Land-use intensity and border structures as determinants of vegetation diversity in an agricultural area

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Summary

1 Agroecosystems have long been viewed as sites of low biodiversity, but their importance for landscape-level diversity is now increasingly recognised. However, our knowledge of the determinants of biodiversity in these widespread and thus important ecosystems is still fragmentary. Land-use intensity and landscape structure seem to be the most important factors.

2 The objective of this study was to examine how the diversity of the vegetation varies within a typical farmland of Central Switzerland (30 ha, with crop fields, pastures and meadows) and to analyse how land-use type and distance from border structures influence these patterns.

3 The vegetation of the study area was surveyed in 481 quadrats (1 m^2) according to a systematic grid design (25 m mesh width). The land-use of these quadrats was categorized into five classes of increasing land-use intensity. Four measures of vegetation diversity were calculated: Shannon's diversity index (alpha diversity), species richness, evenness, and floristic dissimilarity among nearby samples (beta diversity). GIS was used to relate the spatial patterns of vegetation to land-use intensity and distance from border structures (such as field and pasture margins or forest edges).

4 A total of 180 non-woody and non-crop vascular plant species were recorded in the study area. The border structures had a comparatively high species richness: they supported 93% of the 180 species although their area accounted only for 3% of the farmland. In contrast, the managed area (97% of the area) included only 55% of the species. Vegetation diversity (both alpha and beta diversity) was negatively related to land-use intensity and tended to decrease from the margins of the study area towards its centre.

5 The key determinant for vegetation diversity in agroecosystems seems to be land-use intensity. Less intensively used spots such as border structures play a crucial role as species reservoirs despite their small area. They may even have some positive 'radiative' effects on vegetation diversity in farmland with a high proportion of border structures.

Keywords: agro-ecosystems, border structures, GIS, spatial distribution

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Introduction

Intensively managed agro-ecosystems have long been considered unnatural and monotonous (e.g. Wood & Lenné 1999). Therefore, research on patterns and processes maintaining biodiversity in the landscape has focused on species-rich, (semi-)natural ecosystems such as wetlands, dry meadows and woodland (e.g. Wheeler 1993; Zobel *et al.* 1994; Ryser *et al.* 1995; van der Maarel *et al.* 1995; Zobel & Liira 1997; Pärtel *et al.* 2000; de Forest Safford *et al.* 2001). In intensively managed landscapes, species diversity and spatial distribution have only been well studied for some animal groups (birds, butterflies, grasshoppers, amphibians, reptiles; e.g. Weibel 1998; Laussmann 1999; Weggler & Widmer 2000; Bosshard & Kuster 2001; di Giulio *et al.* 2001). Plants have rather been neglected in this respect until recently (but see Marshall 1989).

The importance of agro-ecosystems for total biodiversity has now been acknowledged on a regional and global scale (e. g. Oppermann 2000; Pfiffner 2000; Edwards & Hilbeck 2001). A large fraction of the Central European Flora could establish or spread due to traditional agricultural use and depends on this use for its maintenance (Korneck & Sukopp 1988; Landolt 1991). Yet, our knowledge of plant species diversity within agricultural areas and of its determinants is still fragmentary. In particular, the role of land-use intensity for species diversity has not yet been firmly established. Burel *et al.* (1998), for example, found that vegetation diversity of (entire) agricultural landscapes was only weakly influenced by land-use intensity. In contrast, Halley & Lawton (1996) suggest that large intensively managed fields affect flora and fauna negatively. Edwards *et al.* (1999) generalise that the pool of plant species decreases with increasing land-use intensity, and Studer (2001) found that a large fraction of the variation in species composition of meadows could be explained by management intensity (fertilisation and mowing frequency).

Border or corridor structures are generally considered particularly valuable for the maintenance of biodiversity within agro-ecosystems (Röser 1988; Duelli 1997; Marshall & Moonen 2002). The structure and species composition of their vegetation has therefore been well studied (e.g. Dierschke 1974; Marshall 1989; Marshall & Arnold 1995; Ullrich 2001; Wagner & Edwards 2001; Théato, unpublished). The importance of these landscape elements, which include field margins, hedgerows, woodland patches, ditches and streams, has a variety of reasons. First, border structures are generally managed less intensively than the adjacent farmland and may for this reason have a greater species pool (Edwards *et al.* 1999). Second, border structures are ecotonal habitats, i.e. transitions between two or more habitat types. Similarly to natural ecotones, they can support species of each habitat type in addition to a specific ecotonal flora, and therefore possess a high alpha diversity (Dierschke 1974; Zelesny 1974). Third, border structures offer a great variety of different habitats and niches. Their vegetation may therefore be more heterogeneous than that of the structurally uniform agricultural land, i.e. present a high beta diversity (Ellenberg 1996). Fourth, corridor structures may alleviate the increasing fragmentation of the landscape by contributing to the exchange of species and genotypes between scattered landscape elements (Fry & Robson 1994).

The influence of border structures on the plant species composition of crop fields seems to be rather weak (Marshall 1989; Marshall & Arnold 1995; Smith *et al.* 1999). This would

contradict the fear of some farmers that diverse border structures are important sources of pest and weed immigration into the fields (Théato, unpublished). Still, Marshall (1989) and Marshall & Arnold (1995) found a decrease in species number from the edge towards the centre of the studied crop fields. The generality of this result, however, still needs to be established.

The present study contributes to increase our knowledge of spatial patterns in vegetation diversity across the agricultural landscape by focusing on the following three questions: (i) How diverse are border structures compared to the managed area? (ii) How is vegetation diversity within the managed area related to land-use intensity? (iii) How does vegetation diversity within the managed area depend on distance from border structures? We examined these questions for a farmland area of 30 ha in Central Switzerland that includes pastures, meadows and arable fields, based on an extensive vegetation survey on a systematic sample grid covering the entire area.

