RESEARCH PAPER

Effects of landscape structure and land-use intensity on similarity of plant and animal communities

Carsten F. Dormann[1]*, Oliver Schweiger[2], Isabel Augenstein[1,9], Debra Bailey[3], Regula Billeter[4], Geert de Blust[5], Riccardo DeFilippi[3], Mark Frenzel[2], Frederik Hendrickx[7], Felix Herzog[3], Stefan Klotz[2], Jaan Liira[8], Jean-Pierre Maelfait[5], Torsten Schmidt[2], Marjan Speelmans[7], Walter K. R. E. van Wingerden[6] and Martin Zobel[8]

[1]*Computational Landscape Ecology, UFZ Centre for Environmental Research, Permoserstrasse 15, 04318 Leipzig, Germany.*
[2]*Community Ecology, UFZ Centre for Environmental Research, Theodor-Lieser-Strasse 4, D-06120 Halle/Saale, Germany.*
[3]*Swiss Federal Research Station for Agroecology and Agriculture, Reckenholzstrasse 191, 8046 Zürich, Switzerland.*
[4]*Swiss Federal Institute of Technology (ETH), Zürichbergstrasse 38, 8044 Zürich, Switzerland.*
[5]*Institute of Nature Conservation, Division of Landscape Ecology and Nature Management, Kliniekstraat 25, B-1070 Brussels, Belgium.*
[6]*Alterra Green World Research, Department of Landscape Ecology, P.O. Box 47, 6700 AA Wageningen, The Netherlands.*
[7]*Terrestrial Ecology Unit (TEREC), Department of Biology, Ghent University, K.L. Ledeganckstraat 35, 9000 Gent, Belgium.*
[8]*Institute of Botany and Ecology, University of Tartu, Lai 40, 51005 Tartu, Estonia.*
[9]*Chair for Landscape Development Strategy and Management, Technical University Munich, Am Hochanger 13, 85354 Freising, Germany.*

*Correspondence: Carsten F. Dormann, Computational Landscape Ecology, UFZ Centre for Environmental Research, Permoserstrasse 15, 04318 Leipzig, Germany. E-mail: carsten.dormann@ufz.de

ABSTRACT

Aim Species richness in itself is not always sufficient to evaluate land management strategies for nature conservation. The exchange of species between local communities may be affected by landscape structure and land-use intensity. Thus, species turnover, and its inverse, community similarity, may be useful measures of landscape integrity from a diversity perspective.

Location A European transect from France to Estonia.

Methods We measured the similarity of plant, bird, wild bee, true bug, carabid beetle, hoverfly and spider communities sampled along gradients in landscape composition (e.g. total availability of semi-natural habitat), landscape configuration (e.g. fragmentation) and land-use intensity (e.g. pesticide loads).

Results Total availability of semi-natural habitats had little effect on community similarity, except for bird communities, which were more homogeneous in more natural landscapes. Bee communities, in contrast, were less similar in landscapes with higher percentages of semi-natural habitats. Increased landscape fragmentation decreased similarity of true bug communities, while plant communities showed a nonlinear, U-shaped response. More intense land use, specifically increased pesticide burden, led to a homogenization of bee, bug and spider communities within sites. In these cases, habitat fragmentation interacted with pesticide load. Hoverfly and carabid beetle community similarity was differentially affected by higher pesticide levels: for carabid beetles similarity decreased, while for hoverflies we observed a U-shaped relationship.

Main conclusions Our study demonstrates the effects of landscape composition, configuration and land-use intensity on the similarity of communities. It indicates reduced exchange of species between communities in landscapes dominated by agricultural activities. Taxonomic groups differed in their responses to environmental drivers and using but one group as an indicator for 'biodiversity' as such would thus not be advisable.

Keywords

Arthropods, birds, community similarity, dispersal, diversity, Europe, fragmentation, landscape ecology, land-use management, pesticide load.

INTRODUCTION

Most studies of the effects of change in land use on biodiversity focus on species richness at the local (α-diversity) or regional (γ-diversity) scale. However, regional land use also acts on ecological processes affecting community composition and the exchange of species among local communities (Thomas *et al.*, 2001; Hutton & Giller, 2003; Burel *et al.*, 2004; Schweiger *et al.*, 2005). Hence, information on the differences between communities (β-diversity) or its inverse, community similarity,

can shed light on the mechanisms by which regional diversity emerges from local species richness and can contribute to the current discussion about biotic homogenization. Biotic homogenization refers to an increase in species similarity across space due to anthropogenic activities, and usually focuses on interactions between non-native species, native species and the environment (McKinney & Lockwood, 1999; Olden & Rooney, 2006). However, in a more general understanding of this concept, ecological processes leading to homogenization need not necessarily include either species invasion or extinction (Olden & Poff, 2003). Such processes rather promote the dominance of some, usually widespread and broadly adapted, species ('winners' in McKinney & Lockwood, 1999) and the decrease or extinction of others ('losers'), most likely rare and specialist species (Davies *et al.*, 2004; Henle *et al.*, 2004).

Understanding which processes potentially lead to homogenization is not only a topic of theoretical interest, but is also important for biodiversity management (Orians & Millar, 1992). Although community similarity may be less intuitive than the common diversity measure of species richness, it has repeatedly proved to be a more sensitive measure of changes in community composition and has been claimed to be a useful measure of ecosystem reliability (Fukami *et al.*, 2001). Anthropogenic land use is one of the most important factors in global change (Sala *et al.*, 2000), and changes in landscape structure and agricultural land-use intensity are very likely to influence community similarity. Alterations in the size, connectivity and shape of semi-natural habitat patches may well have severe impacts on exchange between communities. The effects of land use will hence be reflected in community similarity within a landscape (Vandvik & Birks, 2004).

The majority of studies of diversity and community similarity report on patterns within landscapes (e.g. Sweeney & Cook, 2001), similarity–distance relationships (e.g. Alard & Poudevigne, 2000), spatial scales of diversity patterns (e.g. Reyers *et al.*, 2002; Sax & Gaines, 2003) or differences between land-use types (e.g. Cousins & Eriksson, 2002). The plethora of publications on fragmentation effects on diversity have provided strong evidence for decreasing α-diversity with increasing fragmentation (e.g. Didham *et al.*, 1998; Fahrig, 2003). However, there is little knowledge about the impact of landscape fragmentation on biotic homogenization (Ohmann & Spies, 1998). Some studies hint at effects of landscape structure on community similarity, e.g. high edge density leading to higher community similarity in bats (Numa *et al.*, 2005) or decreased plant community similarity as a result of fragmentation (Pardini, 2004) and succession (Hernandez-Stefanoni & Ponce-Hernandez, 2004).

Furthermore, relatively few studies have attempted to analyse drivers of community similarity, such as landscape structure or land-use intensity, *across* different landscapes (e.g. Ohmann & Spies, 1998). However, comparisons of community composition across large spatial scales such as continental transects may be confounded by changing regional species pools (e.g. Phillips *et al.*, 2003; Tuomisto *et al.*, 2003). If species pools at the opposite ends of transects are completely different, comparisons of community composition among very distant sites will tell us little about the effect of landscape-scale drivers of diversity.

To overcome these problems, a nested sampling design is required, with several sample locations *within* each of several landscapes. Such a design allows the calculation of community similarity for each particular landscape. Next, the effects of different land use on community similarity can be analysed across all landscapes (for examples see Kluth & Bruelheide, 2004). This approach corrects for differences in regional species pools when comparing data collected across large geographical distances.

