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Spider, bee, and bird communities in cities are shaped by environmental control and high stochasticity

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Abstract. Spatially organized distribution patterns of species and communities are shaped by both autogenic processes (neutral mechanism theory) and exogenous processes (niche theory). In the latter, environmental variables that are themselves spatially organized induce spatial structure in the response variables. The relative importance of these processes has not yet been investigated in urban habitats. We compared the variance explained by purely spatial, spatially structured environmental, and purely environmental components for the community composition of spiders (Araneae), bees (Apidae), and birds (Aves) at 96 locations in three Swiss cities. Environmental variables (topography, climate, land cover, urban green management) were measured on four different radii around sampling points (<10 m, 50 m, 250 m, 1000 m), while Moran's eigenvector maps (MEMs) acted as spatial variables. All three taxonomic groups showed weak spatial structure. Spider communities reacted to very fine-scaled environmental changes of lawn and meadow management and climate. Bird community composition was determined by woody plants as well as solar radiation at all radii, the scale of the influence varying among species. Bee communities were weakly explained by isolated variables only.

Our results suggest that the anthropogenic structuring of urban areas has disrupted the spatial organization of environmental variables and inhibited the development of biotic spatial processes. The near absence of spatial structure may therefore be a feature typical of urban species assemblages, resulting in urban community composition mainly influenced by local environmental variables. Urban environments represent a close-knit mosaic of habitats that are regularly disturbed. Species communities in urban areas are far from equilibrium. Our analysis also suggests that urban communities need to be considered as being in constant change to adapt to disturbances and changes imposed by human activities.

Key words: Apidae; Aranae; Aves; beta diversity; built environment; cities; disturbance; MEM; spatial process; Switzerland; urban; variation partitioning.

Introduction

Identification of the factors and underlying processes explaining species distribution by means of environmental and spatial models are vividly discussed ecological topics (e.g., Legendre 1993, Koenig 1999, Wagner 2003, Legendre et al. 2005, 2009). The spatial processes shaping community composition generally pertain to two sources (Legendre 1993, Legendre and Legendre 1998, Fortin and Dale 2005): (1) Autogenic spatial structure is generated by biotic processes such as dispersal, growth, mortality, interspecific competition, or predation. The neutral theory of biodiversity (Bell 2000, Hubbell 2001) predicts that such processes lead to spatial autocorrelation, which can be assessed as a pure spatial component using variation partitioning (Borcard and Legendre 2002, Borcard et al. 2004). (2) Exogenous spatial structure stems from the classical environmental control model by selection of the species' ecological niche (Hutchinson 1957) and arises when species respond to environmental variables that might be themselves spatially structured. This is sometimes called spatially structured or induced environmental dependence (Borcard and Legendre 2002, Borcard et al. 2004). It is challenging to untangle the relative contributions of these processes, and to determine the scales at which they are operating (Borcard and Legendre 1994, Jones et al. 2008).

Relationships between communities and both environmental and spatial variables are assessed with canonical ordination methods, especially redundancy analysis (RDA; Rao 1964). Variation partitioning untangles the relative importance of unique and shared effects of different explaining data sets (Borcard et al. 1992, Borcard and Legendre 1994, Legendre et al. 2005). The obtained ecological information is important for basic ecological knowledge of species or communities

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(Böhning-Gaese 1997, Cushman and McGarigal 2002), as well as for judging the effectiveness of (potential) conservation measures (Betts et al. 2006, Kivinen et al. 2007, Johnston et al. 2008). Variation partitioning lends itself to the study of complex ecosystems.

The relative importance of autogenic and exogenous factors is especially poorly known in urban ecosystems. Urban areas are ecosystems (Sukopp and Wittig 1998) that are characterized by a unique environmental complexity, which is often referred to as the "urban mosaic" (Rebele 1994; Sattler et al. 2010). Variation partitioning, however, has rarely been applied in this environment to investigate the relative contributions of different components affecting species communities. Species composition in the close-knit urban matrix may be influenced by the availability of many, often fine-scaled habitat types (e.g., trees, meadow, bushes, ornamental plants, gardens, lawns, etc.), built structures (buildings, sealed areas), regional effects, topography, climate (Urban Heat Island effect; Pickett et al. 2001), pollution, and traffic. Current knowledge of species distributions in urban environments is often based on studies dealing with single taxa at a single spatial scale (Palomino and Carrascal 2006, Devictor et al. 2007). This limits our understanding of how environmental and spatial factors affect community composition at different scales.

In our study, we used three model communities (spiders, bees, birds) to address the following questions: (1) What environmental variables measured at which spatial scale (radius) best explain community composition in urban areas? (2) How much of the variation in community composition is explained by environmental variables measured at four radii, individually, or in combinations? (3) What is the relative importance of the purely environmental (PE), the spatially structured environmental (SSE), and the purely spatial (PS) components on local community composition? With this last question, which to our knowledge has not yet been addressed for urban environments in any taxonomic group, we identify the processes (niche, neutral) that best explain the observed community compositions.

