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Do protected areas in urban and rural landscapes differ in species diversity?

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Abstract Previous studies from Central Europe and North America showed that species richness is higher in urban than in rural landscapes. Do protected areas, which can be found in both city and countryside, reflect this species richness pattern? The impact of urban land-use might reduce conservation success and necessitate special management strategies. We compared species richness and species spatial turnover of selected animal and plant taxa (carabids, butterflies, snails, birds, lichens, mosses, vascular plants) in 30 protected areas in the city of Halle and 56 protected areas in the adjacent rural district of Saalkreis (Central Germany). Species were mapped by experienced biologists within a systematic species inventory. We corrected species numbers for the effects of landscape structure (e.g. size, shape and distance of habitats) which might influence species diversity beyond urbanisation effects. Butterflies, birds and lichens had significantly higher species numbers in the rural protected areas. Species spatial turnover was higher among urban areas than among rural areas or pairs of urban and rural areas for most taxa. Diversity in all taxa depended on the size of a protected area. We discussed these patterns in the context of the general urban-rural species diversity patterns. Our results indicate an increasing isolation

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of species assemblages with urbanisation and highlight that space for protected areas is even more limited in urban than rural areas. An effective conservation of urban species diversity should include both typical urban and semi-natural habitats to cover the full range of species living in cities.

Keywords Biodiversity · Conservation planning · Germany · Isolation · Landscape structure · Urban ecology · Urban–rural gradient

Abbreviation

ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
a.s.l	Above sea level
MPAR	Mean perimeter-to-area ratio
MPS	Mean patch size
NN_DIST	Distance to nearest neighbour
NSH_MDIST	Mean distance to nearest similar habitat
NUMP	Number of patches

Introduction

Cities are hotspots of species diversity, harbouring more species than rural landscapes, as shown at least for Central Europe and North America for various organisms and at various scales (Walters 1970; Pyšek 1993; Dobson et al. 2001; McKinney 2002; Araújo 2003; Deutschewitz 2003; Hope 2003; Kühn et al. 2004; Hoechstetter et al. 2005; Wania et al. 2006). The import of food and materials, the patchiness and existence of early and mid-successional habitat stages, the often high geological diversity associated with cities and the introduction and invasion of alien species contribute to this high species richness (Pyšek 1995; Niemelä 1999a; Kühn et al. 2004; McKinney 2006). However, not only alien species richness is increased in urban areas but also native species richness (Kühn et al. 2004).

On the other hand, there are taxa that increase in species numbers along urban-to-rural gradients, a pattern that also depends on scale: the positive relationship between species richness and urban land-use is especially strong at coarse scales and gets weaker the smaller the scale of a study is (Pautasso 2007). It can even turn negative, but there are examples of positive relations on small scales as well (Leveau and Leveau 2005; Wania et al. 2006). The taxa with usually increasing numbers along urban-to-rural gradients (butterflies, birds, lichens and mosses) seem to be especially sensitive to urban land-use and illustrate the negative impact that urbanisation can have on species diversity (Gilbert 1968; Seaward 1982; Blair 1999).

Due to the co-occurrence of high species diversity and intensive human impact in cities (Cincotta et al. 2000; Liu et al. 2003), species conservation should not only concentrate on natural areas but also on urban areas. Classical instruments of species conservation are nature reserves, which can be found in both cities and countryside. However, protected habitats in cities are generally not typical urban habitats, but semi-natural habitats within an urban landscape. Since protected areas are not isolated from the surrounding landscape matrix, reserves in urban and rural regions are exposed to different environmental conditions. Although they are at a different scale than cities, protected areas within a city are influenced by the urban climate, e.g. the heat island effect and air pollution (Landsberg 1981; Oke 1982). They should also be more prone to the invasion of alien species than reserves in a rural matrix, because the regional pool (Zobel 1997) of alien species is larger in cities than in the countryside. Thus, we need special management strategies to handle the specifics of urban ecosystems (Niemelä 1999b).

To efficiently conserve urban habitats and species, we should monitor and measure species diversity. The most common approximation for species diversity is species richness (Gaston 2000; Purvis and Hector 2000; Magurran 2004), also known as α- and γ- diversity (for local and regional species richness, respectively; Whittaker 1972). By contrast, species spatial turnover, or β-diversity (Whittaker 1972), is often neglected (Koleff et al. 2003). Species turnover shows how similar the communities of two habitats are, by taking species numbers and species identities into account. The consideration of both species spatial turnover and species richness allows a more comprehensive assessment of the processes contributing to species diversity than considering species richness only.

The main aim of our study was a broad evaluation of the success of species conservation in urban protected areas in comparison to that in rural protected areas. Therefore, we compared α-, β- and γ-diversity of carabid beetles, butterflies, snails, birds, lichens, mosses and vascular plants in the protected areas of Halle (Saale), Central Germany, and the adjacent rural district of Saalkreis. The protected areas were established to conserve valuable habitats typical for the region without examining species occurrences in the first place but with the aim to inventory the species and later checking the reserves' representativeness with respect to the regional species pool and to adjust nature conservation strategies, if necessary (Ebel and Schönbrodt 1988). Earlier studies showed that the city of Halle is richer in species than its rural surroundings (Wania et al. 2006). From this and other studies on urban–rural gradients (e.g. Klotz 1990; Kühn et al. 2004) we would expect that protected areas harbour more species when situated in urban rather than in rural environments, if they sampled the same amount of species from their respective species pools. We asked

(a) whether there are differences in α-, β- and γ-diversity between the urban and rural protected areas and
(b) whether landscape structure explains possible differences.