Methods

Study site

The study site, located in Oberwil-Lieli AG, 10 km SE of Zurich (47°20' N, 8°24' E; 590 m a.s.l.), was a farmland area of 30 ha surrounded by beech and spruce forest. The farmland has been intensively managed by the Farm Litzibuch and is representative for agricultural land-use practice in the agricultural belt of the Swiss plateau. The whole area is flat or weakly sloped. Management includes dairy farming with pasturing and crop cultivation. About two thirds of the area (21.5 ha) are rotational crop fields. In the study year, barley, wheat, spelt and maize were grown on parts of these fields (12 ha), along with intensively managed meadows (9.5 ha). The rest of the area consisted of extensively managed meadows (2.8 ha) and cattle and horse pastures (5.5 ha). Several farm buildings are situated in the centre of the area (Fig. 1).

The soil types of the studied area are cambisols and gleysols that are susceptible to water-logging and shrinkage crevices, depending on precipitation. The climatic conditions of the area are humid-temperate. Mean annual temperature in Zurich is 7.9 °C, and mean annual precipitation is 1100 mm/yr, most of which falls in summer.

For the purpose of this study five types of land use were distinguished, representing different degrees of land-use intensity (according to the frequency of ploughing and mowing or grazing). In sequence of decreasing intensity, the types are cereal fields (barley, wheat, spelt and maize), intensive meadows, permanent pastures, extensive meadows and border structures. All but the last category are referred to as the 'managed area' hereafter. Intensive meadows are sown on rotational crop fields, mown 3 to 4 times a year, and ploughed again after one or two years. They are characterised by a mixture of sown grass species (*Dactylis glomerata, Festuca pratensis, Festuca rubra, Lolium multiflorum, Lolium perenne, Phleum pratense, Poa pratensis*) with a high content of clover (*Trifolium pratense, Trifolium repens*). Extensive meadows are mown two or three times a year, and their species composition is not influenced by sowing. Border structures are partly mown, but not ploughed; they include forest edges, field and pasture margins, a few ruderal sites and a single young hedge. They are consistently termed 'border structures' hereafter. Most of the border structures are rather narrow (mean width of 2 m, ranging from 0.4 to 9 m); their total length is 6600 m, and their total area, 1.2 ha.

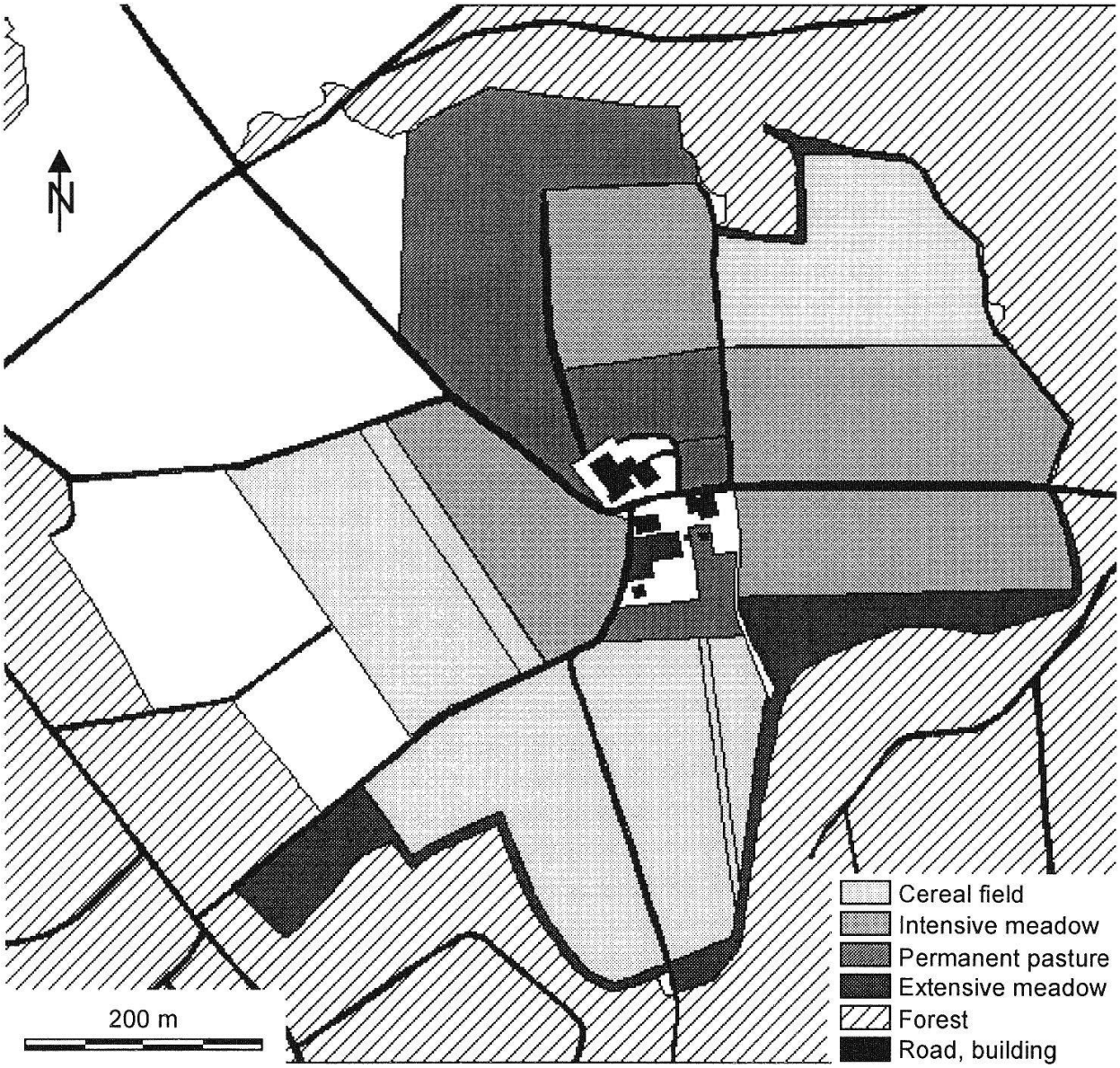

Fig. 1. *Map of the farm Litzibuch. The northwestern side is open towards a neighbouring farm. White areas indicate either uncultivated areas (central settlement) or cultivated areas belonging to the neighbouring farm.*