METHODS

Study sites and sampling design

Data were collected in the three Swiss cities of Lucerne, Zurich (both north of the Alps), and Lugano (south of the Alps), representative of small- to medium-sized European cities (53 000–371 000 inhabitants) of central European lowlands (273–436 m above sea level [asl]).The three cities were chosen due to their similar landscapes, as they all border a lake and are partially surrounded by mountains of 800–2100 m asl. Each settlement usually continues in neighboring lowland areas outside the city border (Lucerne and Lugano have ~4 km diameter of continuous settlement; Zurich ~7 km). All three cities are characterized by historical centers (basic structure of buildings often 300–400 years old), residential areas including old gardens, parks, and cemeteries (often >100 years), business quarters, and former but discontinued industrial areas, which are being transformed for new purposes. They experience a temperate climate (in the north, the average January temperature is 1°C and July is 17°C; in the south, the average January temperature is 3°C and July is 20°C).

We selected three taxonomic groups that we expected to respond to environmental variables at different spatial scales: spiders (Araneae), bees (Apidae), and birds (Aves). Community composition of all three species groups was surveyed at the same 32 study locations in each city to give a total number of 96 study locations. For each city, we selected sampling locations along three gradients; namely, (1) the age of green areas, (Lugano, 1–106 yr; Lucerne, 1–156 yr; Zurich, 1–156 yr), (2) amount of urban green areas in 50 m radii around the sampling locations, (Lugano, 14.8–89.4%; Lucerne, 13.7–93.5%; Zurich, 8.2–97.5%; 100% = 0.79 ha) and (3) management intensity of the meadow/lawn plots (Lugano, 1–20 cuts/vegetation period; Lucerne, 0–16; Zurich 1–13). We chose a reasoned choice sampling strategy to maximize variation along these main gradients, including all possible combinations of minimum and maximum values. The study locations included private gardens, semipublic spaces between apartment buildings, public parks, and courtyards of industrial buildings (detailed locations in Germann et al. 2008).

Arthropod sampling

At each of the 96 study locations, surface-dwelling arthropods were sampled using three pitfall traps (cups with opening diameter of 72 mm; transparent roofs 10 cm above the cups provided rain protection), arranged in an isosceles triangle with 1-m sides. Flying invertebrates were sampled using a nondirectional window interception trap in combination with a yellow pan trap (diameter 44 cm) placed at 1.5 m above ground (Duelli et al. 1999). The pitfall and combination traps were filled with the same 0.2% Metatin solution (bactericide; Acima, Buchs, Switzerland). Arthropods were caught during seven weeks in the period of highest species richness in Central Europe (Duelli et al. 1999). Traps were opened between 13 and 15 June 2006 (depending on cities) and then emptied weekly until closure between 1 and 3 August 2006 (Sattler et al. 2010). Based on previous Swiss arthropod projects that sampled during the whole season (Duelli 1997, Duelli et al. 1999, Moretti et al. 2004), we estimate the proportion of species sampled in these seven weeks to be 74.2% ± 8.7% (±SD; $n = 16$) for spiders and 67% ± 10.3% ($n = 13$) for bees.

Bees and spiders were sorted from the remaining arthropods and identified and counted by specialists (see *Acknowledgments*). Juvenile spiders, as their determination at species level is not reliable, and the European honey bee (*Apis mellifera*), since we are not interested in this species cultured by humans, were excluded from the analysis. Bee keeping is relatively rare in Swiss cities; we therefore expected the density of the honey bee to be low at our study sites and that it would not influence the results of the bee community analysis through competition.

Bird survey

We applied the point count method in the early morning (Bibby et al. 2000) to record birds at the same sampling points as the arthropods. Each of the 96 points was visited six times between 15 April and 13 June 2007 (corresponding to the breeding season), and bird species were surveyed visually and acoustically within a radius of 50 m for 15 min (=90 min per sampling point; 144 h overall). The observer stayed on the central point for the initial 10 min and checked hidden areas, such as behind buildings in the last 5 min. Since the time of day affects bird activity, which in turn affects detection probability, the order of sampling points was alternated between the start (one hour before sunrise) and end (usually four hours after sunrise) of each tour. When counting birds, we took special care that individuals were counted once only. Birds flying overhead were counted only when they showed connection to the ground environment (i.e., searching for food). Abundance for each species and sampling point was defined as the maximum number of individuals present during any of the six visits.

