

RESEARCH
PAPER



Local vs. landscape controls on diversity: a test using surface-dwelling soil macroinvertebrates of differing mobility

Jens Dauber^{1*}, Tobias Purtauf¹, Andreas Allspach², Johannes Frisch³, Karin Voigtländer⁴ and Volkmar Wolters¹

¹Department of Animal Ecology, IFZ, Justus-Liebig-University, Heinrich-Buff-Ring 26-32, 35392 Giessen, Germany; ²Wetzlarer Strasse 50, 35398 Giessen, Germany; ³Humboldt-Universität zu Berlin, Museum für Naturkunde, Invalidenstrasse 43, 10115 Berlin, Germany; and ⁴State Museum of Natural History Görlitz, Department of Soil Zoology, PF 30 01 54, 02806 Görlitz, Germany

ABSTRACT

Aim A better understanding of the processes driving local species richness and of the scales at which they operate is crucial for conserving biodiversity in cultivated landscapes. Local species richness may be controlled by ecological processes acting at larger spatial scales. Very little is known about the effect of landscape variables on soil biota. The aim of our study was to partly fill this gap by relating the local variation of surface-dwelling macroarthropod species richness to factors operating at the habitat scale (i.e. land use and habitat characteristics) and the landscape scale (i.e. composition of the surrounding matrix).

Location An agricultural landscape with a low-input farming system in Central Hesse, Germany.

Methods We focused on five taxa significantly differing in mobility and ecological requirements: ants, ground beetles, rove beetles, woodlice, and millipedes. Animals were caught with pitfall traps in fields of different land use (arable land, grassland, fallow land) and different habitat conditions (insolation, soil humidity). Composition of the surrounding landscape was analysed within a radius of 250 m around the fields.

Results Factors from both scales together explained a large amount of the local variation in species richness, but the explanatory strength of the factors differed significantly among taxa. Land use particularly affected ground beetles and woodlice, whereas ants and rove beetles were more strongly affected by habitat characteristics, namely by insolation and soil characteristics. Local species richness of diplopods depended almost entirely on the surrounding landscape. In general, the composition of the neighbouring landscape had a lower impact on the species richness of most soil macroarthropod taxa than did land use and habitat characteristics.

Main conclusions We conclude that agri-environment schemes for the conservation of biodiversity in cultivated landscapes have to secure management for both habitat quality and heterogeneous landscape mosaics.

Keywords

Agri-environment schemes, Carabidae, Diplopoda, Formicidae, habitat quality, Isopoda, landscape composition, multiscale control, soil fauna, Staphylinidae.

*Correspondence: Jens Dauber, Department of Animal Ecology, IFZ, Justus-Liebig-University, Heinrich-Buff-Ring 26-32, 35392 Giessen, Germany. E-mail: jens.dauber@allzool.bio.uni-giessen.de

INTRODUCTION

Habitat type and quality are known to be important drivers of local species richness (Rosenzweig, 1995), but additional patterns and processes causing variation in local species richness often operate simultaneously across a range of scales (Kotliar & Wiens, 1990; Ricklefs & Schluter, 1993; Whittaker *et al.*, 2001). Differences in local species richness may be caused by ecological

processes acting at larger spatial scales, and species differing in size and mobility can be regulated by different processes at the same spatial scales as well (Olf & Ritchie, 2002). To determine the causes of variation, it is necessary to link the scales at which variation in diversity is measured to the scales at which the processes potentially affecting diversity actually operate (Huston, 1999). Models of species distribution based only on local environmental conditions may thus be inadequate for most taxa

(Mazerolle & Villard, 1999). This is notably palpable for animals that depend on combinations of different habitats in the landscape to maintain viable populations (Noss, 1990; Dunning *et al.*, 1992; Söderström & Pärt, 2000; Weibull *et al.*, 2000; Steffan-Dewenter *et al.*, 2002; but see Collinge *et al.*, 2003). The search for drivers of local species richness across different spatial scales is of special importance in cultivated landscapes, where current trends of intensification and marginalization affect both habitat quality and landscape structure (Jongman, 2002). Knowing about the processes and the scales at which they operate might help to establish efficient agri-environment schemes for the conservation of biodiversity in cultivated landscapes.

Very little is known about the effect of landscape variables on soil biota (Wolters, 2001). The aim of the study presented here was to partly fill this gap by relating the local variation of soil macroarthropod species richness to factors operating at the habitat scale (i.e. land use and habitat characteristics) and the landscape scale (i.e. composition of the surrounding matrix). The focal habitats are situated in a cultivated landscape of Central Hesse (Germany). The small-scale mosaic of land-use types in this region (Hietel *et al.*, 2004) gives the opportunity to compare habitat patches differing in the composition of the surrounding landscape, without geographical differences causing a major bias. However, short spatial distances between study sites make it necessary to restrain the focus of the study to the analysis of the landscape in the immediate vicinity (250 m radius in our case). The response of taxa that might very well be affected by landscape features of a wider spatial scale (several staphylinids and carabids) was the subject of complementary analyses and is presented elsewhere (Höhn *et al.*, 2002; Purtauf *et al.*, 2002). We included five taxa of surface-dwelling soil macroarthropods (for a definition of this term see Swift *et al.*, 1979), which significantly differ in mobility and ecological requirements in our study: ants (Hymenoptera: Formicidae), ground beetles (Coleoptera: Carabidae), rove beetles (Coleoptera: Staphylinidae), woodlice (Isopoda: Oniscidae) and millipedes (Myriapoda: Diplopoda). Due to limited dispersal ability most soil macroarthropods should be particularly sensitive to characteristics of contiguous patches (cf. Dunning *et al.*, 1992).

