cause for the high share of β -diversity in the bee data set. Bees were collected by sweep-netting, which is a less sampling-intensive technique than trapping. In addition, although bees can be good colonizers, site fidelity as well as the strong reliance on suitable nesting habitats outside the arable fields (Westrich 1996; Gathmann & Tscharrntke 1999), is likely to decrease the average amount of bee species found per field and to explain the high spatial turnover in species composition. The availability of nesting habitats may not have been captured appropriately by the landscape composition factors used in our analysis, which did not show any correlation between variability in landscape composition and species composition.

EFFECTS OF ORGANIC MANAGEMENT ON α - AND β -DIVERSITY

The effect of an agri-environment scheme on total species richness depends on both α - and β -diversity. This work is novel in that it tests the effect of management on both components, β -diversity having being ignored in such studies to date. α -Diversity was higher in organic than in conventional fields for plants and bees, but not for the surface-dwelling arthropods sampled. Studies evaluating biodiversity benefits of organic farming generally find an increase across all taxa considered (Hole *et al.* 2005; Bengtsson, Ahnström & Weibull 2005), although variation in response of α -diversity between taxa to organic farming has been shown elsewhere (Fuller *et al.* 2005). Interestingly, the results of our study suggest that the strong positive response of plants to organic management is relayed to the pollinators (wild bees), while epigeaic arthropods benefit less (or not at all) from organic farming (Purtauf *et al.* 2005). Limited use of insecticides in conventional fields (only nine of 21 fields were sprayed, with a single application) or the use of comb-harrowing in organic fields (15 of 21 fields, 10 of those more than once during the season), which may be detrimental to the epigeaic fauna, may explain partly the absence of differences. In addition, plants may directly benefit from less intensive management through extensification and pollinator availability (Gabriel & Tscharrntke 2007) and are allowed to build up a seed bank in organic fields which leads to a progressive increase in species richness. Unlike most organic fields, conventionally managed fields contain few broad-leaved flowering plant species which can attract bees, which may explain why species richness of bees is higher in organically managed fields (Holzschuh *et al.* 2007). Many epigeaic arthropods, on the other hand, need to

overwinter outside arable fields due to tillage (Pfiffner & Luka 2000; Thorbek & Bilde 2004). For these groups, the limiting factor may be the availability of the overwintering sites rather than the management of the field. The analysis of β -diversity in the context of comparing alternative management schemes is a new approach. It has also been shown that more intensive management may result in larger heterogeneity between plots and thus increase β -diversity, albeit on a temporal and not on a spatial scale (Tylianakis, Klein & Tscharrntke 2006). However, we expected β -diversity to be higher in organic fields than in conventional fields because organic fields tend to be managed more heterogeneously from farm to farm than conventional fields (Y. Clough unpublished results), where systematic use of synthetic fertilizers and pesticides, especially herbicides, are expected to reduce the differences between the fields. Our findings matched our expectations for the plants and bees, the two taxonomic groups which showed higher α -diversity in organic fields. However, the between-site β -diversity of spiders was greater in conventional fields than in organic fields, resulting in greater total species richness in conventional fields. This pattern can be explained partly by the fact that the species composition of spiders varies more strongly with landscape composition than in organic fields.

EFFECTS OF LOCATION IN FIELD ON α - AND β -DIVERSITY

Edges of wheat fields contained a higher α -diversity for all species groups considered. Edges are less subject to management effects because they are close to the perennial boundary, which allows more spill-over than in the field centre (Coombes & Sotherton 1986; Bowie *et al.* 1999). In addition, agrochemical applications may be less intensive at the edge of the fields than at the centre (Kleijn & van der Voort 1997). The pattern in between-site β -diversity is similar to a large extent to the pattern of α -diversity, with higher values in the edge than at the centre of the fields. While this cannot be tested with the present data set, heterogeneity in species composition between edges can be expected to be larger than between centres of fields, because the variability within the ecotone most probably mirrors the variability of adjoining habitat, which may be another arable field with little or no boundary, a grass strip, a ditch or a hedge.

IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

Organic farming enhances species richness in agricultural habitats for plants and the most important insect group pollinating them, the bees, but not for surface-dwelling arthropods such as carabids, staphylinids and spiders. Diversity of all taxa was higher at the edge of the fields, due presumably to spill-over effects from the

adjacent boundary habitats. Our case study demonstrates clearly that the analysis of well-replicated biodiversity data benefits from the inclusion of β -diversity analyses. Although we did not find that β -diversity analyses reversed the overall conclusions on effectiveness of the agri-environment scheme that could be made with α -diversity analyses, β -diversity was the source of hidden species richness benefits in organic fields for two of the taxa. For another group, the spiders, β -diversity was larger in conventional fields while no differences were detected with the α -diversity analyses. These analyses show how heterogeneously species turnover can be affected by management factors depending on the species group upon which one is focusing. Across species groups, β -diversity enhances species richness at between-site as well as between-regional scales. As discussed above, the causes for this pattern may be multiple, but we could show that the variability in landscape composition plays a role in increasing β -diversity.

Based on our results we make the following recommendations: (1) given its large contribution to total species richness, β -diversity should be included in evaluations of the effectiveness of agri-environment schemes whenever species richness, and not a small set of specific species, is targeted (Olson *et al.* 2002); (2) organic agriculture benefits some groups, such as plants and bees, but for other species groups more targeted measures are needed; (3) biodiversity benefits of organic agriculture would be threatened by an intensification of management through repeated mechanical weeding; if biodiversity is to be an integral part of organic agriculture implementing explicit measures to conserve a minimal weed cover and diversity might be appropriate; and (4) implementing agri-environment schemes in contrasting landscapes and in different regions may result in a larger increase of total species richness in areas covered by the scheme through enhanced between-site and between-region β -diversity.

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