DATA COLLECTION

The vegetation of the managed area was surveyed according to a regular grid of sample points that covered the entire area. The spacing of sample points was chosen such as to keep the amount of field work feasible while ensuring a sufficient density of sample points for spatial analysis. Thus, the mesh width of the grid was 25 m in both directions, which yielded a total of 481 sample points, of which 188 were in cereal fields, 145 in intensive meadows, 83 in pastures, 32 in extensive meadows, and 33 in other areas. A corrected GPS (Trimble Pro XR/XRS, Sunnyvale, USA; accuracy ± 1 m) was used to obtain the map coordinates of each sample point for GIS analysis. Vegetation relevés were performed at each sample point within quadrats of 1 m^2 (cf. Fig. 4). This rather small plot size allowed us to sample many plots and to detect variations in species composition at microsite scale.

Border structures, which represented only 3% of the area, would not have been adequa-

tely sampled by the grid method and were therefore treated separately. All border structures were partitioned into visually homogeneous sections of 21–285 m length (mean = 119 m). In each of the 56 resulting sections, three randomly placed quadrats of 1 m^2 were surveyed; average cover values of the species in these three quadrats were used in data analysis.

All field work was carried out from May to July 2001. To obtain comparable results, care was taken to survey all quadrats of a specific land-use type at the same phenological state of the vegetation. Early relevés were re-visited in July for the addition of species that were possibly missed in May. The abundance-dominance of each vascular plant species (nomenclature according to Binz & Heitz 1990) was assessed on an extended Braun-Blanquet scale with nine levels (Wilmanns 1989). The numbers 1 to 9 were assigned to the ordered levels of this scale, with 0 for absence. For numeric analysis, cover estimates were transformed into fractions from 0 (= 0% cover) to 1 (= 100% cover).

DATA ANALYSIS

The diversity of the vegetation was characterised by four different indices: species richness S and Shannon's diversity index H' as measures of alpha diversity; evenness E' (H'/log S) as measure of dominance patterns; mean dissimilarity of neighbouring quadrats as a measure of beta diversity (i.e. heterogeneity). Dissimilarity was quantified by the squared Euclidean distance D (Kent & Coker 1992). For each quadrat, squared Euclidean distances from the four rectangular neighbours were calculated, and D was the mean of the four values. The squared Euclidean distance is very sensitive to differences in species dominance. Thus, in extreme (rather theoretical) cases, it is possible that two sites without any common species and with high evenness seem to differ less from each other than two sites that share some subordinate species but have different dominants (Legendre & Legendre 1998). This may be an undesirable effect, but in our case, differences in species dominance did appear most relevant for the assessment and ecological interpretation of dissimilarity. By contrast, the presence or absence of subordinates may be due to chance in the rather disturbed agricultural ecosystem, so that it seemed sensible to give it little weight in the assessment of dissimilarity. As border structures had not been sampled in a systematic way, vegetation heterogeneity was determined only in the managed area.

The four indices of vegetation diversity were subjected to a nested ANOVA testing the effect of management type against variation among lots and variation among lots against variation among individual quadrats. If the effect of management was significant, the four types were compared pairwise with the Tukey HSD test to determine which management types differed significantly from each other.

For spatial analysis we used a raster GIS (Idrisi 32, Clark University, USA). A map of the study area (1: 5000) provided the basis for a raster image on which several vector layers were superimposed. The vector layers represented the different types of land use as well as landscape structures such as forest, roads, border structures and fields. For each sample point (relevé), the perpendicular distance from the closest border structure was calculated with GIS. Linear regression was used to analyse how vegetation diversity depended on distance from border structures. Only Shannon diversity and heterogeneity were considered in these analyses as measures of alpha and beta diversity, respectively. To test whether the most diverse border structures influenced the diversity of the managed area stronger than average, distances of relevés from border structures

Table 1. *Floristic composition of the study area, based on 481 quadrats of 1 m^2.*

	All plots	Managed area	Border structures
Total	180	98	167
Graminoid species	38	26	37
Fabaceae	6	5	6
Other forbs	136	67	124

Table 2. *Vegetation diversity in the four main types of border structures on the farmland Litzibuch (mean* ± SD; n *= number of visually homogenous border sections defined for each type).*

	n	Shannon index	Species richness	Evenness
All	56	2.44 ± 0.65	12.91 ± 3.73	0.71 ± 0.16
Road margins	34	2.31 ± 0.53	11.56 ± 2.57	0.72 ± 0.14
Field limits	1	2.40	9.00	0.74
Forest borders	18	2.63 ± 0.83	15.50 ± 4.46	0.69 ± 0.20
Ruderal areas	3	2.77 ± 0.61	14.00 ± 2.00	0.71 ± 0.15

were re-calculated using only the 28 border structures with a Shannon diversity greater than the mean of all border structures; vegetation diversity was also regressed against these distances. These analyses were carried out for the managed area as a whole and separately for every single management type.

Results

VEGETATION DIVERSITY IN BORDER STRUCTURES AND IN THE MANAGED AREA

A total of 180 non-woody and non-crop plant species were found in the study area (Table 1; Appendix 1). Only 55% of these species (98) were present in the managed area, whereas 93% of them (167) were present in border structures, although the latter represented only 3% of the study area (less than 1.2 ha). Species that occurred only in the border structures included several predominantly forest species (according to Lauber & Wagner 1998) and a few regionally rare or protected species according to the red list of Landolt (1991): *Hieracium lactucella, Gnaphalium uliginosum, Holcus mollis, Stachys palustris, Vicia tetrasperma* and *Dactylorhiza maculata* (see Appendix 1). Border structures were particularly rich in forb species (Table 1): 51% of the forb species found in the study area occurred only in border structures, compared to 32% of the graminoid species (Poaceae, Cyperaceae, Juncaceae) and one of six legumes (Fabaceae). The few species exclusive to the managed area all occurred in the cereal fields and were mainly crop weeds and specialised species of ruderal areas (see Appendix 1).