Dispersal of most ant species results from mating flights of alates. Subsequent establishment of nests is influenced by a variety of factors including land-use type, abiotic conditions (especially temperature) and primary productivity (Folgarait, 1998; Kaspari *et al.*, 2000; Gómez *et al.*, 2003). Most carabids disperse by means of walking during foraging, mating or egg laying, but many species are also capable of flying (Nelemans, 1987). Habitat choice of carabids is influenced by land use and habitat quality (Kromp, 1999; Eyre *et al.*, 2003; Purtauf *et al.*, 2004a). Since requirements are different for feeding, hibernation and reproduction, carabids may depend on the availability of a variety of habitats in their environment (Wallin, 1985). Staphylinids are good dispersers, either actively (flight) or passively (wind; Bohac, 1999). Most species prefer dark or shady microhabitats (Bohac, 1999). Habitat preference of staphylinids is influenced by surrounding fields (Hulster & Desender, 1984; Dennis & Lys, 1992). The mobility of isopods depends on their life form, with 'long-legged runners'

being as mobile as non-flying carabids, 'rollers' often being less mobile, and some interstitial forms being very stationary (Wolters & Ekschmitt, 1997; Paoletti & Hassall, 1999). Isopods are common in agroecosystems but diversity is low (Davis & Sutton, 1978). They are sensitive to cultivation practices (Paoletti & Hassall, 1999), with moisture being the most important environmental factor affecting habitat selection (Wolters & Ekschmitt, 1997). Diplopods colonize open agricultural landscapes mostly by active migration (Wanner *et al.*, 1998) but in low species numbers (e.g. Dunger & Steinmetzger, 1981; Voigtländer, 1996). They are sensitive to regular disturbances, adverse microclimate (in particular low humidity), insufficient food resources, and monotonous habitat structures (Wolters & Ekschmitt, 1997).

The aim of the study was to identify the relative importance of patch factors (land use and habitat characteristics) in comparison to landscape effects as drivers of local species richness. Our hypotheses were that: (i) land use has a major effect on species richness of all taxa, due to considerable differences in disturbance regimes and vegetation structure between the types of land use; (ii) land-use effects on species richness are modulated by topographic influences on habitat characteristics like microclimate and soil conditions; and (iii) effects of the surrounding landscape on species richness vary with the mobility and multi-habitat requirements of the taxa considered. We used general regression models for statistical analyses. Multi-scale variance partitioning is a very powerful tool for testing hypotheses about hierarchical perspectives in statistical analyses (Borcard *et al.*, 1992; Cushman & McGarical, 2002). We expected taxa that are more specialized in habitat and resource requirements and/or that have more limited dispersal capabilities (i.e. ants, isopods and diplopods) to show a greater response towards patch factors, whereas more generalist taxa with higher movement capacities (i.e. carabids and staphylinids) should be more concerned with the composition of the landscape (With & Crist, 1995; Suarez-Seoane & Baudry, 2002).

MATERIALS AND METHODS

Study area and study sites

The study was carried out in the rural district of Hohenahr-Erda (270–385 m a.s.l., 50°42' N, 8°30' E), which is situated in a highland region (Lahn-Dill-Bergland, Central Hesse; Germany). A fine-grained mosaic of different land-use types covering about 465 ha characterizes the cultivated area of this district (Fig. 1). Mean size of single agricultural fields is about 0.3 ha for managed grassland, 0.4 ha for arable land and 0.3 ha for fallow land. Major soil types are acidic regosols and moderately deep cambisols. Mean annual temperature is 8 °C, and mean annual precipitation amounts to 700–800 mm (Deutscher Wetterdienst, 1981; Frede & Bach, 1999). The study focused on three different types of land use: (A) arable land cultivated with either wheat, barley, or spelt; (G) grasslands, managed by mowing in spring and grazing in autumn; and (F) fallow land with shrubby vegetation of Scots Broom *Cytisus scoparius*. The focal sites were interspersed within the study area and included 12 crop fields, 12 grasslands

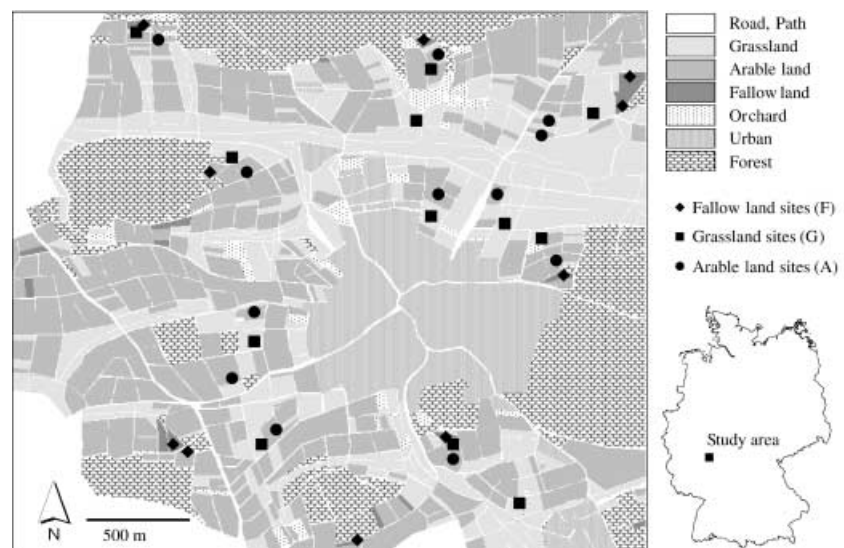


Figure 1 The landscape mosaic of the study area Hohenahr-Erda (270–385 m a.s.l., 50°42' N, 8°30' E), which is situated in a highland region (Lahn-Dill-Bergland, Central Hesse; Germany), and locations of the study sites.