Materials and methods

Study area

The study area is situated in Central Germany in the eastern foreland of the Harz Mountains (Fig. 1). It comprises the city of Halle (Saale) (Northern part of town: 51°30′ N, 12° E) and the surrounding administrative district of Saalkreis. Together, these areas cover approximately 755 km^2, reaching altitudes between 70 m and 250 m a.s.l. The river Saale flows through the study area. With a mean annual temperature of 9°C and an annual precipitation of 480 mm, the climate is subcontinental and relatively dry, at least in the Central European context (Müller-Westermeier et al. 1999, 2001). The low precipitation is due to the location in the rain shadow of the Harz Mountains.

During the last ice-age, the region was located at the southern edge of the glaciers covering Northern Europe where loess accumulated (Lang 1994). Hence, the soils in the study region are mainly Chernozems and therefore highly suitable for agriculture

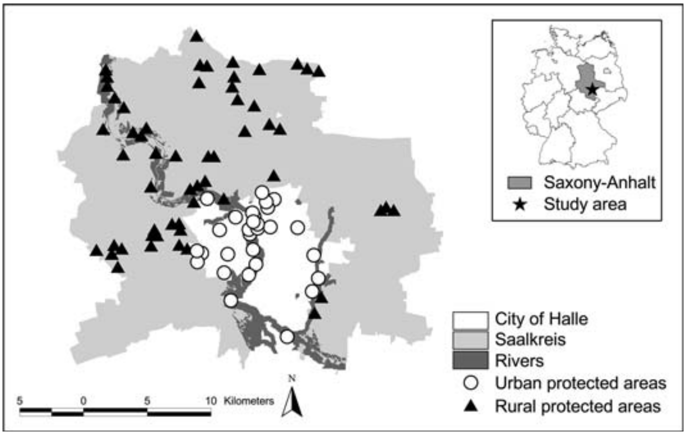

Fig. 1 Location of urban and rural protected areas in the study area (city of Halle and administrative district of Saalkreis, Central Germany). The small inset shows the location of the study area in Germany

(Ministerium für Raumordnung 1996). Besides, there are Podzols, Gleysols, Rendzinas, Cambisols and anthropogenic soils. The Saale valley is dominated by Fluvisols and Cambisols (all according to FAO classification).

We selected 86 protected areas, 30 in the city of Halle and 56 in the rural district of Saalkreis (Fig. 1). They fall into the following legal protection categories (Table 1): nature protection areas, nature monuments (up to a size of 0.05 km^2), protected landscape components and protected parks. The urban areas mainly comprise alluvial habitats and porphyric rocks. These make up a considerable part of the rural areas as well. Half of all

Table 1 Nature protection categories in Halle and Saalkreis (Central Germany) included in the analyses, corresponding laws, subjects and purpose of protection

Protection category	Law	Subjects/purpose of protection
Nature protection area	Nature conservation law (Naturschutzgesetz) Saxony-Anhalt from 23. July 2004	Conservation, development or recreation of habitats and communities of special wild animal and plant species
		Scientific, historic or cultural reason
Nature monument		Due to rarity, special characteristics or beauty
		Scientific, historic or cultural reason
Protected landscape component		Due to rarity, special characteristics or beauty
Protected park	State cultivation act (Landeskulturgesetz) GDR from 14. May 1970, protection status ensured by the nature conservation law (Naturschutzgesetz) Saxony-Anhalt from 23. July 2004	Conservation, development or recreation of ecosystem services
		Structuring or fostering of the local or natural scenery
		Prevention of damage
		Due to the importance as habitats for special wild animal and plant species

urban areas are located in the Saale valley. The rural areas are concentrated west and north of Halle and are embedded in a matrix dominated by agriculture.

Data sources

Species data

The species inventories in the protected areas of Halle and Saalkreis took place during several years in the 1980ies and 1990ies (published for the rural protected areas in Ebel and Schönbrodt 1988, 1991, 1993a, b; and for the urban protected areas in Buschendorf and Klotz 1995, 1996; the former provided digitally by the Environmental State Agency Saxony-Anhalt; Landesamt für Umweltschutz Sachsen-Anhalt 2005a, b, c). Mapping was conducted by experienced zoologists and botanists and although the inventories in the urban and rural protected areas were organised separately due to administrative reasons, it were the same persons who mapped a species group in both urban and rural protected areas in most cases. Because the protected areas were mapped in different years (many of the urban protected areas were established right after the German reunification in 1990, while most rural protected areas were established earlier), we tested the comparability of mapping intensities with species-area curves (see "Data analysis").

