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Indicators for biodiversity in agricultural landscapes: a pan-European study

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Summary

1. In many European agricultural landscapes, species richness is declining considerably. Studies performed at a very large spatial scale are helpful in understanding the reasons for this decline and as a basis for guiding policy. In a unique, large-scale study of 25 agricultural landscapes in seven European countries, we investigated relationships between species richness in several taxa, and the links between biodiversity and landscape structure and management.

2. We estimated the total species richness of vascular plants, birds and five arthropod groups in each 16-km^2 landscape, and recorded various measures of both landscape structure and intensity of agricultural land use. We studied correlations between taxonomic groups and the effects of landscape and land-use parameters on the number of species in different taxonomic groups. Our statistical approach also accounted for regional variation in species richness unrelated to landscape or land-use factors.

3. The results reveal strong geographical trends in species richness in all taxonomic groups. No single species group emerged as a good predictor of all other species groups. Species richness of all groups increased with the area of semi-natural habitats in the landscape. Species richness of birds and vascular plants was negatively associated with fertilizer use.

4. *Synthesis and applications.* We conclude that indicator taxa are unlikely to provide an effective means of predicting biodiversity at a large spatial scale, especially where there is large biogeographical variation in species richness. However, a small list of landscape and land-use parameters can be used in agricultural landscapes to infer large-scale patterns of species richness. Our results suggest that to halt the loss of biodiversity in these landscapes, it is important to preserve and, if possible, increase the area of semi-natural habitat.

Key-words: arthropods, birds, habitats, indicator taxa, monitoring, semi-natural plants, species richness

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Introduction

Europe has a rich diversity of agricultural landscapes that differ greatly in types of land use, sizes and shapes of fields, and the abundance and pattern of semi-natural elements. Most of these landscapes, especially those with a fine-grained mosaic and low-intensity production systems, were formerly rich in biodiversity (Edwards, Kollmann & Wood 1999). In recent decades, however, many previously common species have become scarce or have disappeared as a result of more intensive forms of agricultural production and an associated decline in semi-natural landscape elements (Krebs *et al*. 1999; Robinson & Sutherland 2002). This loss of biodiversity in agricultural landscapes has been particularly marked in many member states of the European Union (EU) (e.g. farmland birds in western EU states) (Stoate *et al*. 2001; Donald *et al*. 2002), reflecting the strong environmental impact of EU agricultural policy. Although most EU countries have introduced schemes aimed at protecting biodiversity and making farming more sustainable (Kleijn *et al*. 2001; Stoate & Parish 2001; Kleijn & Sutherland 2003), many experts fear that the decline of species and habitat diversity will continue unless there are major changes in policy based on improved technology and scientific knowledge (Sala *et al*. 2000; Tilman *et al*. 2001).

Among possible factors influencing large-scale patterns of biodiversity in agricultural landscapes, habitat heterogeneity (Benton, Vickery & Wilson 2003; Tews *et al*. 2004) and land-use practices – especially the application rates of fertilizers and pesticides – are thought to be particularly important. Many studies have been performed to investigate the influence of landscape structure on particular species or groups of species (e.g. Mason & Macdonald 2000; Weibull, Bengtsson & Nohlgren 2000; Atauri & de Lucio 2001; Steffan-Dewenter *et al*. 2002; Steffan-Dewenter 2003; Purtauf, Dauber & Wolters 2005; Vanbergen *et al*. 2005). Although the conclusions tend to vary according to the spatial scale and taxon investigated, all studies suggest that either heterogeneity, or connectivity, or area of semi-natural elements has a positive influence on species richness and abundance. The picture concerning land use is less clear, and the results depend very much on which land-use parameters were measured; few studies have used a broad set of variables covering several aspects of land use.

To avoid the considerable practical problems of assessing total species richness in agricultural landscapes, ecologists have explored the use of particular taxa, especially vascular plants and arthropods, as general indicators of biodiversity (Duelli 1997; Duelli & Obrist 1998; McGeoch 1998; Pharo, Beattie & Binns 1999). However, the growing literature on this topic reveals that, although numbers of species in different taxa are often positively correlated (Pearson & Cassola 1992; Kati *et al*. 2004), these relationships are usually too weak to be useful in predicting species richness in other taxa (McGeoch 1998; Sauberer *et al*. 2004). Moreover, most of these studies have been performed at a relatively small spatial scale, and it is uncertain whether the findings can be applied at a larger spatial scale.

The few studies of agro-biodiversity performed at a continental scale have all had a rather narrow taxonomic focus (from our data: arthropods, Schweiger *et al*. 2005; Hendrickx *et al*. 2007; plants, J.L., unpublished data), and none has had the aim of establishing general relationships between species richness and landscape attributes that are valid for a wide range of taxa. From a European viewpoint this is unfortunate, as agricultural policies with far-reaching consequences for local biodiversity are determined centrally by the authorities of the EU. There is a danger that lessons learnt from small-scale studies, or from one or few taxonomic groups, may lead to suboptimal management practices if applied more generally. For this reason, a combination of small- and large-scale studies is needed as a basis for improving the management of agricultural landscapes (Grashof-Bokdam & van Langevelde 2005; Tscharntke *et al*. 2005).