Table 1 Range of variation (maximum vs. minimum) of habitat and landscape variables, latter measured within a radius of 250 m surrounding the study sites. Data are given separately for arable land sites (A), grassland sites (G) and fallow land sites (F). CA = area of arable land, CF = area of fallow land, CG = area of grassland, FE = length of forest edge, SI = insolation, CTI = compound topographic index

		CA (m ²)	CG (m ²)	CF (m ²)	FE (m)	SI (kW m ⁻²)	CTI
A (<i>n</i> = 12)	max	100,719	145,799	13,963	1044	0.31	9.97
	min	21,327	22,127	0	0	0.26	6.88
G (<i>n</i> = 12)	max	102,534	127,627	13,939	1079	0.32	10.86
	min	36,580	12,276	0	0	0.24	6.67
F (<i>n</i> = 10)	max	128,240	82,467	19,319	1082	0.32	10.08
	min	41,736	0	1,144	557	0.24	6.29

and 10 areas of fallow land located at slopes of different aspect (Fig. 1).

Sampling and species determination

Surface-dwelling soil macrofauna were sampled with pitfall traps consisting of 500 mL polyethylene beakers (diameter 85 mm) filled with approx. 170 mL of an ethanol–glycerine solution (2 : 1). A detergent was added to reduce surface tension. Rain covers (acrylic glass, 250 mm × 250 mm) were placed approximately 10 cm above each trap to prevent flooding by rain. Five pitfall traps were placed about 10 m from each other at the centre of each site. The majority of samples were taken during two four-week periods in May and September in 1997. Three additional crop fields and four fallow lands were sampled using the same approach during similar sampling periods in 1998. Catches of pitfall traps were pooled to total number of species per site. All taxa were determined to the species level using standard keys.

Habitat characterization

We have chosen environmental variables following two criteria: (i) provision of a reasonable gradient, and (ii) likelihood to affect

the focal taxa. All taxa included in this study are sensitive to temperature and humidity (Dunger, 1983). We therefore chose insolation and soil humidity to characterize habitat conditions. Both parameters were calculated by means of a digital elevation model with 20 m grid size (DEM; Hessische Verwaltung für Regionalentwicklung, Kataster und Flurneuordnung, Wiesbaden), using the primary topographic attributes *slope* and *aspect* (ArcView 3.2 GIS, ESRI, New York, USA). Insolation (SI) was calculated as the mean annual intensity of solar radiation (kW m⁻²) that reaches a position on the earth surface. Soil humidity was calculated using the CTI (compound topographic or wetness index; Beven & Kirkby, 1979), showing the effect of topography on the location and size of areas of water accumulation in soils. The range of variation of habitat characteristics is given in Table 1.

Landscape analyses

The landscape surrounding each individual study site was analysed within a radius of 250 m. The study was designed to focus on effects of the neighbouring landscape, and possible landscape effects of the wider spatial context (> 250 m radius) were not within the scope of this paper. The study sites were selected to

show a high variation of landscape composition within the radius of 250 m (Table 1), but due to the short geographical distances between the study sites, very small variation in landscape data would have to be expected at larger spatial scales due to overlap of radii. We calculated the cover of arable land (CA), grassland (CG) and fallow land (CF) in square metres and the length of forest edges (FE) in metres from a digital thematic vector map of land use that was drawn based on field surveys of 1996 and 1997, using ArcView 3.2 GIS software (ESRI, New York, USA).

Data analyses

The impact of land use and habitat characteristics of the study sites and of the composition of the landscape surrounding the study sites on the species richness of the macrofauna taxa were tested simultaneously in multiple models by means of General Regression Models (GRM), using the forward stepwise procedure to eliminate non-significant parameters from the models. GRM implements stepwise and best-subset regression for Analysis of Covariance (ANCOVA) design with categorical and continuous predictor variables (StatSoft, Inc., 2001). Land use (A, G, F) was included in the regression models as a categorical predictor variable, whereas all other variables (SI, CTI, CA, CF, CG, and FE) were included as continuous predictor variables. We also considered possible interactions between land use and the continuous variables, as certain habitat characteristics might enhance landscape effects and vice versa for a given taxon (Mazerolle & Villard, 1999). The part of variance explained by each variable was estimated from the SS-values (sum of square errors).

Prior to analyses we checked for homogeneity of variances by calculating Levene's test. All data were standardized to z-scores (Zar, 1999) to allow for a comparison of the differently scaled predictor variables in variance partitioning. The Unequal N HSD post hoc test was used to test for significant differences in the mean species richness between the different types of land use (Winer *et al.*, 1991). In cases of significant interactions between land use and a continuous predictor variable we calculated the residuals of species richness for the respective variable adjusted for the other variables in the model. A comparison of the original variable against the residuals makes it possible to discriminate between the effects of different types of land use in the regression model. All statistical treatments were performed using the STATISTICA for Windows Package version 6 (StatSoft, Inc., 2001).

