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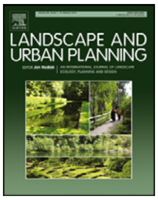

Testing taxonomic and landscape surrogates for biodiversity in an urban setting

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ABSTRACT

Cities often have higher species diversity than the surrounding landscape. This diversity is important for both nature conservation and urban planning. The recreation of residents and the protection of species and habitats are simultaneous targets of maintaining urban green spaces. Data about the distribution and richness of species and their habitats have been compiled frequently; however, it is difficult and costly to measure the complete biodiversity of a region, necessitating useful surrogates. We tested species and habitat data in 27 protected areas in a Central German city and asked (1) whether the diversity of selected taxa acts as a surrogate for the diversity of other taxa and total investigated diversity, and (2) whether landscape structure and human impact explain species richness. Landscape structure metrics were based on soil and habitat types; human influence was measured as the degree of hemeroby. We tested and accounted for sample bias prior to analyses. (1) Vascular plant species richness explained total richness and single taxon richness best. (2) The size of a protected area was the most important predictor of species richness. After correcting for the effect of size, shape complexity, isolation, and matrix properties remained significant. Accordingly, the type of data frequently used for urban planning – collected over several years, by various persons for various purposes – is suitable regarding systematic conservation planning for species richness. The surrogate taxa concept applies in urban areas but with restrictions. Additionally, species richness should be examined in the context of both the city and its surrounding countryside.

1. Introduction

Cities and towns possess specific characteristics, e.g., high levels of air pollution, high disturbance intensity, high abundance of exotic species as well as high landscape heterogeneity (Pickett et al., 2001; Sukopp, 2004). The diversity of human activities in cities creates and maintains a variety of habitats for animals and plants, ranging from fairly natural ones to highly modified ones. This heterogeneity of habitat types together with many existing sources of immigration for both native and exotic species are main causes for the high species richness of urban landscapes that often exceeds the richness of non-urban areas (e.g., Kühn et al., 2004a; Pautasso, 2007).

Protecting the high species and habitat richness of cities should ideally be a main goal for urban planning to be realised simultaneously with the improvement and maintenance of human recreation and well being (Breuste, 2004). However, the specific characteristics of cities (e.g., limitation of semi-natural habitats and open space, habitat fragmentation by built areas) challenge urban planning with respect to the protection of species and habitat diversity (e.g., limitation of migration barriers, promotion of habitat connectivity by corridors or stepping stones). The knowledge of species and habitat distribution provides the basis for a systematic conservation planning (Margules and Pressey, 2000). Thereby, to be suitable for conservation planning, compilations of species and habitat data have to be tailored to the problem under investigation, for instance in the light of defined conservation goals. In Germany, habitat distributional data have been collected in surveys of habitat and land-use types that were established in the 1980s and also covered urban areas. This was also the case for the city of Halle/Saale in Central Germany (see Fig. 1), where the flora and fauna of the city's protected areas has been mapped as well (Buschendorf and Klotz, 1995, 1996).

One main purpose of protected areas is to represent the total biodiversity of the region (Margules and Pressey, 2000). However, the total diversity of all living organisms in a given area is too complex to be measured (Gaston, 1996). Therefore, adequate measurable correlates or surrogates of biodiversity have to be found. Such surrogates can be used as indicators for the quality of biodi-

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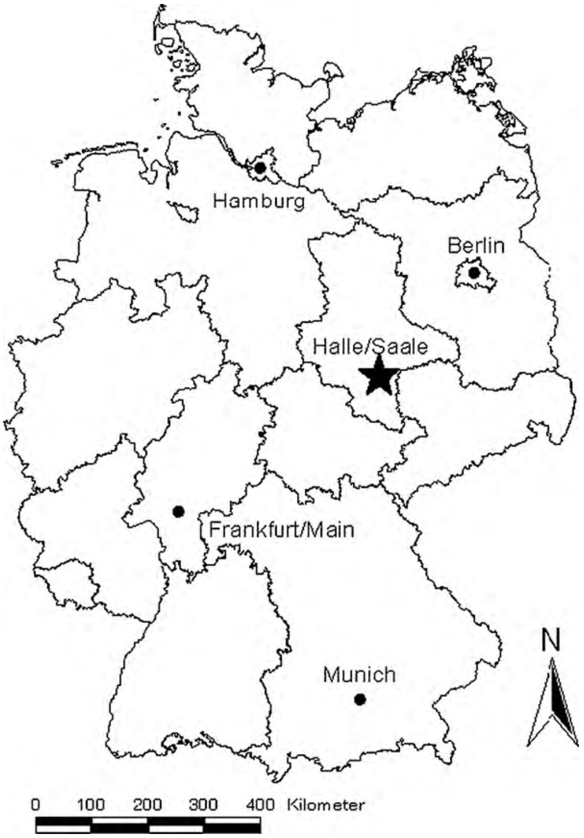

Fig. 1. Location of the study area in Germany.

versity management and of ecologically oriented urban planning (Pullin, 2002). One approach to biodiversity surrogates is the surrogate taxa concept, which postulates that the species richness of one taxon can be representative for the richness of other single taxa and for the total biodiversity of a given area (Margules and Pressey, 2000). Numerous species groups have already been proposed for measuring biodiversity in cultivated areas, mostly plants, birds and butterflies (Duelli and Obrist, 1998). In particular, the species richness of vascular plants and birds were stated to be efficient shortcuts for covering overall species richness (Sauberer et al., 2004). Furthermore, the close relationship of butterflies and plants is well documented (e.g., Su et al., 2004; Schweiger et al., 2008). Moreover, because more than 90% of all genetic variability is contributed by invertebrates, their use as correlates for overall biodiversity seems convincing as well (Duelli and Obrist, 1998).

At a higher level of integration, evaluation of biodiversity can be based on landscape parameters, i.e. landscape structure is used to predict species richness. Key factors for explaining species richness on the landscape scale are landscape structure (Wagner and Edwards, 2001) and geological diversity (Kühn et al., 2004a). As soils are typically influenced by the underlying geological material they mirror geology and geological diversity. Hence, landscape structure metrics based on soil types can be used to explain species richness. Landscape structure metrics based on habitat types or land use, respectively, are also popular for this purpose (Duelli and Obrist, 1998; Deutschewitz et al., 2003).

Moreover, as species richness is not only influenced by natural conditions, but also by human activity, it makes sense to investigate the influence of anthropogenic landscape metrics on species richness: each land-use type selects species from the regional species pool that can cope with the specific conditions of this land-use type (environmental filters, see, e.g., Williams et al., 2009). Thus, different land-use types select different types and numbers of species. In an urban context, highly built areas select different sets of species than, e.g., openly built areas or remnants of semi-natural areas; high amounts of sealed surfaces limit habitat space for many species (Stasch and Stahr, 1999). One parameter that summarizes the impact of human activities on vegetation is the degree of hemeroby (Sukopp, 1969; Kowarik, 1988), which shows the independence of natural processes from human impact.

Besides the properties of protected areas (size, isolation, landscape structure, and hemeroby), properties of the surrounding landscape matrix affect species richness in protected areas: heterogeneous surroundings provide larger species pools than homogeneous surroundings; while the increase of built areas decreases the amount of semi-natural habitats, and hence, should decrease species richness.