Land-use data

Maps showing the location of the protected areas in Halle (at a scale of 1:20,000) were provided digitally by the Environmental Agency Halle (Stadt Halle 2003a). The corresponding maps for the district of Saalkreis were provided partly in digital and partly in non-digital form (we digitised the latter by ourselves) by the Environmental State Agency Saxony-Anhalt and the Environmental Agency Saalkreis, both at a scale of 1:10,000.

Habitat and land-use types in the city of Halle were mapped several times between 1997 and 2001 (at a scale of 1:5,000 and 1:2,000). Maps were improved by analysing aerial infrared photographs, taken in 1998 and 1999. The maps were provided digitally (Stadt Halle 2003b). Saalkreis habitat and land-use maps (at a scale of 1:10,000) are based on aerial infrared pictures taken in 1992. They were provided in digital form by the Environmental State Agency Saxony-Anhalt.

Habitat and land-use types were subdivided in main units and subunits following Peterson and Langner (1992) and Pohl (2003). The main units are agricultural land-use forms, built-up areas, public parks, vegetation-free areas, water bodies, herbaceous vegetation including reed, grove, and forest. They are further subdivided; forest, for example, is split up into deciduous forest, coniferous forest, mixed forest and further.

Data analysis

We performed all statistical analyses with the open source software R, Version 2.0.1 (R Development Core Team 2004) and all geostatistical analyses with ArcView GIS Version 3.1 (Environmental Systems Research Institute, Redlands, CA). As level of significance we chose $\alpha = 0.05$.

Species data

We calculated α-, β- and γ-diversity from species lists separately for each species group. For α-diversity, we counted all species of a group per protected area. As the species-area-relationship can be modelled using either the logarithmic model of Arrhenius or the semi-logarithmic model of Gleason (Rosenzweig 1995), we tested which of the two yielded the better fit for each species group. The semilog model performed better for all taxa but butterflies, so the model after Arrhenius was chosen only for this group. In the following, "size of area" is used synonymously with "logarithm of size of area" and "number of butterfly species" synonymously with "logarithm of number of butterfly species". We used the species-area-curves to get a rough estimate for varying mapping intensities among the reserves and to identify outliers according to visual assessment (exemplarily shown for carabid beetles in Fig. 2). Disproportionally mapped reserves were excluded from all further analyses.

After normalising and standardising all dependent variables to zero mean and unit standard deviance (butterflies: double log-transformation, vascular plants: log-transformation, else: square root-transformation), we analysed differences between the categories of protected areas to see whether these have any effect on species richness. We used analysis of covariance (ANCOVA) and the R-function estimable (Warnes 2006) with species numbers as the response variable and size of protected area and protection categories as explanatory variables (Crawley 2002). Next, we analysed differences in urban and rural α-diversity with another ANCOVA controlling for size of protected area.

For β-diversity, the β_{sim} similarity index was calculated from presence-absence tables for each pair of protected areas within Halle, within the district of Saalkreis and among Halle and Saalkreis as follows (Lennon et al. 2001; Koleff et al. 2003):

$$\beta_{sim} = a/(a + \min(b, c)),$$

where a is the number of species shared between two protected areas and b and c are the numbers of species unique to either one or the other protected area. This index is a measure

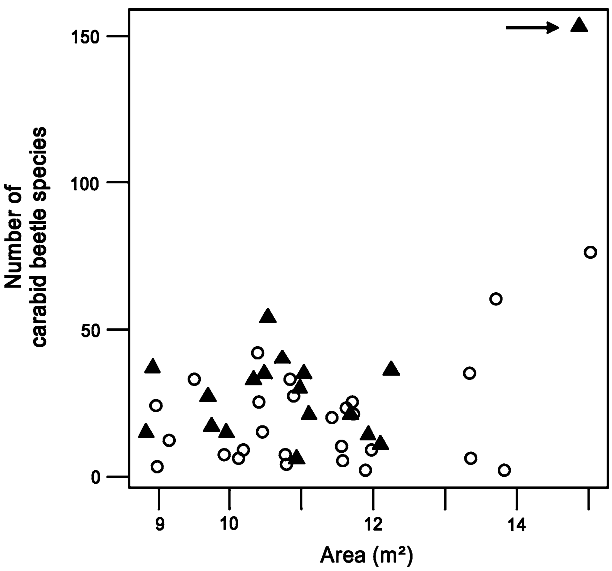

Fig. 2 Species-area-relationship of carabid beetles in urban (white circles) and rural (black triangles) protected areas in Halle and Saalkreis (Central Germany). The arrow shows the protected area that was excluded from the analysis as an outlier

of similarity taking into account all species that are shared by two areas and the smaller number of species not shared. Its values range from zero to one; the upper limit indicating complete similarity of communities and the lower limit indicating no similarity at all. It is less prone to differences in species richness than other indices, such as the popular Jaccard index (Lennon et al. 2001; Koleff et al. 2003). Note that an increase in β_{sim} is considered a decrease in β-diversity. We tested for significant differences in urban vs. rural index values by comparing their medians with the non-parametric Mann–Whitney–Wilcox *U*-Test (Crawley 2002), whose test statistic is not affected by inflated sample size of similarity matrices (resulting in $(N(N-1))/2$ samples from N locations).