The work described here had two main objectives. First, we wanted to investigate relationships between species richness in different taxonomic species groups at a continental scale. Our motivation was to establish whether certain taxa can be used as indicators of overall species richness, thereby streamlining biodiversity assessment efforts performed at a large spatial scale. Although potential indicator taxa are often selected using correlation analysis (Lamoreux *et al*. 2006), this method does not provide information about the predictive power of the indicator (McGeoch 1998). We therefore adopted an alternative approach designed to identify which taxonomic groups can reliably be used to predict species richness in other groups. Our second objective was to investigate whether there are consistent relationships between species richness in selected taxa, and the structure and management of the agricultural landscape. If such large-scale relationships were demonstrated, they would provide a useful basis for biodiversity monitoring and improved landscape planning and management (Fahrig & Jonsen 1998; Brooks & Kennedy 2004).

The study was conducted in 25 agricultural landscapes of 16 km^2 distributed across seven European countries (France, Belgium, the Netherlands, Germany, Switzerland, Czech Republic and Estonia). In a study area extending across half a continent, many factors apart from landscape and land-use variables – including climate, soil conditions and management history – also influence local species richness. Indeed, some of these factors are likely to be more important than landscape variables in determining the absolute number of species present. The analysis presented here was designed to exclude these variables so that the focus could be exclusively on how landscape structure and land-use intensity influence species richness. In each landscape we estimated the total species richness of vascular plants, birds and five arthropod groups, recorded various measures of landscape structure, and assessed the intensity of agricultural land use. In assessing landscape structure, we considered the diversity, area, and spatial arrangement of landscape elements; in assessing the intensity of agriculture, we recorded crop diversity, livestock density, and fertilizer and pesticide use. These variables cover many more aspects of the structure and management of landscapes than have been considered in most previous studies.

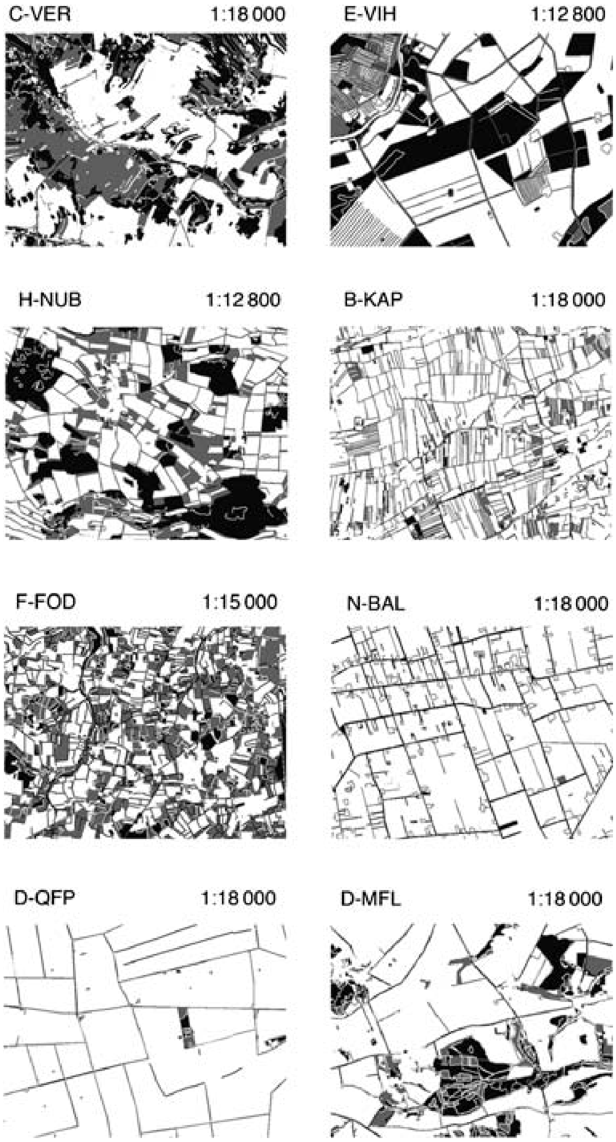

Fig. 1. Maps of eight representative study sites, which are characteristic for all sites surveyed. For site descriptions see Table 3 and Table S1 in Supplementary material. Grey = herbaceous semi-natural patches; black = woody semi-natural patches; white = arable land and other non-semi-natural patches.

Materials and methods

STUDY SITES

Landscapes of 16 km^2 were chosen to cover broad ranges in both land-use intensity and landscape structure, with both factors varying independently as far as possible (Table S1 in Supplementary material; Fig. 1). The sites were selected to avoid strongly contrasting types of land use such as urban areas or broad river corridors. Each study site could be regarded as typical of the region, being located within a much larger agricultural area with similar landscape structure and land-use intensity. In all countries the study sites were squares of 4×4 km, except in Switzerland, where the selection criteria could only be met by choosing sites of more irregular shape.

