RESEARCH ARTICLE

Quantifying determinants contributing to plant species richness in mosaic landscapes: a single- and multi-patch perspective

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Abstract Despite good theoretical knowledge about determinants of plant species richness in mosaic landscapes, validations based on complete surveys are scarce. We conducted a case study in a highly fragmented, traditional agricultural landscape. In 199 patches of 20 representative multi-patch-plots (MPPs, 1 ha) we recorded a total of 371 plant species. In addition to an additive partitioning of species diversity at the (a) patch- and (b) MPP-scale, we adopted the recently proposed 'specificity' measure to quantify the contribution of a spatial subunit to landscape species richness (subunit-to-landscape-contribution, SLC). SLC-values were calculated at both scales with respect to various spatial extents. General regression models were used to quantify the relative importance of hypothesis-driven determinants for species richness and SLC-values.

At the patch scale, habitat type was the main determinant of species richness, followed by area and elongated shape. For SLC-values, area was more important than habitat type, and its relevance increased with the extent of the considered landscape. Influences of elongated shape and vegetation context were minor. Differences between habitat types were pronounced for species richness and also partly scale-dependent for SLC-values.

Relevant predictors at the MPP-scale were non-linear habitat richness, the gradient from anthropogenic to seminatural vegetation, and the proportions of natural vegetation and rare habitats. Linear elements and habitat configuration did not contribute to species richness and SLC. Results at the MPP-scale were in complete accordance with the predictions of the mosaic concept. Hence, our study represents its first empirical validation for plant species diversity in mosaic landscapes.

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Introduction

Landscape ecology is widely recognised to provide a theoretical basis for nature conservation (Hansson and Angelstam 1991). Its concepts and methods are envisioned to convey biological conservation and natural resource management (Gutzwiller 2002; Liu

and Taylor 2002; Wiens 2005). The majority of studies in this field is still, however, conceptually based on the classical focal patch approach. By adopting the patch-mosaic paradigm (Forman 1995), biotic response variables of interest (usually endangered specialist species) are sampled in homogeneous patches and studied for effects of the surrounding landscape structure (cf. Fahrig 2005).

In the context of the Convention of Biological Diversity and the current reform of the Common Agricultural Policy, strategies in European conservation planning, however, shifted focus from patch-based concepts for endangered species towards landscape-oriented strategies that consider the diversity of the 'ordinary' agricultural landscape (Tilzey 2000; Stoate et al. 2001; Gerowitt et al. 2003; Hoffmann-Kroll et al. 2003; Jeanneret et al. 2003; Peterseil et al. 2004; Weber et al. 2004; Firbank 2005). Consequently, the quantification of the relative importance of determinants of species richness in the agricultural landscape at multiple spatial scales becomes an increasingly important task for landscape ecological research (Burel et al. 1998; Baudry et al. 2000; Le Coeur et al. 2002; Dauber et al. 2003; Jeanneret et al. 2003).

For plants, as sessile organisms, agricultural landscapes consist of a mosaic of habitat patches, which are widely congruent with human-perceived patches of land use: Under given site conditions, a certain management leads to comparably homogeneous living conditions for plant species, resulting in species assemblages that are adapted to the respective environmental conditions and management scheme. In mosaic landscapes, virtually all patches are vegetated: A 'nonhabitat' matrix has therefore not to be considered in landscape-oriented analyses of plant species richness. Instead, agricultural fields (and their associated linear landscape elements) form 'patch neighbourhoods' (Forman 2002) or 'multi-habitat environments' (Tjørve 2002).

The aim of this paper is to disentangle the patterns of plant species richness and diversity found in (a) homogeneous patches and (b) in patch neighbourhoods (or multi-patch plots; MPPs) of a highly fragmented, traditional agricultural landscape. The central objective was to quantify the determinants of (i) species richness and (ii) the specific contribution of patches and MPPs to landscape species richness. We thus address questions that are important for our basic ecological understanding of species patterns

and of interest for nature conservation and land management. The present study was part of a larger project focussing on the development of predictive models for patterns of plant species diversity at multiple spatial scales (Waldhardt et al. 2004).

We conducted complete surveys of plant species composition in twenty MPPs (each 1 ha) from four sites. Species composition and cover was recorded separately for each homogeneous patch found in the MPPs. Data analysis took advantage of two landscape ecological methods, which have been somewhat neglected in the analysis of species distribution patterns in agricultural mosaic landscapes. These are the (a) additive partitioning of diversity, and (b) the 'habitat specificity' approach.

(a) Additive partitioning of diversity components

Unlike Whittaker's (1972) 'classical' multiplicative conception of α-(within habitat) and β-(between habitat) diversity building up the γ-diversity of a larger spatial unit ($\alpha \times \beta = \gamma$), the formula for diversity partitioning proposed by Lewontin (1972), Allan (1975), and Lande (1996) conceives the relationship to be additive, i.e. $\alpha + \beta = \gamma$. The pooled diversity of a collection of sampling units constitutes γ-diversity. This 'total' diversity can then be partitioned into its additive components α and β, where α is the average diversity of a sampling unit, and β simply the difference between γ and α (Wagner et al. 2000), or, in other words, the average diversity absent from a sampling unit (Veech et al. 2002). Beta-diversity here is thus expressed in the same dimension as α and γ and not as in more classical approaches as a dimensionless metric of (dis-)similarity or species turnover (cf. Magurran 2004). The additive partitioning provides a useful basis for investigating and understanding species patterns (Wagner et al. 2000), and makes the additive concept particularly applicable for hierarchical designs across multiple spatial scales (Crist et al. 2003). We applied the additive approach to understand species richness patterns across the patch-, MPP-, and site scale.

(b) Habitat specificity—the 'subunit to landscape species richness contribution'

In the past, landscape ecological research has often neglected one important question: Which parameters

determine the contribution of spatial subunits (i.e. patch or MPP) to landscape species richness? Are these parameters coinciding with those determining species richness, and is their quantitative impact similar? As most species occur with different proportions of their total occurrences in many subunits, the contribution of a subunit to landscape species diversity will always be lower than its species richness. It is a function of (i) the number of species present in a subunit, (ii) the number of species shared with other subunits, and (iii) the proportions of the occurrences of these species that are found in the subunit. Wagner and Edwards (2001) provided a straightforward way to quantify the 'subunit-to-landscape contribution'. They proposed the 'habitat specificity' measure, which is based on one general assumption: Plant species occurrence is a continuum with the conceptual habitat generalists and habitat specialists being special cases on its either end. Therefore, the 'subunit to landscape species richness contribution' (SLC) equals the sum of the proportional occurrences of all species that fall into this subunit.

The contribution of a given spatial unit to landscape species richness is scale-dependent, i.e. it varies with the extent of the landscape under consideration: A patch with a high density of widespread species contributes much to species richness in its vicinity; but for a larger landscape, the contribution of the same patch will be comparatively small, as its species are also found in many other patches. In contrast, patches with only a few species will contribute little to local species richness. If these species are rare at a broader scale, however, this patch will gain importance to species richness at broader scales. We thus calculated SLC-values for homogeneous patches and MPPs with respect to different spatial extents, and analysed the relative importance of the determinants of SLC-values and species richness in general regression models (GRM).

Determinants at the patch-scale

The prevailing determinants of plant species richness in patches are well known: Area and habitat type. The species–area relation is one of the few general laws in ecology (cf. Rosenzweig 1995), and principle differences in species densities of habitat types are basic knowledge in vegetation ecology (cf. Ellenberg 1996). We were interested in their average impact on

species richness and on SLC-values for different spatial extents. Also, we analysed differences between habitat types.

Theory and empirical evidence further suggest that patch shape is important (Huston 1994; Forman 1995; Kunin 1997; Bossuyt and Hermy 2004). Our hypothesis regarding shape was two-tailed: Compact patches may, due to their larger core area, contain more interior species and thus have higher species richness and SLC-values. In contrast, elongated patches encounter relatively larger sections of underlying abiotic environmental gradients. This may result in an increased turnover of widespread species and thus a higher species richness (Kunin 1997).

