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Determinants of species richness within and across taxonomic groups in urban green spaces

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Abstract Urban green spaces provide habitat for numerous plant and animal species. However, currently we have little knowledge on which determinants drive the species richness within and across taxonomic groups. In this paper we investigate the determinants of total, native, and endangered species richness for vascular plants, birds, and mammals within and across taxonomic groups. We examined a stratified random sample of 32 urban green spaces in Hannover, Germany. Species inventories for plants and birds were generated on the basis of line transect surveys. Mammals were surveyed by means of point counts using camera traps. Using a principal component analysis and multiple regression models, we tested 10 explanatory variables for species-area effects, distance effects, and the effects of habitat structure of green spaces on species richness. When analyzing single explanatory variables, we determined that the species richness of all groups was significantly positively correlated to patch area, number of habitat types, and a short distance to the nearest green space. Testing combined effects of variables showed that patch area in combination with habitat heterogeneity was most important for plants (total, native, and endangered), birds (total and native), and overall species richness. This emphasizes the importance of the species-area effect and the

effects of habitat structure on species richness in urban green spaces. We conclude that, in the context of urban planning, it is important to conserve large green spaces that include a high diversity of habitats to maintain high species richness.

Introduction

Green spaces in cities, such as parks, allotments, cemeteries, and wastelands, are important components of green infrastructure (EC – European Commission 2013) and provide habitats for numerous animal and plant species (Cornelis and Hermy 2004; Angold et al. 2006). Over the last decades, many studies have shown high species richness and abundance in urban green spaces. This has particularly been the case for studies on birds (e.g. Husté and Boulinier 2007; Carbó-Ramírez and Zuria 2011) and plants (e.g. Fischer et al. 2013; Matthies et al. 2013), but also for other taxa such as mammals (e.g. Garden et al. 2007), butterflies (e.g. Snep et al. 2011), and carabid beetles (e.g. Knapp et al. 2008). These relationships have been found in several cities in Europe (e.g. Bräuniger et al. 2010; Fischer et al. 2013), Asia (e.g. Saito and Koike 2013; Koh and Sodhi 2004), and North America (e.g. Oliver et al. 2011; Turner et al. 2005).

In order to clarify the relevance of urban green spaces for nature conservation it is, in addition to total species richness, valuable to assess the number of endangered and native species (e.g. Pyšek et al. 2004). The richness of plant and animal species in urban green spaces has often been studied in relation to alien species (McKinney 2006; La Sorte et al. 2014). For instance, Pyšek et al. (2004) found that green spaces support a large number of non-native plant species in the city of

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Plzen, Czech Republic. DeCandido (2004) documented a decline in plant species richness in a park in New York City from 1947 to 1994, which was partly due to increasing numbers of exotics. High numbers of non-native species have also been documented for birds (e.g. Shwartz et al. 2008; Platt and Lill 2006) and selected invertebrates (e.g. Tonietto et al. 2011; Vilisics and Hornung 2009). Therefore, it has often been argued that high species numbers in urban green spaces are caused by high numbers of alien species (e.g. McKinney and Lockwood 2001). Nevertheless, a variety of other studies found evidence that also native species (Wania et al. 2006; Kühn et al. 2004) and endangered species (Meffert and Dziock 2012; Matthies et al. 2015) reach high species numbers in urban green spaces. These findings consistently show that different species groups within taxonomic groups contribute to the species richness in urban green spaces (cf. McKinney 2008).

Urban green spaces can be seen as habitat islands within the urban matrix. A key finding of the urban habitat island approach is that green spaces show patterns of species-area relationships as observed in island biogeography (e.g. MacGregor-Fors et al. 2011). The species-area effect explains how larger areas usually facilitate greater species richness (MacArthur and Wilson 1967). For urban green spaces, an increasing number of species with increasing patch areas has been shown for vascular plants (Angold et al. 2006; Li et al. 2006), birds (van Heezik et al. 2013; Carbó-Ramírez and Zuria 2011; Chamberlain et al. 2007; Husté et al. 2006), and mammals (Hodgkison et al. 2007). In contrast, no significant species-area relationships have been found for butterflies and carabid beetles in urban green spaces (Bräuninger et al. 2010; Lizée et al. 2016).

Certain patch configurations modify, to various extents, the underlying species-area relationship of green spaces. For instance, the distance effect describes how species richness is affected by immigration and emigration rates of species, which are affected by the distance of an island from a source habitat (MacArthur and Wilson 1967). The distance effect refers to connectivity and, at the same time, it also refers to isolation. Therefore, green space connectivity is an important determinant for the persistence of species and populations in highly fragmented urban landscapes (Zipperer et al. 2000), mainly related to migration rates and (re)colonization probability (cf. Crooks et al. 2001; Opdam 2002; Uezu et al. 2005). Species numbers in green spaces are likely to be negatively affected by an increasing distance to the surrounding landscape, if the surrounding landscape acts as a potential source habitat. However, each city develops differently and there are different theories and models that describe and explain the spatial form and the evolution of urban areas (cf. Czamanski et al. 2008). A distance effect was documented for taxonomic groups of highly mobile species, e.g. birds (MacGregor-Fors and Ortega-Álvarez 2011; Sandström et al. 2006) and