To measure γ-diversity, we counted all species in urban and rural protected areas, respectively. This measure only consists of one number per category, so no statistical tests were possible.

Landscape metrics

Maps of habitat and land-use types were combined with the maps showing the location of protected areas in ArcView. Size and perimeter of the protected areas were supplied with the maps. Additionally, we calculated several landscape metrics on the basis of habitat and land-use types (Table 2), using the ArcView Extensions Patch Analyst (Elkie et al. 1999) and Nearest Features v. 3.8a (Jenness 2004). These metrics are based on McGarigal and Marks (1994). Mean distance to nearest similar habitat (NSH_MDIST) was used as an indicator for the influence of the landscape matrix surrounding the protected areas: the predominant habitat and land-use type was calculated for each protected area. For each patch of this dominant habitat and land-use type within the protected area, we calculated the distances to the nearest adjacent patch of the same type outside the protected areas and averaged these for each protected area.

Table 2 Overview of landscape structure metrics on the basis of habitat and land-use types used as explaining variables for species richness in the protected areas of Halle and Saalkreis (Central Germany)

Landscape metrics	Abbreviation	Description	Unit
Area	–	Absolute size of a protected area	m^2
Perimeter	–	Lenght of the borderline of a protected area	m
Number of patches	NUMP	Number of all habitat and land-use patches in a protected area based on subunits	–
Mean patch size	MPS	Mean size of all habitat and land-use patches in a protected area based on subunits	m^2
Mean perimeter-to-area ratio	MPAR	Mean ratio of patch-borderline lenght to patch size of all habitat and land-use patches in a protected area based on subunits	m^{-1}
Distance to nearest neighbour	NN_DIST	Shortest distance between two adjacent protected areas, measured from edge to edge	m
Mean distance to nearest similar habitat	NSH_MDIST	Mean distance of all habitat and land-use patches based on main units which belong to the land-use type with the highest share in the size of a protected area to the next patch of the same land-use type but outside protected space, measured from edge to edge	m

Main units are the broad categories of habitat and land-use types, subunits are a further division of main units

To detect differences in the relationship of urban and rural α-diversity with land-use, we performed one ANCOVA per species group. The location in city or countryside was the main explanatory variable and all landscape metrics were covariables. Before performing the ANCOVA, the landscape metrics were tested for pairwise rank correlations. To avoid the problem of collinearity, we excluded one of two variables from further calculations if Kendall's correlation coefficient was $\tau \geq 0.55$. Due to its importance for species richness (MacArthur and Wilson 1967; Rosenzweig 1995), we always kept the variable "size of protected area" but excluded variables that were correlated with several other variables. Kendall's τ is preferable to Pearson's r because it takes non-normally distributed variables into account and has less statistical restrictions (regarding sample size and ties) than Spearman's rank correlation (Röhr et al. 1983). Starting the ANCOVA with a full model, we reduced each model via backward selection until we achieved its minimal adequate version (Mac Nally 2000). After each step of selection, achieved and previous models were compared in an ANOVA to prevent oversimplification (Crawley 2002).

Results

Characteristics of the protected areas

On average, the rural protected areas are smaller than the urban protected areas (Table 3). In the district of Saalkreis, four reserves belong to the category of nature protection areas, 52 reserves are nature monuments. The city of Halle contains eight nature protection areas, twelve nature monuments, nine protected landscape components and one protected park. Generally, the different categories of protected areas have no effect on species richness. Only vascular plant species have significantly higher species numbers in nature protection areas than in protected landscape components ($P < 0.05$).

For carabid beetles, lichens, mosses and vascular plants we excluded one protected area each due to disproportional mapping. As each species group does not occur in every protected area or was at least not recorded in every area, the number of protected areas for analysis differs between species groups (Table 4).

Except for public parks, which are exclusively urban, all habitat and land-use types are represented in the protected areas of both Halle and Saalkreis. Only the relative distribution of habitat and land-use types differs (Table 5). Several landscape metrics in the protected areas are intercorrelated ($\tau \geq 0.55$). Therefore, we retained all variables except "perimeter

Table 3 Statistical parameters for the distribution of size of the protected areas in Halle and Saalkreis (Central Germany)

	Size of protected areas [km^2]	
	Urban	Rural
Minimum	$7.8e^{-3}$	$1.7e^{-3}$
1st Quartile	$3.2e^{-2}$	$1.1e^{-2}$
Median	$7.3e^{-2}$	$2.1e^{-2}$
3rd Quartile	$1.5e^{-1}$	$5.8e^{-2}$
Maximum	3.4	2.9
Mean	$3e^{-1}$	$1.1e^{-1}$
Standard deviation	$6.5e^{-1}$	$3.9e^{-1}$

Table 4 Total number and γ-diversity of urban and rural protected areas analysed per species group (Halle and Saalkreis, Central Germany)

	Urban protected areas		Rural protected areas	
	Total number	γ-Diversity	Total number	γ-Diversity
Carabid beetles	27	149	17	212
Butterflies	16	408	6	575
Snails	18	88	26	84
Birds	27	133	51	139
Lichens	28	84	19	82
Mosses	29	154	29	124
Vascular plants	27	806	56	991

of protected area", which was excluded for all species groups, and "number of patches" (NUMP), which was retained for carabid beetles and lichens only.