Two main ecological processes, usually treated independently, influence community similarity at the landscape scale: (1) loss of specialist and rare species (e.g. due to habitat loss or high pesticide burden; Tscharntke & Brandl, 2004; Vickery *et al.*, 2004; Lavergne *et al.*, 2005), leading to homogenization because of high similarity of the remnant communities consisting mainly of generalists; and (2) disruption of the exchange of species between local communities (e.g. due to fragmentation; Hanski & Gilpin, 1997), consequently promoting the differentiation of local communities. Here we argue that loss of rare species and loss of dispersal may interact, leading to a whole range of responses of community similarity to changes in land use. We illustrate their possible ways of interaction, and their consequences for community similarity, in Fig. 1. Local extinction following from intensification of land use, habitat loss or fragmentation is
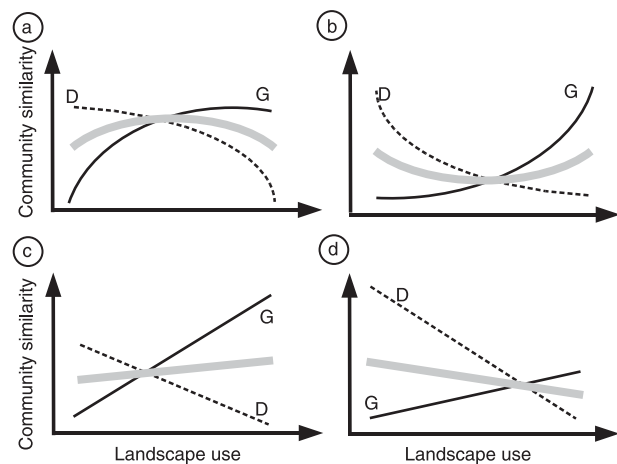

Figure 1 Concept of how dispersal and loss of specialists affects community similarity. The importance of dispersal (D) or the percentage generalist species (G) for community similarity depends on the way these two factors are affected by land use. Landscape quality (structure or use) decreases towards the right. Grey lines are the net outcome of both processes. The response type (a) depicts communities of 'specialists/good dispersers': a rapid increase in the percentage of generalists in the community, i.e. a rapid loss of specialists. At the same time most species still disperse effectively until the environment declines to a low quality. The response type (b) is the opposite, i.e. 'generalist/bad dispersers': the importance of dispersal is quickly reduced as landscape quality erodes, while most species are able to tolerate this environment until eventually most species disappear in rapid sequence. The two lower scenarios illustrate the effect of different slopes on net community similarity. Panel (c) depicts groups where dispersal is less affected by land use than the selection of generalists, while for panel (d) it is the opposite.

determined in part by species traits related to persistence, such as the degree of specialization, as well as by traits related to dispersal, such as mobility or number of offspring. How community similarity relates to land use should depend on the shape of these functions. Any relationship, from monotonic increasing or decreasing to hump-shaped and U-shaped is possible, and may even be expected. If this concept is realistic, the type of response may reveal information about the way in which changes in land use impact upon relative effects of loss of dispersal and loss of rare species.

In this study, we evaluate the concept presented in Fig. 1 using data from a European study on community similarity of seven different groups of organisms: vascular plants, birds, wild bees (Apidae), ground beetles (Carabidae), true bugs (Heteroptera), hoverflies (Syrphidae) and spiders (Araneae). The study design addresses the concerns mentioned earlier about the confounding of species pool and community similarity by comparing community similarity *within* sites, and relating the observed pattern to site characteristics *across* the European transect. Our focus is on identifying the potential mechanism behind community similarity in different landscapes. Specific questions are: (1) do landscape characteristics correlate with community similarity; (2) does increasing land-use intensity lead to more homogeneous communities; (3) does increasing fragmentation lead to more heterogeneous communities; and (4) do land-use intensity and fragmentation interactively influence community similarity?

METHODS

The analysis of species numbers at the site level (i.e. γ-diversity) is the subject of a different paper (R. Billeter *et al.*, unpublished data) and will only be considered here as far as it is important to our results.

Study sites and environmental variables

Vascular plants, birds and five arthropod taxa (wild bees, true bugs, carabid beetles, hoverflies and spiders; Table 1) were sampled in 25 sample sites of 16 km^2 in agricultural landscapes distributed over seven European countries: France (three sample sites), Belgium (four), the Netherlands (four), Switzerland

(three), Germany (four), Czech Republic (three; in one site only plant and bird data were collected) and Estonia (four; Fig. 2). Sample sites were predominantly agricultural (between 40% and 98% of the area being agricultural), flat (thus potentially suitable for intensive agriculture), located below 400 m a.s.l., homogeneous and representative of a larger area. Together, they covered a wide range of both agricultural land-use intensity and landscape structure (see Herzog *et al.*, 2006, and Table S1 in Supplementary Appendix S1).

We recorded environmental data about land-use intensity of arable fields and landscape structure (focusing on semi-natural elements). The intensity of agricultural land use was evaluated at the level of the sample site by standardized interviews with farmers about management practices on arable fields (Herzog *et al.*, 2006). The number of crops in rotation, pesticide applications (insecticides, herbicides, fungicides) and the amount of nitrogen fertilizer applied per hectare and year were recorded and transformed to cropping, pesticide and nitrogen indices, respectively, by ranging them from 0 to 100 (Legendre & Legendre, 1998; see Herzog *et al.,* 2006, for further details).

Landscape structure was evaluated from digitized habitat maps (see also Bailey *et al.*, 2007). Habitats were mapped using ortho-rectified aerial photographs with spatial resolutions better than 1×1 m and ArcGIS software (ESRI, 2003). Classification of the habitats was based on the European Nature Information System (EUNIS) habitat classification (available at http:// eunis.eea.eu.int/habitats.jsp), which was adapted to the requirements of the project. We aggregated the EUNIS habitats into woody, herbaceous and semi-natural habitat (= woody plus herbaceous) to contrast them with the highly anthropogenic elements of arable land and built-up areas. Two indices describing landscape composition and configuration were retrieved from FRAGSTATS analyses (McGarigal *et al.*, 2002). *Proximity* is an ecologically intuitive measure describing the size-weighted geographical distance between habitat patches: the larger and closer patches of the same type are to each other, the larger is the proximity value for this habitat type. However, proximity has poor mathematical properties, such as a high sensitivity to very small changes and a very nonlinear response to continuous fragmentation, which led to the development of the *splitting index* (Jäger, 2000). The number given by the splitting index equals the number of equal-sized habitat patches needed to produce the same degree of landscape division as is found in the landscape under consideration (Jäger, 2000). The higher the value of the splitting index, the more fragmented a landscape is. Both indices were log-transformed because of their strong positive skew.

Plant survey

The vegetation of each sample site was surveyed using a stratified random sampling scheme, where 2×2 m plots (20×20 m for woody vegetation) were randomly placed across all habitat types. Each habitat type was sampled proportional to its area. On average, 240 plots were correspondingly distributed over the different habitat types per sample site (see Table 1). The final data set comprised 5926 plots. For the description of
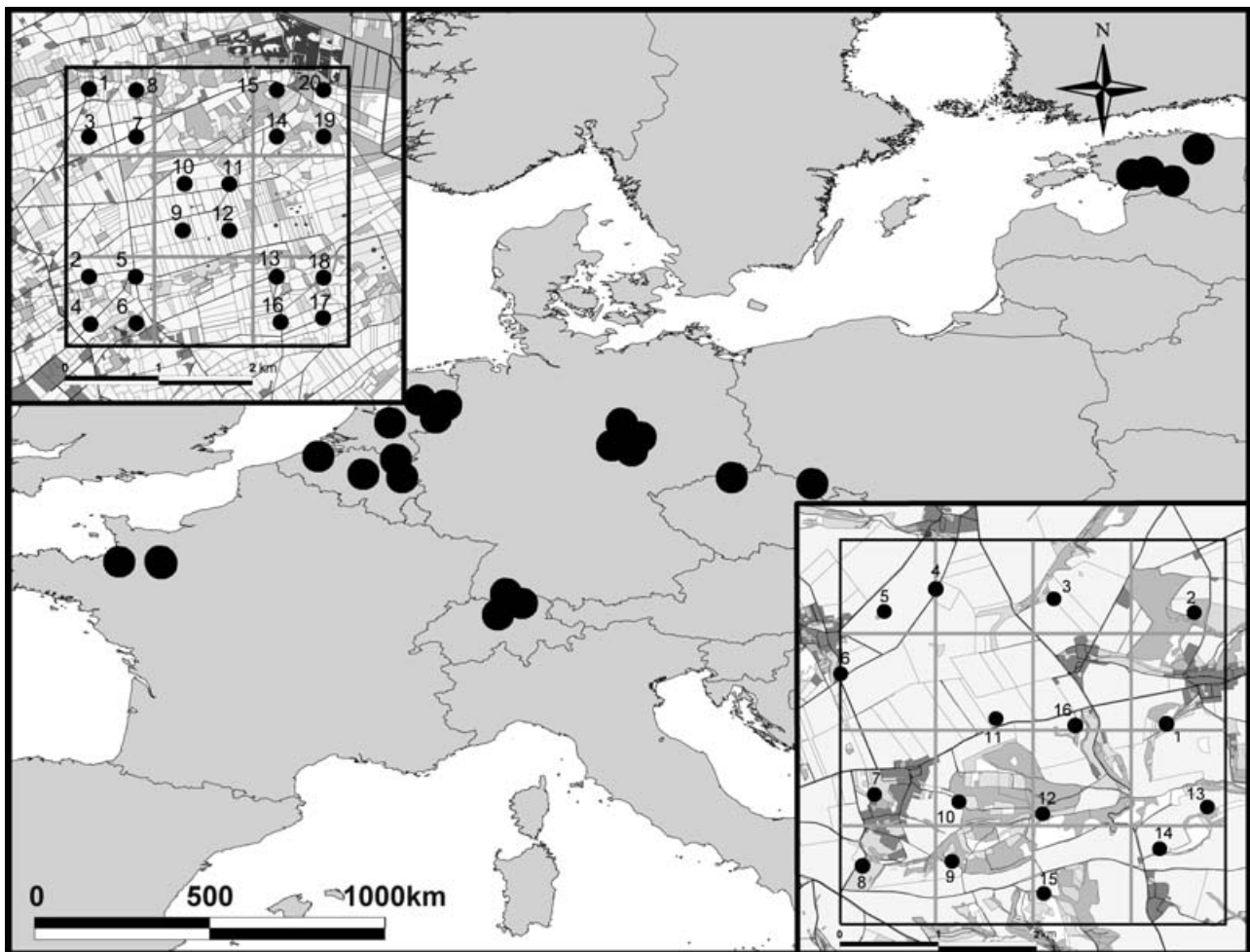
Table 1 Mean local species richness (± 1 SD) and community similarity for the seven investigated groups. Sample sizes (numbers of samples within sites and number of sites) differ between groups.