mammals (Saito and Koike 2013). Besides the distance to the border of the adjacent landscape, the surrounding green infrastructure is considered an influencing factor for species richness in green spaces, especially for birds (Ferenc et al. 2014). The total amount of tree cover in the surroundings has been found to determine, for instance, species richness of woodland avifauna (Ferenc et al. 2014). Pellissier et al. (2012) found that the composition, measured by the proportion of different types of buildings and green spaces, and configuration of the surrounding of green spaces, measured by heterogeneity and spatial arrangement of green spaces, is relevant for bird species abundance. For instance, the tree nester abundance was positively influenced by building heterogeneity, but also by the amount of trees (Pellissier et al. 2012). For large and mid-sized mammals, a decrease in species numbers was detected in a gradient from forest landscapes to urban cores in Tokyo (Saito and Koike 2013). The significance of a gradient of urbanization within a city, with less urbanized areas supporting high species numbers, has also been demonstrated for plant species (Guntenspergen and Levenson 1997; Čepelová and Münzbergová 2012), although this taxonomic group is less mobile.

Habitat structure is also an important factor to consider when assessing the species richness of urban green spaces (Bell et al. 1991). The proportion of core habitat to edge habitat affects species richness, with increasing edge habitat leading to increases in species richness (Ricklefs and Miller 2000). For instance, Li et al. (2006) demonstrated a significant, positive correlation between the number of shrub species in urban parks and the compactness of green spaces as a measure of patch shape. Furthermore, increasing habitat heterogeneity increases species richness. Many studies have shown a relationship between habitat heterogeneity and species richness in urban green spaces (cf. Cornelis and Hermy 2004). High habitat heterogeneity positively affected the number of mammal species (Garden et al. 2007; Hodgkison et al. 2007). Zerbe et al. (2002) detected a correlation between plant species richness and the number of land use types within equally sized study areas along a transect from the center to the outskirts of Berlin. Additionally, a correlation was found between plant species numbers and the intensity of management in different habitat structures. High diversity of tree and shrub species and shrub cover positively affected bird species richness (Husté et al. 2006; Pellissier et al. 2012). Natural structures within urban green spaces, such as dying trees, stumps, and old wind throws, increased bird species richness (Sandström et al. 2006). However, González-Oreja et al. (2012) measured habitat heterogeneity in urban green spaces in Puebla, Mexico, by 14 floristic and 6 physical descriptors but found no significant effects on bird species richness.

Species richness in the urban system is driven by various interacting factors (e.g. Knapp et al. 2008). As many studies have already emphasized the importance of patch metrics,

habitat heterogeneity, and patch connectivity as determinants of species richness in urban green spaces, an investigation of combined effects of these factors on species richness within and across several taxonomic groups would be beneficial (cf. Nielsen et al. 2014). An important issue in analyzing determinants of species richness is the consideration of their potential autocorrelation in statistical analyses (Lichstein et al. 2002). These have often been neglected by previous analyses in the urban context due to single variable analysis, but have been taken into account for example by Kühn et al. (2004). However, species richness in green spaces is known to correlate with a number of single and combined factors (Matthies et al. 2015; MacGregor-Fors and Ortega-Álvarez 2011; Bräuniger et al. 2010). For instance, Jokimäki (1999) demonstrated that the occurrence of breeding bird species in urban parks depends on park size, habitat structure within the park, and landscape structure outside the park. Moreover, Jokimäki (1999) proved that groups of bird species react differently, since species with lower area demands occurred closer to the city center than species with greater area demands. Therefore, research on the factors driving species richness in urban areas need to address multiple explanatory factors, as well as response variables addressing species richness within and across taxonomic groups, in order to advance the understanding of species richness and its determinants in urban green spaces (Nielsen et al. 2014; Knapp et al. 2008; Garden et al. 2006; Angold et al. 2006).

The aim of this study was to detect determinants of species richness in urban green spaces within and across taxonomic groups. We focus on explanatory variables relevant to species-area effects, distance effects, and the effects of habitat structure, since these are important determinants of species richness. First we investigate effects of single and combined explanatory variables on the numbers of total, native, and endangered vascular plant, bird, and mammal species. We address the questions, which single explanatory variables determine species richness within taxonomic groups and which combinations of explanatory variables best explain variance of the species richness. Then we analyze the effects of combined explanatory variables on the overall species richness across all examined taxonomic groups. In this way we test whether the determinants of species richness within taxonomic groups are confirmed for species richness across taxonomic groups.

Methods

Study area and study sites

We conducted our study in Hannover, Germany (52°22′ 32.72 N, 9°43′54.49 E). Within Hannover a total of 32 urban green spaces were selected as study sites using patch area and

distance to the urban edge in a stratified random selection approach. These variables were measured using detailed land cover data from a digital landscape model (LGN 2007). The urban edge was defined as the border of the coherent built-up area (measured as all land cover class objects from the digital landscape model dominated by sealed surface, for example residential building area, industrial area) to the landscape with gaps not exceeding 100 m. Please refer to Matthies et al. (2015) for details on the selection of study sites. The 32 selected study sites included forests, parks, cemeteries, allotments, and fallow lands, covered 0.7 ha to 71.3 ha, and were located 190 m to 2872 m from the urban edge (cf. Online Resource 1).