Further, we hypothesised that the vegetation context may be important for the SLC-value of a patch: The more similar the surrounding vegetation is to the vegetation of a respective patch, the less is the specific contribution of this patch to landscape species richness, since its species may also occur in the other habitat patches.

Determinants at the MPP-scale

For patch-neighbourhoods (MPP), which we here define as an arbitrarily delimited set of homogeneous patches with a standard plot size, we also have a clear theoretical understanding about the determinants of species richness: As an alternative to island biogeography, Duelli (1992, 1997) developed the 'mosaic concept' for the prediction of species richness in mosaic landscapes. According to this concept, species richness in mosaic landscapes depends on (a) habitat variability (number of habitat types), (b) habitat heterogeneity (number of patches), and (c) the surface proportions of natural, seminatural and anthropogenic vegetation.

Another widely discussed determinant of plant species richness in agricultural mosaic landscapes is the occurrence and habitat quality of linear elements associated with fields (e.g., managed and unmanaged field edges, grass roads, herbaceous fringes, hedges etc.). Species composition of linear elements has been subject to many studies over the past decades (Marshall and Moonen 2002), but only recently in larger spatial contexts (Baudry et al. 2000; Le Coeur et al. 2002; Ma et al. 2002). Most studies on the significance of linear habitats were, however, set in highly intensive, large-scale landscapes and little is

known about their relevance in traditional, low input, small-scale mosaic landscapes.

Habitat types are distributed unevenly in a landscape. MPPs with habitats rare at the landscape scale thus contribute most likely more to landscape species richness, than MPPs with common habitat types. Therefore, we have to consider habitat rarity as an additional determinant of SLC-values at the MPP-scale.

Based on the previous discussions, we may frame our research questions into the following three topics:

1. How are α-, β- and γ-components of plant species diversity distributed across spatial scales represented in the surveyed patches, MPPs, and sites?
2. What is, at the patch-scale, the relative importance of habitat type, area, shape and vegetation context for species richness and SLC-values for various spatial extents? How do habitat types differ in species richness? Are there scale-dependent differences in SLC-values between habitat types?
3. Do, at the MPP-scale, the predictions of the mosaic concept hold true for plant species richness and SLC-values? Do linear elements and habitat rarity contribute to species richness and SLC-values in MPPs? Are there scale-dependent differences in the importance of determinants?

Methods

Study region

We conducted our case study in the Lahn-Dill Highlands (Hesse, central Germany), a low mountainous region with altitudes between 200 and 600 m a.s.l. (Fig. 1a). Mean annual temperature ranges from 6 to 8 °C and average annual precipitation is between 650 and 1100 mm. The region represents the eastern ridge of the Rhenish Uplands and is mainly composed of clay schist, siliceous schist, and greywacke. Overall, unproductive soils (cambisols and leptosols) predominate in this traditional agricultural mosaic landscape. Forests cover around 50% of the area (Hietel et al. 2004). Agriculture has always been a matter of small-scale part-time farming and traditional heritage customs led to a severe land fragmentation (Hietel et al. 2005). Mean field size today is around 0.4 ha, but one field spans often more than five estates. This combination of unfavourable abiotic

and socio-economic conditions has produced a traditional small-scale mosaic in nonforested areas with arable fields, rotational fallows, grassland, old fields with shrub succession, and a large proportion of linear elements, such as grass strips, grass roads, herbaceous fringes, and hedges.

Study sites

We selected sites (each 25 ha) in four municipal districts with a traditional land-use mosaic (Fig. 1a, b). As our study focussed on the effects of landscape structure, we chose sites with comparably short abiotic gradients. Thus, all sites were located on moderate south-facing slopes, since southern exposed slopes in the region tend to feature the highest variability and heterogeneity in land use. As a general tendency, all sites revealed a very gentle moisture gradient from moderately dry to moderately moist following the north–south direction.

Study plots

The central objective for the study of multi-patch plots (MPPs) was to test the predictions of the mosaic concept. Therefore, the selection of MPPs aimed at the consideration of the full range of habitat complexity found in one hectare of our sites. Additionally, we wanted to include representative proportions of the main habitat types occurring at the sites. As a first step in a stratification process, we carried out a black and white orthophoto-interpretation of all readily identifiable habitat types at each site using ArcView GIS 3.2. We then overlaid the produced habitat maps with a 1-ha square grid (Fig. 1b). Area proportions of the identified habitat types in all 25 grid cells per study site were calculated. These (log-transformed) data were used to perform a k-means-Cluster Analysis separately for each site with a default number of five clusters. From each of the five clusters per site (results not shown), one grid cell was randomly chosen for field surveys, resulting in a total of 20 MPPs. The selection of the MPPs was bound to the restriction of not sharing a border with other selected plots. Note that the stratification process was solely based on the areal distribution of the main land-use types. The number of patches and other structural parameters were not included in the plot selection process and were thus random.
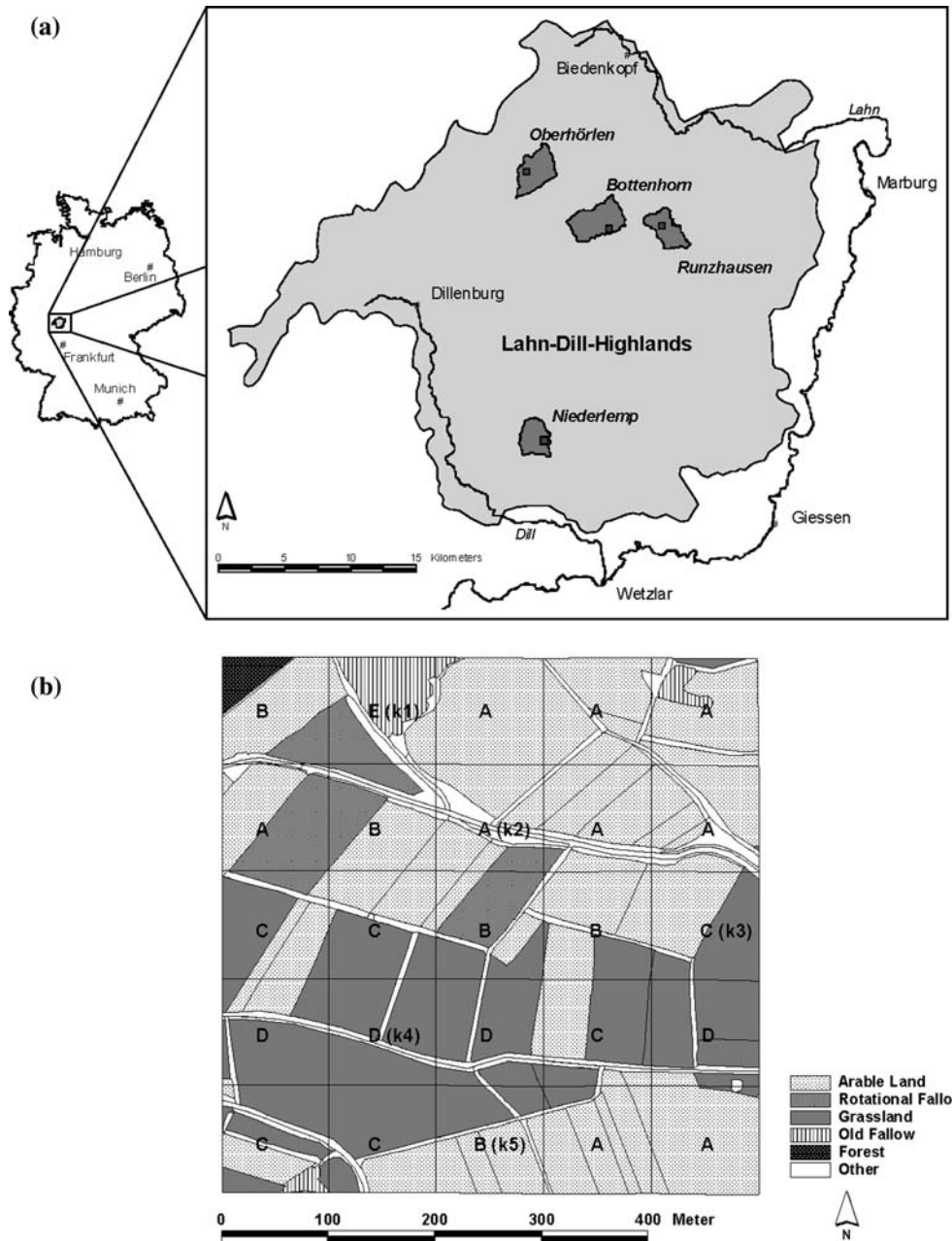
Fig. 1 (**a**) Location of the Lahn-Dill Highlands in Germany and the four districts Bottenhorn (B), Niederlemp (N), Oberhörlen (O), Runzhausen (R) with study sites (small squares). (**b**) Study site (25 ha) in R. The map shows patches as delineated in orthophoto interpretation and main land-use types as verified in the field. The letters A–E refer to the group the grid cells were assigned to in *k*-means Cluster Analysis (see text for details). k1 to k5 denote the selected 1-ha study plots (MPPs)