	n (samples | sites)	Local species richness	Community similarity
Plants	100–300 | 25	11 ± 2.7	0.14 ± 0.03
Birds	20 | 25	16 ± 4.1	0.49 ± 0.12
Bees	16 | 24	14 ± 10	0.52 ± 0.10
Bugs	16 | 24	11 ± 6.0	0.39 ± 0.13
Carabids	16 | 24	22 ± 6.8	0.54 ± 0.12
Hoverflies	16 | 24	6.5 ± 2.3	0.48 ± 0.14
Spiders	16 | 24	21 ± 4.6	0.51 ± 0.08

Figure 2 Geographical distribution of sample sites across Europe and sampling design for birds in a regular checkerboard pattern (upper left inset), and for arthropods in a stratified random way (lower right inset).

community composition within each plot, all vascular plant species and their cover-abundance values were recorded. Estimation of cover-abundance values followed the Braun–Blanquet abundance scale (Bonham, 1989), ranging from rare (r) to very abundant (5): (r) species occurring with fewer than 5 individuals; (+) 5–50 individuals; (1) more than 50 individuals but cover-abundance is lower than 5%; (2) cover-abundance of 5–25%; (3) cover-abundance of 25–50%; (4) cover-abundance of 50–75%; and (5) cover-abundance of 75–100%. For analysis, the Braun–Blanquet scale was transformed into 0.5, 0.75, 1, 15, 37.5, 61 and 87.5%, respectively. Mosses and lichens were not considered.

Arthropod sampling

Sample sites were divided into 16 cells of 1 km² each. Spiders and carabid beetles were captured with pitfall traps. Wild bees, true bugs and hoverflies were sampled with combined flight traps (a combination of flight and yellow pan traps; see Duelli *et al.*, 1999). In every grid cell a trap set was placed at a randomly chosen ecotone between a semi-natural habitat and an agricultural field

(Fig. 2). Ecotones, such as field margins, are less sensitive to field productivity and management than the field itself (Smart *et al.*, 2002) and promote high species numbers due to edge effects. Each trap set consisted of two trap units spaced between 25 and 50 m apart. A trap unit was composed of one pitfall and one combined flight trap. In consequence, a total of 16 trap sets comprised 32 pitfall traps and 32 combined flight traps per sample site. Sampling was carried out according to Duelli (1997). In order to minimize the sampling effort while maximizing the efficiency, we restricted sampling to two periods of maximum activity and density of the species (7 weeks in autumn 2001 and 5 weeks in early summer 2002). To correct for climatic and consequently phenological differences between the countries, we used full bloom of *Taraxacum officinale* Wiggers as a guide for commencing sampling. The traps were emptied weekly. To account for differences in weather conditions between the sample sites during the sampling periods, we considered only the samples with most specimens for the analysis (4 weeks from the autumn period and 3 weeks from the early summer period). The samples of each trap set were pooled and the specimens were identified to species level by specialists.

Bird survey

A central core area of 3 × 3 km within each sample site was divided into nine square cells of 1 km^2 each. Birds were recorded by 20 point counts in five cells selected in a checkerboard pattern (Fig. 2). Within each of these five cells, four observation points were selected and at each point sightings and hearings of birds were counted for 5 min (Bibby, 2000). This was repeated three times, in April, May and June 2001, from half an hour before until 2 hours after sunrise. Only presence/absence of a species was considered for further analysis. Note that, in contrast to plant and arthropod sampling, bird surveys include species from a rather large area (e.g. even woodland birds will be heard on a nearby field), and the similarity of survey points in local habitats is unlikely to be a good predictor of bird community similarity. However, survey points were located far enough apart (> 500 m) to sample spatially distinct bird communities within each site.

Statistical analysis

Response variables

First, community similarity was calculated between sample points within each sample site. We used the same similarity measure for all groups, although for arthropods and plants similarity was calculated based on log-transformed abundances, while for birds it was done on presence/absence data. The (dis-)similarity measure used was the Horn–Morisita index, which is able to handle any type of abundance data and is robust with respect to sample sizes (Krebs, 1989). Secondly, dissimilarities were averaged per sample site. The resulting value for each site thus expresses the average dissimilarity between local communities. Similarity was calculated as 1 minus dissimilarity. We chose similarity over dissimilarity because it is more intuitive, and because of semantics: dissimilarity is sometimes referred to as β-diversity, although this is not the originally proposed measure (Harrison *et al.*, 1992). Despite community similarity being constrained to fall into the interval between zero and one, residuals were normally distributed and could hence be analysed by analysis of (co-)variance.

Explanatory variables

To correct for the fact that different habitats were sampled, we included a variable coding for habitat similarity within a site: a buffer of 50 m (200 m for birds) was placed around every sampling point in a geographical information system (GIS) and the cover of all habitat types according to the EUNIS classification was determined. The similarity of sampling point buffers was calculated using the Horn–Morisita index and averaged per sample site. The resulting similarity was used as the co-variate in further analyses.

Our list of pre-selected explanatory variables thus comprised 10 variables: mean local habitat similarity, log-transformed proximity and splitting indices for the three habitat types *herb*, *woody* and *semi-natural habitat*, percentage semi-natural habitat, and pesticide and nitrogen application indices.

MANOVA *and CCA*

A multivariate analysis of variance (MANOVA) was carried out on the similarity data of all groups against the above 10 explanatory variables. Based on the results of the MANOVA, we carried out a canonical correspondence analysis (CCA) to visualize the effect of significant environmental variables on the seven different species groups.

Spatial analysis

Within a site, geographical distances between sampling points were correlated with community similarity using a Mantel test (1000 permutations, Spearman's rank correlation). Overall, this correlation was very weak (see Table S2 and Fig. S1 in Appendix S1), but in several cases a strong correlation existed. We thus used the harmonic (as well as arithmetic) mean distance between all sample points within a site as a co-variable in the analysis, but it was rejected for all organism groups. Hence, the geographical arrangement of sampling points was no major determinant of community similarity along the entire transect, although it was important in some sites.

ANCOVA

Community similarity values were related to explanatory variables by a best subset regression analysis (Neter *et al.*, 1993). We allowed for nonlinear effects of the explanatory variables by incorporating second-order terms of all the remaining nine variables into the full model. Additionally, we incorporated the interaction of all proximity and splitting indices with pesticide index. A first analysis had shown that percentage semi-natural habitat and nitrogen application did not interact with landscape metrics. Next, we determined all subsets of the full model up to eight explanatory variables in terms of adjusted R^2. Following this, we compared the best models of increasing complexity with each other, starting with the simplest. We accepted a more complex model if the increase in model fit was significant according to F-test statistics (Burnham & Anderson, 2002). Models were further simplified by deleting non-significant terms, if dropping them from the model did not cause a significant reduction in model performance (F-test). As landscape configuration indices for the three habitat types were sometimes correlated, we allowed only uncorrelated terms to be in the final model. Therefore we deleted the less important of two correlated terms and simplified the model further. In order to reduce collinearity between the different interaction terms, all explanatory variables were scaled to mean 0 and standard deviation of 1 prior to analysis (Quinn & Keough, 2002), but the final model was identical for scaled and unscaled models and only the latter are presented here.