Data sources

Response variables: Vascular plant, bird, and mammal species data

The vascular plant species were surveyed from June to August 2011 and March to May 2012. We conducted complete field surveys (true census, systematic total count), with the aim of recording every species in study sites (cf. Krebs 1989; Chiarucci and Palmer 2005). In Germany, a complete field survey is an accepted and often used survey method, for instance, for the collection of data for distribution maps and atlases (cf. Seitz et al. 2012). We refrained from using any sample-based method to survey plant species, as some of the study sites (especially allotments, cemeteries) were highly heterogeneous. Advantages of the complete field survey include a comparable survey effort, a better accuracy of species numbers compared to estimation of species numbers from sample plots, and the possibility to identify native and endangered species. All species occurring in each green space, including ornamentals but excluding submersed species, were recorded for main habitats (e.g. deciduous forest, lawn). The nomenclature followed Buttler and Hand (2008) for native, established, and ephemeral non-native and Erhardt et al. (2008) for ornamental vascular plant species.

Bird surveys were conducted during the breeding season from March to June in 2012. Bird species were surveyed using line transects following Bibby et al. (1995) and Südbeck et al. (2005). Transect routes went through or close to all different habitats and were chosen to cover each study site evenly. The length of transects was standardized to the size of study site (cf. Online Resource 2). Birds were identified visually and acoustically. Birds were only recorded if they exhibited behavior indicating that the study site was part of their habitat, for instance, those that were singing or searching for food. Each study site was visited 8 times with at least 7 days in between visits. Surveys started no earlier than 30 min before and ended no later than 4 h after sunrise. Nomenclature

followed the species list for Germany (Barthel and Helbig 2005).

Mammals were surveyed by point counts using camera traps. This method allows for the detection of medium-sized to large mammals. In each study site, surveys were conducted with three replications (Sept. to Nov. 2012, Dec. 2012 to Feb. 2013, and March to May 2013). Camera traps were installed at the same locations for 7 days and nights. One camera was installed for every approximately 2 ha of study site (cf. Online Resource 3). Cameras were placed evenly within study sites and in as many different habitats as possible. Each camera was mounted to a fixed point (e.g. tree) at a height of 40 cm above ground, due to activation sensitivity (cf. Widdows et al. 2015). For best sensor performance, cameras pointed towards an open area with a dimension of 12 m × 12 m (cf. Bushnell 2011). Camera traps took pictures with 8 M Pixel image size. Three photos were taken per capture and the interval in between captures was set to 1 s.

The response variables used were total, native, and endangered species numbers for vascular plants and birds; for mammals only total and native species numbers were used (Table 1). The endangered mammal species (pine marten, *Martes martes*) was excluded from the analysis, as only one endangered species was found in our study. As we had missing mammal data for two study sites because permission to set up camera traps was not granted, we computed the missing data. We used the mean species number of small study sites, as the number of total and native mammal species showed strong positive correlations to the area of study sites.

In order to assess potential redundancy between the species richness data of these 8 species groups, we performed principal component analysis. The variable NAT_BIRD was excluded from analysis, as it was highly correlated with TOTAL_BIRD. The components were clearly differentiated and a meaningful interpretation was obvious for components 1 to 3 (details shown in Online Resources 5 and 6): The first component can be interpreted as the overall richness of vascular plant, bird, and mammal species (C1_OVERALL_RICH) (Table 1), i.e., species-rich urban green spaces tend to show high species numbers for all investigated taxonomic groups. The second component referred to relatively high mammal and relatively small vascular plant species richness related to overall species richness (C2_ + MAM-PLANT). Finally, the third component referred to relatively small endangered bird species richness related to overall species richness (C3_-END_BIRD).

Explanatory variables: Patch metrics, habitat heterogeneity, and connectivity of green spaces

We used ten explanatory variables describing patch metrics, habitat heterogeneity, and connectivity of green spaces, to test

Table 1 Overview of response variables

	Variable	Abbreviation	Description
Species richness within taxonomic groups	Total number of vascular plant species	TOTAL_PLANT	Sum of recorded vascular plant species (self-established and planted)
	Number of native vascular plant species	NAT_PLANT	Sum of native species (including archeophytes) (following Garve 2004)
	Number of endangered vascular plant species	END_PLANT	Sum of species with red list status 1, 2, 3, R, G, or V (following Garve 2004)
	Total number of bird species	TOTAL_BIRD	Sum of recorded bird species
	Number of native bird species	NAT_BIRD	Sum of native bird species (following Krüger and Oltmanns 2007)
	Number of endangered bird species	END_BIRD	Sum of endangered bird species (following Krüger and Oltmanns 2007)
	Total number of mammal species	TOTAL_MAM	Sum of recorded mammal species (incl. domesticated species)
	Number of native mammal species	NAT_MAM	Sum of native mammal species (following Heckenroth 1993)
Species richness across taxonomic groups	Component 1: Overall species richness	C1_OVERALL_RICH	Overall richness of vascular plant, bird, and mammal species
	Component 2: High mammal and small vascular plant species richness	C2_ + MAM-PLANT	Relatively high mammal and relatively small vascular plant species richness related to overall species richness
	Component 3: Small endangered bird species richness	C3_ -END_BIRD	Relatively small endangered bird species richness related to overall species richness

for species-area effects, effects of habitat structure, and distance effects on species richness. A species-area effect was investigated with the variable patch area, which was calculated from GIS data. The effects of habitat structure were investigated by the proportion of edge to core habitat, measured as patch shape, as well as by habitat heterogeneity measured as the number and the diversity of habitat types within green spaces. Distance effects were tested by the structural (or physical) component of green space connectivity, which refers to the spatial arrangement of different green spaces in the urban area, without any requisite reference to the movement of organisms or processes across the urban area (cf. Crooks and Sanjayan 2006). Tested explanatory variables were distance to the urban edge, distance to the nearest green space, as well as density, percentage, connectivity, and diversity of the green spaces in a 500 m buffer. Please refer to Table 2 for detailed descriptions of the generation of explanatory variables.