As there is no best surrogate for biodiversity that is globally applicable (Margules and Pressey, 2000), the decision on which surrogate to use depends on many factors, for example the availability of data and resources for data analysis. We ask whether the data available for our analysis – which represent the type of data generally collected for nature oriented spatial planning (i.e. collected over long time periods, by various persons from various institutions such as universities or administrative agencies and thus also for various purposes and not always specifically for the conservation of species richness) – are really suitable for reaching conclusions regarding systematic conservation planning in urban settings. A suitable data set for the systematic conservation of species richness should, amongst others, be based on a selection of species that represent the majority of species in the area of interest; be targeted towards the purpose in focus; the data compilation itself often must not be too expensive or too time-consuming. Protection of species in protected areas can follow different targets, e.g., protecting rare species, regionally typical species, or as many species as possible. In our study, we concentrate on species richness, because biodiversity loss is not restricted to rare species but has also been reported for common species (Gaston and Fuller, 2008). Moreover, one main characteristic of urban nature is its high biodiversity (Kühn et al., 2004a).

We investigate if the species richness of specific single taxa, landscape structure and hemeroby of protected areas, as well as the amount of built areas and habitat diversity in the protected areas' surroundings serve as surrogates for the species richness of lichens, mosses, vascular plants, birds, butterflies, carabid beetles, and snails in the protected areas. Additionally, we test whether the total richness of investigated species in the protected areas is explained by the aforementioned parameters. Thus, we use the data on flora and fauna of Halle's protected areas and data on landscape structure to test two approaches of biodiversity surrogates following Margules and Pressey (2000) and Pullin (2002) – i.e. surrogate taxa and/or environmental variables are predictors of species richness – and their applicability in an urban context.

2. Materials and methods

2.1. Study area

The study was conducted in the city of Halle/Saale in Central Germany (Fig. 1), which is situated at the foothills of the Harz Mountains in the Central German loessic belt formed during the last ice age. The Saale is the main river flowing through the city. Halle covers an area of 13,500 ha and has a population of 230,900 people (Stadt Halle, 2008). The city has dense built-up areas in the historical inner city, and newer residential estates from the second half of the 20th century consisting of prefabricated concrete elements in the South and West. Further, the city has many ecologically valuable areas and green spaces. First of all is the Saale

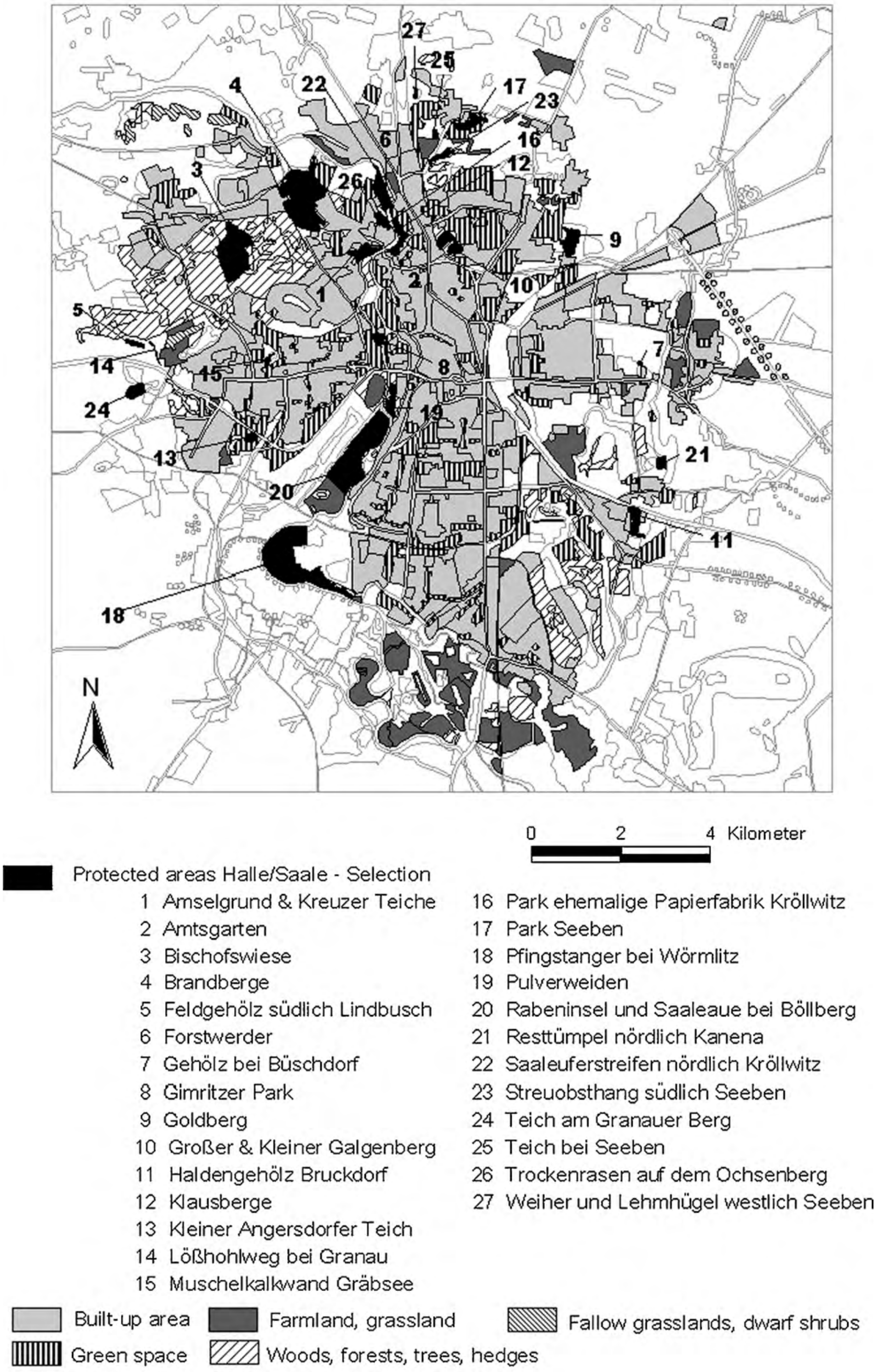

Fig. 2. The study area showing the location of the 27 selected protected areas within the city of Halle/Saale.

floodplain, where many of the protected areas are located representing riparian forests and dry lawns on porphyric rocks. Many of these protected areas are directly adjacent to older residential estates. Additionally, an area of woods and forests is located on the Northwestern fringe of the city. We selected 27 protected areas (Fig. 2) varying in area size from 0.79 ha to 102.05 ha, with a total of 504.48 ha.

2.2. Data sources

2.2.1. Species data

Species numbers of flora and fauna were available from published lists (Buschendorf and Klotz, 1995, 1996) that sum up different sources (i.e. literature, observations and mapping by different persons over a long period) from 1980 to 1995. We selected a

Table 1
Hemeroby levels according to Stasch and Stahr (1999).