Of the four main types of border structures, forest borders and ruderal sites had the highest alpha diversity and the highest species richness (mean species richness of the three sample quadrats) (Table 2).

VEGETATION DIVERSITY IN RELATION TO LAND-USE INTENSITY

Within the managed area, lots with different type of management differed considerably in mean vegetation diversity (Table 3). Gener-

Table 3. *Results of nested Anova (F-ratios, significance) testing whether vegetation diversity differs among management types and among lots with the same management type. Vegetation diversity was measured as H', Shannon index; S, species richness; E', evenness; D, mean floristic dissimilarity of neighbouring quadrats. Significance levels are **, P < 0.01; ***, P < 0.001.*

	df	H'	S	E'	D
Management type	3	16.14 ***	8.17 **	19.91 ***	9.81 **
Lot {management type}	13	28.85 ***	16.85 ***	31.16 ***	6.97 ***
Quadrat {lot} = residual	431				

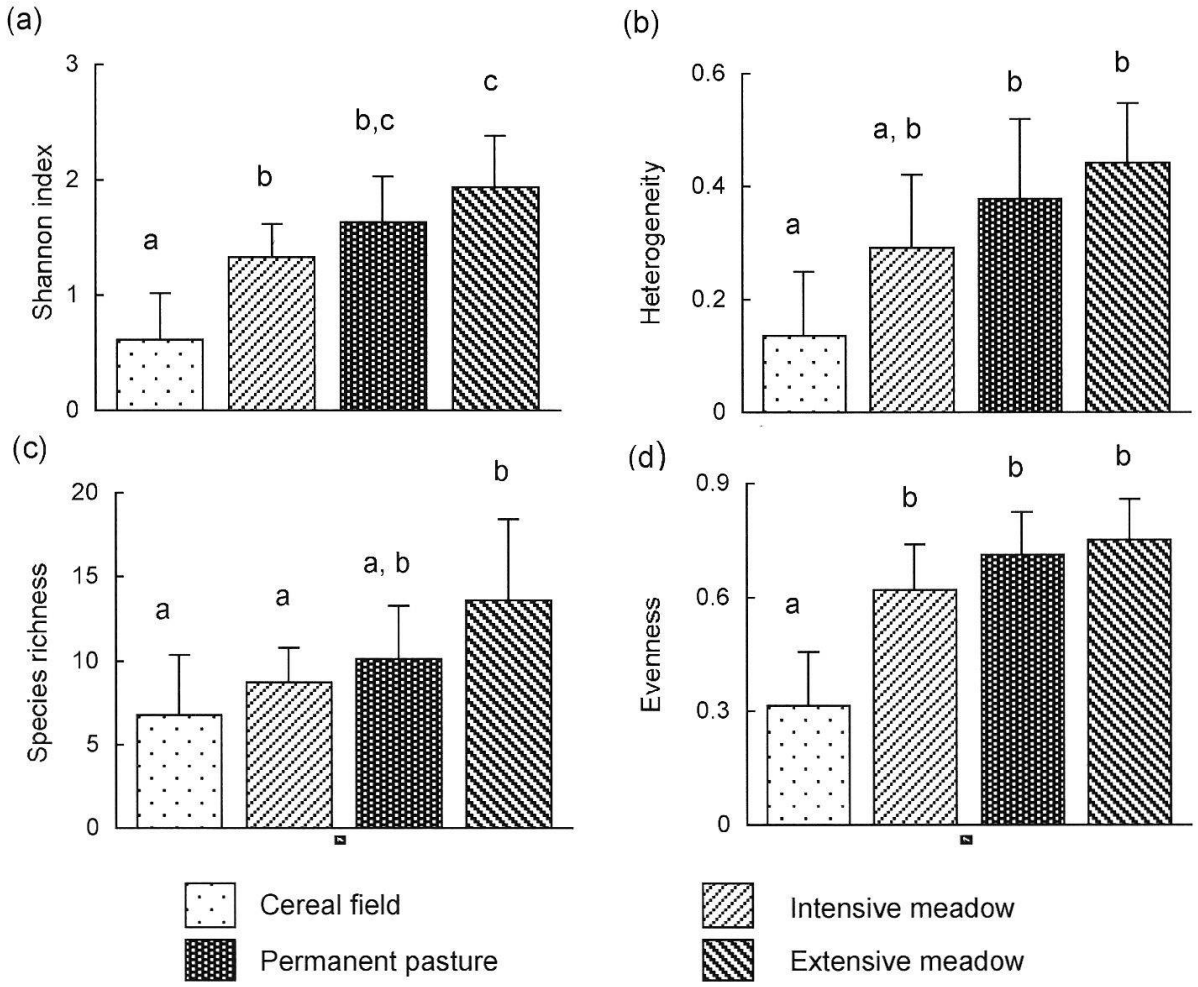

Fig. 2. *Diversity of the vegetation measured as (a) Shannon diversity, (b) heterogeneity (mean floristic dissimilarity of neighbouring quadrats), (c) species richness and (d) evenness in relation to the type of management (mean + SD). Different letters indicate significantly different means.*

ally, diversity increased with decreasing land-use intensity: the four diversity indices all had lowest values in cereal fields and highest values in extensive meadows (Fig. 2). Differences among management types were relatively greatest for Shannon diversity (Fig. 2a). Cereal fields were significantly less diverse than extensive meadows and, with one exception, permanent pastures for all parameters (Fig. 2a-d).