We examined scatter plots and histograms to identify explanatory and response variables with extreme data points and skewed distributions, in order to smooth distributions for the statistical analysis. As a consequence, the variables TOTAL_PLANT, NAT_PLANT, END_PLANT, TOTAL_BIRD, NAT_BIRD, and END_BIRD, as well as AREA, DIST_GS, and CON_GS, were transformed by taking the natural logarithm (ln) (cf. Forman 1995; Knapp et al. 2008). The variables TOTAL_MAM and NAT_MAM were added by 1 and afterwards transformed using the natural logarithm (ln) to account for zeros in the dataset (ln(TOTAL_MAM + 1) and ln (NAT_MAM +1), respectively).

Data analysis

Spearman's rank correlations (r_s) were used to detect correlations between single explanatory variables for patch metrics (AREA, SHAPE, DIST), habitat heterogeneity (NO_HAB, DIV_HAB), and connectivity (DIST_GS, DEN_GS, PER_GS, CON_GS, DIV_GS) and species richness within taxonomic groups (TOTAL_PLANT, NAT_PLANT, END_PLANT, TOTAL_BIRD, NAT_BIRD, END_BIRD, TOTAL_MAM, NAT_MAM). The Spearman's rank correlation was chosen because it is a robust measure and does not require a linear relationship.

To explore the dependencies among the explanatory variables, we computed pairwise correlation coefficients (r_s) and detected some correlations (Table 3). Then we performed principal component analysis (PCA) after log-transforming AREA, DIST_GS, and CON_GS and scaling all variables to unit variance. We computed the variance inflation factor as a measure of multicollinearity when including the explanatory variables jointly in a multiple regression model. Because the components identified in the PCA had no obvious interpretation, and the overall variance was distributed over many

components, we decided to proceed using multiple regression models for the original explanatory variables.

The main objective of our data analyses was to perform statistical tests for the effects of the explanatory variables of patch metrics, habitat heterogeneity, and connectivity, on species richness within taxonomic groups. To avoid overstating significance and the volatile inclusion or exclusion of correlated explanatory variables, we refrained from any method of automated or data-driven model selection (cf. Burnham and Anderson 2002). Rather, we defined groups of variables corresponding to a given overall hypothesis and added them sequentially to the multiple regression model in a pre-defined (i.e., data-independent) sequence (Faraway 2005). The cumulative effect of variables added for a given overall hypothesis was tested using F-tests (type I sum of squares), comparing the extended model with a nested model in which all slopes of added variables are set to 0 (cf. Harrell 2001; Weisberg 2005). A significant effect in such tests means that the group of added variables explains a significant part of the variation of the species richness, which could not be explained by those variables added earlier in the sequence.

By grouping explanatory variables and through the order of inclusion, we were able to test for the added effect of variables after accounting for trivial effects earlier in the sequence, and used statistical tests that are not affected by multicollinearity within a group of variables with similar meaning. The order of adding variables to the sequential regressions was determined by the following reasoning: one major objective of the study was to test the importance of AREA and DIST, the two variables were (nearly) independent of each other due to the stratified sampling; SHAPE was found to be uncorrelated to AREA and DIST and thus there is no problem of collinearity between the three variables and, thus, no ambiguity between their effects. It was also clear before analysis that the two measures of habitat heterogeneity were highly correlated with each other and with AREA (cf. Kallimanis et al. 2008; Cornelis and Hermy 2004). Therefore, they are jointly included in the model and tested after accounting for the (trivial) effect of AREA and previously mentioned variables. Finally, the set of connectivity measures was split into one group of variables describing the connectivity of green spaces quantitatively (DIS_GS, DEN_GS, PER_GS, and CON_GS) and another variable describing the connectivity of green spaces qualitatively (DIV_GS). These groups were added after accounting for patch metrics and habitat heterogeneity. This procedure was performed for species richness within each taxonomic group. Only the adjusted r^2 (adj. r^2) value, as well as the significance level of the test for the sequentially added term, are shown in the main text body, whereas the detailed results are provided in Online Resource 9 to 16. After fitting the sequential regression models, the