Hemeroby level	Degree of human influence	Classification for calculation of landscape metrics	Land-use type (used by Magnucki, 2003b)	Corresponding habitat types in our study (Table 2)
(a) Mesohemerob	Low to very low	1–2	Woods, trees, hedges, ruderal area, grassland, and parks	BIO.G, BIO.H, BIO.K, BIO.M, BIO.N, BIO.P, BIO.R, and BIO.W
(b) Euhemerob	Low			
(c) Euhemerob	Medium to low	3–4	Farmland, horticulture	BIO.A
(d) Euhemerob	Medium			
(e) Polyhemerob	High to medium	5–6	Built-up area (sealing 40–80%)	BIO.B
(f) Polyhemerob	High			
(g) Polyhemerob	High to very high	7–8	Built-up area (sealing 80–100%), railways, roads	BIO.B
(h) Metahemerob	High			

variety of species groups reflecting different dispersal abilities such as dispersal by wind or animals in the case of the flora and such as low or high migration capacity and small-sized or large-sized territorial requirements in the case of the fauna. These were lichens (lichenophyta), mosses (bryophyta), vascular plants (pteridophyta et spermatophyta), birds (aves), butterflies (lepidoptera), carabid beetles (carabidae) and snails (gastropoda).

We divided the vascular plant flora into three status groups of immigration: native vascular plants (indigenous to Germany), archaeophytes (pre 1500 AD aliens, promoted by agriculture from the Neolithic prior to the discovery of the Americas) and neophytes (post 1500 AD aliens, introduced due to long distance transport subsequent to the discovery of the Americas) as this is well established for Central Europe (Pyšek et al., 2004). We distinguished the status groups because alien plant species behave differently from native plant species, for example in ecology (different groups occupy a different variety of habitats) and in evolutionary history (Kühn et al., 2004a). Archaeophytes display intermediate behaviour, which is often even closer to native plants than to neophytes, although archaeophytes are alien plant species themselves (e.g., Pyšek, 1998; Kühn et al., 2003). Immigration status was assigned according to the BiolFlor database (Kühn and Klotz, 2002; Kühn et al., 2004b).

Furthermore, we divided the bird species into four ecological groups, according to their breeding ecology. Thus, four groups of nesting guilds were distinguished: cavity-nesting birds, tree-nesting birds, shrub-nesting birds and ground-nesting birds. Data on nesting guilds were taken from the database BioBase (Centraal Bureau voor de Statistiek, 1997) and from Flade (1994).

2.2.2. *Landscape structure metrics*

To quantify landscape structure, we calculated landscape structure metrics after McGarigal and Marks (1994) using GIS (Arc/View Version 3.2 and ArcGIS 9.3.1), Environmental Systems Research Institute, Redlands, CA) based on the digital map with polygon-topology of protected areas in the city of Halle at a scale of 1:20,000 (Stadt Halle, 2003b). The map of protected areas was intersected with three thematic digital maps with polygon-topology: these were maps of soil types, habitat types and hemeroby levels after Stasch and Stahr (1999; see Table 1). The landscape metrics were calculated on the basis of patches, a patch being defined as an area that is relatively homogeneous and can be clearly separated from its surrounding patches with respect to the parameter of interest (e.g., soil type, habitat type, and hemeroby level). The total number of patches of the same type forms a class.

Soil data were provided by the digital soil map at a scale of 1:50,000 (Magnucki, 2003a) and were used to calculate 17 landscape structure metrics per protected area (patch density and size metrics, edge metrics, shape metrics and diversity metrics). The soil types were aggregated into ten classes (Table 2).

Habitat data were provided by the digital map of habitat types of the city of Halle (Stadt Halle, 2003a) based on area-wide habitat mapping at a scale of 1:5000 in 1998, on selective habitat mapping at a scale of 1:2000 from 1998 onwards, and on aerial infrared photographs taken in 1998 and 1999; and by the digital map of habitat types in the district of Saalkreis surrounding Halle (this map provided data for buffers around some protected areas at the urban fringe; the data are described by Petersohn and Langner, 1992). We aggregated 12 classes (Table 2) and calculated 17 landscape structure metrics per protected area according to soil types. Additionally, we created 100 m and 500 m buffer zones around each protected area (in accordance with Piessens et al., 2004) and calculated the proportion of built areas (from the digital land-use map, Stadt Halle, 2002) and the number of non-built habitat types (from the habitat maps mentioned above) in the buffers. With these matrix predictors, we accounted for the properties of the urban matrix surrounding the protected areas.

For information on hemeroby levels (which are defined as the degree of anthropogenic influence through different land-use types on soil properties and thus, its effect on soil as a resource for flora and fauna, Table 1, according to Stasch and Stahr, 1999), we used the digital map of degree of human influence 1:25,000 (Magnucki, 2003b), which is based on the digital land use map (Stadt Halle, 2002) and the scale of hemeroby by Stasch and Stahr (1999). From this we calculated 17 landscape structure metrics per protected area according to soil types and aggregated four classes (Table 2).

To summarize, 83 landscape metrics were available for analysis: the 17 landscape structure metrics (patch density and size metrics, edge metrics, shape metrics and diversity metrics) calculated for the aggregated classes for soils, habitat types and hemeroby; the total landscape area metric, the distance to nearest neighbour metric, and the matrix predictors in the 100 m and 500 m buffer zones each (Table 2). All metrics were calculated using Patch Analyst (Elkie et al., 1999) except distance to nearest neighbour (after Jenness, 2003), percentage of soil types, habitat types, and hemeroby levels per protected area, and matrix predictors, which were calculated manually.

2.3. *Data analysis*

We selected 27 out of 40 existing protected areas in the city of Halle. For 11 protected areas, data on soils, habitat type, or hemeroby level were not available. Furthermore, one poorly mapped area and one area with a mapping quality above average were visually identified as outliers and were removed from the analysis to adjust for sample bias. We used the number of species (species richness) as an approximation of species diversity. If necessary, species numbers were transformed by sqrt(x) or $\log_{10}(x)$ to approach normal distribution.

Table 2
Overview on calculated landscape structure metrics in the protected areas of the city of Halle. Indices at landscape level (i.e. metrics integrated over all patches and classes over the full extent of the entire landscape, here: one protected area) were related to soil types (BOD.~), habitat types (BIO.~) and hemeroby levels (HEM.~). The following indices were calculated at class level: percentage of soil types, percentage of habitat types and percentage of hemeroby levels per protected area. Patch density and size metrics, edge metrics, shape metrics and diversity metrics were linked with soil types, habitat types and hemeroby levels each; **bold**: groups of landscape metrics, ha: hectare, m: meter, *n*: number of patches.