All analyses were carried out in the free software R (R Development Core Team, 2005), using the packages car, leaps and vegan.

Table 2 Correlation matrix of community similarities for the different groups. Values are Pearson's r, critical value for $P = 0.05$ is $r = \pm 0.520$ (bold). $n = 25$ for plants and birds and 24 for arthropods.

	Plants	Birds	Bees	Bugs	Carabids	Hoverflies	Spiders
Plants	1						
Birds	−0.003	1					
Bees	0.197	0.229	1				
Bugs	0.227	−0.133	**0.616**	1			
Carabids	−0.007	0.055	0.192	0.170	1		
Hoverflies	0.141	0.133	0.204	**0.580**	0.140	1	
Spiders	0.019	0.085	0.206	0.274	**0.781**	0.268	1

RESULTS

Environmental relations of community similarity across all groups

Within-site community similarities of species groups were largely uncorrelated (Table 2), with a few exceptions: true bug community similarity was related to that of bees and hoverflies, and ground beetle community similarity was related to that of spiders (3 out of 21 comparisons). Thus, generally each group seems to respond differently to landscape structure and land use. This questions the usefulness of using one species group as a surrogate for any other and the umbrella concept of nature conservation (Lambeck, 1996) for our study organisms.

Similarity of all seven groups combined was significantly related only to the splitting index for herbaceous habitat and pesticide index (Pillai's $F_{1,21} = 0.66$, $P < 0.01$ and $F_{1,21} = 0.61$, $P < 0.05$, respectively). Higher values of the splitting index correlated with lower community similarity for all groups, with the exception of bugs, where an effect was absent.

The biplot of the CCA illustrates the ordination of the seven groups of organisms with respect to pesticide index and splitting index for herbaceous habitats (Fig. 3). Overall, only plants and spiders cluster similarly in their response, while all other species distribute widely over the two CCA axes. With respect to pesticides, the similarities of wild bees and hoverflies were the most negatively affected, while bird, plant, spider and bug communities seemed to have no such problems. Ground beetle similarity on the other hand was associated with high levels of pesticides. Similarly, fragmentation of grassland (SPLIT_herb) led to increased community similarity in wild bees and true bugs, while ground beetle, bird and hoverfly community similarity was reduced.

The final univariate models differed considerably in their complexity, indicated by the number of model parameters (Table 3). For example, the model for hoverflies contained only the correction for local habitat similarity and the quadratic regression on pesticides, whereas for ground beetles the model contained the local habitat correction and six parameters. Adjusted R^2 values ranged from 0.26 to 0.74 and were uncorrelated with model complexity. In four of the seven cases, correction for local
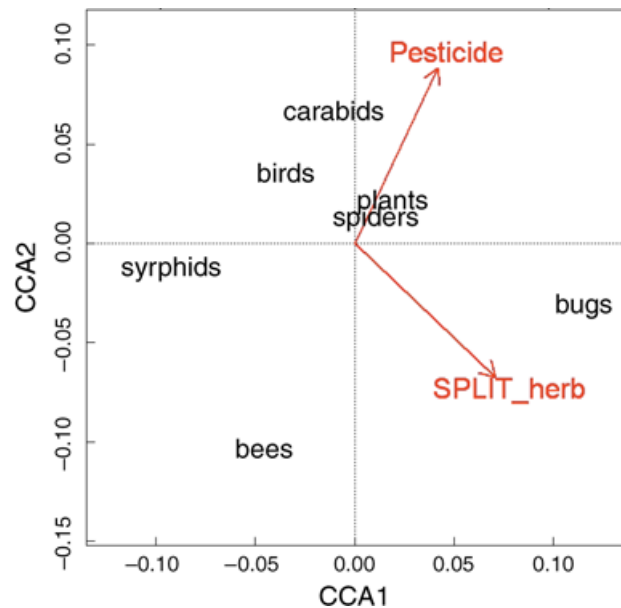

Figure 3 Comparing the responses of the seven different communities to land-use intensity (pesticide index) and landscape structure (splitting index of herbaceous vegetation). MANOVA results were used to identify environmental variables used in canonical correspondence analysis. Positions towards the arrowhead indicate positive correlation with that arrow. Bird community similarity, for example, is negatively related to landscape fragmentation and not influenced by pesticides.

habitat similarity was important. It was most important for hoverflies, ground beetles and spiders, for which community similarity increased with habitat similarity.

Community similarity and γ-diversity

Four groups displayed a significant correlation between species richness at the site (γ-diversity) and community similarity at that site. Bee and ground beetle community similarity was significantly but only weakly related to γ-diversity (with Pearson's $r = -0.37$, $P < 0.01$ and -0.42, $P < 0.01$, respectively). This relationship was stronger for true bugs ($r = -0.60$, $P < 0.01$) and nonlinear for hoverflies ($r^2 = 0.33$, $P < 0.01$: community similarity $= 1.3 - 0.05\gamma + 0.0006\gamma^2$). For plant, bird and spider communities, no relationship between community similarity and species richness was detectable. The overall lower community similarity at higher species richness hints at species-rich landscapes comprising different communities, while species-poor landscapes consist of variations on the same community.

Community similarity by group

Plant community similarity values were the lowest, indicating the least exchange of species between communities (Table 1). Community similarity values showed a U-shaped relationship with the percentage of semi-natural habitat (Fig. 4), indicating that homogeneous habitats on the one hand, and highly

Table 3 Explained variance by different environmental factors for the final model fitted to community similarity data. Partial R^2s do not add up to adjusted R^2 in the last column, as this corrects for the number of parameters in the model and as the intercept of the model also carries some (trivial) explained variance. Note that model selection was not based on the significance level of the effect in the model, but on the comparison of models with and without the respective effect (*F*-test). R^2 values are based on 'type III sum of squares'. See Table S3 for correlation of environmental variables.

Group	Local habitat	Pesticide index	Pesticide²	% SNH	%SNH²	log(proximity_SNH)	log(proximity_SNH)²	log(proximity_wood)	log(proximity_wood)²	log(split_SNH)	log(split_SNH)²	log(split_wood)	Pesticide×log(proximity_SNH)	Pesticide×log(split_SNH)	Pesticide×log(split_wood)	Total model
Plants		0.09*		0.09*	0.13**	0.09*						0.07*	0.09*			0.26†
Birds		0.13*		0.14*		0.09*	0.08*				0.08*	0.08*				0.52**
Bees	0.08*		0.04†	0.07*								0.06*			0.09*	0.55**
Bugs		0.11†						0.24**		0.01n.s.				0.12*		0.28*
Carabids	0.13***	0.08**			0.04*			0.11***	0.08**	0.09**				0.10**		0.74***
Hoverflies	0.26**		0.11*													0.42**
Spiders	0.13***	0.04†										0.10**			0.05†	0.44**

SNH, semi-natural habitat.

Significance values of the model term (in the final model) are: n.s., $P > 0.1$; †, $P < 0.1$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

fragmented landscapes on the other, led to highest similarity among local plant communities. The significant interaction of pesticide index and proximity index for semi-natural habitat is depicted in Fig. 5. A bisector line indicates the axis of worsening environmental conditions, with the best (i.e. most natural) situation in the top left corner and the worst diagonally opposite. Along this axis, community similarity first increases and then decreases again, as is indicated by the darker shading towards the centre. Plant communities are least similar both at the benign and malign ends of the environmental gradient.

Bird community similarity was positively related to the similarity of habitats sampled (Table 3), simply indicating that communities were relatively habitat specific. This is also reflected by the fact that various measures of landscape integrity are correlated with bird community similarity (Table 3). The larger the area of semi-natural habitat that was available the higher was the similarity of bird communities in that landscape (Fig. 4). Similarly, sampling points in landscapes with larger and nearer patches of semi-natural habitats (i.e. higher proximity) harboured more similar bird communities. Bird community similarity furthermore corresponded with the coarse measure of how much semi-natural habitat was available, explaining 14% of all variation (Table 3). More semi-natural habitats also meant higher avian community similarity.