Environmental predictors

The choice of the environmental predictors was driven by the ecology of the selected taxa, i.e., temperature variables for the arthropod groups (sun exposure, solar radiation, topography) and suspected key habitat variables (e.g., soil density for bee nesting, tree cover for birds). In addition, the three main gradients for the selection of the sampling location (age of green areas, urban green areas in 50 m radii, management intensity) were chosen as they represent three factors directly influenced by human decisions. An overview of the four data sets used as environmental variables is presented with some explanations in Table 1. The first data set, which is measured locally, i.e., within a radius of <10 m (“R<10m”), consists of six topographical variables and four variables describing additional local conditions. The topographical variables labeled slope, easterly aspect trap, and northerly aspect trap were measured directly at the trapping location while the variables labeled elevation, easterly aspect hillside, and northerly aspect hillside were obtained from a Digital Elevation Model (the two latter obtained from aspect calculated on 250-m grid cells). The additional variables were labeled age, management intensity, soil density, and sun exposure. We asked property owners to indicate the age of their green areas, which we defined as the time since their last important structural modification or renewal. We counted the number of cuts of the grass or meadow plots during regular visits over the whole vegetation period (26 weeks from mid-April to mid-October) to determine management intensity. Soil density corresponds to the penetration depth of an iron stick combined with a constant weight. Hours of sun exposure was measured with a hemispheric sundial, which took into account distant hills and close buildings and trees.

The other three environmental data sets were integrated over areas of three different radii around the sampling points (“R50m,” “R250m,” and “R1000m”). Land cover variables, labeled agriculture, roads, and urban green (unbuilt and unpaved area), were measured as frequencies (percentages) obtained from theme-specific layers of the topographic map 1:25 000 of Switzerland. Agriculture was not included in R50m, as few locations featured this variable within the 50-m radius. The land cover type “building” was not included in the analysis because it correlated highly with other variables ($r > 0.7$).

Digital Surface Models for Switzerland depict the elevation including vegetation and buildings (Artuso et al. 2003) using airborne laser scanning methods (LIDAR). These data are available in cell sizes of 2.5 × 2.5 m and have an accuracy of ±0.5 m in open terrain and ±1.5 m in terrain with vegetation. We used the module “Area Solar radiation” of ArcMap 9.3 (ESRI 2008) to calculate solar radiation (expressed in watt hours per square meter) for all cells. Shade caused by buildings and trees was taken into account for the calculation of solar radiation. The sum of solar radiation of all cells (solar_SUM) of a given radius is indicative of sun availability and thus indirectly of temperature. The standard deviation of solar radiation for all cells of a given radius indicates its variability for the focal radius (solar_STD). Based on the same digital surface model, we additionally obtained an index for the land cover variable called woody plant cover (trees and bushes). All cells higher than 1 m that are not depicted as buildings in the building layer of the land cover layers of the topographic map 1:25 000 were classified as woody plants. The laser scanning method used in the creation of the digital surface models underestimates the height of trees and bushes as the laser is not always reflected by the top foliage and is mostly reflected by lower levels. So, our measurement of woody plants is a minimum value.

Land cover is often measured in concentric rings of different radii around the sampling location and examined with circular analysis (e.g., Steffan-Dewenter et al. 2002, Pellet et al. 2004). The results are then sometimes generalized as the influence of *spatial scale*, which is potentially misleading since the term *space* is used in multiple ways (Dungan et al. 2002).

In this study, we measured land cover variables at different radii (extent) and reserve the term *spatial variables* to descriptors derived from the geographical location of the sites.

To allow for curvilinear effects of the explanatory variables, we incorporated linear and quadratic terms

TABLE 1. Environmental variables used to analyze urban communities of spiders, bees, and birds.

Name	Explanation	Unit
Local variables measured on a radius <10 m		
Elevation		meters above sea level (m asl)
Slope		%
Easterly aspect trap	exposition of trap location with respect to east	gradient: −1 to 1
Northerly aspect trap	exposition of trap location with respect to north	gradient: −1 to 1
Easterly aspect hillside	exposition of hillside with respect to east	gradient: −1 to 1
Northerly aspect hillside	exposition of hillside with respect to north	gradient: −1 to 1
Age	time since last structural modification of green area	years
Management intensity	cutting frequency of meadow/lawn during the vegetation period	number of cuts in 26 weeks
Soil density†	soil density index	centimeters
Sun exposure	time of sun exposure in July	hours
Land cover map and solar radiation measured in radius 50 m, 250 m, and 1000 m (R50m, R250m, R100m, respectively)		
Agriculture‡	agricultural area (only radius 250 m and 1000 m)	square meters
Roads‡	area sealed by roads (width according to road class)	square meters
Urban green‡	area of urban green (unbuilt and unpaved area)	square meters
Woody plants§	area of trees and bushes	square meters
Solar_STD§	standard deviation of solar radiation	watt hours per square meters
Solar_SUM§	sum of solar radiation	watt hours per square meters

Notes: Variables are split into locally measured variables (at a radius smaller than 10 m) and variables obtained from GIS and LIDAR data at 50 m, 250 m, and 1000 m radius.

† Penetration depth measured with a self-made iron stick and a constant weight.

‡ Obtained from theme-specific layer of the topographic map 1:25 000 of Switzerland.

§ Obtained from Digital Surface Model (LIDAR-data; Artuso et al. 2003).

for all but the four measures for exposition. In total we had 16 predictor variables for the environmental data set R<10m, 10 for the data set R50m (no agriculture in this radius), and 12 each for R250m and R1000m.