RESULTS

The total number of species was 25 for ants, 95 for carabids, 130 for staphylinids, 13 for isopods, and 11 for diplopods (see Appendix S1 in Supplementary Material). Species richness of carabids was highest in arable land sites, while that of all other taxa was highest in fallow land sites (Table 2). General regression models on species richness were significant at $P < 0.001$ for all taxa (Table 3). The effects of the individual variables included in the models were at least significant at $P < 0.05$. Taxon-specific species richness varied with land use, habitat characteristics and

Table 2 Total and mean species richness of replicate sites and standard deviations of five taxa in different land-use types sampled with pitfall traps in the district of Hohenahr-Erda in Central Hesse, Germany. Different letters indicate that values are significantly different ($P < 0.05$; Unequal N HSD Test)

		Arable land ($n = 12$)	Grassland ($n = 12$)	Fallow land ($n = 10$)
Carabids	total	75	57	64
	mean	$26.6 \pm 3.7a$	$19.3 \pm 4.9b$	$20.4 \pm 4.6b$
Staphylinids	total	71	70	97
	mean	$18.8 \pm 6.1a$	$21.7 \pm 7.0a$	$33.3 \pm 6.3b$
Ants	total	17	17	21
	mean	$6.3 \pm 2.5a$	$7.0 \pm 3.4a$	$9.1 \pm 3.2b$
Isopods	total	6	10	12
	mean	$1.1 \pm 1.0a$	$2.1 \pm 0.8b$	$3.0 \pm 1.5c$
Diplopods	total	9	10	11
	mean	$2.0 \pm 1.2a$	$2.7 \pm 1.4a$	$4.0 \pm 0.9b$

Table 3 Multiple coefficients of determination and P -levels of the general regression models calculated for the five taxa. ****, $P < 0.0001$

	R^2	P
Carabids	0.68	****
Staphylinids	0.74	****
Ants	0.83	****
Isopods	0.77	****
Diplopods	0.43	****

landscape variables (Fig. 2). For all taxa other than diplopods, landscape variables explained less variance than land use and habitat characteristics (Fig. 2).

Land use at the study sites explained more than 40% of the variance of carabid species richness. Significantly more carabid species occurred in arable land than in grassland and fallow land (Table 2). Soil humidity was negatively correlated to carabid species richness. Landscape variables explained approximately 15% of total variance. Species richness increased with the increasing length of forest edges and decreased with the increasing amount of fallow land cover.

Species richness of isopods also largely depended on land use. It was significantly higher in fallow land than in grassland and significantly lower in arable land than in grassland (Table 2). Species richness of isopods was slightly positively related to insolation. The significant interaction reflects that the effect of soil humidity varied among land use types. A comparison of the CTI against its adjusted residuals revealed a positive correlation between isopod species richness and soil humidity in arable land and grassland, and a negative correlation in fallow land (Table 4). The effect of the landscape also depended on the land use of the study sites. Cover of arable land in the vicinity had no effect on species richness in arable fields, whereas it had a positive effect in grassland and a negative effect in fallow land (Table 4).

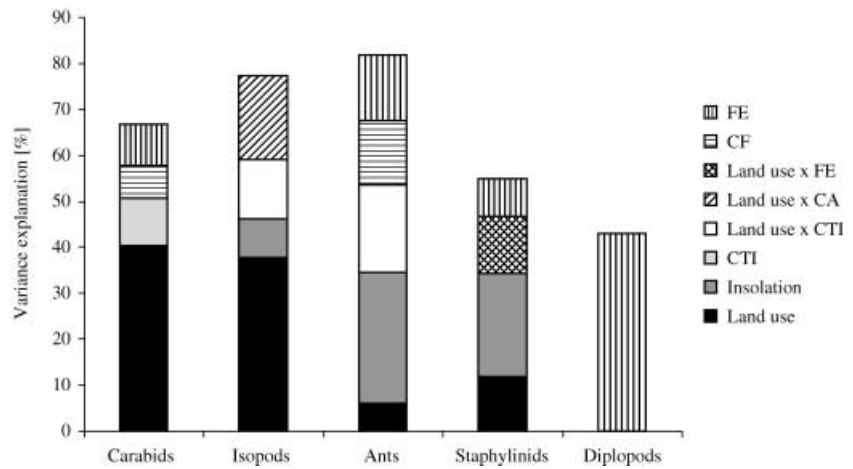


Figure 2 Decomposition of variance explanation of the general regression models for the five taxa. The different parts of the columns show the proportion of variance explained by the respective variable. FE = length of forest edge (m), CF = area of fallow land (m²), CA = area of arable land (m²), CTI = compound topographical index.

Table 4 A coarse classification of the interactions between land use and habitat characteristics or landscape variables as predictors of species richness of the given taxa. The classification is based on a comparison of the original variable against the adjusted residuals, which allows for a differentiated interpretation of the result of the regression for the single types of land use. 0 = no correlation, – = negative correlation, + = positive correlation between the residuals of species richness and the habitat/landscape variable for a certain type of land use. A = arable land; G = grassland; F = fallow land; FE = length of forest edge (m); CTI = wetness index; CA = cover of arable land (m²) in surrounding landscape ($r = 250$ m)

		Land use			P-level
		A	G	F	
Staphylinids	FE	0	+	+	0.04
Ants	CTI	0	–	+	0.00008
Isopods	CA	0	+	–	0.0004
Isopods	CTI	+	0	–	0.002

Species richness of ants was strongly positively related to insolation, which accounted for more than 28% of the total variance (Fig. 2). As for isopods, the impact of soil humidity strongly depended on the land use of the study sites. A comparison of the CTI against its adjusted residuals revealed a positive relationship between soil humidity and ant species richness in fallow land, a negative relationship in grasslands, and no relationship in arable land (Table 4). Though the effect of land use on species richness was comparatively low, there were significantly more species in fallow land than in the other two land use types (Table 2). The fact that local species richness increased with increasing length of forest edges and decreased with increasing cover of fallow land indicates a significant effect of the surrounding landscape.

Similar to ants, species richness of staphylinids was more related to habitat characteristics than to land use (Fig. 2). Insolation explained the highest share of the total variance. In contrast to ants, however, species richness of staphylinids was negatively related to higher insolation values. There were significantly more species found on fallow land than on arable land or grassland

(Table 2). Length of forest edges was positively correlated with species richness, but the strength of the effect varied with land use (Fig. 2). The comparison of the original variable against its adjusted residuals revealed a positive effect of forest edges on species richness of both fallow land and grassland, whereas this effect was not significant in arable land (Table 4).