The similarity of *wild bee communities* was affected by the similarity of the local habitat (8%), by the percentage of semi-natural habitat at a site (7%) and most of all by pesticide burden, landscape structure and their interaction (19%; Table 3). While the percentage of semi-natural habitat impacted upon bird and bee communities, they responded, however, in the opposite way (Fig. 4): the fewer semi-natural habitats in a landscape, the

higher the bee community similarity. The effect of landscape fragmentation of woody habitats (i.e. the splitting index) depended on the intensity of pesticide applications. At low levels of pesticide load, community similarity decreased with habitat fragmentation, while at high pesticide levels, community similarity increased with habitat fragmentation (Fig. 6a). To aid interpretation, the bisector again goes from best to worst environmental conditions. Thus, community similarity was highest under the worst conditions such as high splitting index and high pesticide level (top-right corner), then decreases towards better environments, to increase again in the best landscapes sampled. This means that fragmentation and pesticides in concert result in a U-shaped response curve. Figure 6(a) suggests that the importance of pesticides is higher in highly fragmented landscapes than in those with a low level of fragmentation, since contour lines are denser at the top than at the bottom of the figure.

True bugs exhibited a similar pattern to that of bees. Instead of percentage semi-natural habitat (bees), similarity of local bug communities was affected by the proximity of woody habitats. Low proximity, i.e. small, distant patches, led to lower similarity in bug communities (Fig. 7). The interaction of pesticides with fragmentation of semi-natural habitats (splitting index) was similar to that for bees. At low levels of pesticide load, habitat fragmentation had little effect on community similarity, while at higher pesticide levels, community similarity increased with fragmentation (Fig. 6b). Thus, community similarity was highest under the worst environmental conditions, such as high splitting index and high pesticide level. Again, similar to wild bees, true bug communities show strong responses to fragmentation except at low pesticide levels, but the response is even stronger.
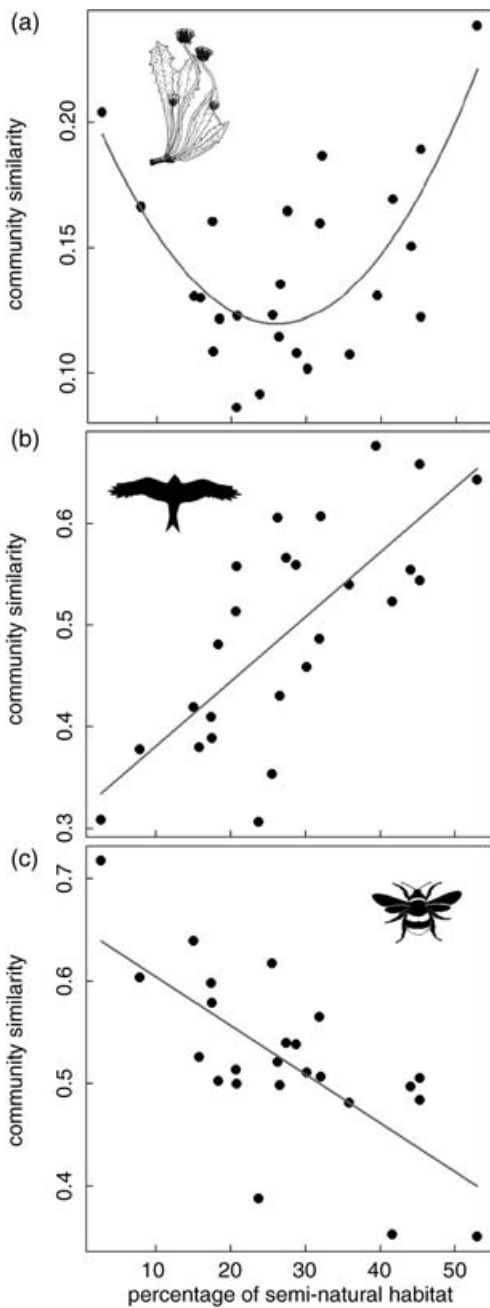
Figure 4 Response of (a) plant, (b) bird and (c) bee community similarity to landscape configuration, as represented by the percentage of semi-natural habitats. Regression lines are based on the parameters of the final model.
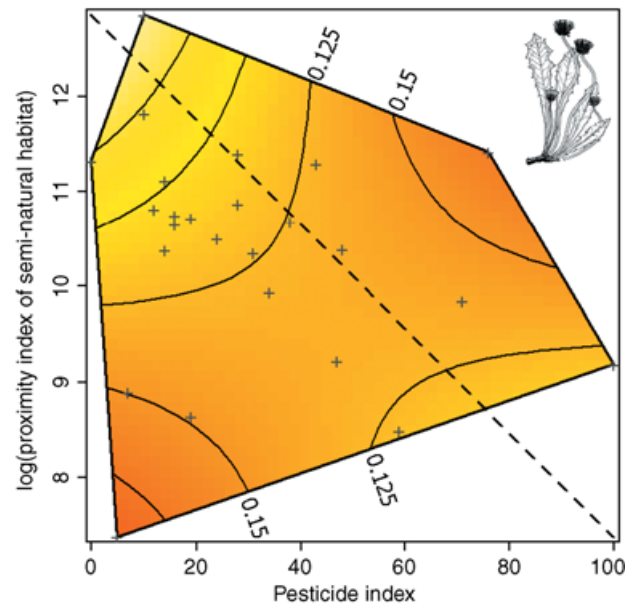

Figure 5 Response of plant community similarity to the interaction of pesticide index and proximity index for semi-natural habitats. The polygon delimits the sample space, i.e. those parameter combinations assessed in our study. Grey crosses indicate the actual parameter values for the 25 sample sites. Contour lines indicate the same level of community similarity (in steps of 0.025 units) and darker shading corresponds to higher similarity. Notice that the bisector line runs from best (top left corner) to worst (bottom right) environmental conditions.

Ground beetle communities showed the most complex response to environmental conditions (Table 3). They also had the highest similarity values of all groups. A higher integrity of woodlands in the landscape (expressed by a higher proximity index) correlated with lower community similarity (Fig. 7). The interaction of pesticides and fragmentation of semi-natural habitats can again be explained in a similar way as for bees and bugs (Fig. 6c). Notice, however, that effects are even stronger in ground beetles, and that maximum community similarity is at low levels of

fragmentation, while for bees and bugs it was found at higher levels of fragmentation (Fig. 6a and b). Nonetheless, fragmentation effects are again strongest at high levels of pesticide application, and weaker at low pesticide levels. Along the bisector community similarity decreases until virtually unique communities are present in the landscape furthest along this axis. This was an extremely agricultural site consisting of practically only arable land.

Hoverfly community similarity was determined mainly by the similarity of sampling points (26%) and pesticide index (11%; Table 3). Hoverflies were the most species-poor group (Table 1) in our data set, and community similarity reflects the fact that only common generalists form the hoverfly community at high pesticide doses. Although data are very scattered (Fig. 8), the significant nonlinear relationship suggests some threshold level for the effects of pesticides, here located at values of about 70.