Species diversity in urban and rural protected areas

α-Diversity of butterflies, birds and lichens is significantly higher in rural than in urban protected areas (Fig. 3). Species numbers of vascular plants and carabid beetles are marginally higher in rural protected areas ($0.1 \geq P > 0.05$). Snails and mosses show no differences (Table 6).

In the protected areas within Halle, the β_{sim} similarity index and therefore the similarity of the species assemblages is lowest for butterflies, snails and all plant taxa. It is lowest for carabid beetles and birds in the protected areas within the district of Saalkreis. Pairs of urban and rural areas are more similar than pairs of urban areas for all species groups (Figs. 4 and 5).

γ-Diversity is higher in rural than in urban reserves for carabid beetles, butterflies and vascular plants, higher in urban reserves for mosses and similar in urban and rural reserves for snails, birds and lichens (Table 4).

Table 5 Percentage of the main units of habitat- and land-use types in the protected areas of Halle and Saalkreis (Central Germany)

Habitat- and land-use type	Percentage in the protected areas	
	Urban	Rural
Agriculture, gardens, vineyards	10.5	15.0
Built-up area	1.1	1.8
Public parks	2.7	0
Vegetation-free area	0.6	1.4
Water bodies	8.8	1.6
Herbaceous vegetation including reed	43.0	49.6
Grove	7.4	4.3
Forest	25.4	26.3
Undefined	0.5	0

Species richness and landscape structure

Location of a protected area in city or countryside remains in the minimal adequate models for the α-diversity of all species groups, also when considering landscape structure. The

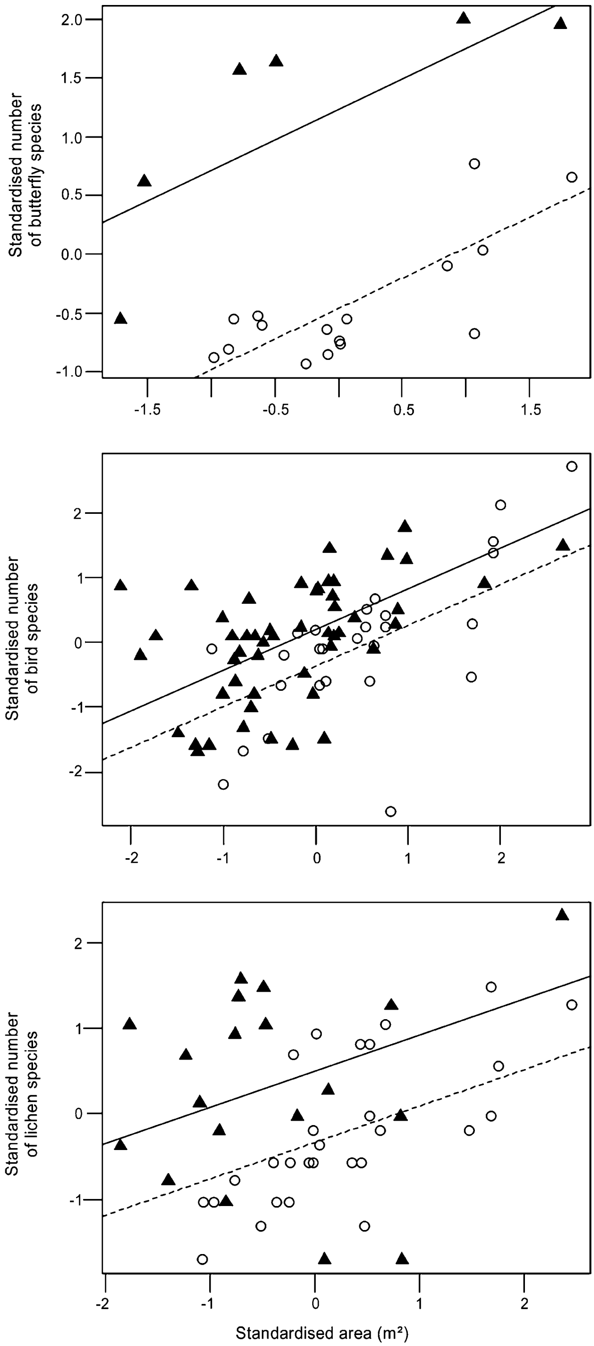

Fig. 3 Regression lines yielded by ANCOVA, illustrating the differences in species numbers between urban (dashed lines, white circles) and rural (solid lines, black triangles) protected areas in Halle and Saalkreis (Central Germany) for butterflies (top), birds (middle) and lichens (bottom). All variables are standardised to zero mean and unit standard deviance. The independent variable "size of area" and the dependent variable "number of butterfly species" are log-transformed

Table 6 Parameters of the ANCOVA models showing differences in species richness between the protected areas in Halle and Saalkreis (Central Germany)