Index	Description	Unit
Area metrics:		
Classes:		
BOD.~	Percentage of soil types per protected area	%
BOD.AB	Fluvic cambisol	
BOD.BB	Eutric cambisol	
BOD.DD	Vertic cambisol	
BOD.GG	Gleysol	
BOD.PP	Podzol	
BOD.RZ	Calcaric cambisol	
BOD.SS	Stagnic phaeozem	
BOD.TT	Chernozem	
BOD.YK	Urbi-anthropogenic regosol	
BOD.YY	Eutric regosol	
BIO.~	Percentage of habitat types per protected area	%
BIO.A	Farmland and horticultural area	
BIO.B	Built-up area	
BIO.F	Rocks and open space	
BIO.G	Water bodies	
BIO.H	Trees and hedges	
BIO.K	Grassland	
BIO.M	Fallow grasslands and dwarf shrub vegetation	
BIO.N	Wetland	
BIO.P	Parks and green spaces	
BIO.R	Ruderal area	
BIO.W	Woods and forests	
BIO.ohne	Undocumented habitat types	
HEM.~	Percentage of hemeroby levels per protected area	%
HEM.1-2	Very low to low hemeroby	
HEM.3-4	Low to moderate hemeroby	
HEM.5-6	Moderate to high hemeroby	
HEM.7-8	High to very high hemeroby	
TLA	Total Landscape Area: size of one protected area in the city of Halle	ha
Nearest neighbour metrics:		
DIST.NN	Distance to nearest neighbour among the protected areas (edge to edge)	m
Matrix metrics (in buffer zones around the protected areas):		
100.BUILT	Proportion of built-up area in 100 m buffer zone	%
500.BUILT	Proportion of built-up area in 500 m buffer zone	%
100.BIO	Number of habitat types and land-use types in 100 m buffer zone	None
500.BIO	Number of habitat types and land-use types in 500 m buffer zone	None
Patch density and size metrics according to BOD.~, BIO.~ and HEM.~:		
PD	Patch density	n/ha
NumCLASS	Number of classes	None
NumP	Number of patches	None
MPS	Mean patch size	ha
MedPS	Median patch size	ha
PSCoV	Patch size coefficient of variance	None
PSSD	Patch size standard deviation	ha
Edge metrics according to BOD.~, BIO.~ and HEM.~:		
TE	Total edge	m
MPE	Mean patch edge	m
ED	Edge density	m/ha
Shape metrics according to BOD.~, BIO.~ and HEM.~:		
MSI	Mean Shape Index	None
AWMSI	Area Weighted Mean Shape Index	None
MPAR	Mean perimeter-area ratio	m/ha
MPFD	Mean patch fractal dimension	None
AWMPFD	Area weighted mean patch fractal dimension	None
Diversity metrics according to BOD.~, BIO.~ and HEM.~:		
SDI	Shannon's Diversity Index	None
SEI	Shannon's Evenness Index	None

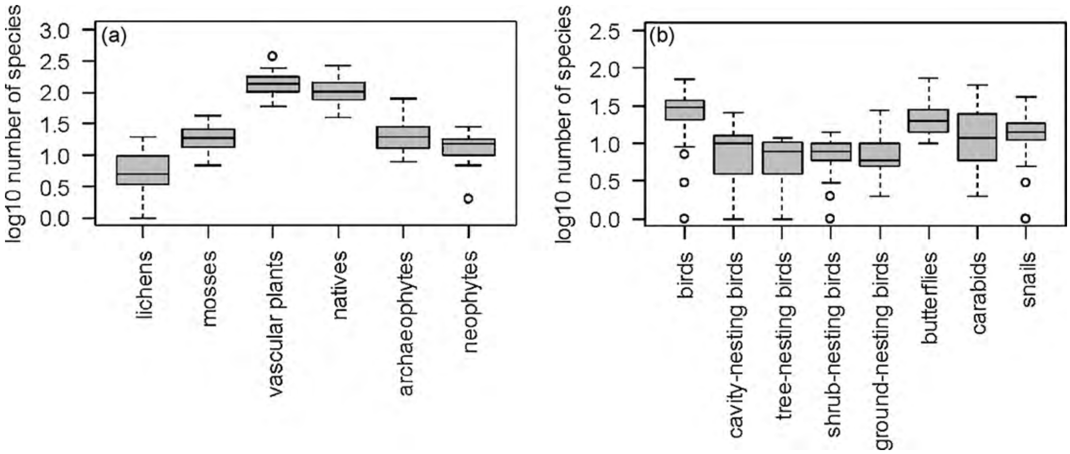

Fig. 3. (a) Species richness of the flora in the protected areas. (b) Species richness of the fauna in the protected areas.

Species richness increases with increasing area or habitat size, respectively, a relationship known as the species–area curve (Rosenzweig, 1995). To account for the correlation with area size we corrected species numbers and landscape variables for area with the species–area relationship. For each species group, we compared the fitness of the semilog model of Arrhenius (1920)

$$S = z\ln(A) + c \tag{1}$$

and of the power model of Gleason (1922)

$$\ln(S) = z\ \ln(A) + c \tag{2}$$

where S is the number of species, A is the area, c and z are constants and ln is the natural logarithm. As the semilog model gave the best fit for most of the species groups, this model was used for further analyses. We performed pairwise Pearson's correlations of the residuals of species number vs. $\log_{10}$ area between the species groups and between the species groups and the total richness of all investigated groups (but excluding the one group used to perform the correlation) to determine surrogate taxa.

To explore the dependence of species richness on landscape structure, the number of landscape structure metrics was reduced by a Principal Component Analysis (PCA) with Varimax rotation to reduce the number of metrics to a smaller set. Since a Principal Component (PC) contains a lot of information and is therefore difficult to interpret, we used the metric with the highest absolute loading per PC, and not the PC itself for further analysis.

To relate the species richness of each group or guild to the landscape variables, we used multiple regression (Crawley, 2002). The response variables were the normalised species numbers of the seven groups (lichens, mosses, vascular plants, birds, butterflies, carabid beetles and snails), the guilds according to immigration status of vascular plants and nesting guilds of breeding birds corrected for area, and all species taken together. The predictor variables were the normalised landscape structure metrics corrected for area. Additionally, we included (1) the percentage of area of trees and hedges on the protected areas (BIO.H) as a relevant landscape structure (e.g., breeding habitat for tree-nesting and shrub-nesting birds) in the regression models for the nesting guilds of breeding birds, and (2) the matrix predictors (100.BUILT, 500.BUILT, 100.BIO, and 500.BIO) as relevant for all investigated taxa. We included the matrix predictors after PCA as we suggest that they are highly relevant for species diversity in the protected areas (providing the local species pool, isolating the protected areas from each other, etc., as Ricketts (2001) states – the matrix matters). Note that butterflies were mapped in a smaller number of protected areas than the other taxa (this reduced the number of degrees of freedom in the regression models, making it necessary to analyse the effects of built-up area und number of habitat types and land-use types separately).

We performed stepwise backward selection for model selection by identifying the minimum value of Akaike's information criterion (AIC) as a measure of goodness-of-fit:

$$AIC = n * \ln\left(\frac{RSS}{n}\right) + 2 * k \tag{3}$$

with n the number of observations, RSS is residual sum-of-squares and k is number of model parameters (Anderson et al., 2000). At each step, the AIC values of all possible models were compared, i.e. the predictor whose omission yielded the lowest AIC was dropped.

Table 3

Results of the regression (species-area relationship) in the protected areas of the city of Halle, for the species richness of different species groups. Dependent variables: species numbers of the selected species groups; Independent variables: area sizes of the protected areas. Note that we refer only to the semilog model of the species-area relationships as this gave the best fit comparing the fitness of semilog model (Arrhenius, 1920) and power model (Gleason, 1922); TLA: total landscape area of the protected areas, n: number of studied protected areas, adj. R^2: coefficient of determination of the regression model adjusted for number of predictors, RSE: residual standard error, F: F-statistic, DF: degrees of freedom.

Species group	Variable in model	Adj. R^2	RSE	F	DF
Lichens ($n = 27$)	TLA	0.31**	4.17	12.7	1, 25
Mosses ($n = 28$)	TLA	0.28**	8.95	11.3	1, 26
Vascular plants ($n = 26$)	TLA	0.46***	51.48	22.2	1, 24
Birds ($n = 25$)	TLA	0.57***	13.34	32.9	1, 23
Butterflies ($n = 14$)	TLA	0.33*	33.21	7.38	1, 12
Carabids ($n = 25$)	TLA	0	14.59	0.17	1, 23
Snails ($n = 17$)	TLA	0.28*	9.99	7.13	1, 15
Total investigated richness	TLA	0.58***	92.58	37.9	1, 26

* Significant ($p < 0.05$).
** Significant ($p < 0.01$).
*** Significant ($p < 0.001$).