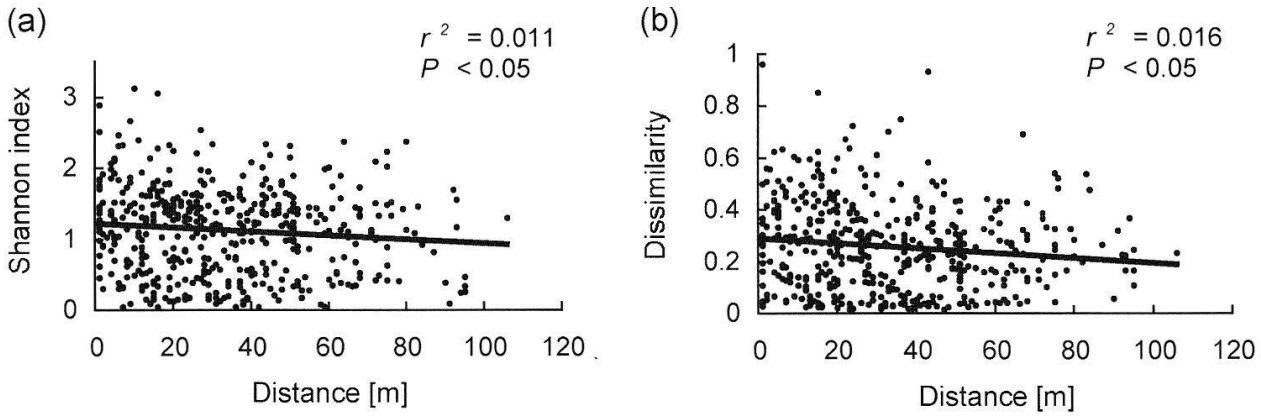

Fig. 3. Linear regression of (a) alpha diversity (Shannon index) and (b) beta diversity (mean floristic dissimilarity of neighbouring quadrats) on distance from border structures. Sample points of the entire managed area are included; all border structures were considered in the calculation of distances.

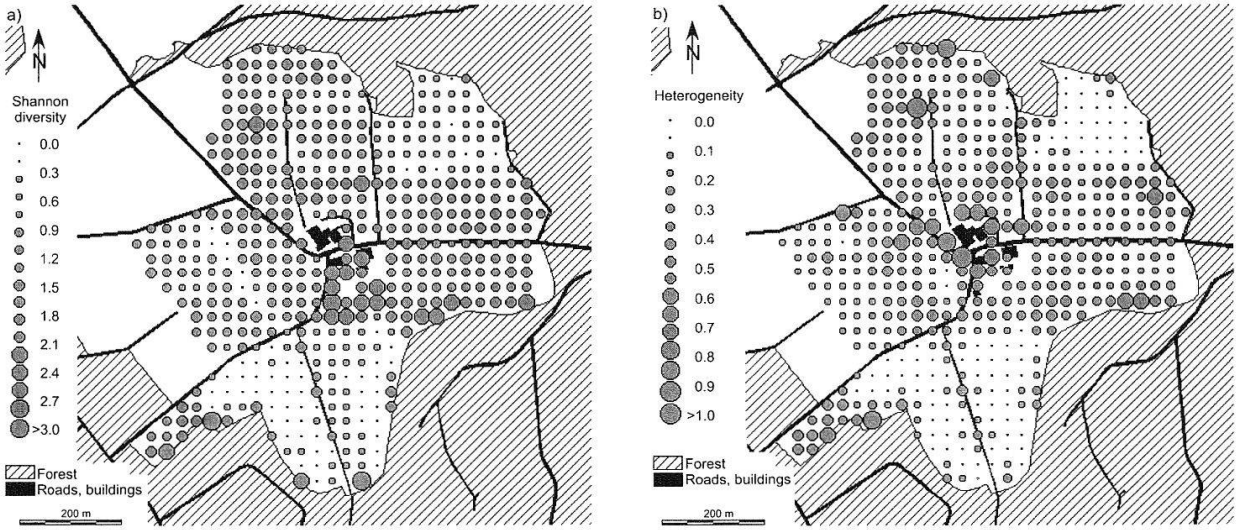

Fig. 4. Spatial distribution of (a) alpha diversity (Shannon index) and (b) beta diversity (mean floristic dissimilarity of neighbouring quadrats) across the study area. The arrangement of points depicts the sample grid. Larger symbols indicate higher diversity. Border structures are continuously adjacent to all forest edges and along all roads.

VEGETATION DIVERSITY IN RELATION TO DISTANCE FROM BORDER STRUCTURES

Considering the entire managed area, alpha and beta diversity (Shannon diversity and heterogeneity) decreased significantly with increasing distance from border structures (Fig. 3). However, this relationship was very weak for both indices (H': $r^2 = 0.011$, $P < 0.05$; D: $r^2 = 0.016$, $P < 0.05$). Fig. 4 shows the spatial pattern of alpha and beta diversity in the study area. While differences among management types are obvious, effects of border structures are less clear, except for a much higher beta diversity around the farm buildings. When only the most diverse border structures were taken into account, relationships between distance from border and vegetation diversity were slightly stronger (H': $r^2 = 0.056$, $P < 0.001$; D: $r^2 = 0.045$, $P < 0.001$).

Separate regression analyses for each management type showed that beta diversity decreased significantly with increasing distance

from border structures within intensive and extensive meadows ($r^2 = 0.046$, $P < 0.05$ and $r^2 = 0.073$, $P < 0.05$, respectively). No significant relationships were found for the other management types or for Shannon diversity.

Discussion

VEGETATION DIVERSITY IN BORDER STRUCTURES

While the total species richness of the study area (180 species) was relatively high for such an intensively managed and weakly structured agricultural landscape (cf. Burel *et al.* 1998; Wagner *et al.* 2000), many species were not abundant in the area and almost 50% of them were restricted to border structures (field and pasture margins, forest edges). Marshall (1989) found even more pronounced differences in species richness between border structures and agricultural area (which in his study included only cereal fields). In contrast, almost all plant species (93%) were present in the border structures, emphasising the importance of these structures for vegetation diversity in an agricultural landscape. Both a more structured habitat type and a lower disturbance frequency seem to explain the higher diversity in border structures (Halley & Lavton 1996; Wagner & Edwards 2001). However, there were also great differences in vegetation diversity among different border structures. For example, many of the species that were only present in border structures (about 35%) were predominantly forest species and were mainly restricted to field margins adjacent to the forest border.