Species richness of diplopods, in contrast to all other taxa, was almost solely related to the composition of the surrounding landscape, with the length of the forest edge explaining over 43% of the total variance (Fig. 2). In addition, species richness of diplopods was significantly higher in fallow land than in the other two land use types (Table 2). However, this effect was not strong enough to become a significant part of the regression model.

DISCUSSION

We compared the effect of factors affecting the local species richness of soil macroarthropods at the patch scale (land use and habitat characteristics) to the effect of the surrounding landscape. The variables included in the GRMs together explained a large amount of the variation of local species richness of most taxa. Moreover, significant interactions between land use and both habitat characteristics and landscape variables indicate that the effects of the different drivers of species richness do not operate independently of each other. The strength of the variables operating at the different spheres differed greatly among taxa. Land use particularly affected carabids and isopods, whereas ants and staphylinids were more strongly affected by habitat characteristics, namely by insolation. Local species richness of diplopods depended almost entirely on the surrounding landscape. It has been concluded from studies with other taxa that agriculture, operating at several levels from field to landscape, induces differential response of communities according to their ecological traits (Burel *et al.*, 2004). Our results confirm the hypothesis that this also applies to surface-dwelling soil macroarthropods.

Our study highlights the positive effect of fallow land on the species richness of all taxa other than carabids. The preference of the latter group for arable fields found in our study has been reported by many authors (cf. Ekschmitt *et al.*, 1997). This is easily explained by the fact that many carabids inhabiting the

cultural landscape of Western Europe originate from open and dry steppes (Andersen, 2000). Other soil arthropods, in contrast, tend to prefer habitats that are characterized by a heterogeneous vegetation structure, accumulated soil organic matter and low disturbance from agricultural production such as fallows. Decomposers like isopods, for example, may profit from a variety of factors including availability of organic matter from different sources, low input of pesticides, diverse habitat structure and accessibility of shelter sites (Pokarzhevskii & Krivolutskii, 1997; Paoletti & Hassall, 1999).

We found that ants are particularly affected by habitat characteristics, namely insolation and soil humidity. This is consistent with the conclusion that the highest species richness of ants in Central Europe is reached in highly insolated habitats with well drained soils and a large supply of possible nesting sites (Seifert, 1996). The relatively sessile soil-nesting colonies depend on a certain envelope of temperature and soil humidity for foraging and successful rearing of the brood. Ants even modify the properties of their nest structures, in order to regulate the microclimate within their nests, particularly with respect to the high temperatures needed for optimal brood rearing (Woodell & King, 1991). The majority of staphylinids, in contrast, prefer dark or shaded microhabitats and their activity is influenced by the intensity of lighting (Bohac, 1999). This explains the negative effect of insolation on staphylinid species richness.

In general, the composition of the neighbouring landscape had a lower impact on the species richness of most soil macroarthropod taxa than did land use and habitat characteristics. This is consistent with the results reported for other animal groups and plants (Söderström *et al.*, 2001; Collinge *et al.*, 2003; Dauber *et al.*, 2003; Jeanneret *et al.*, 2003; Weibull & Östman, 2003; Krauss *et al.*, 2004; Virkkala *et al.*, 2004). However, landscape variables still explained a certain amount of the local variation in species richness of all taxa and thus cannot be ignored. The particularly strong effect of forest edges on diplopods (43% of variance explanation) confirms that many species of this taxon need forests in the vicinity to serve as refuges and sources of recolonization (Dunger & Voigtländer, 1990; Scheu, 1996; Tajovský, 1999). Similarly, surrounding forests have been shown to play a major role in the colonization of mining sites (Dunger & Voigtländer, 1990) and fallow lands (Strüve-Kusenber, 1981). Consequently, most diplopod species found at our study sites are forest species with a comparatively good — but still limited (cf. Paoletti & Hassall, 1999) — dispersal capability. With a few exceptions, agricultural management thus does not increase diplopod diversity at the landscape level, by allowing the invasion of new species from more distant open habitats (Wolters, 2001). Many species found in grassland and arable land can be characterized as forest species and were caught on the sites by ‘accident’, i.e. they most probably do not belong to the site but were travelling through.

Mobile taxa should respond more strongly to features of the surrounding landscape than less mobile taxa (With & Crist, 1995). Though information concerning this issue is still sparse for soil macroarthropods other than carabids (e.g. Kinnunen *et al.*, 1996; Niemelä, 2001; Wolters, 2001), this has been proven for various other taxa such as pollinators (Weibull *et al.*, 2000;

Steffan-Dewenter *et al.*, 2002; Hirsch *et al.*, 2003), as well as herbivorous beetles and their parasitoids (Thies *et al.*, 2003). In contrast, we have found that good dispersers (e.g. staphylinids) were equally or even less affected by the neighbouring landscape than bad dispersers (e.g. diplopods). The low spatial extent of the surrounding landscape chosen for our analysis can partly explain the somewhat deviating result of our study. This conclusion is supported by the strong landscape effects on carabids and staphylinids revealed by complementary studies that were carried out in the same region but addressed a much larger spatial scale (Höhn *et al.*, 2002; Purtauf *et al.*, 2002; Purtauf *et al.*, 2004b). However, the fact that good dispersers are affected by both the neighbouring matrix and the wider landscape highlights the need for multiscale approaches to biodiversity analyses, simultaneously including variables operating at different spatial and perhaps temporal scales (e.g. Cushman & McGarical, 2002).