Table 2 Overview of explanatory variables

	Variable	Abbreviation	Description
Patch metrics	Patch area	AREA	Absolute area of study site [ha]
	Patch shape	SHAPE	Shape index (SI) calculated by perimeter of a study site divided by 2*square root of π times area: $$SI = \frac{P}{2\sqrt{\pi * A}}$$ P is equal to the perimeter and A is equal to the area of a green space. The shape index equals 1.0 for a circle and increases with decreasing compactness (cf. Angel et al. 2010; Lang and Blaschke 2007)
	Distance to the urban edge	DIST	Shortest distance from the centroid of a study site to the urban edge measured with the ET Geowizard "point to distance" tool [m] (Tchoukanski 2011)
Habitat heterogeneity	Number of habitat types	NO_HAB	Number of habitat types within a study site based on existing (urban) habitat classifications (cf. Drachenfels 2011; Freeman and Buck 2003; Herrny and Cornelis 2000; Löfvenhaft et al. 2002; Qiu et al. 2013) (Online Resource 7)
	Diversity of habitat types	DIV_HAB	Shannon Diversity Index (SHDI) calculated from habitat types within a study site: $$SHDI = \sum_{i=1}^{m}(pi*\ln pi)$$ p_i is equal to the proportion of one habitat type (Lang and Blaschke 2007); the proportion of each occurring habitat type within a study site was estimated on the basis of aerial photographs
Connectivity	Distance to nearest green space	DIST_GS	Shortest distance from the edge of a study site to the nearest edge of a green space [m] (Tchoukanski 2011)
	Green space density	DEN_GS	Number of green spaces/ 1 ha in a 500 m buffer around a study site
	Percentage of green spaces	PER_GS	Calculated by dividing the area covered by green space by the area of a 500 m buffer around a study site times 100
	Connectivity of green spaces	CON_GS	Proximity Index Variante C (PX_fg) (Lang and Blaschke 2007) calculated for the green spaces within a 500 m buffer around a study site: $$PXfg = \sum_{i=1}^{n}\frac{Ai}{di2}$$ At refers to the area of the green space and d to the distance from the study site to the specific green space; green spaces stretching beyond the buffer were taken into account if at least some parts were located within the buffer
	Diversity of green spaces	DIV_GS	Shannon Diversity Index (SHDI) calculated from single land use types of existing digital land cover data (LGN 2007) summarized as green space in a 500 m buffer around a study site (Lang and Blaschke 2007) (Online Resource 8); p_i is equal to the proportion of one land use type (cf. description for DIV_HAB)

Table 3 Results for Spearman's rank correlations (r_s) between explanatory variables. For abbreviations see Table 2

	AREA	SHAPE	DIST	NO_HAB	DIV_HAB	DIST_GS	DEN_GS	PER_GS	CON_GS
SHAPE	0.177								
DIST	-0.011	-0.122							
NO_HAB	0.817***	0.063	-0.067						
DIV_HAB	0.345	-0.040	-0.182	0.607***					
DIST_GS	-0.551**	-0.413*	-0.197	-0.410*	-0.068				
DEN_GS	-0.130	-0.231	0.147	-0.116	0.093	-0.038			
PER_GS	0.065	0.142	0.555***	-0.049	-0.295	-0.604***	0.218		
CON_GS	0.362*	0.250	0.449***	0.212	-0.209	-0.810***	0.070	0.726***	
DIV_GS	0.078	0.113	-0.263	0.142	0.238	-0.145	0.318	-0.108	-0.013

*. Correlation is significant at the 0.05 level (2-tailed)

**. Correlation is significant at the 0.01 level (2-tailed)

***. Correlation is significant at the 0.001 level (2-tailed)

potential deviation from the normality assumptions and potential non-linear relations were visually assessed by Q-Q-plots and plots of the residuals vs. explanatory variables. No violations were detected.

In order to identify the effects of combined explanatory variables on species richness across taxonomic groups, we also conducted sequential regressions using principal components as response variables. We performed multiple linear regressions with tests for sequentially added sets of variables as described above for the first three components: overall species richness (C1_OVERALL_RICH), high mammal and small plant species richness (C2_ + MAM-PLANT), and small endangered bird species richness (C3_-END_BIRD). Again, no indications for non-linear relationships were detected by inspecting Q-Q-plots and plots of the residuals vs. explanatory variables.

Results

Species richness of vascular plants, birds, and mammals in green spaces

We recorded a total of 1372 vascular plant species in the investigated study sites (cf. Online Resource 4), which included 577 native species and 108 endangered species. The minimum and maximum total numbers of vascular plant species for one study site were 95 and 736, respectively (native species: Min = 80, Max = 319; endangered species: Min = 2, Max = 50). Additionally, we recorded a total of 83 bird species across all investigated study sites (cf. Online Resource 2). Of these, 80 bird species were native and 23 species were endangered. The maximum total bird species richness for a single green space was 61 species and the minimum was 14 species (native species: Min = 14, Max = 60; endangered species: Min = 1, Max = 12). The lowest species richness

was found for mammals, with a total of 14 mammal species recorded (cf. Online Resource 3). The highest number of mammal species recorded in one study site was 11 species. The pine marten (*Martes martes*) was the only endangered species, and 9 native species were recorded.