Spider communities were mainly determined by the similarity of habitats sampled and the interaction of pesticide index and fragmentation of woody habitat (Table 3). Figure 6(d) shows that the pattern of spiders is comparable to that of wild bees, although the effects are weaker, indicated by contour lines that are spaced further apart. It also differs in that maximum community similarity is found under optimal conditions, i.e. low fragmentation and low pesticides. In contrast to the other groups with a significant interaction, spider communities responded to landscape
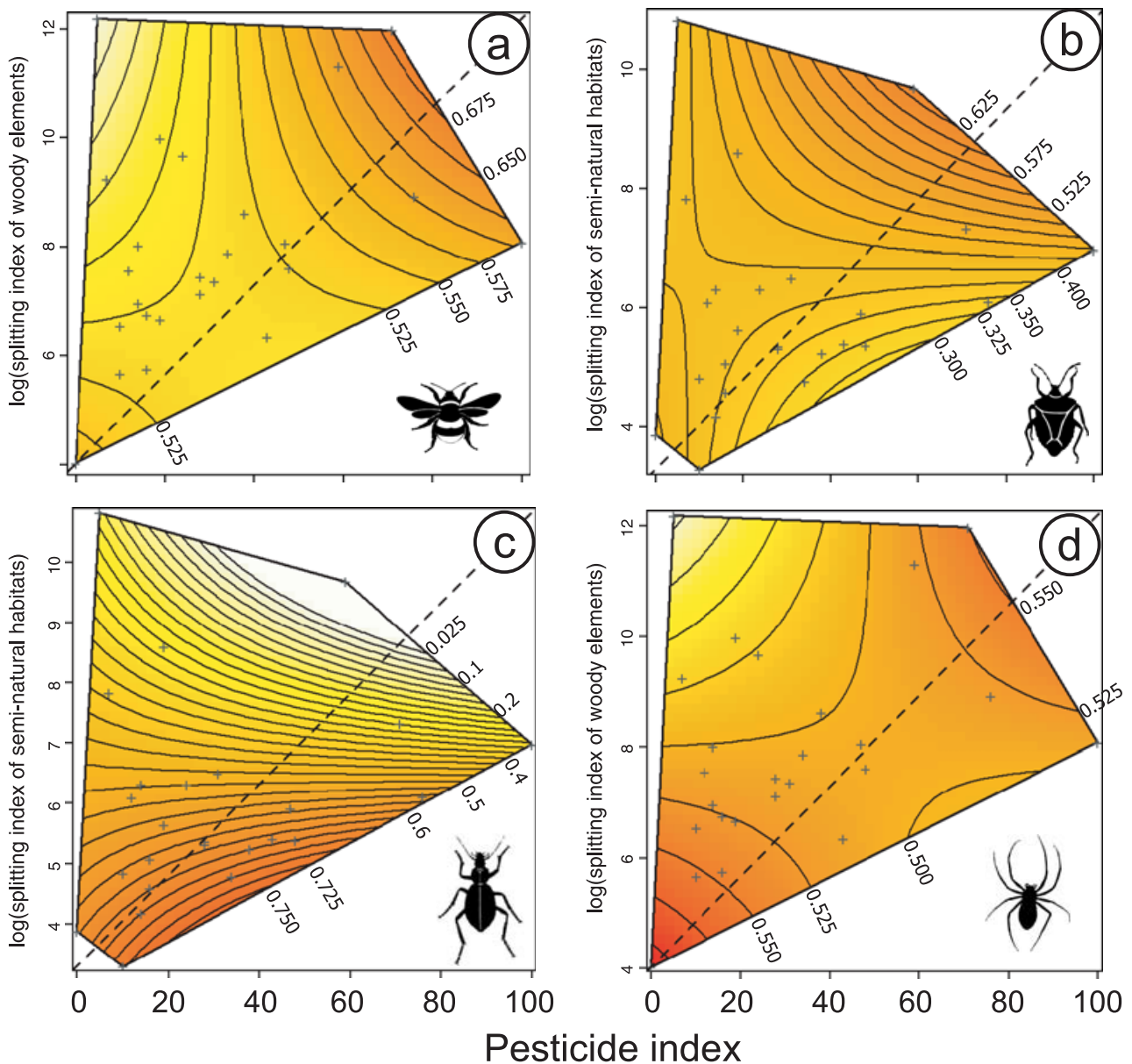
Figure 6 Interaction plots for community similarity of (a) wild bees, (b) true bugs, (c) ground beetles and (d) spiders to pesticide index and landscape structure (splitting index of woody elements or semi-natural habitats). See caption to Fig. 5 for details.

fragmentation only at low pesticide levels. Fragmentation was of little relevance at medium to high pesticide burdens. Community similarity changes only very little along the bisector line.

DISCUSSION

Do landscape characteristics correlate with community similarity?

Several factors acting at different spatial scales may contribute to the observed diversity pattern (Wagner *et al.*, 2000). Habitat similarity is expected to influence community similarity (Harrison *et al.*, 1992) as does regional landscape structure and land-use intensity (Tscharntke *et al.*, 2002). In our analysis, community similarity is determined to a varying extent by habitat similarity. However, after correcting for local effects, landscape structure and land-use intensity did seriously affect the similarity of plant, bird and arthropod communities (Table 3). Hence we provide clear indications of regional effects on the composition of local communities.

Most studies investigating community similarity have reported a high correlation between different groups (birds, amphibians, reptiles and lepidopterans, Atauri & de Lucio, 2001; butterflies and birds, Fleishman *et al.*, 2003; butterflies and dragonflies, Cleary *et al.*, 2004; birds, butterflies and plants, Su
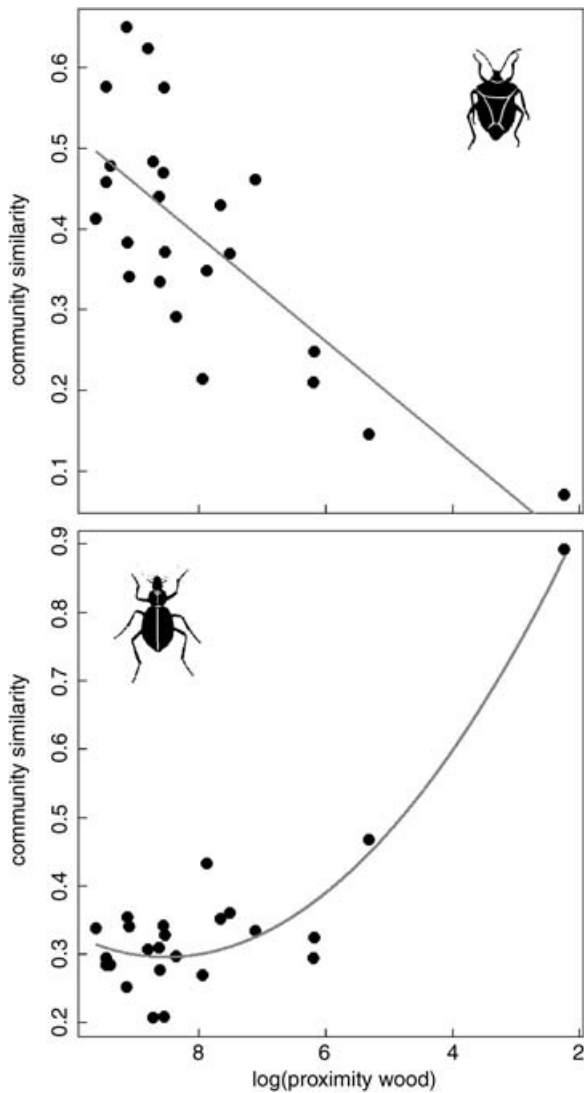
Figure 7 Response of true bug (top) and ground beetle (bottom) community similarity to landscape configuration as represented by the proximity index for woody habitats. For consistency with other figures the *x*-axis is inversed to have lower-quality landscapes to the right of the graph.

Figure 8 Response of hoverflies community similarities to land-use intensity as represented by the pesticide index.

et al., 2004). This was not the case in our study (Table 2). Even among groups using comparable resources and sharing similar movement patterns (bees and hoverflies) or that are trophically linked (plants and bees), community similarities were unrelated. However, two groups sharing similar habitats were similar in their response: carabid beetles and spiders. As a consequence of this idiosyncratic response, only fragmentation of herbaceous habitats and pesticide index had explanatory power for community similarities across all groups (see multivariate analysis). The univariate analyses on the other hand showed that species groups differed because they responded to different aspects of land use (Table 3). Nevertheless, some generic pattern emerged since the observed pattern can be assigned to one of the four response types proposed in Fig. 1.
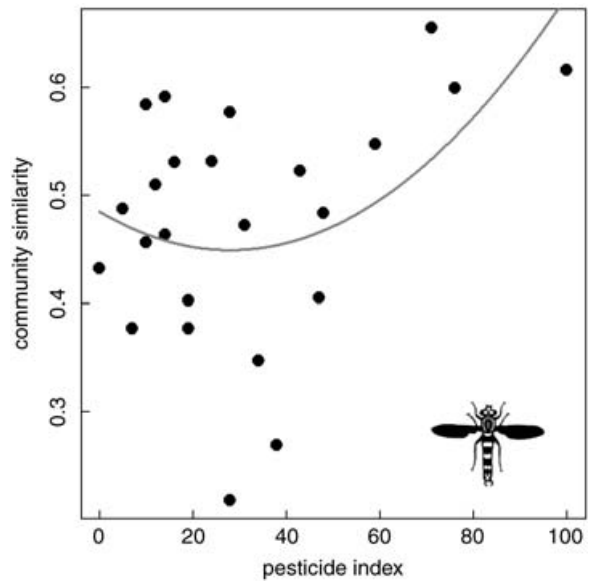
Does increasing fragmentation lead to more heterogeneous communities?