CONCLUSIONS

Noss (1983) suggested that management of a landscape mosaic would provide a more efficient conservation strategy than the management of single sites. This suggestion is in accordance with the ‘habitat heterogeneity hypothesis’, which assumes that structurally complex habitats — comprising spatial scales from patch to landscape — may provide more niches and ways of resource exploitation and thus increase species diversity (MacArthur & Wilson, 1967; Tews *et al.*, 2004). Intensification of agricultural production or marginalization of whole regions threatens the biodiversity of Europe’s cultural landscapes by reducing spatial heterogeneity (Jongman, 2002). Mazerolle & Villard (1999) suggested that the inclusion of landscape characteristics would enhance conservation strategies if the landscape scale were properly defined with respect to the taxon or taxa under investigation. On the one hand, our results corroborated these findings, showing that the composition of habitats in a landscape has to be considered for the prediction and conservation of local species richness. On the other hand, we have to stress that habitat quality, either expressed by the type of land use or by microclimate and soil condition are of great importance for the taxa studied. Therefore, we conclude that agri-environment schemes for the conservation of biodiversity in cultivated landscapes have to secure management for both habitat quality and heterogeneous landscape mosaics. Furthermore, our results clearly demonstrate that the use of single indicator taxa for the elaboration and or evaluation of biodiversity conservation measures of habitats and landscape mosaics has to be criticised (compare, e.g. Noss, 1990; Lambeck, 1997; Söderström *et al.*, 2001; Dauber *et al.*, 2003; Weibull *et al.*, 2003). We agree that there are no general rules relating species diversity to habitat and landscape features, but that the relationship strongly depends on the organism and the region under study (cf. Jeanneret *et al.*, 2003).

ACKNOWLEDGEMENTS

We thank Thorsten Behrens for his support in GIS analyses. Sabine Hassek assisted in field work and carabid determination.

Patrick Höhn assisted in staphylinid determination. The digital thematic vector map of land use was drawn up and provided by the Division of Landscape Ecology and Landscape Planning of the Justus-Liebig-University Giessen. Matty Berg, Jan Lagerlöf, David Currie and two anonymous reviewers provided valuable suggestions and comments on the manuscript. The work was supported by the German Research Foundation (DFG; SFB 299).

SUPPLEMENTARY MATERIAL

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/GEB/GEB150/GEB150sm.htm>

Appendix S1 Species list of Staphylinidae, Carabidae, Formicidae, Isopoda and Diplopoda sampled in arable land, grassland and fallow land in the district of Hohenahr-Erda (270 to 385 m a.s.l., 50°42' N, 8°30' E) in central Hesse, Germany.

REFERENCES

- Andersen, J. (2000) What is the origin of the carabid beetle fauna of dry, anthropogenic habitats in western Europe? *Journal of Biogeography*, **27**, 795–806.
- Beven, K.J. & Kirkby, M.J. (1979) A physically based, variable contributing area model of basin hydrology. *Hydrological Sciences Bulletin*, **24**, 43–69.
- Bohac, J. (1999) Staphylinid beetles as bioindicators. *Agriculture, Ecosystems and Environment*, **74**, 357–372.
- Borcard, D., Legendre, P. & Drapeau, P. (1992) Partialling out the spatial component of ecological variation. *Ecology*, **73**, 1045–1055.
- Burel, F., Butet, A., Delettre, Y.R. & Millan de la Pena, N. (2004) Differential response of selected taxa to landscape context and agricultural intensification. *Landscape and Urban Planning*, **67**, 195–204.
- Collinge, S.K., Prudic, K.L. & Oliver, J.C. (2003) Effects of local habitat characteristics and landscape context on grassland butterfly diversity. *Conservation Biology*, **17**, 178–187.
- Cushman, S.A. & McGarical, K. (2002) Hierarchical, multi-scale decomposition of species–environment relationships. *Landscape Ecology*, **17**, 637–646.
- Dauber, J., Hirsch, M., Simmering, S., Waldhardt, R. & Otte, A. & Wolters, V. (2003) Landscape structure as an indicator of biodiversity: matrix effects on species richness. *Agriculture, Ecosystems and Environment*, **98**, 321–329.
- Davis, R.C. & Sutton, S.L. (1978) A comparative study of changes in biomass of isopods inhabiting dune grasslands. *Scientific Proceedings Royal Dublin Society Series A*, **6**, 223–233.
- Dennis, P. & Lys, G.L.A. (1992) Field margins: can they enhance natural enemy population densities and general arthropod diversity on farmland? *Agriculture, Ecosystems and Environment*, **40**, 25–31.
- Deutscher Wetterdienst (1981) *Standortkarte von Hessen: Das Klima*. Hessisches Landesamt für Ernährung, Landwirtschaft und Landesentwicklung, Wiesbaden.
- Dunger, W. (1983) *Tiere im Boden*. A. Ziemsen Verlag, Wittenberg.
- Dunger, W. & Steinmetzger, K. (1981) Ökologische Untersuchungen an Diplopoda einer Rasen-Wald-Catena im Thüringer Kalkgebiet. *Zoologisches Jahrbuch Systematik*, **108**, 519–533.
- Dunger, W. & Voigtländer, K. (1990) Succession of myriapoda in primary colonization of reclaimed land. *Proceedings 7th International Congress of Myriapodology* (ed. by A. Minelli), pp. 219–227. E.J. Brill, Vittorio Veneto, Italy.
- Dunning, J.B., Danielson, B.J. & Pulliam, H.R. (1992) Ecological processes that affect populations in complex landscapes. *Oikos*, **65**, 169–175.
- Ekschmitt, K., Wolters, V. & Weber, M. (1997) Spiders, carabids, and staphylinids: the ecological potential of predatory macroarthropods. *Fauna in soil ecosystems: recycling processes, nutrient fluxes, and agricultural production* (ed. by G. Benckiser), pp. 307–362. Marcel Dekker, New York.
- Eyre, M.D., Luff, M.L., Staley, J.R. & Telfer, M.G. (2003) The relationship between British ground beetles (Coleoptera: Carabidae) and land cover. *Journal of Biogeography*, **30**, 719–730.
- Folgarait, P.J. (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and Conservation*, **7**, 1221–1244.
- Frede, H.-G. & Bach, M. (1999) Perspectives for peripheral regions. *Zeitschrift für Kulturtechnik und Landentwicklung*, **40**, 193–196.
- Gómez, C., Casellas, D., Oliveras, J. & Bas, J.M. (2003) Structure of ground-foraging ant assemblages in relation to land-use change in the northwestern Mediterranean region. *Biodiversity and Conservation*, **12**, 2135–2146.
- Hietel, E., Waldhardt, R. & Otte, A. (2004) Analysing land-cover changes in relation to environmental variables in Hesse, Germany. *Landscape Ecology*, **19**, 473–489.
- Hirsch, M., Pfaff, S. & Wolters, V. (2003) The influence of matrix type on flower visitors of *Centaurea jacea* L. *Agriculture, Ecosystems and Environment*, **98**, 331–337.
- Höhn, P., Purtauf, T., Wolters, V. & Dauber, J. (2002) Landscape effects on rove beetles (Coleoptera: Staphylinidae) in wheat fields. *Verhandlungen der Gesellschaft für Ökologie*, **32**, 46.
- Hulster, M.D. & Desender, K. (1984) Ecological and faunal studies of Coleoptera in agricultural land. IV. Hibernation of Staphylinidae in agroecosystems. *Pedobiologia*, **26**, 65–73.
- Huston, M.A. (1999) Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos*, **86**, 393–401.
- Jeanneret, P.H., Schüpbach, B. & Luka, H. (2003) Quantifying the impact of landscape and habitat features on biodiversity in agricultural landscapes. *Agriculture, Ecosystems and Environment*, **98**, 311–320.
- Jongman, R.H.G. (2002) Homogenisation and fragmentation of the European landscape: ecological consequences and solutions. *Landscape and Urban Planning*, **58**, 211–221.
- Kaspari, M., Alonso, L. & O'Donnell, S. (2000) Three energy variables predict ant abundance at a geographical scale. *Proceedings Royal Society London B*, **267**, 485–489.
- Kinnunen, H., Järveläinen, K., Pakkala, T. & Tiainen, J. (1996) The effect of isolation on the occurrence of farmland carabids in a fragmented landscape. *Annales Zoologici Fennici*, **33**, 165–171.