Habitat classification and field data collection

We collected field data in the summer of 2001. The selected MPPs were localised in the field using a GPS. Dimensions and classification of the homoge-

neous patches inside the MPPs were readjusted and complemented by additional smaller patches that had been not identifiable in the preliminary remote mapping process. All spatial elements that were, regardless of their size, visually homogeneous and

distinguishable from their surroundings, were mapped as a patch and assigned to one of 11 habitat types (classification in Table 3). Depending on the size and location of the elements in the MPP, a patch represented therefore either an entire field/linear element, or – as in many cases – homogeneous patch fragments of various sizes, delimited by the outer borders of the 1-ha plot. For the determination of patch area and perimeter, we transferred the positions and dimensions of the patches back to the GIS.

Habitat types were classified as either 'nonlinear' types (i.e. arable fields, fallows, grassland, old fields, forest), or 'linear' types. The latter (field margins, grass strips, grass roads, fringes and hedges) usually exhibit an elongated, narrow shape (Table 3). Also, we classified habitat types regarding to their vegetation structure, i.e. the fractions of anthropogenic, seminatural and natural vegetation in a respective habitat patch. We defined anthropogenic vegetation, according to Duelli (1997), as composed of mainly annual vegetation, seminatural vegetation as dominated by perennial forbs and grasses, and natural vegetation as dominated by shrubs and trees. While most habitat types were assigned entirely (1/1) to either one of the three groups, some 'hybrid types' were divided into fractions of the three structural types, based on rule of thumb expert knowledge (Table 3). These fractions were later used to calculate vegetation context variables for patch-scale analysis, and proportions of the three structural vegetation types for MPP-scale analysis (see below).

We carried out a complete census of vascular plant species separately for each patch within the 20 MPPs. Sampling effort was proportional to area and we continued the exhaustive search until no new species were encountered for 20 min. If necessary, patches were visited twice to account for temporal variation in species occurrences during growing season. We visually estimated percentage cover values for all species within the Braun-Blanquet cover classes (Kent and Coker 1992). Note that, unlike in the traditional Braun-Blanquet approach, our cover estimates did not relate to a predefined standard relevé or quadrat size, but to the entire patch surface.

Additive partitioning of diversity

We partitioned diversity into its components at four spatial scales. Mean species richness was calculated

at the patch (α_{PATCH}) and multi-patch-plot (α_{MPP}) scale. At the site scale, we calculated pooled species richness of the five surveyed MPPs (α_{SITE}), and γ-diversity was the pooled total species number found in all 20 MPPs. The respective β-diversities were accordingly expressed by the difference between the α-diversities (or γ) of a higher and the next lower level.

Response variables: SLC-values and species richness at the patch and MPP-scale

We calculated the contribution (SLC-value) of a patch or MPP to the species richness of a larger spatial unit according to Wagner and Edwards (2001, see Table 1 in their paper for the formulae): The specificity S_{ij} of a species i to a spatial element j (e.g. a patch) is defined as the proportion of the species' total occurrence that is concentrated in this element. To this end, we first estimated the area covered by each species in each patch by multiplying each species' Braun-Blanquet cover-class mean with the patch area. The obtained values were summed for each species across all patches and set to 1. Thereafter, the proportions S_{ij} of the total occurrences of each species that fell into the respective patch were calculated. The SLC measure was finally derived by summing up the S_{ij} scores of all species found in a patch. Although Wagner and Edwards (2001) termed this estimate also the 'specificity' (S^{aj}_{j}) of a spatial element of the size a, we find that 'subunit contribution to landscape species richness' is a better expression and therefore introduced the acronymised term 'SLC-value'.

To clarify the nature of the SLC-values we provide an example: A generalist species that occurs in 10 patches of a landscape with abundance equally distributed among the patches will contribute with 0.1 to each patch's SLC. In contrast, a specialist or rare species that occurs concentrated in only one patch, contributes with 1 to this patch's SLC, independently of its abundance. As the proportions of all species occurrences in the larger referential spatial unit are divided among all patches, the sum of SLC-values of all patches equals the number of species in the larger spatial unit. Hence follows that SLC-values are purely additive: SLC estimates of patches belonging to one patch neighbourhood (MPP) may be summed up to express this neighbourhood's total contribution to landscape level species richness.

Table 1 Classification and definition of habitat types according to differences in management and vegetation structure

Habitat type	Vegetation structure type (fractions)			Vegetation Management
t	Anthropogenic vs_{1t}	Seminatural vs_{2t}	Natural vs_{3t}	
Linear types				
1 Gravel road	1/1			Sparse annual and herbaceous vegetation due to high frequency of utilisation and unfavourable substrate
2 Cultivated arable field margin	1/1			Narrow strips with annual vegetation along field edges; only distinguished when management was distinctively different to the actual fields
3 Grass strip	1/3	2/3		Grass-dominated strips along fields and roads; rel. high frequency mechanical disturbances
4 Grass road		1/1		Roads with grass-dominated vegetation; mown once or twice a year
5 Herbaceous fringe		1/1		Linear elements with perennial vegetation; infrequent disturbance
6 Hedge		1/4	3/4	Shrub dominated hedges with little herbaceous vegetation; occasional pruning
Nonlinear types				
7 Arable field	1/1			Fields with annual vegetation; crops: barley, oat, wheat, rapeseed, maize
8 Rotational fallow	1/2	1/2		Ex-arable field for 1–3 years, sometimes sown with a grass-clover mixture, large proportions of arable weeds; not mown, or once a year
9 Grassland		1/1		Established grasslands; annual or biannual mowing and/or grazing
10 Old field		1/2	1/2	Old fields overgrown with shrubs and large open areas with herbaceous vegetation; occasional interferences
11 Forest			1/1	Forest stands without regular disturbance within decades

See Methods for details

With our multi-scale design, we were able to calculate SLC-values of a patch or MPP for different spatial extents by enlarging the referential spatial unit. Consequently, we calculated SLC at the patch-scale with respect

(i)   to the MPP, the patch was located in (SLC$_{Patch}$ 1 ha),

(ii) to the total of the five MPPs at its site (SLC$_{Patch}$ 5 ha),

(iii) to the overall area of the twenty MPPs from all four sites (SLC$_{Patch}$ 20 ha).
      Accordingly, SLC-values for the 20 MPPs were derived by pooling the SLC$_{Patch}$ 5 ha and SLC$_{Patch}$ 20 ha-values to receive the contribution of a MPP

(iv) to site species richness (SLC$_{MPP}$ 5 ha), and

(v)   to the species richness of the total area (SLC$_{MPP}$ 20 ha) (Appendix A).

Hence, together with species richness, which we also calculated at the patch- and MPP-scale, we received seven response variables for analyses.