VEGETATION DIVERSITY IN RELATION TO LAND-USE INTENSITY

Vegetation diversity generally decreased with increasing land-use intensity. Thus, on extensively used land more species could be encountered per 1-m^2 plot (species richness; cf. Studer 2001) and in total (species pool; cf. Edwards *et al.* 1999), species were more uniformly distributed within plots (evenness, Shannon diversity), and species composition varied more between individual plots (beta diversity).

However, there is probably a threshold of land-use intensity below which species richness and evenness do not increase further (Swift *et al.* 1996). In our study, species richness and evenness were higher in extensive meadows than in border structures. Various studies have shown that grasslands mown or grazed twice a year are more species-rich than those managed only once a year if nutrient supply is relatively high (Smith *et al.* 2000; Rosenthal 1992). Total abandonment of grazing or mowing has severely reduced species richness in formerly managed grasslands (Müller *et al.* 1992; Smith & Rushton 1994; Linusson *et al.* 1998; Köhler 2001), and abandonment was classified as the second most important cause of species endangering in the analysis of Korneck & Sukopp (1988). On the other hand, species richness is generally lower in fertilised than in unfertilised grasslands (Berendse *et al.* 1992; Smith *et al.* 2000, Gough *et al.* 2000). Thus, in evaluating the effect of land-use intensity on species richness, it is important to distinguish between the effects of disturbance (ploughing, mowing, grazing) and those of fertilisation. Except for very unproductive vegetation types (cf. Proulx & Mazumder 1998), disturbance is needed for the preservation of species diversity. In addition, we found that 7% of the species in our study area were confined to the most intensively managed area (cereal fields). Thus, the maintenance of these intensive structures is also necessary for maximal overall diversity.

Another effect could be responsible for the higher species richness per quadrat of extensive meadows compared to border structures. Extensive meadows were mostly situated adjacent to border structures in the studied area. In a small transition zone both border species and meadow species can co-exist (cf. Marshall 1989; Zelesny 1994), which may explain the high species richness of extensive meadows. Alternatively, while within-plot diversity may be high in an intensively managed area, e.g. due to a smaller size and therefore, a larger number of plants per plot (cf. Stevens & Carson 1999), overall diversity may still be lower than in a less intensively managed area (Wagner & Edwards 2001). This seems to hold for our study, as heterogeneity increased with decreasing land-use intensity.

Our results demonstrate substantial differences in vegetation diversity among different management types within a single farmland. For a full evaluation of the contribution of different agricultural habitats to regional vegetation diversity, it would be necessary to include between-farm diversity, since the spatial scale of ecological processes such as species dispersal may be different among the different management types (Swift *et al.* 1996; Oppermann 2000; Pfiffner 2000).

VEGETATION DIVERSITY IN RELATION TO DISTANCE FROM BORDER STRUCTURES

Generally, alpha and beta diversity of the vegetation were weakly, but significantly, related to distance from border structures. Our hypothesis that the spatial pattern of diversity and heterogeneity within the vegetation of managed areas is influenced by border structures was therefore confirmed by our study, but the effects were rather weak. Two processes may be particularly important for increased diversity in the vegetation of the marginal zones of managed fields: (i) 'propagule radiation' from border structures with higher diversity and/or different species composition into neighbouring areas, and (ii) increased heterogeneity in site conditions (mechanical disturbance, inhomogeneous treatments) in the transition zone (Fielder 1987). In our study area, intense management probably prevented these processes from causing more obvious effects. In addition, the border structures were rather narrow and most of them were not highly diverse. We found a slightly stronger relationship between diversity and distance from border structures when we restricted our analysis to the most diverse borders (e.g. forest margins), even though this decreased the number of borders included in the analysis. This suggests that an even stronger relationship might have been found if all border structures in the study area had been more diverse, and that border structures of lower diversity are considerably restricted in their ability to act as a propagule source.

Our findings may be typical for many intensively used landscapes in Central Europe. They suggest that agro-ecosystems should not be disregarded when regional vegetation diversity is considered, since they can include a respectable diversity. While it is well known that broad, extensively managed border structures like wildflower strips represent biodiversity hot-spots in their own right (e.g. Ullrich 2001), our results show that even relatively narrow and intensively used border strips can substantially increase overall vegetation diversity of a farmland. In addition, despite its weak magnitude, 'diversity radiation' from border structures into managed areas may also increase total biodiversity. This effect is likely to be most pronounced if the ratio of border structure length to managed area is high, if border structures feature particularly high diversity or if management in-

tensity is reduced near the margins of managed areas.

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References

Berendse, F., Oomes, M.J.M., Altena, H.J. & Elberse, W.T. (1992) Experiments on the restoration of species-rich meadows in The Netherlands. *Biological Conservation,* **62,** 59–65.

Binz, A. & Heitz, C. (eds.) (1990) *Schul- und Exkursionsflora für die Schweiz.* 19th edition. Schwabe & Co AG, Basel.

Bosshard, A. & Kuster, D. (2001) Bedeutung neu angelegter Extensivwiesen für Tagfalter und Heuschrecken. *Agrarforschung,* **8,** 252–257.

Braun-Blanquet, J. (1964) *Pflanzensoziologie.* 3rd edition. Springer, Wien.

Burel, F., Baudry, J., Butet, A., Clergeau, P., Delettre, Y., Le Coeur, D., Dubs, F., Morvan, N., Paillat, G., Petit, S., Thenail, C., Brunel, E., Lefeuvre, J.-C. (1998) Comparative biodiversity along a gradient of agricultural landscapes. *Acta Oecologica,* **19,** 47–60.

Cox, T.S. & Wood, D. (1999) The nature and role of crop biodiversity. *Agrobiodiversity: Characterization, Utilization and Management* (eds. D. Wood & J.M. Lenné), pp. 35–58. CABI Publishing, Wallingford.