Table 4

Correlations across the species richness of selected species groups in the protected areas of the city of Halle corrected for area size (correlations of residuals species number vs. $\log_{10}$ area size of protected areas). n: Number of studied protected areas, r: Pearson's correlation coefficient.

Species groups	n	Mosses r	Vascular plants r	Birds r	Butterflies r	Carabids r	Snails r	Total investigated richness r
Lichens	25	0.42^{*}	0.4	−0.17	0.52	0.29	0.34	0.46^{*}
Mosses	25	1	0.4^{*}	−0.33	0.4	0.17	0.34	0.37(.)
Vascular plants	24		1	0.17	0.67^{**}	0.41^{*}	0.21	0.72^{***}
Birds	21			1	0.04	0.09	0.2	0.14
Butterflies	10				1	0.67^{*}	0.15	0.02
Carabids	23					1	−0.07	0.45^{*}
Snails	15						1	0.22

(.) Significant ($p < 0.1$).

* Significant ($p < 0.05$).

** Significant ($p < 0.01$).

*** Significant ($p < 0.001$).

The model with the minimum AIC was selected for the next step. Thus, we obtained the model that best explains the variation of the dependent variable (species richness) with a minimum of explanatory variables.

Furthermore, for partitioning the explained variation among the landscape variables we applied Hierarchical Partitioning (Chevan and Sutherland, 1991; Mac Nally, 1996). This method shows how much variance is explained independently by one predictor and jointly by several predictors. The significance of the predictor variables revealed by Hierarchical Partitioning was tested by 1000 randomisations using the z scores [observed value − mean (randomised values)/standard deviation (randomised values)] as test statistics (Mac Nally and Walsh, 2004). We used the R^2-coefficient of the model as goodness-of-fit measure. This assisted the assessment of statistical and biological significance.

All analyses were performed using the program R (http://www.r-project.org/, R Development Core Team, 2009).

3. Results

3.1. Species richness

Across all protected areas, there were 1740 species: 84 lichens, 153 mosses, 806 vascular plants, 104 birds, 352 butterflies, 153 carabid beetles, and 88 snails. The median number of vascular plants (138.5) was the highest, while the lowest was the median number of lichens (5.0) (see Fig. 3a and b for details). All species–area relationships were significant (except for carabid beetles) with an explained variance ranging from 28% to 58% (Table 3).

3.2. Relationships of species richness between species groups and between single taxa and total investigated richness

Five out of 21 correlations of species richness among mosses, lichens, vascular plants, birds, butterflies, carabid beetles and snails, corrected for area, were significant; all were positive (Table 4). The highest significant correlations were given by both the species richness of vascular plants with butterflies and of butterflies with carabid beetles ($r = 0.67$, each). Additional significant correlations existed between the species richness of vascular plants and two other groups (carabid beetles, $r = 0.41$; mosses, $r = 0.4$) as well as the species richness of lichens and mosses ($r = 0.42$). Total investigated species richness was correlated positively and significantly with the species richness of vascular plants ($r = 0.72$), lichens ($r = 0.46$) and carabid beetles ($r = 0.45$); all corrected for area. The number of moss species marginally increased with total species richness ($r = 0.37$; see Table 4 for all correlations).

3.3. Landscape variables

The first seven out of 27 PC's explained 67% of total variance. The other PC's did not contribute a relevant amount of explanation. Thus, we derived seven landscape structure metrics for multiple regression, each presented the highest loading variable for each Principal Component: mean perimeter–area ratio based on soil types (BOD.MPAR in PC 1 = 0.97, $R^2 = 0.15$), mean shape index based on soil types (BOD.MSI in PC 2 = 0.98, $R^2 = 0.12$), mean patch fractal dimension based on hemeroby levels (HEM.MPFD in PC 3 = 0.98, $R^2 = 0.10$), mean patch fractal dimension based on habitat types (BIO.MPFD in PC 4 = −0.98, $R^2 = 0.08$), distance to nearest neighbour among the protected areas (DIST.NN in PC 5 = −0.91, $R^2 = 0.07$), percentage of area of woods and forests on the protected areas (BIO.W in PC 6 = 0.99, $R^2 = 0.06$) and mean perimeter-area ratio based on hemeroby levels (HEM.MPAR in PC 7 = 0.98, $R^2 = 0.06$).

3.4. Relationship between species richness and landscape structure

The minimal adequate models explaining the species richness of lichens, vascular plants, native vascular plants, shrub nesting birds, ground-nesting birds, and all species with landscape structure were significant; ground-nesting bird richness was explained best ($R^2 = 0.45$; Table 5 shows all minimal adequate models). Moss richness and snail richness could not be explained with landscape structure; all other models were not significant, but still better than null-models (according to AIC).

The shape complexity variables BOD.MSI, HEM.MPFD, and HEM.MPAR had significant effects on all birds (HEM.MPAR, positive), tree nesting birds (HEM.MPAR, negative), shrub nesting birds (HEM.MPFD, positive), and ground-nesting birds (BOD.MSI, positive).

BIO.W, i.e. percentage of wood and forest area in the protected areas, was significantly and negatively related to ground-nesting bird richness and total investigated richness.

The isolation metric “distance to the next adjacent protected area” (DIST.NN) had significant effects on the richness of all birds (negative) and ground-nesting birds (positive).

Lichen richness increased significantly with the percentage of built-up area in the 500 m buffer zones around the protected areas (500.BUILT).

The number of habitat- and land-use types in the 100 m buffer zones around the protected areas (100.BIO) positively influenced the species richness of vascular plants and native vascular plants. This effect was also visible for total investigated species richness. For marginally significant and not significant effects of landscape variables on species richness within the best predicting model, see Table 5.

Table 5
Results of the stepwise multiple regression analyses (minimal adequate model) in the protected areas of the city of Halle, explaining the species richness of different taxa, immigration status groups of plants and nesting guilds of birds corrected for area (residuals of species number vs. $\log_{10}$ area size of protected areas) with landscape structure metrics; predictors are corrected for area, too (residuals of predictor variables values vs. $\log_{10}$ area size of protected areas). For details see text. *n*: number of studied protected areas, slope +/−: positive/negative effect of landscape variable on species richness, adj. R^2: coefficient of determination of the minimal adequate model adjusted for number of predictors, RSE: residual standard error, *F*: *F*-statistic, DF: degrees of freedom, AIC: Akaike's information criterion.