Predictor variables

Patch-scale

A patch, in this study, was conceived as any homogeneously vegetated stand within a MPP that was assigned to a habitat type (cf. Table 3). Area (m^2) and perimeter (m) were derived from the GIS database. We did not differentiate between patches that were recorded entirely, or only fractional. However, varying proportions of our patch-perimeters were 'artificial', i.e. determined by the outer borders of the 1 ha plots. To control for the potential influence of 'true' vs. 'artificial' patch boundaries on the effects of the

variables shape and area, we included (a) the total length, and (b) the proportional length of 'true' patch boundaries as variables in the GRM analysis (see below). Both variables did not yield significant results, thus we concluded that the artificial delimitation of patches did not effect the results.

The shape of a patch j was, in accordance with Wagner and Edwards (2001), measured as circularity C_j (Griffith 1982; Davis 1986; Forman 1995). Circularity is an area a_j and perimeter p_j based function that quantifies the deviation from a circular shape and is thus a measure of compactness (Eq. 1). Possible values range between 0 and 0.32 (perfect circle) Higher values indicate a more compact shape, while elongated patches exhibit low values.

$$C_j = \frac{4a_j}{p_j^2} \tag{1}$$

The vegetation context of a patch was accounted for by estimating the amount of 'Potential Suitable Habitat Area' (PSHA) that is available to the species of a patch. Most plant species are rather confined to a certain structural type of vegetation than to a certain habitat type. Distinguishing the three structural types (anthropogenic, seminatural and natural vegetation), PSHA was therefore defined as the area outside a respective patch (in a defined spatial context) that belongs to the same structural type. The PSHA of, e.g., the species of one meadow patch, is the sum of all areas of seminatural vegetation that occurs in the spatial unit of interest, minus the patches' own area. The overall areas VS_i of the three structural types were calculated for each MPP $k=1,..., 20$. MPPs k are represented by a vector $(a_{k1},...,a_{k11})$, where a_{kt} is the area (m^2) covered by habitat type $t=1,...,11$. With this notation, the overall proportion of anthropogenic VS_1, seminatural VS_2 and natural vegetation VS_3 can be calculated as

$$VS_1 = \sum a_{kt} vs_{1t}, \quad VS_2 = \sum a_{kt} vs_{2t},$$
$$VS_3 = \sum a_{kt} vs_{3t} \tag{2-4}$$

The values of vs_{1t}, vv_{2t}, and vs_{3t} are listed in Table 3. Analogously, we calculated VS_i with respect to the extent of the site (5 ha) and the landscape

(20 ha). Given a MPP k, each patch j is represented by its area a_j and habitat type t. For the PSHA calculation, we distinguished two cases of habitat types (Table 1) 'pure' habitat types with only one nonzero vs_i-value, and (ii) 'hybrid' types with two nonzero vs_i-values. Employing the ceiling function $\lceil x \rceil$, PSHA was calculated as

$$PSHA_j = \left(\sum_{i=1}^{3} \lceil vs_i \rceil \cdot VS_i \right) - a_j \tag{5}$$

Accordingly, we calculated PSHA for the extent of the site (sum of five MPPs per site; 5 ha) and landscape (sum of 20 MPPs from all sites; 20 ha).

MPP-scale

On the MPP-scale, our analysis focussed on the predictions of the mosaic concept and the relevance of linear elements and habitat rarity. The variables considered in the analysis are listed in Table 4, and their values are given in Appendix A. The mosaic concept (Duelli 1997) differentiates between the number of habitat types (habitat variability) and the number of patches (habitat heterogeneity). As we intended to discriminate also between the effects of linear and nonlinear habitats, we counted types and patches separately for both classes. Linear elements were additionally accounted for by calculating their total area in the MPP. We also considered the spatial configuration of elements by calculating Evenness J (Magurran 2004) separately for linear and nonlinear patches. Hence, in contrast to common GIS practices (McGarigal and Marks 1995), we used Evenness as a class metric.

Further, the mosaic concept considers the proportions of anthropogenic, seminatural and natural vegetation. The proportions of the three structural types inside a 1-ha MPP were calculated from the results of Eqs. 2–4.

As they are likely to contain a specific set of species, we also considered the occurrence and amount of rare habitats as an additional variable that may determine SLC-values in multi-patch plots. Thus, to account for rare habitats inside a MPP with respect to the extent of the site (5 ha) or landscape (20 ha), we computed a habitat rarity index (HR_k):

$$\mathrm{HR}_k = \sum_{j=1}^{\Pi} \frac{a_j}{A_k} * \frac{a_j}{A_t} \qquad (5)$$

where π is the respective number of patches in MPP k, A_k the area of MPP k, and A_t the overall area of habitat type t at either the site or landscape scale. Thus, given equal weights to each habitat type, high values indicate the occurrence of more and/or larger patches of habitat types that are rare at the respective spatial extent.

Note that due to the large number and multiple intercorrelations of predictors and the rather small sample size of 20 MPPs, we applied Factor Analysis as a data reduction method (Riitters et al. 1995) to derive a reduced set of predictor variables on MPP-scale (see below).

Statistical procedures

Since the patches sampled in 1-ha MPPs were either adjacent or at least very close to each other, they were thus probably not to be treated as independent samples in statistical analyses. We therefore conducted a series of Mantel tests on patch data to test response and predictor variables for spatial autocorrelation (Mantel 1967; Legendre and Legendre 1998). A spatial distance matrix was computed from pairwise distances (m) between the centroids of patches. Pairwise differences between values were used to construct distance matrices for all predictor and response variables. All matrices were log-transformed prior to analysis. Significance was tested for by Monte-Carlo Tests (9999 permutations), followed by a Bonferroni-Holm Correction ($P < 0.05$) to account for multiple testing (Legendre and Legendre 1998). The tests revealed marginal effects for species richness (r_M=0.03, P=0.02) and PSHA 5 ha values (r_M=0.05, P=0.008), but these became insignificant after Bonferroni–Holm Correction. Thus, it seemed reasonable to conclude that patch data were not spatially autocorrelated. Our patches were therefore treated as independent samples. However, in the stepwise regression procedures, spatial structure was additionally accounted for by including the categorical factors 'Site' and 'MPP' in patch-scale analysis, and 'Site' alone in MPP-scale analysis (see below).

To quantify the relative importance of determinants of species richness and SLC-values for patches

and MPPs, we followed the same scheme for both scales: Predictor variables were included in a multivariate GRM analysis (using stepwise-forward regression and Wilks Lambda) with species richness and SLC-values as response variables. These were followed by separate univariate stepwise-forward GRM procedures for each response variable. Estimates of variance explained (EV%) were calculated from the ratios of the sums of squares of a significant predictor variable to the total sum of squares in the respective univariate general regression model.

Due to many intercorrelated predictors on MPP-scale, we employed Principal Component Factor Analysis (FA, standard varimax axis rotation) for data reduction purposes and to avoid problems with multicollinearity (Stevens 2002). FA resulted in the extraction of four independent, orthogonal factors (with a predetermined minimum Eigenvalue >0.70). These were interpreted and labelled according to the factor loadings of the original predictors (Table 3). Subsequently, the obtained factor scores were used as independent surrogate variables in the GRMs on MPP-scale.

All analyses were performed with log10-transformed and standardised variables. Log-transformation was applied, firstly, to meet the assumptions of normality in GRM. Secondly, as our data were sampled in a limited spatial extent (1 ha), the response variables as well as some predictors (such as area, number of habitats) have an intrinsic maximum. Thus, we assumed that the curves of these predictors vs. species richness/SLC are likely to follow a saturating function. By transformation into logarithmic space, we therefore obtained linear relations as required in GRM and FA. Standardisation of variables was carried out to enable direct comparisons of the parameters and to receive a zero-intercept, which simplified matters for variance partitioning (Legendre and Legendre 1998).

All analyses were carried out with Statistica 6.0 (Statsoft 2001) and PC-ORD (McCune and Mefford 1999).