	Slope	Intercept for the protected areas		*P*-value for difference between intercepts	R^2—explained variance of the model	*P*-value for the model
		Urban	Rural			
Carabid beetles	0.2	−0.24	0.38	0.053	0.06	0.1
Butterflies	0.52	−0.46	1.23	$6e^{-6}$***	0.69	$6e^{-6}$***
Snails	0.56	−0.20	0.14	0.24	0.25	0.0011**
Birds	0.63	−0.37	0.20	0.009**	0.32	$2e^{-7}$***
Lichens	0.42	−0.33	0.49	0.005**	0.20	0.003**
Mosses	0.63	0	0	0.53	0.41	$2e^{-7}$***
Vascular plants	0.6	−0.28	0.14	0.055	0.29	$5e^{-7}$***

R^2 is adjusted for the number of predictors

** Very significant (≤0.001), *** Highly significant (≤0.001)

most important landscape metrics determining species richness are the size of a protected area or its number of habitat and land-use patches (Table 7). Note that area and NUMP are strongly correlated, with correlation coefficients varying from $\tau = 0.46$ for carabid beetles to $\tau = 0.61$ for butterflies, because they both represent a measure of area size.

For butterflies, snails and vascular plants, protected area size is the main predictor of α-diversity. The three groups differ in the relationship of richness and landscape structure between urban and rural protected areas: butterfly species richness decreases with mean perimeter-to-area ratio in the protected areas of Halle and Saalkreis, but in the latter the slope is much steeper. Besides MPAR, area and location, the number of butterfly species depends on mean patch size. Snail species numbers decrease in urban but increase in rural protected areas with mean distance to the nearest similar habitat. The number of vascular plant species increases with the size of a protected area, but with a steeper slope in urban than in rural areas. Besides, vascular plant species richness decreases with MPAR in urban but increases in rural protected areas.

The relationship of species richness and landscape structure for carabid beetles, birds, lichens and mosses does not vary between urban and rural protected areas. For carabid beetles, NUMP is the only landscape metric predicting species richness; for birds, lichens and mosses it is the size of a protected area.

Discussion

Our results confirm the well known pattern that area size is one of the most important determinants of species richness (MacArthur and Wilson 1967; Rosenzweig 1995). The larger an area, the more different habitats and the more species it can contain. Additionally, in smaller areas the risk of local extinctions is higher (MacArthur and Wilson 1967). Thus, area size is also among the most important determinants for the effectiveness of nature reserves in terms of conserving species richness (Nebbia and Zalba 2007). It is noteworthy that protected areas in the rural district of Saalkreis support more species than Halle's protected areas of equal size, at least concerning butterflies, birds, lichens and, to a minor degree, carabid beetles and vascular plants. Depending on the species group considered,

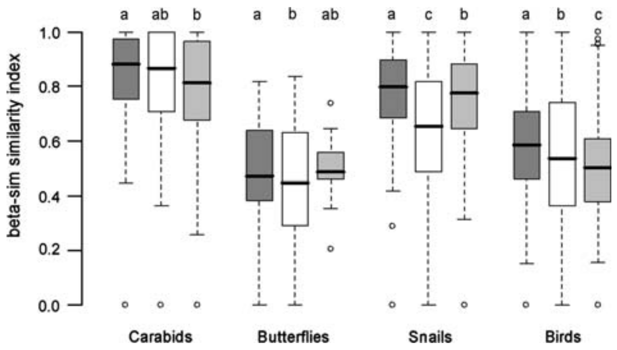

Fig. 4 Boxplots showing the β_{sim} similarity index for carabid beetles, butterflies, snails and birds for pairs of urban and rural (dark grey bars), urban (white bars) and rural (light grey bars) protected areas (Halle and Saalkreis, Central Germany). The boxplots represent median (line), 25–75% quartiles (boxes), ranges (whiskers) and extreme values (circles). The letters above the boxplots indicate significant differences between them

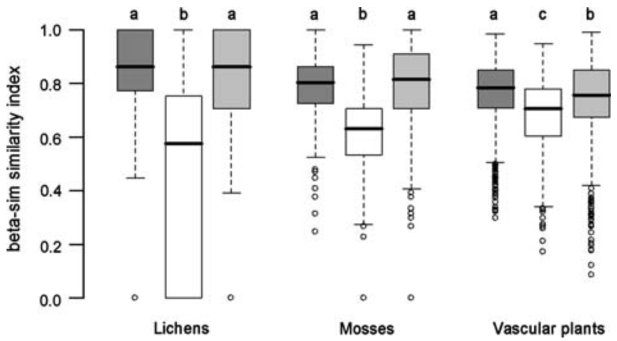

Fig. 5 Boxplots showing the β_{sim} similarity index for lichens, mosses and vascular plants for pairs of urban and rural (dark grey bars), urban (white bars) and rural (light grey bars) protected areas (Halle and Saalkreis, Central Germany). The boxplots represent median (line), 25–75% quartiles (boxes), ranges (whiskers) and extreme values (circles). The letters above the boxplots indicate significant differences between them