- Kotliar, N.B. & Wiens, J.A. (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos*, **59**, 253–260.
- Krauss, J., Klein, A.-M., Steffan-Dewenter, I. & Tscharrntke, T. (2004) Effects of habitat area, isolation, and landscape diversity on plant species richness of calcareous grasslands. *Biodiversity and Conservation*, **13**, 1427–1439.
- Kromp, B. (1999) Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. *Agriculture, Ecosystems and Environment*, **74**, 187–228.
- Lambeck, R.J. (1997) Focal species: a multi-species umbrella for nature conservation. *Conservation Biology*, **11**, 849–856.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton.
- Mazerolle, M.J. & Villard, M.-A. (1999) Patch characteristics and landscape context as predictors of species presence and abundance: a review. *Ecoscience*, **6**, 117–124.
- Nelemans, M.N.E. (1987) Possibilities for flight in the carabid beetle *Nebria brevicollis* (F.). *Oecologia*, **72**, 502–509.
- Niemelä, J. (2001) Carabid beetles (Coleoptera: Carabidae) and habitat fragmentation: a review. *European Journal of Entomology*, **98**, 127–132.
- Noss, R.F. (1983) A regional landscape approach to maintain biodiversity. *Bioscience*, **33**, 700–706.
- Noss, R.F. (1990) Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology*, **4**, 355–364.
- Olf, H. & Ritchie, M.E. (2002) Fragmented nature: consequences for biodiversity. *Landscape and Urban Planning*, **58**, 83–92.
- Paoletti, M.G. & Hassall, M. (1999) Woodlice (Isopoda: Oniscidae): their potential for assessing sustainability and use as bioindicators. *Agriculture, Ecosystems and Environment*, **74**, 157–165.
- Pokarzhevskii, A.D. & Krivolutskii, D.A. (1997) Problems of estimating and maintaining biodiversity of soil biota in natural and agroecosystems: a case study of chernozem soil. *Agriculture, Ecosystems and Environment*, **62**, 127–133.
- Purtauf, T., Dauber, J. & Wolters, V. (2004a) Carabid communities in the spatio-temporal mosaic of a rural landscape. *Landscape and Urban Planning*, **67**, 185–193.
- Purtauf, T., Dauber, J. & Wolters, V. (2004b) The response of carabids to landscape simplification differs between trophic groups. *Oecologia*. DOI: 10.1007/s00442-004-1740-y.
- Purtauf, T., Wolters, V., Tscharrntke, T., Schmidt, M. & Dauber, J. (2002) Landscape complexity and biodiversity of carabids in wheat fields. *Verhandlungen der Gesellschaft für Ökologie*, **32**, 34.
- Ricklefs, R.E. & Schluter, D. (1993) Species diversity: Regional and historical influences. *Species diversity in ecological communities: historical and geographical perspectives* (ed. by R. E. Ricklefs and D. Schluter), pp. 350–363. University of Chicago Press, Chicago.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Scheu, S. (1996) Changes in the millipede (Diplopoda) community during secondary succession from a wheat field to a beech-wood on limestone. *Acta myriapodologica* (ed. by J. J. Geoffroy, J. J. Mauries and M. Nguyen Duy-Jaquemin), pp. 647–656. Mémoires du Muséum national d'Histoire naturelle, **169**, Paris.
- Seifert, B. (1996) *Ameisen beobachten, bestimmen*. Weltbild Verlag, Augsburg.
- Söderström, B. & Pärt, T. (2000) Influence of landscape scale on farmland birds in seminatural pastures. *Conservation Biology*, **14**, 522–533.
- Söderström, B., Svensson, B., Vessby, C. & Glimskär, A. (2001) Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. *Biodiversity and Conservation*, **10**, 1839–1863.
- StatSoft, Inc. (2001) STATISTICA (data analysis software system), version 6. www.statsoft.com, Tulsa, USA.
- Steffan-Dewenter, I., Münzenberg, U., Bürger, C.H., Thies, C. & Tscharrntke, T. (2002) Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, **83**, 1421–1432.
- Strüve-Kusenber, R. (1981) Sukzession und trophische Struktur der Bodenfauna von Brachlandflächen. *Pedobiologia*, **21**, 126–137.
- Suarez-Seoane, S. & Baudry, J. (2002) Scale dependence of spatial patterns and cartography on the detection of landscape change: relationships with species' perception. *Ecography*, **25**, 499–511.
- Swift, M.J., Heal, O.W. & Anderson, J.M. (1979) *Decomposition in terrestrial ecosystems*. Blackwell Scientific Publications, Oxford.
- Tajovský, K. (1999) Epigeic activity of millipedes (Diplopoda) in abandoned fields. *Soil zoological problems in Central Europe* (ed. by V. Pižl and K. Tajovský), pp. 351–356. ISB ASCR, České Budjovice.
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M. & Jeltsch, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, **31**, 79–92.
- Thies, C., Steffan-Dewenter, I. & Tscharrntke, T. (2003) Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos*, **101**, 18–25.
- Virkkala, R., Luoto, M. & Rainio, K. (2004) Effects of landscape composition on farmland and red-listed birds in boreal agricultural-forest mosaics. *Ecography*, **27**, 273–284.
- Voigtländer, K. (1996) Diplopoden und Chilopoden von Trockenstandorten des Hallenser Raumes (Ostdeutschland). *Hercynia N. F. Halle*, **30**, 109–126.
- Wallin, H. (1985) Spatial and temporal distribution of some abundant carabid beetles (Coleoptera: Carabidae) in cereal fields and adjacent habitats. *Pedobiologia*, **28**, 19–34.
- Wanner, M., Dunger, W., Schulz, H.-J. & Voigtländer, K. (1998) Primary immigration of soil organisms on coal mined areas in Eastern Germany. *Soil zoological problems in Central Europe* (ed. by V. Pižl and K. Tajovský), pp. 267–275. ISB ASCR, České Budjovice.
- Weibull, A.-C.H., Bengtsson, J. & Nohlgren, E. (2000) Diversity of butterflies in the agricultural landscape: the role of farming system and landscape heterogeneity. *Ecography*, **23**, 743–750.