Results

All 20 MPPs contained anthropogenic (1–96% cover) and seminatural vegetation (4–99% cover), while only seven MPPs contained natural vegetation

(3–71% cover). Regarding habitat variability and habitat heterogeneity (*sensu* Duelli 1997), the selected MPPs varied from 3 to 8 habitat types, and 5 to 18 habitat patches, respectively (Appendix). This resulted in a total of 199 patches found in the 20 MPPs. Overall mean size of the patches was 1000 m^2, varying from 6 to 7.595 m^2. Areal proportion of linear elements per MPP varied between 2% and 23%. One MPP did not contain any linear structures.

Diversity partitioning

A total of 371 species (= γ-diversity) were found in the 20 MPPs. Partitioning of α– β-diversity patterns within and among sites revealed a strong 'between site' effect (β_{SITE}), which accounted for 36% of total species richness (Fig. 2). Another 30% of γ, and 42–52% of species richness at the site scale (α_{SITE}), were due to 'between MPP' diversity (β_{MPP}), and thus an

effect of small-scale spatial variation in species distributions within a site. While a 1-ha MPP contained on average (α_{MPP}) around 33% of γ, and around 50% of α_{SITE}, the β-diversity within a MPP accounted for 23% of γ, and for 34–41% of α_{SITE}. Mean α-diversity of a patch was 10% of γ, and 14–18% of α_{SITE}. These seemingly homogeneous patterns of species diversity at the patch and MPP-scale have to be relativised considering the broad range of minima and maxima values, with α_{patch} reaching almost 40%, and α_{MPP} exceeding 60% of a site's total species richness in some cases. The next results will shed light on the determinants of this heterogeneity.

The patch perspective

Multivariate GRM confirmed area, habitat type, shape, and vegetation context (PSHA 1 ha, PSHA 5 ha) in ascending order of Wilks-Lambda values to
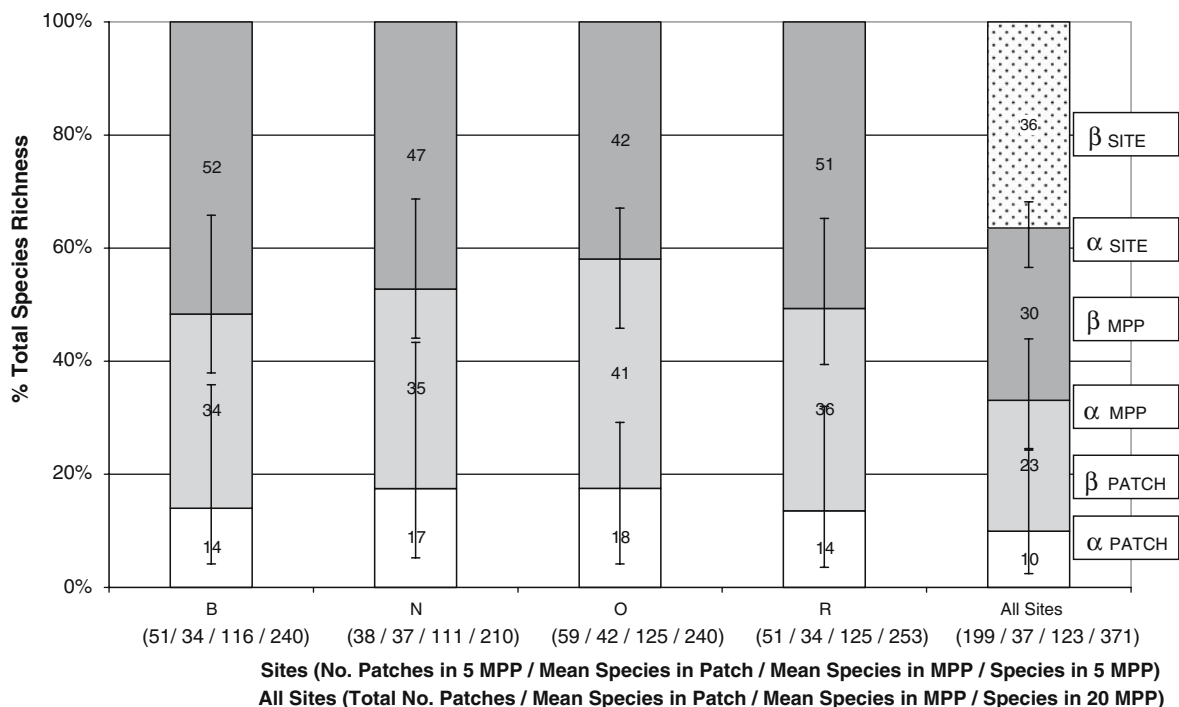
Fig. 2 Additive partitioning of species richness in the four study sites at patch, multi-patch-plot (MPP 1 ha), site (5 ha) and landscape scale (all sites, 20 ha). Abbreviations of sites as in Figure 1a. Figures in the columns give percentages; the real figures of α-components and number of patches are provided beneath abscissa labels. White column sections indicate mean 'within patch' species richness (α_{PATCH}), light grey sections 'between patch diversity' within a 1-ha MPP (β_{PATCH}). The sum of both sections represents mean 'within MPP' species richness (α_{MPP}). Error bars indicate minima and maxima on patch and MPP-scale. Dark grey sections account for β-diversity among the five MPPs of a site (β_{MPP}). Added up with the former two sections, they represent total species richness of a site in five MPP plots ($\alpha_{SITE} = 100\%$). The fifth column shows the results related to γ diversity (total species richness found in 20 MPPs) and complemented by 'between site diversity' (dotted section, β_{SITE})

Table 2 Patch-scale results of GRM on the effects of location (site, pattern), habitat type, area, shape, and vegetation context (PSHA) in the respective area unit on species number and SLC-values for three spatial extents (1, 5, 20 ha)

Effects	Multivariate GRM		Univariate GRM's																				
$n=199$			Species richness					SLC_{Patch} 1 ha					SLC_{Patch} 5 ha					SLC_{Patch} 20 ha				
	Wilks Λ	P	β	MS	df	P	EV%	β	MS	df	P	EV%	β	MS	df	P	EV%	β	MS	df	P	EV%
Intercept	0.96	0.159	−0.03	0.12	1	0.603		−0.02	0.05	1	0.679		0.02	0.04	1	0.682		0.12	1.21	1	0.025	
Habitat type	0.45	<0.001		6.09	10	<0.001	**33.2**		2.31	10	<0.001	**15.6**		1.87	10	<0.001	**13.1**		1.63	10	<0.001	**11.2**
MPP	0.52	0.003			0					0					0					0		
Area	0.35	<0.001	0.48	26.40	1	<0.001	**14.3**	0.73	59.41	1	<0.001	**39.9**	0.80	69.23	1	<0.001	**48.5**	0.85	81.68	1	<0.001	**56.3**
Shape	0.80	<0.001	−0.44	13.71	1	<0.001	**7.5**	−0.32	7.34	1	<0.001	**4.9**	−0.31	7.08	1	<0.001	**5.0**	−0.18	2.40	1	0.002	**1.7**
PSHA 1 ha	0.81	<0.001			0			−0.20	6.02	1	<0.001	**4.1**										
PSHA 5 ha	0.84	<0.001											−0.16	1.53	1	0.014	**1.1**					
Error	–	–		0.44	186		**45.0**		0.29	185		**35.5**		0.25	185		**32.5**		0.24	186		**30.8**

See Methods for details. df = degrees of freedom, MS= mean squares, P = P-level; EV% = explained variance, β = standardised regression coefficient; the spatial factor 'Site', PSHA 20 ha and the interactions of habitat type with all continuous variables were included in the multivariate analysis, but excluded in the stepwise regression procedure

be important determinants of species richness and SLC-values at the patch-scale (Table 2). While a significant effect of the spatial factor 'MPP' in multivariate analysis indicated an overall small-scale spatial patterning of the response variables, this factor did not reach statistical significance in any of the univariate models.