A GIS program (ARCGIS 8·1; ESRI) was used to map each study site at 1-m resolution from aerial photographs and topographical maps. The different habitat types were classified using the EUNIS Habitat Classification System (Davies & Moss 1999). To calculate landscape and class metrics (Table 1), habitat types were aggregated into three categories: woody semi-natural habitats, herbaceous semi-natural habitats, and all other habitats. Some metrics were calculated using all three categories separately, while for others the woody and herbaceous habitats were combined into a single category (Grashof-Bokdam & van Langevelde 2005). Landscape and class measures were calculated at 1-m resolution using the software package FRAGSTATS (McGarigal *et al*. 2002). Information on land-use intensity was obtained by interviewing about 10 farmers who between them managed at least 10% of the study site. The interview contained questions about crop rotation, crop management, fertilizer and pesticide use, and livestock management (Table 1). Fertilizer input, pesticide use and livestock units were calculated per hectare of utilized agricultural area (UAA; cropland and permanent grassland).

Landscape structure varied widely in terms of the extent and types of semi-natural habitats (Fig. 1): while some landscapes had a fine-grained structure with many hedgerows separating small fields (e.g. Brittany, France), others exhibited little structural diversity, being dominated by large patches of semi-natural elements (e.g. Estonia) or large fields (e.g. Querfurt, Germany). The total area of semi-natural elements in the landscapes ranged from 2 to 50%, and the type and intensity of land use also varied greatly. Nitrogen input varied from 34 kg ha^{-1} $year^{-1}$ in one Estonian site to 361 kg ha^{-1} $year^{-1}$ in a Dutch site (Table S1). The number of crops cultivated in one year ranged from 1 to >7 per farm. More descriptors and the relationships among them are given by Herzog *et al*. (2006) and Bailey *et al*. (2007).

BIODIVERSITY ASSESSMENT

The taxa studied were vascular plants, birds, bees (Apoidea), true bugs (Heteroptera), carabid beetles (Carabidae), hoverflies (Syrphidae) and spiders (Araneae). Plants and birds were surveyed in all sites, and arthropods in 24 sites.

The plots for recording plants were located using a stratified random sampling scheme. The plots for recording the herbaceous layer were 2×2 m, and those for the shrub and tree layer, if present, 20×20 m. The sampling protocol required the plant plots to be distributed among agricultural, semi-natural and linear elements in the ratio 1 : 4 : 5 – to avoid over-representation of particular habitat types – and with a total sample of 200–250 plots per site. In practice, the sample size ranged between 86 and 323 per study site, but the ratios among the elements remained constant. To facilitate comparisons, the mean numbers of plant species in 86 plots, rarefied from the original data, are presented as well as the original data in Table 2. As the Spearman correlation coefficient between observed herb-layer richness and rarefied richness was very high (herbs $r = 0{\cdot}96$; $P < 0{\cdot}001$; woody plants $r = 0{\cdot}92$, $P < 0{\cdot}001$), the observed data set was used for statistical analyses; the variation in sampling intensity of vegetation was taken into account with a continuous factor 'log-transformed number of samples', utilizing the species–area accumulation curve (Arrhenius 1921).

For bird sampling, the study site was divided into 1-km^2 grid cells. Bird diversity was measured by making point-counts in five central grid cells selected in a checkerboard pattern. Within each cell, four observation points were selected, and at each point sightings and hearings of birds were counted for 5 min from 30 min before until 2 h after sunrise. This procedure was repeated in April, May and June.

Arthropods were sampled using 16 pairs of pitfall traps and 16 pairs of combined flight-intercept traps (combined window-glass and yellow-pan trap) located using a stratified random distribution,

Table 1. Explanatory variables used in the statistical analysis

Variable name	Explanation	Range (min–max)
Country	Country	
Taxonomic group	Taxonomic or morphological group of species	
Vegetation period	Length of vegetation period (average number of days 1982–2001 with daily temperature >5 °C)	235–291 days
Number of plots	Number of vegetation sample plots in study site	84–323
Land-use intensity parameters		
Crop diversity	Average number of crops cultivated on a farm	1·2–7·7
Fertilizer input ha^{-1} UAA	Average nitrogen input scaled to the UAA	34–361 kg ha^{-1} $year^{-1}$
Intensely fertilized land	Share of intensively fertilized arable area (>150 kg N ha^{-1} $year^{-1}$) scaled to the UAA	0–98·6%
Livestock units	Average amount of livestock units per farm in study site, scaled to the UAA	0–4·7 lu
Pesticide application	Average number of pesticide applications per field in study site, scaled to the UAA	0–5·8
Landscape parameters		
Share of semi-natural elements	Area (m^2) of semi-natural habitats in study site	2·69–52·96%
Habitat diversity	Number of semi-natural habitat types in study site	12–23
$Patch.No_{WH}$	Number of patches of woody and herbaceous semi-natural habitats	126–2027
$Patch.Area_{GV}$	Average size of a semi-natural patch	1965–29136 m^2
$Patch.Density_{GV}$	Number of patches of woody and herbaceous semi-natural habitats per 100 ha	7·88–126·69
$Edge.Density_{GV}$	Average edge density of semi-natural habitats in study site	97·65–579·63 m ha^{-1}
ENN_{GV}	Average euclidean-nearest-neighbour distance between semi-natural landscape elements in study site	9·51–53·02 m
$Contag_{GV}$	Contagion index of woody and herbaceous semi-natural landscape elements	37·61–76·73%
$Prox_{GV}$	Proximity of woody and herbaceous semi-natural elements within a 5000-m radius	295·07–60321·11

UAA = utilized agicultural area.