Spatial predictors

Moran's eigenvector maps (Dray et al. 2006) were used to obtain spatial predictor variables that can be used in regression or ordination. MEMs represent the generalized form of the previously developed principal coordinates of neighbor matrices (PCNM; Borcard and Legendre 2002). Both methods use the eigenfunctions of spatial configuration (= connectivity) matrices. The resulting variables (eigenvectors) are orthogonal to each other, so they can be used to build additive, scale-specific models (Borcard and Legendre 2002, Borcard et al. 2004, Dray et al. 2006). MEM variables are more flexible to geographically irregular sampling schemes, as it was the case in our cities, and a wider array of connectivity matrices can be applied than in the classical PCNM approach. According to Dray et al. (2006), we proceeded as follows: (1) We obtained a connectivity matrix ($\mathbf{B} = [b_{ij}]$) based on coordinates of sampling locations. We used Delaunay triangulation (Legendre and Legendre 1998) to define neighboring locations. We thereby excluded connections that cross lakes, as we assume that spatial processes crossing the open water are insignificant in our context. (2) We then computed a Euclidean distance matrix ($\mathbf{D} = [d_{ij}]$) between neighboring locations and derived a weighting matrix **A** where $[a_{ij}] = 1/[d_{ij}]$. (3) The connectivity matrix **B** is weighted according to this distance, meaning that locations that are closer together are given greater weight ($1/d$) in the analysis. The final, spatial weighting matrix **W** results from the Hadamard (i.e., term-by-term) product of **B** and **A**. (4) Moran's eigenvectors and eigenvalues are calculated on the spatial weighting matrix **W**. The resulting variables are continuous. (5) The eigenvectors with positive eigenvalues, representing positive spatial autocorrelation, were included in the data analyses as spatial predictor (MEM) variables.

The MEM variables associated with small eigenvalues consist of fine waves with high frequency patterns and represent local structures, while those associated with large eigenvalues exhibit broadscale frequency and represent scales on the maximum distances between sampling locations for each city (Lugano = 3.5 km, Lucerne = 4.3 km, Zurich = 6.2 km; Borcard and Legendre 2002, Dray et al. 2006). MEM eigenfunctions were created using the R package "spacemakeR" (Dray 2008).

Data analysis

An overview of the data sets used and of the different steps of analysis to answer questions 1–3 is given in Fig. 1. Unless otherwise stated, we used the R language v2.6.0 (R Development Core Team 2007) for all statistical analyses. We Hellinger-transformed all community data (site by species matrices) to make them appropriate for linear analyses (Legendre and Gallagher 2001). We tested the general null hypothesis that species community was not related to environmental or spatial variables.

Question 1.—For each of the three cities separately, we explained community composition of the focal taxa (birds, bees, spiders) with four environmental data sets measured at the four different radii by redundancy analysis (RDA). For each of the four environmental

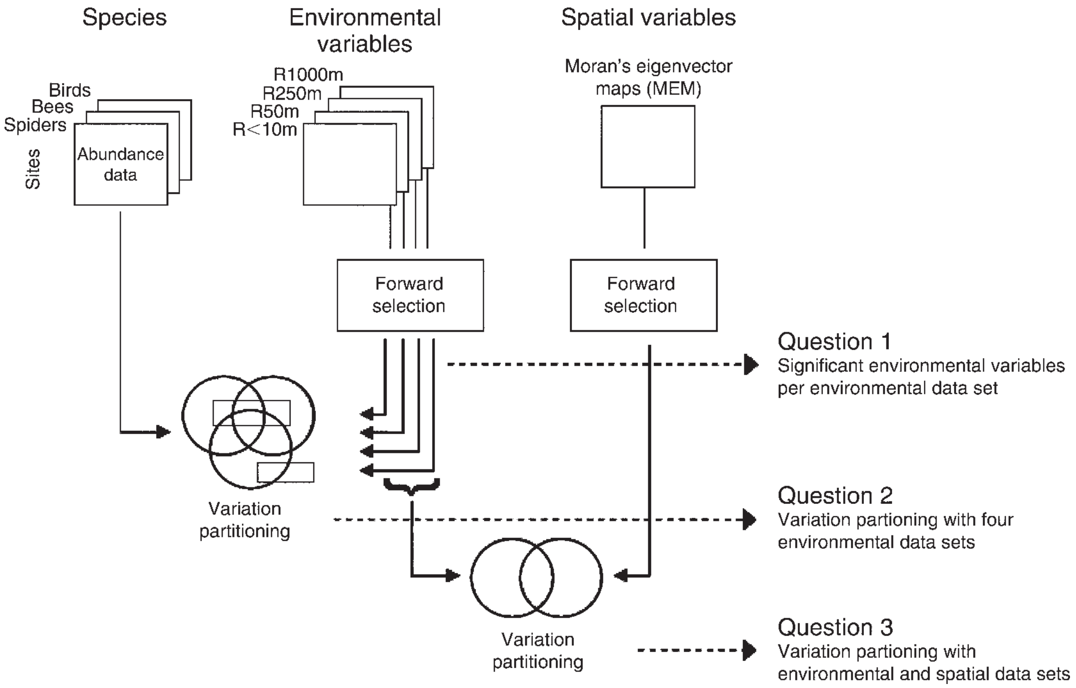

FIG. 1. Diagram of the different data sets used and the analytical steps performed with respect to the three study questions. These steps were repeated for every city individually. Areas of four different radii around the sampling points are abbreviated R<10m, R50m, R250m, and R1000m.