Total variance explained in the univariate GRMs was lower for patch species richness (55%) than for the three SLC-values (65%, 68%, 69%). The amount of variation explained (EV) by area was higher for SLC-values than for species richness (14% EV) and increased with spatial extent from 1 to 20 ha (40%, 48%, 56% EV). Accordingly, the standardised regression coefficient (0.48) for area was considerably smaller for species richness than for the SLC-values (0.73–0.85). This result indicated an overproportional increase of specific contributions to landscape species richness with area.

The influence of patch shape (circularity) followed the opposite direction: Despite a positive correlation between area and shape ($r=0.48$; $P < 0.001$), GRMs revealed a negative effect of a compact shape on both species richness (7.5% EV), and SLC- values. The influence of shape on SLC-values became marginal with increasing spatial extent (5–1.7% EV), however. Thus, elongated patches tended to have more species than more compact shapes, but these species contributed comparably less to species richness at broader scales.

Vegetation context (PSHA) contributed marginally, though significantly to patch SLC-values at the 1-ha (4% EV) and 5-ha extent (1% EV), but was insignificant in the landscape context (20 ha).

The identity of habitat type proved to be the most important predictor of species richness (33% EV), while the effect on SLC-values was considerably smaller and decreased with spatial extent (16–11% EV). To detect differences between habitat types, we regressed the response variables on their respective set of continuous predictors, using the regression coefficients from the univariate models (Table 2). The resulting residuals were then portioned according to the underlying habitat type and tested for differences with Tukey-HSD (for unequal N). Independent of area, shape and PSHA, the habitat types revealed significant differences in species richness, as well as various scale-dependent effects in SLC-values (Fig. 3).
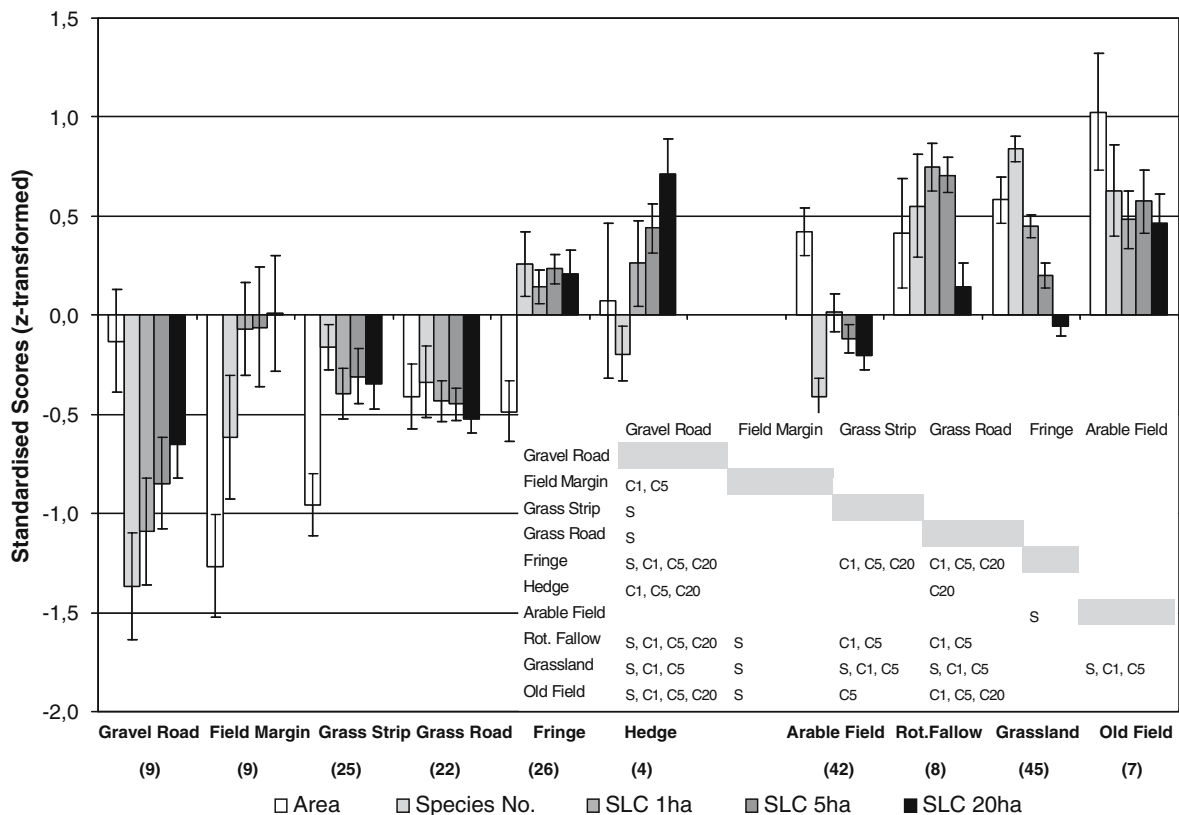
Fig. 3 Comparison of habitat types (*n*) at the patch scale regarding area, species numbers, and SLC-values for three spatial extents (1, 5, 20 ha) (mean±SE). Values of the four dependent variables represent residuals after regressing the original data against significant predictors in the respective GRM (Table 2), i.e., after accounting for all other determinants. Zero of the standardised scores represents the overall mean of the respective variable, 1 its standard deviation. Due to their low number, forest patches are not shown. The matrix in the right corner shows significant differences (post hoc tests, $P < 0.05$) between habitat types for the four dependent variables: S=species number, C1, C5, C20=SLC 1, 5, 20 ha

While species richness and SLC-values of most linear habitat types were well below average, the situation was different for herbaceous fringe vegetation and hedges. As the only linear habitat type, fringe vegetation showed above-average species richness *and* SLC-values, the latter remaining constant at the three spatial extents. Hedges, in contrast, revealed average species richness, but SLC-values increased with spatial extent. Although not significant, they showed highest SLC-values of all habitat types at the 20 ha extent. Despite their small size and low species richness, cultivated field margins featured comparably high SLC-values.

Among the nonlinear habitat types, only arable fields showed species richness and SLC-values below the average. They equalled those of single cultivated field margins. Grassland patches featured a significant higher species richness and contributed more to

MPP (1 ha) and site (5 ha) richness than arable fields. At the landscape scale (20 ha), SLC-values of grassland patches were, in contrast, below the average and equal to arable fields. The same pattern, high species richness and high SLC-values at the 1-ha and 5-ha extent, and a decrease in SLC at the landscape scale, was detected for rotational fallows. Old fields, in contrast, revealed high species richness and specificity at all spatial extents.

The MPP perspective

Factor Analysis on intercorrelated predictor variables in MPP-scale analysis extracted four independent factors, explaining a total of 86% of the original heterogeneity in the data set (Table 3). Factor 1 had highest loadings for habitat rarity at both extents (5 and 20 ha), and the amount of natural vegetation. As

Table 3 Factor loadings and Eigenvalues of Principle Component Factor Analysis on MPP-scale

n=20	Factor 1: Habitat rarity/natural veg.	Factor 2: Linear habitats	Factor 3: Nonlinear habitats	Factor 4: Anthropog. Seminatural veg.
Habitat rarity 5 ha	0.93			
Habitat rarity 20 ha	0.92			
Natural vegetation (%)	0.94			
Configuration nonlinear patches	−0.75			
Area linear types (%)		0.96		
Number linear types		0.93		
Number linear patches		0.93		
Configuration linear patches		0.72		
Number nonlinear patches			0.89	
Number nonlinear types			0.87	
% Anthropogenic vegetation				0.91
% Seminatural vegetation				−0.89
Eigenvalue	3.98	2.95	1.83	1.28
Explained variance (%)	33.15	24.66	15.24	12.96

The scores of the factors 1–4 were used as independent variables in GRM on MPP-scale (Table 4)

patches of natural vegetation were among the rarest types, this is a reasonable combination. Additionally, this factor had a high loading for an uneven spatial configuration of nonlinear habitat patches. Factor 2 represented a combination of the overall area, number and configuration of linear habitats within the MPPs. Factor 3, in contrast, was a surrogate variable for the number of nonlinear habitats (types and patches). Factor 4 represented a linear gradient from MPPs dominated by seminatural vegetation to MPPs dominated by anthropogenic vegetation. Scores of all four factors were used as independent surrogate variables in the GRMs to quantify the relative importance of the four combinations of determinants (Table 4).