Effects of single explanatory variables on species richness within taxonomic groups

The single variables patch area (AREA), number of habitat types (NO_HAB), and distance to the nearest green space (DIST_GS), significantly affected species richness within all tested species groups (Table 4). Increasing patch area, increasing numbers of habitat types, and decreasing distance to the nearest green space, increased species numbers. The diversity of habitat types (DIV_HAB) was positively correlated with the response variables of vascular plants and birds, but did not significantly affect mammals. Increasing connectivity of green spaces (CON_GS) increased the number of NAT_PLANT and TOTAL_MAM. Thus, three of the individually tested explanatory variables relevant to species-area effects, distance effects, and the effects of habitat structure of urban green spaces (AREA, NO_HAB, DIST_GS), affected all species groups. Two of the variables (DIV_HAB, CON_GS) just affected certain species groups and five variables (SHAPE, DIST, DENS_GS, PER_GS, DIV_GS) did not significantly affect species richness in any of the tested taxonomic groups.

Effects of combined explanatory variables on species richness within taxonomic groups

Patch area (AREA) and the variables describing habitat heterogeneity (NO_HAB + DIV_HAB) showed the strongest effects on species richness within taxonomic groups, if tested in combination with other explanatory variables (Table 5).

Table 4 Results for Spearman's rank correlations (r_s) for explanatory and response variables. For abbreviations see Table 1 and Table 2

	TOTAL_PLANT	NAT_PLANT	END_PLANT	TOTAL_BIRD	NAT_BIRD	END_BIRD	TOTAL_MAM	NAT_MAM
AREA	0.804***	0.903***	0.742***	0.873***	0.863***	0.538**	0.619***	0.680***
SHAPE	-0.110	0.243	-0.029	0.109	0.106	0.151	0.262	0.287
DIST	-0.159	-0.024	-0.128	0.033	0.026	0.152	0.091	-0.031
NO_HAB	0.832***	0.857***	0.760***	0.876***	0.873***	0.557***	0.590***	0.653***
DIV_HAB	0.574***	0.404*	0.601***	0.537**	0.543**	0.454**	0.288	0.310
DIST_GS	-0.401*	-0.644***	-0.354*	-0.460**	-0.446*	-0.374*	-0.625***	-0.581***
DEN_GS	-0.116	-0.124	-0.052	-0.176	-0.178	-0.098	-0.114	-0.135
PER_GS	-0.052	0.187	-0.056	0.078	0.066	0.118	0.232	0.127
CON_GS	0.215	0.423*	0.195	0.295	0.280	0.207	0.367*	0.331
DIV_GS	0.134	0.168	0.157	0.154	0.155	0.109	0.098	0.139

*. Correlation is significant at the 0.05 level (2-tailed)

**. Correlation is significant at the 0.01 level (2-tailed)

***. Correlation is significant at the 0.001 level (2-tailed)

The variables AREA, DIST, and SHAPE, as well as the variables describing habitat heterogeneity (NO_HAB + DIV_HAB), showed significant effects on TOTAL_PLANT. The inclusion of additional variables improved the model from 52% (only AREA) to 76% of explained variance (all five variables). The AREA and the variables describing habitat heterogeneity (NO_HAB + DIV_HAB) showed significant effects on NAT_PLANT, END_PLANT, TOTAL_BIRD, and NAT_BIRD. For NAT_PLANT the model including habitat heterogeneity was improved by 10% to a total explained variance of 82%. For END_PLANT, TOTAL_BIRD, and NAT_BIRD, the model improved by 15%, 10%, and 9%, respectively, to 56%, 89%, and 88% of the explained variance. AREA was the only variable that showed significant effects on

END_BIRD, TOTAL_MAM, and NAT_MAM. The explained variance was 31%, 36%, and 45%, respectively. Therefore, for five of the eight tested species groups, the consideration of combined explanatory variables significantly improved the model and the explained variance.

Effects of combined explanatory variables on species richness across taxonomic groups

The patch area and the habitat heterogeneity (NO_HAB + DIV_HAB) were the significant variables across taxonomic groups, if tested in combination with other explanatory variables (Table 6). The patch area (AREA) showed highly significant effects on the first principle component regarding

Table 5 Results for the sequential regressions for species richness within taxonomic groups showing the adj. r^2 values with the level of significance. The variables/variable groups newly included in the model are written in bold letters. For detailed results of the sequential regressions see Online Resource 9 to 16

Model	ln (TOTAL_ PLANT)	ln (NAT_ PLANT)	ln (END_ PLANT)	ln (TOTAL_ BIRD)	ln (NAT_ BIRD)	ln (END_ BIRD)	ln (TOTAL_ MAM + 1)	ln (NAT_ MAM + 1)
~ ln(AREA)	0.52***	0.72***	0.41***	0.79***	0.79***	0.31**	0.36***	0.45***
~ ln(AREA) + **DIST**	0.54*	0.73	0.43	0.79	0.78	0.30	0.36	0.44
~ ln(AREA) + DIST + **SHAPE**	0.58*	0.72	0.42	0.78	0.78	0.28	0.36	0.46
~ ln(AREA) + DIST + SHAPE + **(NO_HAB + DIV_ HAB)**	0.76***	0.82**	0.56**	0.89***	0.88***	0.33	0.35	0.45
~ ln(AREA) + DIST + SHAPE + (NO_HAB + DIV_ HAB) + **(ln(DIST_GS) + DEN_GS + PER_GS + ln(CON_GS))**	0.81	0.84	0.62	0.88	0.87	0.26	0.32	0.42
~ ln(AREA) + DIST + SHAPE + (NO_HAB + DIV_ HAB) + (ln(DIST_GS) + DEN_GS + PER_GS + ln(CON_GS)) + **DIV_GS**	0.80	0.83	0.60	0.88	0.88	0.23	0.29	0.40