The hypothesis that community similarity depends on the level of landscape fragmentation received substantial support. All of the seven groups were affected to some extent by fragmentation (measured as splitting or proximity index – both quantify spatial arrangement of habitats; Table 3). However, a simple linear relationship between community similarity and fragmentation was only observed for true bugs, for which similarity decreased with increasing fragmentation (Fig. 7). Bird community similarity also showed a near-linear, monotonic decreasing function of fragmentation, while ground beetles only responded at very high levels of fragmentation (i.e. low proximity; Fig. 7). The observed pattern for bugs, carabids and birds indicates an increasing disruption in the exchange of species between local communities in fragmented landscapes since landscape structure affects dispersal, especially at low levels of habitat connectivity (King & With, 2002). For birds, whose community similarity was negatively affected by fragmentation, our findings are not fully in tune with other studies on bird community similarity (Clergeau *et al.*, 2001; Jokimäki & Kaisanlahti-Jokimäki, 2003). They report little response of birds to habitat structure.

The remaining groups showed a more complex picture discussed below: fragmentation interacted with land-use intensity, indicating a linkage between landscape structure and land-use factors in their effects on the similarity of local communities.

Does increasing land-use intensity lead to more homogenous communities?

Our analyses show that habitat loss and land-use intensity significantly affect community similarity. Both factors often favour the

dominance of generalist species while decreasing that of rare and specialized ones (Andrén, 1994; Warren *et al.*, 2001). Thus, one might expect an increase in community similarity with habitat loss or increasing land-use intensity, since it is most likely that local communities will consist merely of the same generalist species that can cope with such adverse conditions (Fig. 1, the 'Generalist' effect). However, these simple expectations were only supported by wild bees, where a decrease in the amount of semi-natural habitat led to an increase in community similarity. Plant communities, on the other hand, at first become *less* similar as the amount of semi-natural habitat decreases (Fig. 4). Once a threshold (here *c.* 18%) is passed, community similarity increases again. We interpret this pattern as conforming to Fig. 1(b), where initially limited dispersal prevents a synchronization of communities, but as loss of habitat continues, habitat specialists are lost and common generalists dominate the pattern (Schweiger *et al.*, 2005).

The effect of land-use intensity (represented in the pesticide index) was in itself evident only for hoverflies. Mostly it interacted with landscape structure (see below). The U-shaped response of hoverfly community similarity (Fig. 8) indicated a slight decrease in similarity within lower ranges of pesticide burden but an increase within higher ranges. Our interpretation is similar to the pattern in plants, i.e. that heavy pesticide burdens reduce hoverfly communities to robust generalists, hence increasing community similarity.

Do land-use intensity and fragmentation interactively influence community similarity?

Despite the ostensible differences of the seven species groups in their reactions to different land-use and structure indices, one generic pattern occurred. Five groups showed an interaction along a gradient from landscapes with low levels of pesticide burden and fragmentation to highly fragmented landscapes with high pesticide pressure (Figs 5 & 6). In all groups, pesticide burden determined the way in which landscape structure influenced community similarity. Three groups (wild bees, true bugs and ground beetles) had *stronger* responses to fragmentation at high pesticide loads (reflected in closer spacing of contour lines towards the right; Fig. 6). For plants and spiders the opposite was true: landscape structure was *less influential* at high pesticide levels and the interaction was less pronounced altogether.

To simplify the interaction, the bisectors from best to worst environmental conditions are added to the interaction plots (Figs 5 & 6). Plants, wild bees and true bugs show a (nonlinear) response along this line, while ground beetle and spider community similarity hardly varied. We interpret this pattern as an interaction of two opposing processes: disruption of dispersal (i.e. the exchange of species between local communities) and selection for generalists (see Fig. 1). Following this idea, plant, hoverfly, wild bee, true bug and spider communities in moderately managed agricultural landscapes would mainly consist of more or less generalist species with limited dispersal capacity (Fig. 1b). With increasing land-use intensity, it is not habitat loss or pesticide burden that mainly affect community similarity but

fragmentation, which rapidly reduces species turnover and thus decreases community similarity. This need not necessarily reduce species richness, since many species in agricultural landscapes are capable of overcoming such problems by intrinsic metapopulation dynamics (Hanski & Gilpin, 1997). Nevertheless, previous analyses of the same data set revealed that further intensification of land use will reduce species richness (R. Billeter *et al.*, unpublished data), most likely because of disrupted meta-population dynamics or the extinction of rare and more specialized species. The percentage of generalist species will increase gradually at low levels but rapidly at very high levels of land use, until only well-dispersing generalists dominate and community similarity is accordingly high (in line with Tockner *et al.*, 1999).

The U-shaped response of community similarity to increasing land use (directly as pesticide index or along the bisector lines) seems to be a common response type. However, birds and ground beetles (Figs 4 & 6c) differed and were best described by Figure 1(d). Here the effect of dispersal disruption is assumed to be stronger than the selection for generalists. Most carabid beetle species in agricultural landscapes might be regarded as generalists, especially when compared with wild bees, true bugs and hoverflies, since they are mainly generalist predators or omnivorous and many of them are able to forage in various habitats. Hence, the selection effect of habitat loss might not come into force within this land-use gradient. However, the question remains: why is it that pesticide application and not fragmentation accounts for a decrease in community similarity and an inferred disruption of dispersal? Many ground beetle species living in agricultural landscapes are able to cover considerable distances between habitat patches across cultivated areas (Kinnunen *et al.*, 1996). However, most of these species are preferably ground dwelling and are therefore exposed to pesticide applications and other, often correlated, adverse management practices when moving between patches (Thacker & Dixon, 1996). The observed decrease in community similarity thus indicates indirect effects of land-use intensity via disruption of species exchange and supports recent findings that it is not always fragmentation affecting dispersal but sometimes matrix quality, too (see Debinski & Holt, 2000).

Bird community similarity decreased with decreasing amounts of semi-natural habitat (Fig. 4). From the concept presented in Fig. 1(d) we deduce that effective bird mobility is strongly reduced by habitat loss, while the level of generalization is little affected. This pattern may be caused by random composition of bird communities. In fragmented landscapes, bird abundance will be lower, due to less available habitat but also larger home ranges of resident species (e.g. Bezzel, 1982). Hence, any bird community will consist of relatively few individuals randomly drawn from a pool of generalists. Thus, continuous habitat loss will cause a decrease in bird species density, and hence in community similarity, indicating more homogeneous communities residing in more intact landscapes.

CONCLUSIONS

Our study suggests that there is no simple relationship between change in land use and biotic homogenization. Moreover,

several, sometimes opposing and interacting, processes at the landscape scale affect the composition and turnover within and between local communities. Usually the response of community similarity to changes in a specific environmental factor, such as pesticide pressure, depends not only on the particular species group but also on other environmental conditions, such as the level of landscape fragmentation. Consequently, different species groups will reveal different impacts, and tailoring the indicator system to the impact is hence crucial although difficult. Nevertheless, observed generalities in the response patterns of community similarity, either U-shaped or simply linear, and interactions of both opposing processes of dispersal disruption and selection for generalists, suggest that conservation management might focus on specific aspects of land use according to pre-conditions of the particular landscape. In intensively utilized agricultural landscapes, focusing on reducing land-use intensity and increasing the amount of semi-natural habitat will be more effective in maintaining overall biodiversity than simply increasing connectivity. More explicitly, planting linear elements such as hedgerows or lines of trees in intensively utilized areas will yield little benefit to overall diversity since the total area of semi-natural habitat is not increased much. In less intensively used landscapes, on the other hand, increasing connectivity *per se* will be more advantageous than assigning more patches to conservation. This provides scope for specific conservation programmes with regard not only to overall biodiversity but also to socio-economic and agri-environmental requirements.

ACKNOWLEDGEMENTS

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BIOSKETCHES

Carsten F. Dormann is senior researcher interested in biodiversity research at the landscape scale. Statistical analyses of species distributions and consequences for their ecosystem services are at the heart of his research.

Oliver Schweiger is a research scientist at the Department of Community Ecology at the Helmholtz Centre for Environmental Research-UFZ. His main research interest is the effects of global change on different levels of biodiversity across temporal and spatial scales.

Editor: Martin Sykes

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Site characteristics, correlation of variables and spatial analysis.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1466-8238.2007.00344.x

(This link will take you to the article abstract).

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Appendix S1. Site characteristics, correlation of variables and spatial analysis

Table S1. Mean values of environmental variables within the sample sites across seven European countries (± one standard deviation).