Multivariate GRM revealed the categorical factor 'Site' and FA factors 4 and 3 to be important determinants of MPP species richness and SLC-values (Table 4). Linear habitats (factor 2) did not contribute to overall variance explanation. Habitat rarity (factor 1) was excluded from the multivariate model, but did significantly increase variance explanation in all three univariate models, while the factor 'Site' was excluded from the univariate models.

Total variance explained in the univariate GRMs was 68% for MPP species richness, and 70% and 51% for both SLC- values. Number of nonlinear habitats (factor 3) accounted for 35% EV in species richness, but contributed only with 9% EV to SLC-values of MPPs at the site scale, while it was not significant for landscape scale SLC-values.

MPPs with higher proportions of seminatural vegetation had higher species richness (23% EV) and contributed even more to site (43% EV) and landscape (33% EV) species richness. The occurrence of rare habitats in the MPPs was the least important variable for species richness (10% EV), but contributed more to SLC-values at both spatial extents.

Discussion

Partitioning of diversity components

The additive formula of diversity partitioning has recently regained much interest in community ecology and landscape ecological applications with a focus on multiple spatial scales (Loreau 2000; Wagner et al. 2000; Veech et al. 2002; Gering et al. 2003; Ricotta 2003; Roschewitz et al. 2005). It has proved to be particularly useful for the investigation of local–regional relationships of species diversity (Gering and Crist 2002) and hypothesis testing with respect to species distribution patterns (Crist et al. 2003). For our completely surveyed patch neighbourhoods we employed the additive formula to present a comprehensive overview of the patterns of species richness found at the patch, multi-patch and site-scale (cf. Fleishman et al. 2003). By comparing the sites, results revealed remarkably homogeneous patterns in species accumulation from one patch, to one MPP, to five MPPs. High β-diversities further indicated heterogeneous species distributions from the local to landscape scale. Thirty-six percent of total species richness was due to β_{SITE}-diversity. We cannot

Table 4 MPP-scale GRM results on the effects of location (site), habitat rarity, linear habitats, and the gradient from anthropogenic to seminatural vegetation on species number and SLC-values for two spatial extents (5, 20 ha)

n=20 Effects	Multivariate GRM		Univariate GRM's														
			Species richness					SLC$_{MPP}$ 5 ha					SLC$_{MPP}$ 20 ha				
	Wilks Λ	P	β	MS	df	P	EV%	β	MS	df	P	EV%	β	MS	df	P	EV%
Intercept	1.00	1.000	0	0.00	1	1.000		0	0.00	1	1.000		0	0.00	1	1.000	
Site	0.26	0.034			0					0					0		
FA 1: Habitat rarity/nat. veg.	1.00		0.32	1.98	1	0.037	**10.4**	0.42	3.42	1	0.007	**18.9**	0.42	3.29	1	0.026	**17.3**
FA 2: Linear habitats	1.00				0					0					0		
FA 3: Nonlinear habitats	0.40	0.022	0.59	6.60	1	0.001	**34.8**	0.30	1.72	1	0.043	**9.1**			0		
FA 4: Anthrop.-seminat. veg.	0.44	0.008	−0.48	4.30	1	0.004	**22.7**	−0.66	8.18	1	<0.001	**43.0**	−0.58	6.32	1	0.004	**33.3**
Error				0.38	16		**32.2**		0.36	16		**29.9**		0.55	17		**49.3**

See Methods for details

df=degrees of freedom, β=standardised regression coefficient, SE=standard error, MS= mean squares, P=P-level; EV%=explained variance

distinguish with this analysis, whether this result indicates heterogeneity in local species pools, or is merely an effect of the additional area and habitats sampled, but it emphasises the necessity to spatially disperse sampling efforts when the goal is to receive an adequate sample of landscape level species diversity.

Patch-scale

Regarding species richness and SLC-values at the patch-scale, however, we did not detect a significant spatial correlation (Mantel tests). This is an interesting result, as it indicates that both aspects of diversity are mainly dependent on patch-specific traits. The spatial structure of patches may therefore be important for species composition, but negligible, if the focus is on plant species *richness* in mosaic landscapes.

Patch-scale results revealed an expected large influence of area (14% EV) on species richness, which can be interpreted as the average area effect across habitat types in the study region. The area effect studied here complies methodologically with an island curve, i.e., each data point was derived from a unique area and contained all species within this area (Scheiner 2003). The regression coefficient (0.48; Table 2) is analogue to the slope z of the species–area relation (log S=z*log A+log c; Arrhenius 1921; Preston 1960) in standardised data space. If we had calculated the model with unstandardised data, we had received a regression coefficient of 0.14, which lies well within the range of previously pub-

lished slopes constructed from mainland subunits (Rosenzweig 1995; Hanski and Gyllenberg 1997).

Area had a stronger effect on SLC-values than on species richness. This effect even increased with the extent of the landscape (1–20 ha). We consider this an important result, which points to a disproportional higher number of rare, specialist species in larger patches. Supported by theory (cf. Connor and McCoy 1979), we thus expect a higher 'within-patch' habitat diversity in larger patches. Though recent research on the old 'habitat diversity vs. area per se' debate still produces contrasting results (Eriksson et al. 1995; Bruun 2000; Brose 2001; Bruun 2001), it is a widely accepted view that both, area and internal habitat diversity, are supplementary to each other (Forman 1995; Triantis et al. 2003; Scheiner 2004).

Elongated shape also contributed to patch species richness and SLC-values. This influence was expectedly weaker than the area effect, but for species richness still half as strong. In contrast to area, though, shape only marginally affected the contribution to landscape species richness (SLC-values). In accordance with our hypothesis, the shape effect is obviously driven by larger environmental gradients in elongated patches (Kunin 1997). Therefore, the shape effect also suggests an increasing 'within-habitat' diversity. However, as a remarkable difference to the area effect, the shape effect seems not to support the occurrence of species that are rare at the landscape scale. Studies on the effects of plot shape on species richness have shown inconsistent results (Stohlgren et al. 1995; Potts et al. 2001; Bossuyt and Hermy 2004). Some studies could not detect significant

effects of plot shape on species numbers (Wagner and Edwards 2001). However, even though Kunin (1997) considered the elongated shape effect on species richness to be scale-independent, there is evidence that it is irrelevant in small plots (Keeley and Fotheringham 2005).

The vegetation context (PSHA) of a patch contributed only marginally to SLC-values at the 1 and 5 ha extent, and was irrelevant at 20 ha. This result confirms that in heterogeneous mosaic landscapes, the specific contribution of a patch to landscape diversity is mainly driven by intrinsic patch-specific traits and only marginally affected by the patterns of the surrounding vegetation.

The most important variable for species richness was the identity of habitat types. The results revealed a striking difference between linear and nonlinear types (Fig. 3). In past decades, there have been numerous studies on the plant species diversity of linear elements. These have been widely appreciated in landscape planning and nature conservation as being important for landscape species richness. In traditional mosaic landscapes, linear elements are usually small, but occur very frequently. Our results showed that species richness and SLC-values of most linear habitat types were very low, with the exception of hedges and fringes. Of all linear elements compared here, these two types experience the least anthropogenic disturbance. The general increase in species richness (and SLC-values) along a gradient of decreasing disturbance from field margins to hedges (Table 1, Fig. 3) suggested that this is the relevant determinant of species richness of linear elements in our region.