Response variable	Slope	Predictor variables in model	Adj. R^2	RSE	*F*	DF	AIC
Lichens (*n* = 25) log-transformed	−	BOD.MPAR	0.29*	0.66	4.28	3, 21	56.01
	−	BIO.W(.)					
	+	500.BUILT**					
Mosses (*n* = 25) log-transformed		No variables					
Vascular plants (*n* = 24) log-transformed	+	100.BIO*	0.15*	0.70	5.35	1, 22	55.06
Native vascular plants (*n* = 24) not transformed	+	100.BIO*	0.18*	0.65	6.34	1, 22	51.31
Archaeophytes (*n* = 24) log-transformed	−	BIO.W	0.15	0.87	3.24	2, 23	71.26
	+	100.BIO(.)					
Neophytes (*n* = 23) log-transformed	+	500.BUILT(.)	0.09	0.62	3.37	1, 21	47.37
Birds (*n* = 21) sqrt-transformed	+	HEM.MPFD(.)	0.23(.)	0.51	2.81	4, 19	42.20
	−	DIST.NN*					
	+	HEM.MPAR*					
	−	500.BIO(.)					
Cavity-nesting birds (*n* = 20) not transformed	+	HEM.MPAR	0.15	0.51	2.13	3, 16	35.71
	+	500.BUILT(.)					
	−	500.BIO(.)					
Tree-nesting birds (*n* = 19) sqrt-transformed	+	BOD.MSI	0.25(.)	0.78	2.97	3, 15	49.81
	+	BIO.MPFD(.)					
	−	HEM.MPAR*					
Shrub-nesting birds (*n* = 20) not transformed	+	HEM.MPFD*	0.34*	0.66	3.43	4, 15	46.34
	+	DIST.NN					
	+	500.BUILT(.)					
	−	500.BIO(.)					
Ground-nesting birds (*n* = 20) log-transformed	+	BOD.MSI*	0.45*	0.61	4.88	4, 15	43.35
	+	DIST.NN**					
	−	BIO.W*					
	+	HEM.MPAR					
Butterflies (*n* = 10) log-transformed	+	BOD.MSI	0.48	0.75	2.39	6, 3	26.48
	−	HEM.MPFD					
	−	BIO.MPFD					
	+	BIO.W					
	−	100.BIO					
	+	500.BIO(.)					
Carabids (*n* = 23) log-transformed	−	BIO.MPFD	0.14	0.96	2.20	2, 20	69.15
	−	BIO.W					
	+	500.BUILT					
Snails (*n* = 15) sqrt-transformed		no variables					
Total investigated richness	−	BIO.W*	0.29**	0.54	6.39	2, 25	50.20
	+	100.BIO**					

(.) Significant ($p < 0.1$).
* Significant ($p < 0.05$).
** Significant ($p < 0.01$).

Including "percentage of area of trees and hedges in the protected areas" (BIO.H) into multiple regression for nesting guilds did not improve the model.

Additionally, Hierarchical Partitioning (see Fig. 4a and b) mainly confirmed the above mentioned results; the variables that proved most important in the minimal adequate models also proved most important in Hierarchical Partitioning: 500.BUILT significantly affected lichen richness; 100.BIO significantly affected the richness of vascular plants, native vascular plants, archaeophytes and all investigated taxa; DIST.NN significantly affected ground-nesting bird richness, and for butterflies and for all investigated taxa, 500.BIO was significant. In contrast to the minimal adequate model, Hierarchical Partitioning showed no significant variables for the species richness of shrub-nesting birds. For mosses, neophytes, all birds, cavity-nesting and tree-nesting birds, carabids and snails no variables were significant.

4. Discussion

4.1. Relationships of species richness between species groups and between single taxa and total investigated richness

For efficient conservation planning, it is essential to identify species groups which confer different aspects of biodiversity. Following Duelli and Obrist (1998) and Margules and Pressey (2000), we tested the use of the surrogate taxa concept for the assessment of biodiversity with data from protected areas in Halle/Saale. Although the seven taxa we used in our study only are a subset of the overall biodiversity in Halle's protected areas, we consider the data set to be representative for overall biodiversity, as it covers flora and fauna, and a range of different dispersal abilities and habitat requirements. In the specific urban context of our study, our results support the surrogate taxa concept, with some restrictions.

Single taxa have only little explanatory power when correlating one taxon to another; i.e. there is no species group that can be used to predict the richness of all other groups, if these are taken separately. In our study, only five out of 21 pairwise correlations across species groups were significant. Three out of these five correlations only explained 16% of variance each (species richness of vascular plants and carabid beetles; vascular plants and mosses; lichens and mosses). Only the correlations between the species richness of butterflies and vascular plants and between butterflies and carabid beetles explained more variance (45%). Focussing on the latter two relationships, we see that the species richness of butterflies positively correlates with the species richness of vascular plants, which is not surprising because plants are the feeding resource for these strict herbivores. Simonson et al. (2001) and Su et al. (2004) also obtained a significant positive correlation between butterflies and vascular plants. The positive correlation between the species richness of butterflies and the species richness of carabid beetles seems to be due to the following reason. High numbers of butterflies and carabid beetles are driven by the same factor at the same time: the two groups shared mean patch fractal dimension based on habitat types (BIO.MPFD) as an explanatory variable, which decreased species richness. Accordingly, both butterflies and carabids tend to be isolated by natural dispersal barriers, a pattern we will discuss below. Similarly, habitat type and high landscape heterogeneity both had major positive effects on the species richness of butterflies and carabids in a study by Weibull et al. (2003).

The low congruence in the species richness of the taxa corresponds with the results of other surveys that were performed at different scales than our study. Howard et al. (1998) found only few significant correlations across pairs of selected taxa using the most extensive data set from the tropics (resolution > 100 km^2, extent 3000 km^2). Su et al. (2004) found only the above-mentioned positive relationship between butterfly and plant species richness (22% explained variance; mean resolution 500 km^2, extent unknown).

Still, the real question is whether the presence of any taxon indicates the presence of several other taxa to an extent that it can be considered as a surrogate for overall biodiversity (Margules and Pressey, 2000). In our study, this is the case for vascular plants, which proved to be the best surrogate for overall biodiversity with 72% of correlation, followed by lichens and carabid beetles with almost 50% each. Simultaneously, vascular plant richness is a sufficient surrogate for several single taxa, if these taken separately as described above.

In conclusion, if species inventories in urban areas aim to record overall biodiversity, but time and money are sparse, it seems most efficient to concentrate on vascular plants. Areas with high vascular plant richness will likely be rich in other taxa as well. In this respect, the surrogate taxa concept is successful, in accordance with various publications (e.g., Wood and Pullin, 2002; Weibull et al., 2003; Su et al., 2004). However, our study also shows that the surrogate taxa concept has to be used carefully, if the focus of an inventory is on single taxa – here, it seems preferable to map the target species and no surrogate taxon, especially if it comes to snails or birds whose