DeForest Safford, H., Rejmánek, M. & Hadac, E. (2001) Species pools and the "hump-back" model of plant species diversity: an empirical analysis at a relevant spatial scale. *Oikos,* **95,** 282–290.

Dierschke, H. (1974) Saumgesellschaften im Vegetations- und Standortsgefälle an Waldrändern. *Scripta Geobotanica,* **6,** 1–246.

Di Giulio, M., Meister, E. & Edwards, P.J. (2001) Enhancing insect diversity in agricultural grasslands: the roles of management and landscape structure. *Journal of Applied Ecology,* **38,** 310–319.

Duelli, P. (1997) Biodiversity evaluation in agricultural landscapes: An approach at two different scales. *Agriculture, Ecosystems and Environment,* **62,** 81–91.

Edwards, P.J. & Hilbeck, A. (2001) Biodiversity of agroecosystems: past, present and uncertain future. *Crop Science: Progress and Prospects* (eds. Nösberger, J., Geiger, H.H. & Struik, P.C.), pp. 213–229. CABI Publishing.

Edwards, P.J., Kollmann, J. & Wood, D. (1999) Determinants of agrobiodiversity in the agricultural landscape. *Agrobiodiversity: Characterization, Utilization and Management* (eds. D. Wood & J.M. Lenné), pp. 183–210. CABI Publishing, Wallingford.

Ellenberg, H. (1996) *Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht.* 5th edition. Ulmer, Stuttgart.

Fielder, A. (1987) Management options for field margins, an agricultural adviser's view. *Field margins, Integrating agriculture and conservation.* BCPC Monographs (eds. J.M. Way & P.W. Greig-Smith), pp 85–95. BCPC Publications, London.

Fry, G.L.A. & Robson, W.J. (1994) The effects of field margins on butterfly movement. *Field margins: Integrating agriculture and conservation.* BCPC Monographs (ed. N. Boatman), pp 111–116, Thorton Heath.

Gough, L., Osenberg, C.W., Gross, K.L. & Collins, S.L. (2000) Fertilization effects on species density and primary productivity in herbaceous plant communities. *Oikos,* **89,** 428–439.

Gustafson, E.J. (1998) Quantifying landscape spatial pattern: what is the state of the art? *Ecosystems,* **1,** 143–156.

Haas, G., Wetterich, F. & Koepke, U. (2001) Comparing intensive, extensified and organic grassland farming in southern Germany by process life cycle assessment. *Agriculture, Ecosystems and Environment,* **83,** 43–53.

Halley, J.M. & Lawton, J.H. (1996) The JAEP ecology of farmland modelling initiative: spatial models for farmland ecology. *Journal of Applied Ecology,* **33,** 435–438.

Kent, M. & Coker, P. (1992) *Vegetation description and analysis:* A practical approach. Belhaven Press, London.

Köhler, B. (2001) *Mechanisms and extent of vegetation changes in differently managed limestone grasslands.* Ph.D. thesis, Swiss Federal Institute of Technology (ETH), Zurich.

Korneck, D. & Sukopp, H. (1988) Rote Liste der in der BRD ausgestorbenen, verschollenen und gefähreten Farn- und Blütenpflanzen und ihre Auswertung für den Arten- und Biotoschutz. Bundesforschungsanstalt für Naturschutz und Landschaftspflege, Bonn-Bad Godesberg.

Landolt, E. (1991) *Gefährdung der Farn- und Blütenpflanzen in der Schweiz: mit gesamtschweizerischen und regionalen roten Listen.* Bundesamt für Umwelt, Wald und Landschaft (BUWAL), Bern .

Lauber, K. & Wagner, G. (1998) *Flora Helvetica.* 2nd edition. Paul Haupt, Bern.

Laussmann, H. (1999) *Die mitteleuropäische Agrarlandschaft als Lebensraum für Heuschrecken. Agrarökologie,* **34.** Bern, Hannover.

Legendre, P. & Legendre, L. (1998) *Numerical Ecology.* 2nd edition. Elsevier, Amsterdam.

Linusson, A.-C., Berlin, G.A.I. & Olsson, E.G.A. (1998) Reduced community diversity in semi-natural meadows in southern Sweden, 1965–1990. *Plant Ecology,* **136,** 77–94.

Londo, G. (1984) The decimal scale for relevés of permanent quadrats. *Sampling methods and taxon analysis in vegetation science* (ed. R. Knapp), pp. 45–49. Dr W. Junk Publishers, the Hague

Mander, U., Mikk, M. & Kulvit, M. (1999) Ecological and low intensity agriculture as contributors to landscape and biological diversity. *Landscape and Urban Planning,* **46,** 169–177.

Marshall, E.J.P. (1989) Distribution patterns of plants associated with arable field edges. *Journal of Applied Ecology,* **26,** 247–257.

Marshall, E.J.P. & Arnold, G.M. (1995) Factors affecting field weed and field margin flora on a farm in Essex, UK. *Landscape and Urban Planning,* **31,** 205–216.

Marshall, E.J.P. & Moonen, A.C. (2002) Field margins in northern Europe: their functions and interactions with agriculture. *Agriculture, Ecosystems & Environment,* **89,** 5–21.

Oppermann, R. (2000) Nature balance scheme – a means to evaluate the ecological benefit of farms. *The relationship between nature conservation, biodiversity and organic agriculture* (eds. S. Stolton, B. Geier, & J.A. McNeely), pp. 160–165. IFOAM, Tholey-Theley.

Pärtel, M., Zobel, M., Liira, J. & Zobel, K. (2000) Species richness limitations in productive and oligotrophic plant communities. *Oikos,* **90,** 191–193.

Pfiffner, L. (2000) Significance of organic farming for invertebrate diversity – enhancing beneficial organisms with field margins in combination with organic farming. *The relationship between nature conservation, biodiversity and organic agriculture* (eds. S. Stolton, B. Geier, & J.A. McNeely), pp. 52–66. IFOAM, Tholey-Theley.

Pfiffner, L., Luka, H. (2002) Effects of low-input farming systems on carabids and epigeal spiders in cereal crops - a paired farm approach in NW-Switzerland. *Basic and Applied Ecology,* in press.