variable sets, we ran a forward selection with the R package packfor (Dray et al. 2007) to identify the significant variables ($P < 0.05$ after 9999 random permutations). We minimized the problems of the classical forward selection by applying the double-step procedure proposed by Blanchet et al. (2008). (1) Inflated Type I error was avoided by forward selecting only models for which a global test with all explanatory variables was significant. (2) To avoid overestimation of the amount of variance explained, another stopping criterion (next to the classical α rejection level) was introduced in that the adjusted coefficient of multiple determination (R^2_{adj}) of the model could not exceed the R^2_{adj} obtained when using all explanatory variables. The variables that fulfilled both stopping criteria were identified as the significant environmental variables shaping the communities of the focal taxa. Only these selected variables were used in subsequent analyses.

Question 2.—We applied variation partitioning to determine the unique and joint fractions of variation explained by the four environmental data sets. Variation partitioning is implemented as function "varpart" in the "vegan"' package (Oksanen et al. 2008). We report the variation explained in each RDA model as the adjusted R^2 (R^2_{adj}), which takes the number of predictor variables and sample size into account to prevent the inflation of R^2 values (Peres-Neto et al. 2006). When a negative R^2_{adj} was obtained, we interpreted it as a zero value (Peres-Neto et al. 2006), meaning that not all fractions of one variation partitioning always add up to a perfect 100%. The first two canonical axes of the RDA analyses were illustrated with biplots using Canoco 4.5 (Ter Braak and Smilauer 2002). To make the fractions of explained variation comparable among analyses, we divided them by the total explained fraction.

Question 3.—We used the environmental variables and the spatial variables in another variation partitioning to assess the unique and joint fractions of variation explained by these matrices. For the environmental information we used the previously forward selected variables. For the spatial information we forward selected the MEM variables with the R package "packfor," but in this case we chose a relaxed, single-criterion forward selection ($\alpha = 0.05$, 9999 permutations). We did so for exploratory purposes, to avoid a too high Type II error level. We repeated this procedure for each city individually so that a different number of MEM variables were selected (Lugano = 9, Lucerne = 10, Zurich = 9). The species matrices (response variables) were checked for linear trends using RDA (explanatory variables: coordinates of sampling locations). Significant linear trends were removed by multiple regression. The original Hellinger transformed species data or the detrended residuals were then used as response variables in the partial RDAs of the variation partitioning.

RESULTS

Overall, we analyzed 21 048 spiders from 163 species, 6194 bees from 139 species, and 4120 birds from 63 species. Species numbers per city were of similar

TABLE 2. Summary statistics for spiders (Aranae), bees (Apidae), and birds (Aves) analyzed per city.

	Aranae			Apidae			Aves		
City	No. individuals	No. species	Species mean ± SD†	No. individuals	No. species	Species mean ± SD†	No. individuals	No. species	Species mean ± SD†
Zürich	6039	94	16.8 ± 4.7 (10–28)	2085	80	15.7 ± 6.0 (7–27)	1321	42	15.0 ± 3.7 (9–25)
Luzern	7707	89	16.3 ± 4.5 (9–26)	1594	73	14.5 ± 5.8 (5–31)	1374	51	17.4 ± 4.4 (9–25)
Lugano	7302	82	14.0 ± 4.5 (5–24)	2515	102	18.8 ± 6.8 (8–35)	1425	40	16.1 ± 3.1 (7–21)
Total	21 048	163		6194	139		4120	63	

† Values in parentheses are the minimum and maximum species mean per sampling location.

magnitude for all groups and cities (Table 2). Detailed information on species' identities, steadiness, and abundances are given in Appendix A.

Variables explaining spider community

Management intensity, i.e., the frequency of lawn/meadow cuttings, and temperature-related variables measured at the local radius (<10 m) are structuring urban spider communities (Table 3). For spider communities, six out of the eight selected variables stem from the R<10m data set, while the remaining two were identified in the next smallest spatial extent, R50m, in Zurich. No environmental variable measured at R250m and R1000m was selected in any of the three cities. Four of the selected variables can be construed as temperature-related with two variables ([sun exposure]^2, solar_SUM under R50m) directly measuring sun intensity and exposition and slope (northerly aspect hillside, [slope]^2) controlling exposure to the sun. Management intensity (selected in two cities) indicates the susceptibility of spider communities to increased lawn/meadow cuttings. The only land cover variable selected ([roads]^2) points to the influence of an intermediate level of sealed area. All environmental variables together analyzed with variation partitioning explained around 10% of the variance (Fig. 2, purely environmental and spatially structured environmental components) in all three cities (Zurich 12.1%, Lucerne 9.4%, Lugano 10.8%).