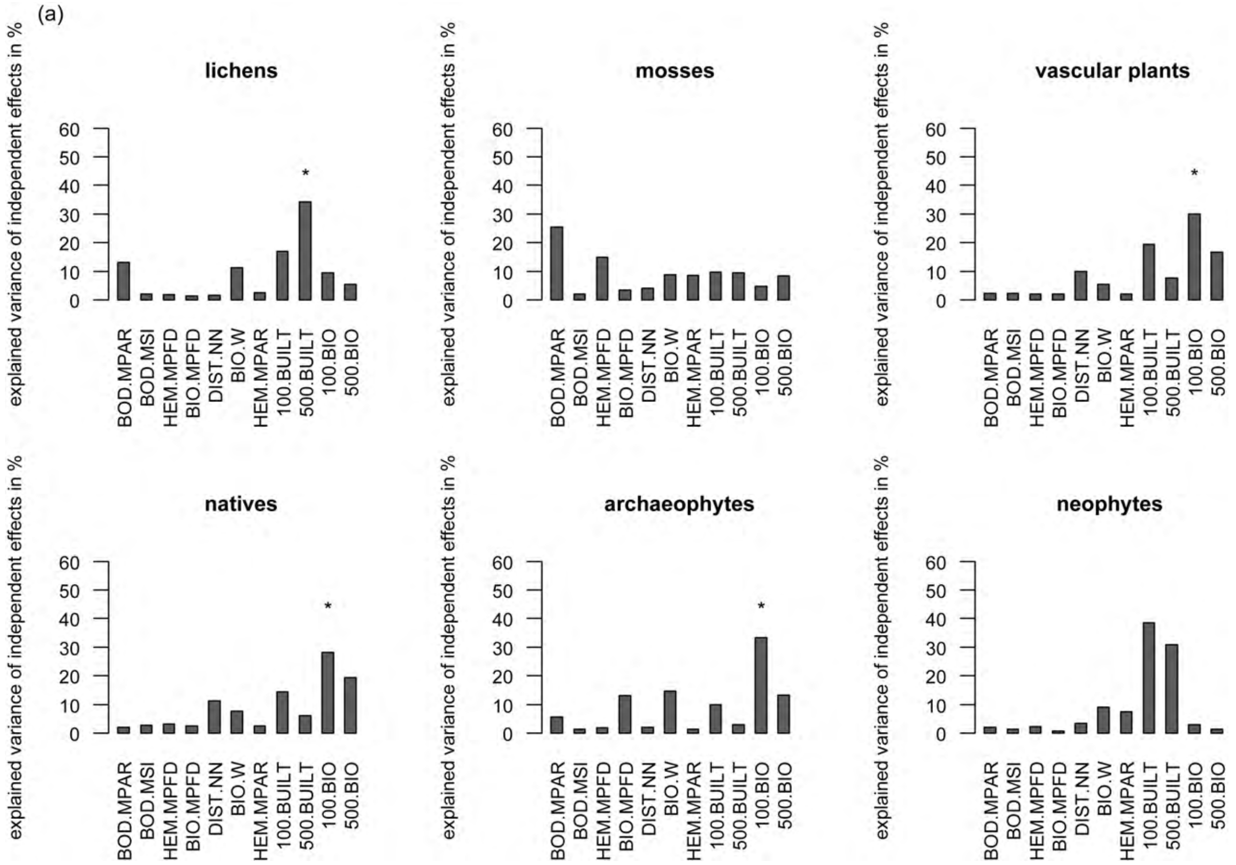

Fig. 4. (a) Hierarchical partitioning of landscape variables explaining species richness of flora within the regression model. (b) Hierarchical partitioning of landscape variables explaining species richness of fauna and of total investigated taxa within the regression model.

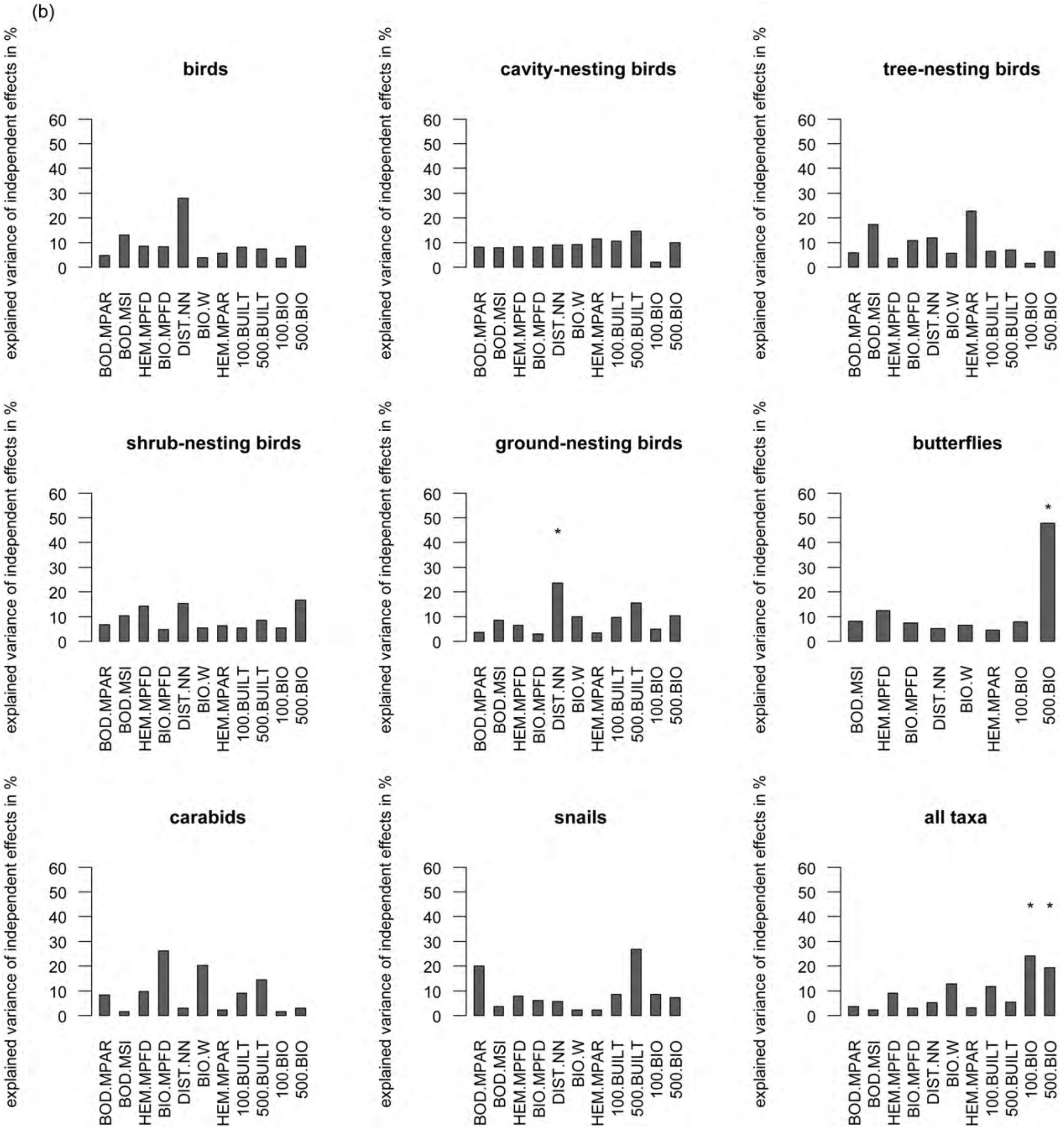

Fig. 4. (*Continued*).

richness was neither correlated to the richness of another taxon, nor to total richness. The independence of bird richness from the richness of other taxa contradicts the recommendation of Sauberer et al. (2004) to use birds as a surrogate group, at least in an urban context. The studies of Howard et al. (1998) and Su et al. (2004) indicate that complementing the surrogate taxa concept by other biodiversity measures, such as complementarity or community similarity, can help to solve such restrictions.

4.2. *Relationship between species richness and landscape structure*

Many studies identified size of area as the main factor explaining the variation in biodiversity indicators, for example Cornelis and Hermy (2004) for urban and suburban parks in Flanders, and Pyšek (1993) for European cities. An earlier study on the protected areas of Halle included area as first predictor in the regression model (Bräuniger, 2004) and showed that it was the main factor explaining species richness. Therefore, to look beyond the influence of area, we accounted for the correlation of landscape variables with area size and did not include area as first predictor in the regression models.