Proulx, M. & Mazumder, A. (1998) Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology,* **79,** 2581–2592.

Reichelt, G. & Wilmanns, O. (1973) *Vegetationsgeographie.* Westermann, Braunschweig.

Rosenthal, G. (1992) Problempflanzen bei der Extensivierung von Feuchtwiesen. *NNA-Berichte,* **5,** 27–36.

Röser, B. (1988) *Saum- und Kleinbiotope: ökologische Funktion, wirtschaftliche Bedeutung und Schutzwürdigkeit in Agrarlandschaften.* Ecomed, Landsberg.

Ryser, P., Langenauer, R. & Gigon, A. (1995) Species richness and vegetation structure in a limestone grassland after 15 years management with six biomass removal regimes. *Folia Geobotanica et Phytotaxonomica,* **30,** 157–167.

Schneider, D.C. (1994) *Quantitative ecology: spatial and temporal scaling.* Academic Press, San Diego.

Smith, H., Firbank, L. G., Macdonald, D.W. (1999) Uncropped edges of arable fields managed for biodiversity do not increase weed occurence in adjacent crops. *Biological Conservation,* **89,** 107–111.

Smith, R.S. & Rushton, S.P. (1994) The effects of grazing management on the vegetation of mesotrophic (meadow) grassland in Northern England. *Journal of Applied Ecology,* **31,** 13–24.

Smith, R.S., Shiel, R.S., Millward, D. & Corkhill, P. (2000) The interactive effects of management on the productivity and plant community structure of an upland meadow: an 8-year field trial. *Journal of Applied Ecology,* **37,** 1029–1043.

Stevens, M.H.H. & Carson, W.P. (1999) Plant density determines species richness along an experimental fertility gradient. *Ecology,* **80,** 455–465.

Studer, S. (2001) *The influence of management on the floristic composition of hay meadows.* Ph.D. thesis, Swiss Federal Institute of Technology (ETH), Zurich.

Swift, M. J., Vandermeer, J., Ramakrishanan, P. S., Anderson, J. M., Ong, C. K. & Hawkins, B. A. (1996) Biodiversity and agroecosystem function. *Functional Roles of Biodiversity* (eds. H.A. Mooney, J.H., E. Medina, O.E. Sala & E.-D. Schulze), pp. 261–298. Wiley, New York.

Ullrich, K.S. (2001) *The influence of wildflower strips on plant and insect (Heteroptera) diversity in an arable landscape.* Ph.D. thesis, Swiss Federal Institute of Technology (ETH), Zurich.

Underwood, A.J. (1997) *Experiments in ecology: their logical design and interpretation using analysis of variance.* Cambridge University Press, Cambridge.

Van der Maarel, E., Noest, V. & Palmer, M.W. (1995) Variation in species richness on small grassland quadrats: niche structure or small-scale plant mobility? *Journal of Vegetation Science,* **6,** 741–752.

Wagner, H.H. & Edwards, P.J. (2001) Quantifying habitat specificity to assess the contribution of a patch to species richness at a landscape scale. *Landscape Ecology,* **16,** 121–131.

Wagner, H.H., Wildi, O., Ewald, K.C. (2000) Additive partitioning of plant species diversity in an agricultural mosaic landscape. *Landscape Ecology,* **15,** 219–227.

Walter, H., Harnickell, E. & Mueller-Dombois, D. (1975) *Klimadiagramm-Karten der einzelnen Kontinente und die ökologische Klimagliederung der Erde: eine Ergänzung zu den Vegetationsmonographien.* Fischer, Stuttgart.

Weggler, M. & Widmer, M. (2000) Vergleich der Brutvögelbestände im Kanton Zürich 1986–88 und 1999. I. Was hat der ökologische Ausgleich in der Kulturlandschaft bewirkt? *Ornithologischer Beobachter,* **97,** 123–146.

Weibel, U. (1998) Habitat use of foraging skylarks (Alauda arvensis L.) in an arable landscape with wild flower strips. *Bulletin of the Geobotanical Institute ETH,* **64,** 37–45.

Wheeler, B.D. (1993) Botanical diversity in British mires. *Biodiversity and Conservation,* **2,** 490–512.

Wildi, O. (1986) Analyse vegetationskundlicher Daten: Theorie und Einsatz statistischer Methoden. *Veröffentlichungen des Geobotanischen Institutes der Eidgenössischen Hochschule, Stiftung Rübel,* **90,** 1–226.

Wilmanns, O. (1989) *Ökologische Pflanzensoziologie.* 4th edition. Quelle & Meyer, Heidelberg.

Wood, D. & Lenné, J.M. (1999) Why agrobiodiversity? *Agrobiodiversity: Characterization, Utilization and Management* (eds. D. Wood & J.M. Lenné), pp. 1–14. CABI Publishing, Wallingford.

Zelesny, H. (1994) Vegetationskundliche und nährstoffökologische Untersuchungen im Übergangsbereich von Mehrschnitt-Wirtschaftsgrünland zu Streuwiese im Württembergischen Alpenvorland. *Dissertationes Botanicae,* **211,** 1–243.

Zobel, K. & Liira, J. (1997) A scale-independent approach to the richness vs. biomass relationship in ground-layer plant communities. *Oikos,* **80,** 325–332.

Zobel, K., Zobel, M. & Rosén, E. (1994) An experimental test of diversity maintenance mechanisms, by a species removal experiment in a species-rich wooded meadow. *Folia Geobotanica et Phytotaxonomica,* **29,** 449–457.

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Electronic Appendix

Appendix 1. List of all non-woody and non-crop plant species recorded in the study area (farm Litzibuch). Abbreviations of management types: C = cereal fields, I = intensive meadow, P = permanent pasture, E = extensive meadow, B = border structures. Abbreviations in plant names: *F.* = *Festuca, L.* = *Lolium, Ch.* = *Chenopodium, Chr.* = *Chrysanthemum, H.* = *Heracleum.*

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