*. Correlation is significant at the 0.05 level (2-tailed)

**. Correlation is significant at the 0.01 level (2-tailed)

***. Correlation is significant at the 0.001 level (2-tailed)

Table 6 Results for the sequential regressions for species richness across taxonomic groups (principle components C1_OVERALL_RICH, C2_ + MAM-PLANT, C3_-END_BIRD), showing the adj. r² values with the level of significance. The variables/variable groups newly included in the model are written in bold letters. For detailed results of the sequential regression for C1_OVERALL_RICH see Online Resource 17

Model	C1_ OVERALL_RICH	C2_ + MAM-PLANT	C3_ -END_BIRD
~ **ln(AREA)**	0.74***	-0.03	-0.03
~ ln(AREA) + **DIST**	0.74	-0.06	0.01
~ ln(AREA) + DIST + **SHAPE**	0.73	-0.00	-0.02
~ ln(AREA) + DIST + SHAPE + **(NO_HAB + DIV_HAB)**	0.86***	-0.03	-0.08
~ ln(AREA) + DIST + SHAPE + (NO_HAB + DIV_HAB) + **(ln(DIST_GS) + DEN_GS + PER_GS + ln(CON_GS))**	0.85	0.03	-0.19
~ ln(AREA) + DIST + SHAPE + (NO_HAB + DIV_HAB) + (ln(DIST_GS) + DEN_GS + PER_GS + ln(CON_GS)) + **DIV_GS**	0.84	-0.01	-0.24

*. Correlation is significant at the 0.05 level (2-tailed)

**. Correlation is significant at the 0.01 level (2-tailed)

***. Correlation is significant at the 0.001 level (2-tailed)

overall species richness (C1_OVERALL_RICH). Additionally, for green spaces with a given area, the habitat heterogeneity (NO_HAB + DIV_HAB) showed highly significant effects. Using a model including AREA, DIST, SHAPE, and NO_HAB + DIV_HAB, a total of 86% of variance in C1_OVERALL_RICH was explained. Regarding the second component (C2_ + MAM-PLANT) and the third component (C3_-END_BIRD), no significant results were detected in our sequential regression models. Therefore, the examination of combined explanatory variables across taxonomic groups highlighted the significance of AREA and habitat heterogeneity (NO_HAB + DIV_HAB) for explaining species richness.

Discussion

We found that patch area and habitat heterogeneity (measured as number and diversity of habitat types) were the most important explanatory variables for plants (total, native, and endangered), birds (total and native), and overall species richness. This emphasizes the relevance of the species-area effects and the effects of habitat structure on species richness in urban green spaces. As patch area and habitat heterogeneity were both significant in the sequential regressions, these variables explain different parts of the variance in the dataset. Even though the variables are correlated, habitat heterogeneity is not simply a surrogate of patch area, but represents qualitative measures of the green space explaining species richness. In contrast, the distance to the nearest green space showed only significant, negative effects on species richness within taxonomic groups when tested as a single explanatory variable. In combination with other variables in the sequential regression, it did not show any significant results. In our sample

we found a clear negative association between distance to the nearest green space and patch area, patch shape, and number of habitat types. This implies that in our study region, green spaces with relatively long distances to the nearest green space, tended to be relatively small, have few habitats and low compactness (as measured by the shape index). In the sequential regressions, there was no additional effect of distance to the nearest green space or other connectivity measures after accounting for the effects of area, distance to the urban edge, shape, and habitat heterogeneity. Although we see a marginal association between distance to the nearest green space and species richness, our data suggest that this could be due to an indirect association with area and habitat heterogeneity (cf. Table 3).

The analysis of the combined explanatory variables reduced the number of identified determinants of species richness for almost all the investigated species groups, although this was not the case for total plant species richness. For total plant species richness, the distance to the urban edge and the shape of the green space were significant in the sequential regressions, in addition to patch area and habitat heterogeneity. The distance to the urban edge and the shape of the green space was not significant in the single explanatory variable analysis. The different determinants of total plant species richness, in comparison to native and endangered species richness, could be due to the high species numbers in total plant species richness, which enables the detection of even weak effects. Additionally, the distance to the urban edge and the shape of a green space could be surrogates for a human impact that is represented in the total plant species richness by non-native species (incl. ornamentals) and is missing from the native plant species richness. Nevertheless, different explanatory variables were significant for species richness

within taxonomic groups (total number of vascular plant species vs. native and endangered), as well as in different taxonomic groups (birds vs. mammals). All this emphasizes the importance of multivariate analysis regarding the explanatory variables as well as the response variables when examining the determinants of species richness in urban green spaces (e.g. Nielsen et al. 2014).