Table 2. Total species numbers of vascular plants (separated into herbaceous and woody plants) and six animal taxa recorded in 25 landscape study sites. Observed and mean species number of herbaceous and woody plants found in 86 plots based upon a rarefaction of the original data are shown

Country	Site code	Herbs (observed)	Herbs (86 plots)	Woody (observed)	Woody (86 plots)	Birds	Spiders	Carabids	True bugs	Hoverflies	Bees
Belgium	B-BRE	240	156·8	36	28·0	63	107	77	36	24	38
	B-HOE	287	187·8	60	41·7	52	74	69	32	22	40
	B-KAP	192	131·2	63	35·7	59	73	67	24	27	15
	B-VOE	284	189·6	56	36·6	58	67	59	36	21	36
Czech Rep.	C-BRO	328	204·4	48	32·0	50	68	47	27	13	63
	C-SVE	274	192·7	41	26·9	56	–	–	–	–	–
	C-VER	339	230·4	57	33·4	47	78	60	88	40	50
Estonia	E-ARE	293	211	30	22·7	52	101	69	48	28	33
	E-VIH	280	204·4	27	22·1	53	118	82	73	35	45
	E-Vii	270	189·6	38	27·0	38	84	75	52	32	40
	E-VMA	255	181·2	37	26·4	37	104	80	75	33	42
France	F-AL	278	204·1	42	29·1	39	79	67	58	23	38
	F-FOD	301	183·4	43	27·3	46	91	79	60	20	44
	F-FOO	274	190	49	31·9	42	92	75	56	17	41
Germany	D-FRI	266	187	27	18·5	63	90	73	69	19	125
	D-MFL	251	163·2	32	24·5	67	105	83	89	49	98
	D-QFP	152	121	24	16·8	50	81	72	68	37	96
	D-WAN	237	170·8	40	25·1	58	89	78	86	26	99
Netherlands	N-BAL	161	159·7	18	17·7	49	74	63	27	28	16
	N-BEN	223	183·8	54	45·6	59	77	54	43	21	32
	N-SCH	143	127·8	33	29·5	56	74	69	32	25	23
	N-WEE	185	157·5	45	38·5	62	73	71	32	19	22
Switzerland	H-KLG	274	196·9	46	29·7	43	62	52	104	26	59
	H-NUB	314	208·3	44	32·1	53	76	61	88	55	64
	H-REE	340	212·3	42	31·1	62	91	66	80	54	62

with two sets of traps in each 1-km^2 grid cell. At each location, two sets of one pitfall and one flight trap each were placed 25–50 m apart at the border between a semi-natural habitat and agricultural land. For a detailed description of the sampling procedure see Schweiger *et al.* (2005). Sampling was carried out according to the procedures of Duelli (1997). Species numbers for all species groups in every landscape are presented in Table 2.

STATISTICAL ANALYSIS

In a first step, we investigated the predictive power of the different species groups. We calculated predictive correlations between species groups using general linear modelling with stepwise selection procedure for all groups of taxa and the factor variable 'country'. Country was used as compound variable to account for biogeographical variation within Europe. If one group is clearly superior as a predictor of species richness, then the final model may include just one species group, or it may include several groups and/or the biogeographical effects if there is no single best indicator group.

Second, we analysed the effect of landscape and land-use parameters on the number of species in different taxonomic or morphological groups. We created general linear mixed models using the statistical package SAS ver. 8·2 (procedure 'mixed'; Littell *et al.* 1996). Separate models were built for plant diversity (two groups: woody and herbaceous), bird diversity (one group) and arthropod diversity (five groups: bees, carabids, true bugs, hoverflies and spiders). Taxonomic groups were analysed in separate models according to the sampling methods. Where more than one species group was involved (plants and arthropods), the species group was treated as a factor with discrete levels. Any regional variation in species richness unrelated to landscape or land-use factors was accounted for by the continuous variable 'length of vegetation period' and the random factor country within the 'country × species group' term. The interaction term 'country × species group' was treated as a random factor as each species group has its own species pool within a country. The 'length of vegetation period' was excluded during the stepwise model building as a non-significant predictor, with only the 'country effect' being used in the final models to account for geographical variations. Because of the random effects in the model, we used the Satterthwaite approximation for the denominator degrees of freedom. We included a repeated statement with an unstructured covariance matrix in the plant and arthropod models; this took account of any autocorrelation caused by sampling both plant species groups or all five arthropod species groups in the same locations within a study site. Landscape and land-use parameters were included in the models as continuous predictors (Table 1). In the plant model, we included the log-transformed number of sample plots to correct for sampling intensity.