Variables explaining bee community

In all three cities, bee communities were scarcely explained by isolated variables without interpretable common ecological pattern. Together and as shown in Fig. 2, the environmental variables explained <6% of the variance in all three cities (Zurich 4.2%, Lucerne 4.0%, Lugano 5.9%).

Variables explaining bird community

The fraction of woody plants (i.e., trees and bushes as a linear or quadratic term; selected eight times), as well

TABLE 3. Environmental variables explaining community composition of the spiders, bees, and birds for each of the four data sets (R<10m, R50m, R250m, R1000m), for each city.

Taxa and city	R<10m	R50m	R250m	R1000m
Spiders				
Zurich	management intensity (5.3%); northerly aspect hillside (2.5%)	roads^2 (3.7%) solar_SUM (4.7%)	ns	ns
Lucerne	management intensity (7.2%); northerly aspect hillside (2.3%)	ns	ns	ns
Lugano	sun exposure^2 (5.5%); slope^2 (5.3%)	ns	ns	ns
Bees				
Zurich	ns	ns	ns	roads^2 (2.9%)
Lucerne	ns	urban green (3.1%)	roads^2 (3.2%)	agriculture (2.7%)
Lugano	age (2.5%)	ns	solar_SUM (2.3%)	ns
Birds				
Zurich	ns	woody plants^2 (6.2%); solar_SUM (3.9%); urban green^2 (2.4%)	woody plants^2 (6.4%); agriculture (4.2%)	solar_STD^2 (4.6%)
Lucerne	elevation (3.6%)	woody plants (7.8%)	solar_SUM (8.8%); woody plants (2.1%)	woody plants (3.4%)
Lugano	elevation (3.8%); slope^2 (2.2%)	woody plants (7.3%); solar_STD^2 (4.5%); solar_STD (2.3%)	woody plants (8.0%); solar_SUM (4.0%)	solar_SUM^2 (3.8%); woody plants (7.1%); agriculture (2.7%); urban green^2 (2.9%)

Notes: Values in parentheses indicate the percentage of explained variance by the respective variable on total variance in community composition. See Table 1 for explanation of abbreviations and variables.

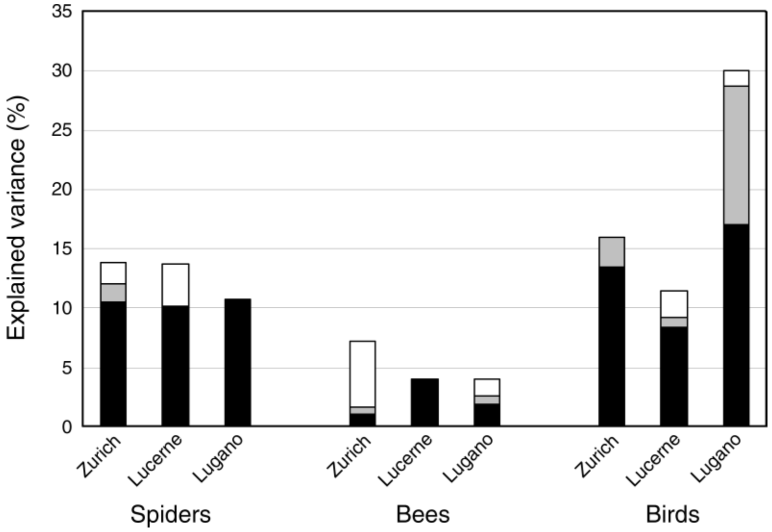

FIG. 2. Results of variation partitioning (Borcard et al. 1992) to separate the purely environmental (black), the spatially structured environmental (gray), and the purely spatial (white) component of variance explaining community composition of the spiders (Aranae), bees (Apidae), and birds (Aves). The selected variables of the four environmental data sets (R<10m, R50m, R250m, R1000m) formed the environmental information; the selected MEM variables were used for the spatial information. See *Methods* for details.

as the quantity and heterogeneity of solar radiation (linear or quadratic; selected seven times) measured at R50m, R250m, and R1000m best explained bird communities (Table 3). Other land cover variables were selected only four times. The R50m data set (one to three variables per city) explained 8–14% of the variance. The R250m data set (two variables per city) explained 11–12%. From the R1000m data set, one variable each was chosen for Zurich and Lucerne (explaining 5% and 3%, respectively), while in Lugano four significant variables explained 17% of the variation. Even the variables measured at the finest radius, R<10m, had some minor relevance, explaining 0–6% in two cities. Fig. 2 shows that all environmental variables together explained 15–29% of the variance in the three cities (Zurich 16.0%, Lucerne 15.2%, Lugano 28.7%).