Our results support the significance of the species-area effect for overall species richness (e.g. Bräuniger et al. 2010; Husté et al. 2006; Hodgkison et al. 2007) in urban green spaces. They also confirm effects of habitat structure, indicated by a better model performance. For bird and plant species richness habitat structure was measured by habitat heterogeneity (e.g. Zerbe et al. 2002; Ferenc et al. 2014) and for less mobile species it was measured by the proportion of edge to core habitat (patch shape) (cf. Li et al. 2006). The significant effect of patch area on endangered birds could be explained by a probably higher proportion of core habitat to edge area in the larger study sites. Nevertheless, we did detect differences in these findings for the species richness within some selected taxonomic groups. For instance, we did not find a significant effect of habitat heterogeneity on total or native mammal species richness. For small mammals, a significant effect of habitat structure and on-site habitat characteristics has been shown (Garden et al. 2007; Hodgkison et al. 2007). As we focused on medium-sized to large mammal species (by using camera traps), this difference is probably due to large mammals requiring larger habitat sizes that can extend beyond the border of our study sites. Furthermore, we defined relatively coarse habitat types, which were neither specifically fitted to the requirements of a specific group of species within a given taxonomic group nor to a single species (cf. Ferenc et al. 2014). Therefore, using habitat types specifically defined for certain mammal species may have led to significant effects but were not addressed in this study. Nevertheless, our coarse habitat types were sufficient to significantly determine plant species richness and the richness of total and native bird species.

In our study we did not confirm a significant distance effect. Our results regarding connectivity are different to those of other studies, in which the significance of the green space surroundings have been clearly shown for birds (Ferenc et al. 2014; Pellissier et al. 2012), mammals (Saito and Koike 2013), and plant species (Čepelová and Münzbergová 2012). In our study, the distance to the urban edge showed significant effects only for total plant species richness in combination with patch area. In contrast, when testing site-specific and landscape traits in Mexico City, MacGregor-Fors and Ortega-Álvarez (2011) found the strongest relationship for bird species richness with the distance from the city border. Additionally, a decrease of large and mid-sized mammals from forest landscapes to urban cores was detected in the Tokyo metropolitan area by Saito and Koike (2013). A likely

explanation for the different findings is that the distance to the urban edge is relatively short in Hannover compared to that in megacities such as Mexico City and Tokyo. Furthermore, it is worth noting that city borders are very different in shape, e.g. very regular or more irregular, which affects the distance to the surrounding landscape (Czamanski et al. 2014). The city matrix of Hannover includes a remarkable amount of green spaces and, therefore, clear distance effects are difficult to identify due to high structural connectivity. As a result, the city matrix is pervaded by urban green spaces and their distance from each other could be more important than the distance to the surrounding landscape, implying a less severe isolation effect (cf. Garden et al. 2010; Oliver et al. 2011). Furthermore, the urban edge can be defined in different ways, e.g. by an administrative border or, as applied in our study, by the border of building development. Therefore, it is possible that the distance to the urban edge measured in Hannover, was inappropriate for the scale of the effect.

A significant distance effect, as measured by the distance to the nearest green space, was only supported in the single variable analysis. However, within the single variable analysis, a significant distance effect was shown for all the investigated taxonomic groups. When analyzing distance effects, after consideration of the species-area effect and effects of habitat structure, we did not find any significance for any of the tested connectivity measures. All our connectivity variables were based on the use of existing digital land cover data (LGN 2007), which is a common way to assess the surroundings (Saito and Koike 2013). We focused on green spaces and their quantitative and qualitative measures. Another common way to assess urban green spaces is the interpretation of aerial photographs or the use of automatic satellite remote sensing (e.g. Toger et al. 2015; Pellissier et al. 2012). These methods facilitate the distinction of very small urban green spaces, like private gardens in between houses. However, such methods are very time and cost intensive. The inclusion of qualitative measures of the predominantly built-up area could be useful for the investigation of structural connectivity measures (e.g. Pellissier et al. 2012). The size of the buffer most likely influences the results as well. For this study, we have chosen to focus on a 500 m buffer as it represents an intermediate dispersal capacity. In habitat network analysis, the distance of the buffer can be adjusted upwards or downwards for either individual taxonomic groups or single species (Verboom and Pouwels 2004). For instance, other studies in urban areas have addressed the surroundings up to 8000 m (Saito and Koike 2013). However, analyzing structural connectivity through any buffer analysis does not imply that the same urban area would have the same connectivity for all species. Instead, a structurally connected landscape may be functionally connected for some species while being disconnected for others. We used a 500 m buffer, as it is a reasonable dispersal distance for vascular plants and birds, as well as mammals. It is consistent

with existing standards for the evaluation of overall habitat connectivity on a local level (Opdam et al. 2008) and, therefore, appropriate for the movement of individuals and species in our investigated taxonomic groups.

Conclusion

We conclude that, in the context of urban planning, it is important to conserve large green spaces that include a high number and high diversity of habitats. Several other studies have identified a minimum threshold size of 10 ha to secure high species richness in urban green spaces (cf. Nielsen et al. 2014). For total plant species richness, a short distance to the urban edge and a compact shape of green spaces could be beneficial. According to our results of the single explanatory variable analysis, a short distance to the next urban green space would also benefit the species richness of all investigated taxonomic groups (cf. Bräuniger et al. 2010). Additionally, a high connectivity of green spaces positively affects native plant and total mammal species richness. Our results provide strong evidence that green space area, as well as habitat heterogeneity, and especially the combination of these two variables, are important determinants of species richness within and across vascular plant, bird, and mammal species richness.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Animal studies This research paper contains data on bird and mammal species. Animals were only identified by sighting or hearing and no animals were captured during data collection. Therefore, the welfare of animals should not be negatively affected by the research.

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