The statistically significant main effects of the environmental variables describe the general pooled trends of all species groups in a model. Significant interaction terms between the species groups and the continuous variables indicate differences in correlation among the environmental parameters and the number of species within a group.

The procedure for model building was stepwise backward. Variables for which neither the main effect nor the interaction term with the species group was significant were excluded step by step, and the procedure stopped when all environmental variables showed either a significant main effect or interaction term ($P < 0{\cdot}05$). To avoid over-parameterization (Shao 1997), Akaike's information criterion (Akaike 1973) was used to test for the optimal set of variables in a model according to its predictive power. The results of the final models are presented with slope parameter estimates for the main effects (interaction term not significant) or separate slope estimates for each species group (interaction term significant, see Table 4). Slope parameters were tested for their difference from zero (t-test) within the mixed model. It is not possible to calculate multiple determination coefficient (R^2) values directly for mixed models with random factors and repeated settings, but the approximate estimate of R^2 was obtained from the likelihood ratio test statistic of a model (Magee 1990).

Results

PREDICTIVE CORRELATIONS AMONG SPECIES GROUPS

Several significant predictive relationships between numbers of species in different taxa were obtained (Table 3), but no taxon proved to be a good predictor for all others. The optimal predictive model for most groups involved one or two indicator groups in combination with the country effect. The descriptive power of the indicator model varied from 34% for woody plants to 94% for bees. Among the individual groups, bees proved to be a good indicator taxon for species richness of herbs, spiders for birds, and carabids for hoverflies. Paired indicator groups were found for three taxonomic groups – bees were best predicted by herbs and hoverflies, carabids by herbs and spiders, and spiders by carabids and birds. Neither species richness of woody plants nor bugs could be predicted by any other group. For most species groups there was a significant country effect, indicating strong biogeographical variation in species numbers. All indicative correlations were positive except for those of carabids against plants, and bees against hoverflies (Table 3).

CORRELATIONS WITH LANDSCAPE AND LAND-USE INDICATORS

For all taxonomic groups, variables describing landscape structure and land-use intensity accounted for a significant part of the variation in species richness. The same analyses were also performed using Simpson's diversity index, but the results are not presented here because the relationships were very similar to those obtained using species richness.

The total number of vascular plant species increased with the area of semi-natural habitat in the study site, and decreased with the percentage of heavily fertilized agricultural land (after considering the variation in sampling intensity; Table 4). Significant interaction terms revealed that these relationships were due to variation in the numbers of herbaceous species and that numbers of woody species were unaffected by these factors (Table 4, Fig. 2).

The trends for birds were similar to those for plants, with the number of species being positively related to the area of semi-natural habitat in the study site and negatively related to fertilizer input (annual N input in kg ha^{-1} utilized agricultural area, Table 4, Fig. 3).

The combined species richness of the five arthropod taxa also increased with the area of semi-natural habitat in the study site (Table 4, Fig. 4). However, unlike for birds and plants,

Table 3. Results of the GLM analysis for predictive correlations. This is a critical list of indicator groups for predicting species richness of each species group, considering factor effect by country. Significant effects are presented with slope estimate and significance class. Estimates for intercept and/or country are not presented. MPE, multiple parameter estimates

	Species richness of group to be predicted							
Indicator group	Herbs	Woody	Birds	Bees	True bugs	Carabids	Hoverflies	Spiders
Herbs				0·204*		–0·098*		
Woody								
Birds								0·873**
Bees	1·356*							
True bugs								
Carabids							0·722*	0·912**
Hoverflies				–0·392*				
Spiders			0·366**			0·551***		
Country	MPE**	MPE*	MPE***	MPE***	MPE***		MPE*	MPE*
adjR^2	0·586	0·338	0·641	0·941	0·660	0·681	0·440	0·739
Model P	0·002	0·036	0·001	0·001	0·001	0·001	0·016	0·001

Presented is a critical list of indicator groups for predicting species richness of each species group, considering factor effect by country. Significant effects are presented with slope estimate and significance class. Estimates for intercept and/or country are not presented. MPE, multiple parameter estimates.
* $P \leq 0·05$; ** $P \leq 0·01$; *** $P \leq 0·001$.

Table 4. Results of GLMM analysis of the relationships between biodiversity and landscape, and land-use variables. Results of individual groups are given with homogeneity group classes of the slope values indicated by superscript labels (for significant interactions terms only). Degrees of freedom were rounded to avoid decimals.