Biplot illustrations for spiders and birds showing the first two canonical axes of the RDA analysis with the selected environmental variables and species are found in Appendix B and C.

Variation partitioning: environmental data sets

Most of the standardized fractions for both spider communities (65–100%) and bird communities (49–72%) were explained by unique fractions (R<10m, R50m, R250m, R1000m), i.e., the joint fractions were small (Table 4). Nevertheless, in some cases, the joint fractions, indicating variation explained commonly by variables measured at different radii, took up significant amounts. For example, bird community in Zurich was explained to 34% by the joint fraction of the R50m and R250m data sets and to 20% by the joint fraction of the R50m, R250m, and R1000m data sets.

Variation partitioning: space–environment

The striking feature of the partitioning is a near absence of spatial component, suggesting that neutral processes do not structure these communities (Fig. 2). Even with an overall liberal, single stopping criterion in the forward selection of the MEM variables, almost no pure spatial structure could be detected in any taxon and city. Both spatial components, unique and joint with the environmental variables, were usually small to negligible. In the case of spider communities, the variation explained by the spatial MEM variables was low (Zurich 3.3%, Lucerne 3.5%) or absent (Lugano). Spatial variables did not substantially increase the already minimal amount of explained variation for the bee community composition. Only in the case of the bird community in Lugano did the spatially structured environmental component reach a comparatively substantial value of 11.4%. In Zurich and Lucerne the MEM variables (unique and joint components) explained little, 2.5% and 3%, respectively.

DISCUSSION

Absence of spatial component

The absence of relevant spatial structure suggests that neutral mechanisms, i.e., biotic processes such as dispersal and interspecific competition, play a subordinate to negligible role in structuring community composition in urban areas. We propose the near absence of spatial structure to be typical to many urban species assemblages. The urban environment as a close-knit mosaic of many different habitat types is disturbed on a regular and frequent basis by the manifold human activities that we suspect to inhibit both the develop-

TABLE 4. Standardized fraction of explained variance (100% = explained variance by all selected variables) by component (environmental data set of a respective radius; in columns) and per taxon and city.

Data set	R<10m (%)	R50m (%)	R250m (%)	R1000m (%)	R<10m ∩ R50m (%)	R50m ∩ R250m (%)	R250m ∩ R1000m (%)	R<10m ∩ R1000m (%)	R50m ∩ R1000m (%)
Aranae									
Zurich	30.6	34.3	ns	ns	35.1	…	…	…	…
Lucerne	100.0	ns	ns	ns	…	…	…	…	…
Lugano	100.0	ns	ns	ns	…	…	…	…	…
Apidae									
Zurich	ns	ns	30.9	7.9	…	…	61.2	…	…
Lucerne	ns			44.2	…	74.2		…	0.4
Lugano	33.6	ns	8.9	ns	…	…	…	…	…
Aves									
Zurich	ns	26.0	12.8	9.9	…	33.5		…	
Lucerne		27.8	17.3	10.4	0.2	8.7	12.1	0.4	
Lugano	6.1	22.4	14.3	28.7	0.8				

Notes: Components including "∩" indicate that the variation explained is shared between the components, meaning that the variation is explained by all radii included. No significant variables identified is abbreviated with "ns"; ellipses (…) indicate that a shared component is not available (at least one set has no significant variables); and cells left blank indicate negative values (omitted because not interpretable, see *Methods*; in cases of negative values, fractions of explained variance sum to >100%). See Table 1 for an explanation of abbreviations.

ment and installation of spatially organized environmental variables and of biotic processes. We hypothesize that the selection pressure imposed by this constant change inhibits the existence of urban species that heavily depend on spatial processes for their survival. Urban species are selected to cope with heavy human influences.

The importance of spatial variables to spider community organization appears to follow a gradient of human disturbance. Spatial variables explain from 24.5% of the variation in spider communities at the alpine timberline (Muff et al. 2009) to 9.7% in dry meadows (Pozzi and Borcard 2001), 4.9% and 4.0% in intensive agricultural areas (Jeanneret et al. 2003), and 0% to 3.5% in urban areas (according to our results). Although methodological differences among these studies, pertaining to the type of spatial variables (trend surface analysis, principal coordinates of neighbor matrices, Moran's eigenvector maps) and extent of the studied areas (a few hundred meters to 80 km), have certainly influenced the results, this overview supports our case that increased human disturbance across ecosystems suppresses the development of spatial structure in spider communities, and possibly in other arthropod taxa, and even in birds. A study applying principal coordinates of neighbor matrices to bird communities in forests, a habitat type with considerably less human disturbance than urban areas, attributed 9–19% variance of bird communities to purely spatial effects (Yamaura et al. 2008), while we found 0–2.2% in urban areas. The cause for the substantial spatially structured environmental component (11.7%) of bird communities in Lugano is uncertain. The bird-relevant environmental variables may be more spatially structured in this than in other cities because the small size of Lugano possibly enables a better connectivity of green areas.