Maximum patch species richness in nonlinear habitats was recorded in rotational fallows, grassland patches and old fields. However, we detected scale-dependent effects on SLC-values: Old fields showed high SLC-values (equivalent to their species richness) at all extents under consideration (Fig. 3). Grassland patches and rotational fallows, in contrast, featured decreasing importance from the local to the landscape scale. Therefore, old fields represent hot spots of diversity at the landscape scale (cf. Simmering et al. 2001). Arable fields, instead, showed an above average species richness, but their contribution to landscape richness was comparably low at all scales. This result is an effect of the general low species density in arable fields, but it also indicates that the surveyed arable fields contained mostly widespread weed species and few specialist species.

MPP-scale

Although Duelli's (1992, 1997) mosaic concept was well perceived in some papers (e.g., Alard and Poudevigne 2000; Wagner and Edwards 2001; Hietala-Koivu et al. 2004; Ortega et al. 2004; Weber et al. 2004), to our knowledge there have yet been no attempts to actually validate its predictions for any group of organisms. The reason for this is presumably that a true validation requires a complete inventory of species richness at a relevant spatial scale. Highly fragmented landscapes offer the opportunity to test the mosaic concept at a relatively small spatial extent, as already small areas, in our case 1 ha MPPs, usually contain large numbers of habitat types and patches. On this scale, vascular plants are furthermore among the view organism groups that are accessible to a complete survey.

Our results at the MPP-scale were completely in accordance with the predictions of the mosaic concept (Duelli 1997). We may therefore explicitly state that the mosaic concept was validated in our study. Species richness was best explained by variations in (i) habitat richness, expressed as a combined variable of (nonlinear) habitat types and patches, (ii) the proportions of anthropogenic and seminatural vegetation, and (iii) the additional occurrence of rare habitats, which correlated closely with the amount of natural vegetation types.

The area and habitat diversity of linear elements did not contribute to MPP species richness. However, results at the patch-scale revealed large differences in species richness and SLC-values between the respective linear habitat types (see above).

The contribution (SLC-values) of the 1-ha MPPs to site (5 ha) and landscape (20 ha) scale species richness was mainly determined by their proportion of seminatural vegetation and the occurrences of rare habitats. Nonlinear habitat richness was only important for SLC-values at the site scale, but not at the landscape scale. These results indicate that highly fragmented patch neighbourhoods (many, but small patches) in mosaic landscapes support a high number of species, as many patches contribute with at least a few exclusive species to MPP species richness. However, they do not support species that are rare at

the landscape scale. This result corresponds with the higher relevance of area for SLC-values than for species richness at the patch-scale. We therefore may conclude that for patches sizes up to 1 ha, rare species are more likely to be found in larger patch.

Conclusions

With our approach to sample representative MPPs, we were able to determine the quantitative impacts of hypothesis-driven predictors on plant species richness from a patch and multi-patch perspective. Our study yielded results that contribute to our basic understanding of species distribution in traditional mosaic landscapes, and shows the merits of transcending landscape ecological methods beyond the focal patch approach. Other studies based on a similar complete survey of MPPs were equally successful in revealing main determinants of species patterns in mosaic landscapes (Neßhöver 1999; Retzer 1999). We

therefore recommend this multi-scale method as a Rapid Diversity Assessment approach for plant species patterns. It may serve as a complement method to those more appropriate for less fragmented landscapes (e.g. Stohlgren et al. 1997). For such derived data, the calculation and analysis of SLC-estimates gives additional insight in the complex structures of species distribution (Wagner and Edwards 2001). The knowledge generated by multi-scale studies is important for the evaluation of land management strategies. Further, it fosters the development of spatially explicit models for the prediction of plant species patterns (Triantis et al. 2003; Steiner and Köhler 2003; Waldhardt et al. 2004).

Appendix Landscape structure, species numbers, and SLC-values of 20 multi-patch plots (MPPs)

Site	Bottenhorn (B)					Niederlemp (N)					Oberhörlen (O)					Runzhausen (R)				
MPP No.	B01	B05	B13	B16	B23	N01	N07	N16	N18	N25	O02	O10	O11	O13	O23	R02	R08	R15	R17	R23
Response variables																				
Species richness MPP	91	124	158	106	101	149	110	107	90	98	161	142	110	123	161	163	148	101	111	101
SLC$_{5haMPP}$	28.8	47.6	70.6	61.5	31.6	75.0	32.4	51.9	23.2	27.5	66.2	48.9	32.0	33.9	59.0	90.8	40.5	33.1	61.4	27.3
SLC$_{20haMPP}$	11.2	24.3	31.7	31.3	8.9	35.5	13.4	17.3	6.8	7.0	22.4	16.4	10.2	10.9	19.6	42.0	17.1	11.2	22.7	10.9
Predictor variables																				
No. habitat types	3	5	7	3	4	3	3	4	3	4	8	6	4	5	6	5	6	3	3	4
No. habitat patches	6	12	17	6	10	6	11	5	7	9	16	12	8	11	12	11	18	6	6	10
Area (%) linear patches	5	12	20	2	5	0	10	10	3	7	16	12	9	8	6	15	23	2	8	7
Configuration linear patches (Evenness)	0.89	0.77	0.78	0.53	0.96	0.84	0.91	0.84	0.97	0.78	0.85	0.84	0.81	0.95	0.90	0.91	0.92	0.83	0.98	0.91
Configuration nonlinear patches (Evenness)	0.61	0.44	0.73	0.57	0.83	0.84	0.91	0.78	0.86	0.52	0.72	0.85	0.63	0.46	0.66	0.80	0.76	0.67	1.00	0.92
Anthrop. veg. (%)	96	18	40	5	61	96	14	1	78	90	8	11	67	3	10	32	74	47	3	59
Seminatural veg. (%)	4	11	35	95	39	96	86	99	22	10	50	89	33	97	66	45	23	53	93	41
Natural veg. (%)	0	71	26	0	0	0	0	0	0	0	42	0	0	0	24	23	3	0	0	0
Habitat rarity 5 ha	29.0	76.6	41.5	39.2	20.4	27.4	8.1	25.7	17.0	33.2	43.3	23.3	59.9	23.8	43.0	66.4	16.1	23.1	18.5	11.4
Habitat rarity 20 ha	8.9	49.0	11.8	6.3	4.0	4.8	2.9	7.2	5.0	7.8	14.7	6.5	7.8	7.3	14.7	21.6	5.8	5.9	4.6	3.0
Linear habitats (no. patches/area%)																				
Gravel road		1/6.4	1/3.1								2/6.2	1/2.9		1/2.3		1/3.4	1/1.1		1/2.6	
Cultivated arable field margin				1/0.2							1/0.1		2/0.8							
Grass strip	2/2.2	5/5.1		1/1.6	1/2.0		1/1.5	1/0.8	2/1.7	1/2.0	1/0.5	1/0.7		1/1.0	1/0.6	2/2.6	3/2.9			1/1.3
Grass road					1/3.3		3/8.2	1/4.0	1/1.2	1/4.5		2/3.0	1/3.5	2/2.1	1/2.7		3/6.1	2/2.3		3/5.9
Herbaceous fringe	1/2.8		4/7.6					1/5.0			3/8.0	3/5.3	2/4.3	3/2.5	2/2.4	4/9.3	3/9.1			
Hedge																	1/4.3		2/5.6	
Nonlinear habitats (no. patches/area%)																				
Arable field	3/95.0	2/8.9	2/34.0	2/4.7	6/56.3	1/3.9	2/12.1		3/76.7	4/85.8	1/1.4		1/64.8		2/9.9	2/15.8	6/66.3	1/46.6		4/58.6
Rotational fallow		1/1.7	1/3.9		1/8.6					1/6.4		1/16.0	1/2.4				1/23.8	1/10.3		
Grassland		2/6.7	1/1.9	2/93.4	1/29.9	4/76.2	5/78.3	2/90.1	1/20.4	1/0.6	4/35.1	4/72.2	1/24.2	4/92.2	5/36.6			3/51.2	3/91.8	2/34.2
Old field			2/40.6			1/20.0					2/10.7				1/47.9	1/45.1				
Forest		1/71.3	1/7.1								1/36.4									

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