Effect	d.f.	F	P	Group	Slope	SE	P
Plants (R^2 = 81·2%)							
Growth form	1,23	51·97	<0·001				
Log (number of plots)	1,22	12·80	<0·002				
Share of semi-natural elements (% area)	1,20	6·02	<0·024				
Growth form × share of semi-natural elements	1,22	7·38	<0·013	Herbs	1·718	0·636	<0·014
				Woody	–0·052	0·195	0·794
Intensely fertilized land (% area)	1,24	5·24	<0·032				
Growth form × intensely fertilized land	1,24	8·38	<0·009	Herbs	–0·717	0·262	<0·012
				Woody	0·065	0·093	0·486
Birds (R^2 = 25·6%)							
Share of semi-natural elements (% area)	1,17	7·36	<0·016		0·282	0·165	
Fertilizer input (kg N ha^{-1} year^{-1})	1,18	4·93	<0·040		–0·037	0·104	
Arthropods (R^2 = 37·1%)							
Taxonomic group	4,22	2·71	0·051				
Share of semi-natural elements (% area)	1,25	13·77	<0·002		0·312	0·061	
Taxonomic group × share of semi-natural elements	4,21	1·09	0·361				
Crop diversity	1,26	7·40	<0·015		2·284	0·426	
Taxonomic group × crop diversity	4,21	1·21	0·437				
Habitat diversity	1,24	0·01	0·935				
Taxonomic group × habitat diversity	4,20	3·21	<0·048	Bees	1·621^{a}	0·574	<0·011
				Bugs	–0·616^{b}	1·167	0·587
				Carabids	–0·405^{b}	0·527	0·450
				Hoverflies	–0·333^{ab}	0·775	0·672
				Spiders	0·786^{ab}	0·967	0·425

crop diversity also had a positive effect on species richness (Table 4, Fig. 4). Species numbers of bees but not of other arthropods were positively related to the diversity of semi-natural habitat types (Table 4, Fig. 4).

No other factors entered into the models explained a significant part of the variation in the species richness of any taxonomic group.

Discussion

PREDICTIVE CORRELATIONS AMONG SPECIES GROUPS

Our results suggest that no single species group can be used as a surrogate measure of species richness for all others. It could

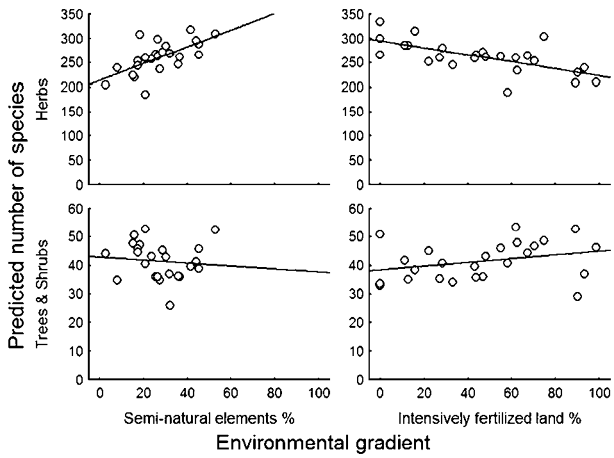

Fig. 2. Relationships between number of plant species in the study sites and landscape structure (percentage of semi-natural habitats, $P < 0{\cdot}014$, for herbs only) and land-use intensity (percentage of intensively fertilized agricultural land, $P < 0{\cdot}012$, for herbs only). Dots represent variation around the model predicted factor effects (solid line).

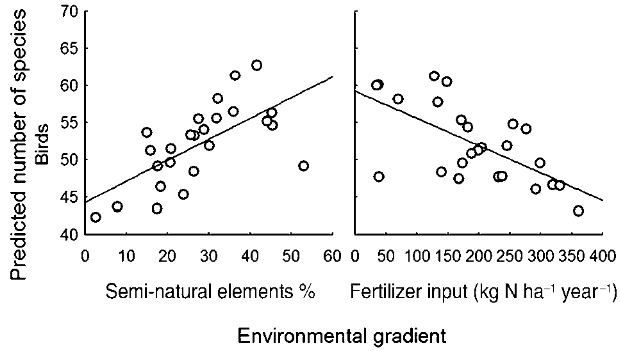

Fig. 3. Relationships between number of bird species in the study sites and landscape structure (percentage of semi-natural habitats, $P < 0{\cdot}016$) and land-use intensity (total nitrogen applied per hectare of agricultural land, $P < 0{\cdot}040$). Dots represent variation around the model predicted factor effects (solid line).