this supports or contradicts previous studies on urban and rural species richness which did not focus on nature reserves. Firstly, an increase of species numbers along urban-to-rural gradients was also found for carabid beetles in Finland, Canada and Bulgaria (Niemelä et al. 2002), for butterflies and birds in the USA (Blair 1999), for birds in Italy, France, Finland and Sweden (Clergeau et al. 2006; Sandström et al. 2006) and for lichens in the UK (Seaward 1982). These studies all took place on similar scales like ours, and the decrease of species numbers for carabids, butterflies, birds and lichens with urbanisation on regional scales seems to be a general pattern and no peculiarity of nature reserves. Secondly, although we expected to find higher species numbers of mosses in rural areas as well (Gilbert 1968; Wittig 2002), moss diversity is higher in the urban protected areas. This might indicate a positive effect of the location of the protected areas on the urban moss assemblages: evapotranspiration in cities is generally lower than in the countryside (Pickett et al. 2001)—an unfavourable condition for mosses. The protected areas however, have a relatively dense plant cover and thus should have an increased evapotranspiration relative to built-up urban habitats, especially when situated in the river valley, where air moisture is

Table 7 Minimal adequate models of ANCOVA showing the relation of species richness and landscape structure and differences in this relation between the protected areas in Halle and Saalkreis (Central Germany)

Minimal adequate model	Slope of the interaction term(s)		Intercept for the protected areas		R^2	*P*-value
	Urban	Rural	Urban	Rural		
Carabid beetles ~ cc + NUMP	–	–	−0.3	0.49	0.24	0.002**
Butterflies ~ cc + area + MPS + MPAR + int(cc, MPAR)	−0.15	−5.65	−0.49	−1.6	0.82	$2e^{-6}$***
Snails ~ cc + area + NSH_MDIST + int(cc, NSH_MDIST)	−0.56	0.13	−0.12	0.12	0.40	$6e^{-5}$***
Birds ~ cc + area	–	–	−0.37	0.20	0.32	$2e^{-7}$***
Lichens ~ cc + area	–	–	−0.33	0.49	0.20	0.003**
Mosses ~ cc + area	–	–	0.07	−0.07	0.41	$2e^{-7}$***
Vascular plants ~ cc + area + MPAR + int(cc, area) + int(cc, MPAR)	0.88 (area)	0.37 (area)	−0.42	1.97	0.33	$7e^{-7}$***
	−0.02 (MPAR)	7.31 (MPAR)				

R^2 is adjusted for the number of predictors

** Very significant (≤0.001), *** Highly significant (≤0.001)

cc = Location of the protected areas in city or countryside, int(x_1, x_2) = Interaction between the explanatory variables x_1 and x_2, MPAR = Mean perimeter-to-area ratio, MPS = Mean patch size, NSH_MDIST = Distance to nearest similar habitat outside protected space, NUMP = Number of patches

increased. Lastly, vascular plant species richness is marginally higher in the rural areas, contrary to studies that did not focus on protected areas (e.g. Walters 1970; Haeupler 1975; Klotz 1990; Pyšek 1993; McKinney 2002), including a study in our study region at the regional scale (Wania et al. 2006). It seems that vascular plant species in rural protected areas represent a larger part of the whole species pool of the Saalkreis district than the species in urban protected areas represent of Halle's species pool. In summary, none of the analysed taxa has significantly higher species numbers in the city areas.

These patterns are neither explained by the differences in the size distribution of protected areas—we corrected for the effect of size—nor by differences between the categories of protected areas—only vascular plants show significantly higher species numbers in nature protection areas than in protected landscape components, but there are even more nature protection areas in the city of Halle than in the district of Saalkreis. One reason for the better performance of the rural protected areas might be their quality: the range of habitats that are interesting for species conservation is probably wider in the countryside than in the city; therefore, also habitats that seem less valuable for conservation purposes than some rural areas got a protection status in the city of Halle. The city's protected areas could also be more frequented by visitors and therefore more disturbed than the rural areas. The contribution of alien species to total species richness is higher in urban than in rural areas but aliens should be less frequent in the urban protected areas than in the rest of the city, because the reserves represent semi-natural habitats (Pyšek 1998). The urban environment may have a stronger isolating effect than the rural environment and thus decrease the probability of species migrations between the urban protected areas. The heterogeneity of habitat and land-use types probably influences species richness as well.

However, the city's protected areas have higher numbers of habitat and land-use patches and are more heterogeneous (data not shown), and should therefore be richer in species (Rosenzweig 1995). The relationship between landscape heterogeneity, isolation and species richness in the urban and rural protected areas is discussed in more detail below.