Country	Pesticide	Nitrogen	%SNH	Proximity
Be (4)	3.1 (±2.3)	238 (±51)	28 (±14)	37 (±27)
Cz (2)	0.8 (±1.2)	55 (±23)	40 (±19)	235 (±207)
Est (4)	0.7 (±0.5)	140 (±135)	31 (±5)	76 (±44)
F (3)	2.3 (±0.3)	206 (±37)	34 (±10)	25 (±17)
D (4)	3.2 (±0.8)	190 (±44)	18 (±11)	52 (±40)
Ch (3)	1.4 (±0.3)	159 (±26)	34 (±15)	24 (±16)
Nl (4)	0.5 (±0.3)	317 (±37)	16 (±6)	23 (±22)

Number behind country code indicates the number of sites.

Pesticide, number of pesticide applications to major crops per year;

Nitrogen, nitrogen application $(kgha^{-1}y^{-1})$;

%SNH, proportion of semi-natural habitats;

Proximity, proximity index of semi-natural elements.

Be, Belgium; Cz, Czech Republic; Est, Estonia; F, France; D, Germany; Ch, Switzerland; Nl, The Netherlands.

Table S2. Mantel correlations (Spearman's rank) between spatial distance between sampling points and community similarity for the 25 sites (24 for arthropods), and the seven groups of organisms. Bold printed coefficients are significant at p < 0.05.

| Site	plants	birds	bees	bugs	carabids	syrphids	spiders
B-BRE	–0.024	–0.114	0.175	0.205	0.033	0.176	0.081
B-HOE	0.015	–0.213	–0.003	0.289	0.009	0.088	0.201
B-KAP	–0.019	–0.194	0.032	–0.069	–0.164	**–0.261**	0.043
B-VOE	–0.007	–0.248	–0.007	0.060	–0.084	–0.098	–0.038
C-BRO	–0.012	–0.039	–0.051	–0.167	–0.175	–0.054	–0.035
C-SVE	–0.003	–0.228					
C-VER	–0.036	–0.061	0.046	**–0.229**	0.065	–0.060	0.009
D-FRI	–0.018	0.071	–0.100	0.042	0.013	0.058	0.083
D-MFL	0.011	–0.020	–0.075	–0.068	0.072	0.107	0.176
D-QFP	–0.001	–0.424	**–0.269**	**–0.268**	0.058	0.012	–0.051
D-WAN	–0.010	–0.205	–0.181	–0.143	–0.016	–0.140	–0.030
E-ARE	0.047	–0.121	–0.021	0.176	0.141	0.090	0.144
E-VIH	**–0.038**	–0.207	0.138	0.042	–0.089	0.048	0.120
E-VII	**–0.039**	–0.074	**–0.206**	0.164	–0.123	0.004	0.180
E-VMA	**–0.040**	–0.23	**–0.241**	–0.040	–0.001	–0.029	–0.186
F-AL	0.004	–0.084	–0.160	–0.057	**–0.268**	–0.107	–0.057
F-FOD	0.009	–0.237	–0.071	0.199	0.055	–0.177	–0.025
F-FOO	**–0.111**	–0.133	0.031	0.164	0.124	–0.102	0.052
H-KLG	**–0.067**	–0.159	0.042	–0.054	**–0.297**	0.046	–0.028
H-NUB	**–0.059**	–0.081	0.109	0.026	0.081	0.017	0.043
H-REE	0.001	–0.246	–0.125	–0.201	0.010	0.060	0.114
N-BAL	**–0.063**	–0.039	–0.006	0.162	–0.155	0.005	0.095
N-BEN	**–0.047**	–0.101	–0.018	–0.163	–0.082	0.089	**–0.223**
N-SCH	–0.014	–0.202	–0.116	0.148	0.151	0.076	0.094
N-WEE	–0.015	–0.243	–0.136	**–0.210**	–0.108	–0.096	–0.128
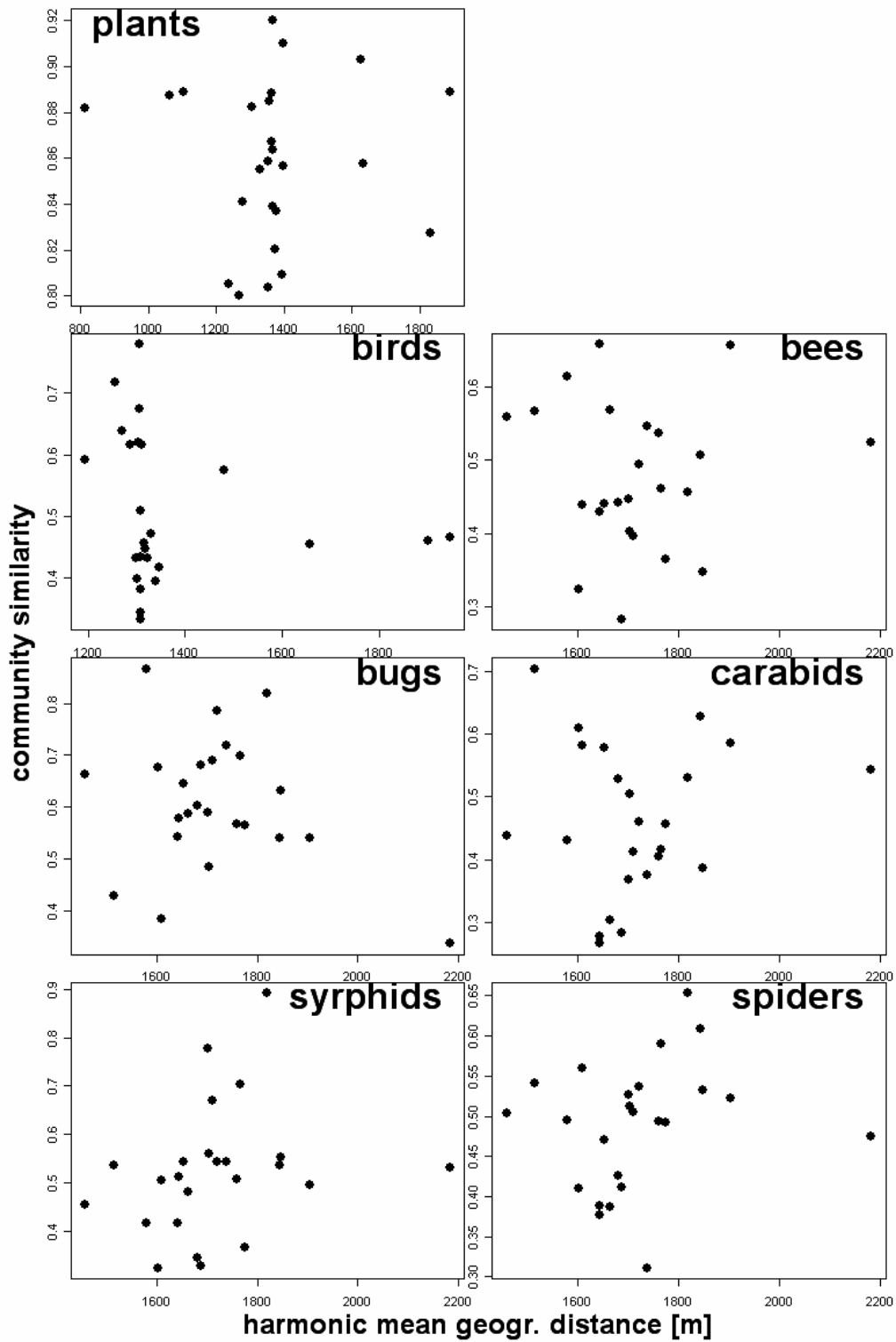
Figure S1. Relationships of community similarity and harmonic mean geographic distance between sampling points within a site. The harmonic mean gives more weight to closer sampling points, which are also more likely to be in exchange with the focal community. Using arithmetic mean yields a very similar picture.

Table S3. Pearson's correlation between explanatory variables. Bold printed coefficients are significant at p < 0.05.

	log(Prox_SNH)	log(Prox_wood)	log(Split_SNH)	log(Split_wood)	log(Split_herb)	%SNH	Pesticide	Nitrogen
Log(Prox_herb)	**0.641**	0.294	–0.550	–0.217	**–0.901**	0.565	0.203	0.348
Log(Prox_SNH)		**0.617**	**–0.877**	**–0.726**	**–0.624**	**0.659**	–0.187	0.157
Log(Prox_wood)			**–0.692**	**–0.748**	–0.455	0.536	–0.122	–0.052
Log(Split_SNH)				**0.846**	**0.636**	**–0.769**	0.204	–0.196
Log(Split_wood)					0.292	–0.599	0.349	0.083
Log(Split_herb)						**–0.669**	–0.247	–0.499
%SNH							–0.331	0.131
Pesticide								0.469