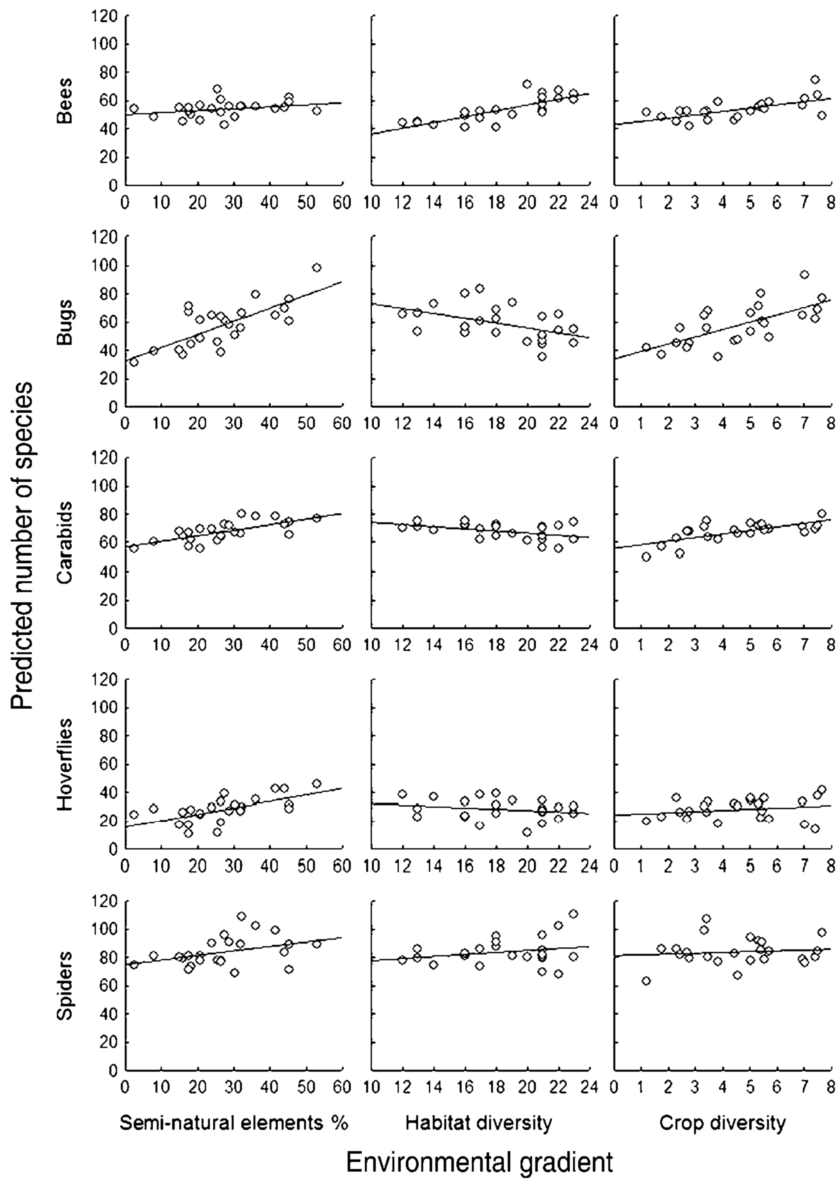

Fig. 4. Relationships between species number of the five arthropod species groups in the study sites, landscape structure and land use (percentage of semi-natural habitats, $P < 0{\cdot}002$; habitat diversity, $P < 0{\cdot}011$, for bees only; crop diversity, $P < 0{\cdot}015$). Dots represent variation around the model predicted factor effects (solid line).

potentially be suggested that the correlation between spiders and carabids may be spurious due to the fact that trapping efficiency of traps can be related to local conditions and installation (Topping & Sunderland 1992). However, the same was not observed for species studied with flight traps. It is likely that simple ecological causes, such as similar habitat preferences or similar prey selection, may also be good explanations for the strong correlation observed between these two groups.

The strong influence of the variable country – which can be interpreted as representing geographical variation in species richness – further complicates the use of individual taxa as indicators of species richness at a continental scale. This finding is consistent with some published studies (van Jaarsveld *et al*. 1998; Vessby *et al*. 2002) but not with others (Pearson & Cassola 1992; Duelli 1997; Kati *et al*. 2004). We suggest two ways to explain this inconsistency. First, few if any other studies have considered such a wide range of species groups, and the positive relationships that have been established among some species groups may not be more generally applicable. Second, many conflicting results may stem from differences in the spatial scale at which the various studies were conducted, underlining the dangers of upscaling conclusions from small-scale studies to regions or continents.

CORRELATION WITH LANDSCAPE AND LAND-USE INDICATORS

The landscapes chosen for our study covered wide ranges of both landscape structure and land-use intensity (Table S1), with the two sets of variables varying more-or-less independently. The landscapes were very different in structure, not only in the total area of semi-natural habitat, but also in the spatial arrangement of the various elements (Fig. 1) and in the land-use intensity. However, despite the structural diversity, two general landscape parameters were distinguished that contributed significantly to explaining species richness across the very different taxonomic groups. By far the most important of these was the share of semi-natural habitat in the study sites, which was positively correlated with species richness for vascular plants, birds and arthropods. The consistent importance of this species–area relationship suggests that, in most agricultural landscapes, the largest contribution to total biodiversity comes from the natural and semi-natural habitats and is directly influenced by their area. Many other studies have shown similarly positive relations between numbers of species and area of semi-natural habitat (Bruun 2000; Steffan-Dewenter *et al*. 2002; Kremen *et al*. 2004). Not only are many species confined to these habitats, but some species closely associated with agro-ecosystems may require the presence of semi-natural habitats. For example, it has been shown that more than 63% of all animal species living in agricultural areas depend on semi-natural habitats for their survival (Duelli & Obrist 2003), demonstrating the crucial importance of these habitats. The only other landscape parameter that contributed significantly to species richness was habitat diversity, which was positively associated with the number of bee species. This is not surprising, as many bee species require several different and sometimes also very specific habitat types to persist in a landscape (Westrich 1996).