- Weibull, A.-C.H. & Östman, Ö. (2003) Species composition in agroecosystems: the effect of landscape, habitat, and farm management. *Basic and Applied Ecology*, **4**, 349–361.
- Weibull, A.-C.H., Östman, Ö. & Granqvist, Å. (2003) Species richness in agroecosystems: the effect of landscape, habitat and farm management. *Biodiversity and Conservation*, **12**, 1335–1355.
- Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453–470.
- Winer, B.J., Brown, D.R. & Michels, K.M. (1991) *Statistical principals in experimental design*, 3rd edn. McGraw-Hill, New York.
- With, K.A. & Crist, T.O. (1995) Critical thresholds in species' responses to landscape structure. *Ecology*, **76**, 2446–2459.
- Wolters, V. (2001) Biodiversity of soil fauna and its function. *European Journal of Soil Biology*, **37**, 221–227.
- Wolters, V. & Ekschmitt, K. (1997) Gastropods, Isopods, Diplopods, and Chilopods: neglected groups of the decomposer food web. *Fauna in soil ecosystems: recycling processes, nutrient fluxes, and agricultural production* (ed. by G. Benckiser), pp. 265–306. Marcel Dekker, New York.
- Woodell, S.R.J. & King, T.J. (1991) The influence of mound building ants on British lowland vegetation. *Ant-plant interactions* (ed. by C. R. Huxley and D. F. Cutler), pp. 521–535. Oxford University Press, Oxford.
- Zar, J.H. (1999) *Biostatistical analysis*. Prentice Hall, New Jersey.

BIOSKETCHES

Jens Dauber leads the landscape ecology group at the Department of Animal Ecology, Giessen. His fields of research are biodiversity in agricultural landscapes, and functioning of ants as ecosystem engineers.

Tobias Purtauf is a PhD student at the Department of Animal Ecology, Giessen. He focuses on the effects of spatio-temporal landscape mosaics on ground beetle communities.

Andreas Allspach is a taxonomist with a special interest in Isopoda.

Johannes Frisch is the curator of the beetle collection at the Museum für Naturkunde, Berlin. His main research interest is the taxonomy of Staphylinidae especially of the genus *Scopaeus*.

Karin Voigtländer is curator in chief of the soil zoological collection of the Museum of Natural History, Görlitz. Her main research interests are focused on the taxonomy of Myriapods, on conservation ecology, and on restoration ecology of mine sites.

Volkmar Wolters is head of the Animal Ecology Group and is the director of the Department of Zoology at the University of Giessen. He has long-term expertise in soil biology, landscape ecology, and ecosystem research.