For the highly mobile fauna (birds and their guilds, butterflies and carabids), different shape metrics, mainly based on soil types and human influence, which represent structural diversity, are important. Complex and structured patch areas with a complex shape (high HEM.MPFD) tend to increase the species richness of all birds and shrub-nesting birds and slightly decrease butterfly species richness (Table 5). For the former, it reflects the availability of many suitable habitats and niches; for the latter it reflects the anthropogenic fragmentation of an area, i.e. decreased sizes of continuous habitats and decreased connectivity (Jones et al., 2000). Moreover, different bird guilds responded differently to the same landscape variable, suggesting that these variables reflect several characteristics of landscape structure. This is the case for increasing HEM.MPAR, which increases the species richness of all birds, slightly increases cavity-nesting bird richness and ground-nesting bird richness but decreases tree-nesting bird species richness. For the former, it reflects human-made structures that act as pathways for dispersal, or structure and habitat diversity (Forman and Godron, 1986; McGarigal and Marks, 1994); for the latter it probably reflects dispersal barriers (e.g., walking ways or trails; Forman, 1995; Gustafson and Gardner, 1996) or the lack of trees. Moreover, increasing BIO.MPFD is an ambiguous landscape variable. It tends to increase the species richness of tree-nesting birds and to decrease the species richness of butterflies and carabid beetles. For tree-nesting birds, it reflects the availability of many natural habitats and niches as well as structural diversity (Forman and Godron, 1986; McGarigal and Marks, 1994); for butterflies and carabids it probably reflects fragmentation with natural dispersal barriers, which is consistent with the findings of Niemelä et al. (2002) that carabid beetles need areas large and undisturbed enough to retain beetle communities.

A high percentage of woods and forests in the protected areas (BIO.W) decreased species richness of lichens, archaeophytes, ground-nesting birds and carabids, and increased species richness of butterflies and the total investigated species pool. More than 50% of the lichen species occurring in our study sites are epilithic lichens, i.e. species that grow on rocks and find suitable habitats on house walls and other built structures. Epilithic lichens were most frequent in other urban areas, too, e.g., in UK urban domestic gardens (Smith et al., 2010). Contrarily, lichens that grow on trees are typically underrepresented in urban areas (Wittig, 2002) and only make up 17% of our study lichen species. Many archaeophytes are associated with agricultural or other non-forest habitats (Lososová et al., 2006). Ground-nesting birds prefer open spaces for their nests (e.g., *Perdix perdix* L.). Carabids in urban areas are mainly associated with open habitats, as shown by Magura et al. (2004), while forest specialists are more common in rural landscapes. In the case of butterflies, we suggest that they accumulate along the forest fringe, which as an ecotone, i.e. a transition zone between two habitats, offers suitable living conditions for species from different habitats (as shown for plants by Waldhardt et al., 2004). Interestingly, butterfly richness was decreased by habitat richness in the close surroundings of the protected areas (100.BIO), but was increased by habitat richness in the wider surroundings (500.BIO). This becomes clearer with the positive effect of BIO.W: there are only few forested areas within the city of Halle, and 500 m buffer zones have a higher chance to include these areas than 100 m buffer zones.

High DIST.NN decreases the richness of all bird species. This reflects the well-known pattern that the most isolated patches in a landscape often have low species richness (e.g., Rosenzweig, 1995). In contrast, the species richness of shrub-nesting birds and ground-nesting birds increases with increasing distances among the protected areas. This seems to contradict the above mentioned results. However, many of the protected areas are located along the margins of the city and are farer away from each other than the protected areas that are closer to the city centre (Fig. 2). Thus, with increasing distances between the protected areas the distance of a protected area to the surrounding countryside decreases, while its distance to the city centre increases. We tested this hypothesis and found a significantly positive correlation between the distances of the protected areas to the city centre and the distances among the protected areas (edge-to-edge). Ricketts (2001) emphasised the importance of the matrix, and the city of Halle is mostly surrounded by farmland and grassland. These are suitable habitats for shrub-nesting birds and ground-nesting birds. It is likely that these species build sink populations within the city supported from sources in the open countryside (source-sink relations; Pulliam, 1988; Hess and Fischer, 2001). Hence, we hypothesise that the species richness of shrub-nesting birds and ground-nesting birds depends on the location of a protected area related to the surrounding countryside. This hypothesis is supported by a study that compared the avian fauna of Halle's protected areas with the avian fauna of the rural surrounding's protected areas and found that bird species richness is higher in the rural than in the urban habitats, respectively (Knapp et al., 2008). Additionally, cavity-nesting and shrub-nesting birds profit from the amount of built areas around the protected areas (500.BUILT); the former can use nesting aids or cave-like structures on buildings, the latter might find shrubs for nesting in gardens. Built structures, or the habitats associated with them, e.g., urban brownfields, also support neophyte richness. These results, together with the increase of plant species numbers and total species numbers with habitat richness in the buffer zones (100.BIO), emphasizes the relevance of the landscape matrix as valuable habitat for a range of species – even in an urban area. Migration takes place between protected areas, between matrix and protected areas, and within the matrix.

Despite the kind of abiotic data we used in the analyses, namely that these were not collected with a special focus on nature conservation-oriented spatial planning, but for a broad range of purposes by different people over a long time (personal communication, T. Katterle, Environmental Agency Halle), we are able to make predictions about the effects of landscape structure on species richness. Still, although we used a broad array of variables, our models were not able to completely explain species richness, i.e. we missed relevant predictors. Bastin and Thomas (1999), for example, explained species distribution in focal habitat patches with the availability of similar habitat in the surroundings of the focal patches. For our study, we only had information about species presence per protected area not per habitat patch. Moreover, Knapp et al. (2008), in a study on the same study area, used the mean distance of habitat patches in a protected area to the patches of the same habitat type in the surroundings of the protected area, and found no relevance for species richness. Therefore, we restricted the matrix variables to the amount of built area and habitat richness in the buffer zones. The selection of predictive variables remains challenging, especially when analysing a range of taxa that have different strategies and requirements. Also, different research questions might require more specific data (e.g., sampled at finer scales) or, in urban contexts, complementary data from the surrounding countryside.

5. Conclusions

It is difficult to measure the total biodiversity of a given area. Hence, the use of biodiversity surrogates that allow assessing the major part of biodiversity is desirable. We found only little evidence that single taxa act as surrogates for other singles taxa. Out of our study groups (lichens, mosses, vascular plants, birds, butterflies, carabid beetles, and snails), vascular plant species richness performed best by explaining the richness of three other taxa. Vascular plant richness also was the best predictor for total investigated richness. Comparing our study on an urban context with studies on different landscape contexts (Simonson et al., 2001; Sauberer et al., 2004; Su et al., 2004), we see that the surrogate taxa concept using vascular plant species is not only specific to urban areas. However, taxon–taxon approaches should be applied carefully, as they might be sensitive to different landscapes and specific to the target taxon.

Related to abiotic landscape variables, one result of our analysis is well-known, namely that the size of protected areas is vital for nature conservation. This is one of the earliest established laws in ecology (MacArthur and Wilson, 1967), but it is still relevant in the current context (Margules and Pressey, 2000). Particularly in cities, the limitation of semi-natural and open space complicates nature conservation. Besides, the conservation of species richness especially requires continuous suitable habitats – not only in protected areas but also in the matrix in-between. Even in cities, this will improve connectivity and thus, species migration and species persistence in small habitat patches.

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