Landscape heterogeneity

Higher geological diversity in urban areas partly explains the high plant diversity of cities (Kühn et al. 2004). Obviously, high geological diversity is unaltered by human land-use. Rather, landscapes with a high geological diversity are favourable to human settlement and this is the reason for the often high urban geological diversity. Half of the protected areas in the city of Halle are situated in river valleys (Fig. 1), so that these only show a part of the city's spectrum of geological substrates. This might explain why we find marginally lower species numbers of vascular plants in the urban than in the rural protected areas, but higher species numbers in the city of Halle than in the surrounding countryside when looking at randomly chosen areas outside of reserves (Wania et al. 2006). Accordingly, not all habitats that exist in the city of Halle also exist in the protected areas. For example, species from ruderal vegetation of urban brownfields, railroad embankments or roadsides are restricted to early and intermediate stages of succession (Strauss and Biedermann 2005), but protected habitats mostly represent older successional stages. We want to emphasise that the species communities in urban protected areas are not typical urban communities. They rather represent semi-natural communities in an urban surrounding, like alluvial forests and dry grasslands on porphyric rock. Species in semi-natural habitats might be especially diminished by increasing urbanisation, and species losses there might be less compensated by immigrating (especially alien) species than in typical urban habitats (Chocholouskova and Pysek 2003). Typical urban communities, e.g. the communities of urban brownfields, are hardly protected in nature reserves. However, these urban communities contribute considerably to the urban hotspot character (Herbst and Herbst 2006). Brownfields often act as analogues of natural habitats and provide suitable living conditions for both rare and common species (Eversham et al. 1996; Lenzin et al. 2007). Hence, we need new conservation strategies complementing already protected areas, if cities are to stay hotspots of plant diversity. These could for example include temporary nature reserves, protecting a constant stock of urban brownfields in early and intermediate stages of succession as proposed by Strauss and Biedermann (2005), or the provision of industrial and municipal areas for the development of spontaneous vegetation as postulated by Wittig (1998).

Isolation

Niemelä (1999a) argued that urban habitats are more island-like than rural habitats, due to the patchiness of city habitats. Thus, the dispersal of taxa with a small dispersal radius should be more problematic within an urban environment. Indeed, our results indicate stronger isolation mechanisms among urban than among rural protected areas: the β_{sim} similarity index of butterflies, snails, lichens, mosses and vascular plants is lowest among urban protected areas, even lower than among pairs of urban and rural protected areas. This suggests that species mainly move between pairs of rural protected areas and between pairs of urban and rural protected areas, but less between pairs of urban protected areas. The spatial parameters distance to nearest neighbour and mean distance to nearest similar habitat do not explain the higher urban isolation mechanisms, at least for the plant taxa: the two parameters were not selected for the minimal adequate models (Table 7). Only for snail species richness, NSH_MDIST appears in the minimal adequate model. However, there is an unexpected increase of snail species numbers with increasing values of NSH_MDIST in the rural protected areas, which may make the relationship spurious.

Accordingly, other factors should cause the increased isolation of species assemblages in urban protected areas. Our results suggest that the type of the landscape matrix surrounding the protected areas plays an important role in the isolation of species assemblages, not distance itself. Densely built-up areas are isolating urban free space much more than agricultural areas. Air pollution and reduced air moisture hinder the dispersion of lichens and mosses (Gilbert 1968; Seaward 1982). The region around Halle was dominated by chemical industries and lignite open mining in the twentieth century, and air pollution was correspondingly high (Neumeister et al. 1997). Additionally, the lack of early successional stages in protected areas and the lack of older successional stages or green spaces in general outside protected areas might increase the isolation of species assemblages in urban protected areas. As agricultural landscapes are dominated by large fields with uniform disturbance regimes (Lososová et al. 2006), they are less varied than urban landscapes, and species movements might be less limited in the countryside. The river valleys that connect city and countryside might act as corridors as well, and facilitate the migration among urban and rural protected areas. In summary, we argue that the built-up urban matrix is more resistant to species migrations than the rural matrix and the river valleys. Although half of the urban protected areas are in river valleys, the other half is more strongly surrounded by built-up area, in contrast to the rural protected areas, so on average, pairs of urban protected areas are isolated more strongly from each other than in the rural environment. This isolation causes lower α-diversity and higher β-diversity in the urban protected areas. Plant populations face a higher extinction risk in more urbanised regions, as was shown for grassland remnants along an urban-to-rural gradient in south-western Australia (Williams et al. 2005). This emphasises the importance of habitat networks and a high landscape permeability for the connectivity between populations especially in urban areas (Von Haaren and Reich 2006), but also between semi-natural habitats in cities with habitats in the countryside.

Conclusions

The protected areas in the rural district of Saalkreis supported more species than Halle's protected areas (corrected for size effects) and simultaneously had a lower spatial species turnover. This shows that β-diversity rather than α-diversity causes the high species richness generally found in urban areas and points to a higher isolation of species in protected areas within an urban matrix. Accordingly, the high human impact in urban areas indeed reduces conservation success with respect to species diversity, as we supposed in the beginning. We therefore suggest broader management strategies in order to conserve the high biodiversity of urban areas. If species richness is distributed over a large area (high β-diversity) more space for protection is needed. This is consistent with the well known pattern that area size is the best predictor for species richness, which our results confirm. This highlights one problem of nature conservation in cities: space for protected areas is limited, even more in urban than in rural areas. However, if we add more flexible management strategies to the existing protected areas, we might be able to protect the full range of species living in cities: the protected areas include semi-natural habitats but no typical urban habitats. The latter are rich in species but do not need a classical protection status, they rather depend on the change of land-use and land-use abandonment (like urban brown-fields). The acceptance and management of typical urban nature e.g. as green space on industrial sites or accompanying roads, should help in the conservation of typical urban biodiversity while protected areas within cities should conserve the semi-natural biodiversity of urban space.

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