Of the five variables used to characterize agricultural land-use, none was consistently important in explaining species richness, but three were significant for particular taxonomic groups. The number of vascular plant species was negatively related to the percentage of intensively fertilized land. This can be readily understood, as fertilizer application is known to reduce plant species richness in both arable fields and agricultural grasslands (Ditommaso & Aarssen 1989; Gough *et al*. 2000; Myklestad & Saetersdal 2005); and non-agricultural habitats can also be affected as a result of the lateral movement of fertilizer in the air and groundwater (Kleijn & Snoeijing 1997; de Snoo & van der Poll 1999; Marshall & Moonen 2002). The numbers of birds were also negatively correlated with the mean input of N. In this case, the effect is likely to be indirect: high levels of agrochemicals have been associated with both a lower availability of weed seeds – which are an important component of the diet of many farmland birds (Watkinson *et al*. 2000; Marshall *et al*. 2003) – and with a lower biomass of many insect species (Di Giulio & Edwards 2003). The third significant land-use variable was crop diversity, which was positively associated with the species richness of arthropods, and particularly of bees, carabids and bugs (interaction not significant, but see Fig. 4). This is an interesting result because it shows that species richness in an agricultural landscape is not solely dependent on the semi-natural habitats, but is also affected by the diversity of forms of agriculture (Tscharntke *et al*. 2005). The case of bees is particularly significant because this group – including many ecologically demanding species requiring specific habitats for foraging and nesting (Westrich 1996) – is economically highly important for agriculture. In summary, our data show species richness at the landscape scale to be predicted by a very few variables representing land-use intensity and the spatial structure of both agricultural and semi-natural areas.

In view of these results, it is appropriate to ask why other landscape parameters had no influence on species richness; the connectivity of habitats, for example, is known to affect the ability of some species to persist in fragmented landscapes (Tscharntke *et al*. 2002; Steffan-Dewenter 2003), yet there were no significant relationships with relevant parameters such as edge density or average Euclidean nearest-neighbour distance between semi-natural elements. One possible reason is that many of the landscape parameters were correlated with each other, and the method of variable selection in the multiple regressions may have excluded some functionally important variables in favour of others. A more basic reason is probably that this study provides the 'large picture', with the results differing from those of smaller-scale studies in important ways. First, the relationships demonstrated here are based on numbers of species within large taxonomic groups, and do not necessarily reflect the needs of individual species. Appropriate measures of connectivity vary greatly according to species, and such detailed information must come from smaller-scale studies focused on individual species groups (Mason & Macdonald 2000; Steffan-Dewenter *et al*. 2002; Steffan-Dewenter 2003; Vanbergen *et al*. 2005). Second, there may be contradictory trends among different taxa within major species groups that are not evident from our broad analysis. Further analyses of our data for individual taxonomic groups at a more detailed scale may yield deeper insights into the relationships between biodiversity and agriculture across temperate Europe. For example Schweiger *et al*. (2005) analysed community composition of the arthropod groups in detail, and found responses to landscape structure and land use not only at the level of species group, but also in relation to trophic status and body size. Hendrickx *et al*. (2007) focused on the roles of α-, β- and γ-diversity in arthropod richness, and could show that the decrease in total species richness could be attributed primarily to a decrease in species diversity between local communities (β-diversity). They concluded that 'the effects of agricultural change operate at a landscape level and that examining species diversity at a local level fails to explain the total species richness of an agricultural landscape.' A detailed analysis of the composition and richness of plant functional groups (J.L., unpublished data) showed that generalizations obtained from mobile taxa such as insects are not applicable to plants, for which habitat availability and quality are the most important determinants at the landscape scale.

IMPLICATIONS FOR MANAGEMENT

Policy-makers increasingly accept that preserving biodiversity is important for the functioning and stability of ecosystems and for the provision of ecosystem services, as well as being justifiable on moral, ethical and aesthetic grounds (Loreau *et al*. 2001; Kremen 2005). For this reason, a major objective of most environmental policies related to the agricultural landscape is to maintain or enhance biodiversity. For practical reasons, most monitoring systems are based on small-scale surveys, but the results of such studies do not necessarily provide useful information about trends at regional, national or even continental scales (Kleijn *et al*. 2001; Robinson & Sutherland 2002). To improve environmental management and policy, however, reliable yet easy-to-use indicators are needed for assessing biodiversity at a large spatial scale.

Our study – one of the first to investigate biodiversity relationships at a pan-European scale – shows that at a large scale it may not be possible to use one species group as an indicator for all others. However, the results do suggest that a small list of landscape and land-use parameters can be used to assess environmental conditions for biodiversity at a large spatial scale in agricultural landscapes (e.g. for the EU Sixth Environment Action Programme, Environment 2010; http://ec.europa.eu/agriculture/capreform/index.htm). In combination with smaller-scale studies of individual species, large-scale studies such as the one presented here will improve our understanding of the mechanisms contributing to the species richness of agricultural landscapes, and help us find ways of preserving this diversity. But without waiting for such studies, a simple, first step to meeting the 2010 target of the EU Action Programme would be to increase the amount of semi-natural habitats per landscape unit. The possible trade-off between conservation benefits and economic losses may cause some discussion, but the gains would seem to be larger than any losses in total production (Green *et al*. 2005).

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Supplementary material

The following supplementary material is available for this article.

Table S1. Description of the landscape study sites.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2664.2007.01393.x.
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