Furthermore, principal coordinates of neighbor matrices and Moran's eigenvector maps usually detect more spatial variance than polynomials and coordinates (Borcard and Legendre 2002, Peres-Neto and Legendre 2010). It is all the more striking that, even though we included advanced Moran's eigenvector map variables to model spatial variables, we found little autogenic spatial structure.

Environmental variables shape community composition

Environmental variables accounted for higher proportions of the total variance in community composition than did spatial variables. Due to the strong disturbance regime in urban areas, we could expect the environmental component to outweigh the spatial component to shape urban communities of most organisms. Our study measuring environmental variables at multiple scales (radii) informed us that different taxonomic groups respond to different spatial scales.

Spider communities are shaped by fine-scaled variables (mainly R<10m). Micro-climatic variables describing exposition and sun intensity are key factors explaining spider communities in Swiss cities (see also Appendix B), conforming to previous studies in U.S. urban-desert landscape (Shochat et al. 2004), in fire-influenced forests (Moretti et al. 2002), and across an alpine timberline (Muff et al. 2009). In two cities (Zurich, Lucerne) we found mowing to be a significant variable structuring spider communities. In grassland, the loss of structural complexity through increased management was also identified by Pozzi and Borcard (2001) as an important variable explaining spider communities. This pattern indicates that small surface-dwelling organisms are very vulnerable to environmental

Table 4. Extended.

R<10m ∩ R250m (%)	R<10m ∩ R50m ∩ R1000m (%)	R<10m ∩ R50m ∩ R250m (%)	R50m ∩ R250m ∩ R1000m (%)	R<10m ∩ R250m ∩ R1000m (%)	R<10m ∩ R50m ∩ R250m ∩ R1000m (%)
...	...	...	...	...	...
...	...	...	...	...	...
...	...	...	...	...	...
...	...	...	...	...	...
...	...	...	26.5	...	...
57.5	...	...	...	...	...
...	...	...	19.8	...	...
15.6		18.0	0.0		0.3
	4.8	1.7	15.5	7.4	5.5

influences at the local scale, especially in disrupted urban habitats.

Environmental variables on all four radii were significant in explaining bird communities (mainly woody plant and solar radiation variables on R50m, R250m, and R1000m; see also Appendix C). These findings agree with those of Melles et al. (2003), who found that both local- and landscape-scale resources were important in determining the distribution of urban birds in British Columbia, Canada. Actually, studies that looked at a specific radius (e.g., house properties [Sattler and Tobler 2004], 25 m radius [Palomino and Carrascal 2006], 1 ha [Goldstein et al. 1986], 1 km^2 [Marzluff 2005], 1000 m radius [Melles et al. 2003]) all found some significant relationships between urban avian diversity and environmental variables at their respective scales. It is suggested that this pattern arises because individual species show variable reactions at different spatial scales (Melles et al. 2003, Donnelly and Marzluff 2004, Betts et al. 2006). The importance of woody plants corroborates several previous studies that found that trees play an important role in explaining urban bird diversity (Goldstein et al. 1986, Palomino and Carrascal 2006, Sandstrom et al. 2006; S. Fontana, T. Sattler, F. Bontadina, and M. Moretti, *unpublished manuscript*), often this relationship seems to be curvilinear (Marzluff 2005). We suggest that the different reaction radius of spiders (mainly to R<10m) and bird communities (mainly to R50m, R250m, R1000m) is caused by their different mobility. Unlike spiders, birds can explore their environment and secure their resources over relatively large areas, which make them more responsive to broader scale organization of their key environmental constraints, thereby corroborating results of Snep et al. (2006), who had modeled butterflies of different mobility and their respective scale of response.

In opposition to spiders and birds, we were unable to explain variation in bee communities with environmental variables across the three cities. Flying distances for bees have long been underestimated, especially in cities (Chapman et al. 2003). The low fraction of explained variance in this group may also be due to methodological issues that did not sufficiently consider the patchy distribution of the bees' two main resources: suitable nesting substrate and nectar-offering plants. A bee collected at one spot may have been there because the spot suited its needs or because the bee was on its route to the foraging ground. This problem is likely to have confused this part of our study. At the least, this tells us that new methodological approaches need to be developed to study small mobile animals in urban environments.

The role of stochasticity

Despite the use of advanced spatial variables and extensive environmental variables measured on four radii, large amounts of variation in community composition of all three taxonomic groups remains unexplained, suggesting that much of the community composition in urban areas is determined by stochasticity. For example, in spider communities, we explained 11–14% of the total variation. These are rather low values compared to other studies. Pozzi and Borcard (2001) explained 29.1% variance in spider communities of dry meadows, Jeanneret et al. (2003) explained 26.3% and 28.6% variance in intensive agricultural areas, while Muff et al. (2009) explained 48.9% variance at the alpine timberline. This overview suggests that urban spider communities are rather stochastic ad hoc assemblages. Dispersal capacities, e.g., by ballooning and passive anthropogenic transportation, seem to allow spiders to colonize suitable fine-scaled habitats (regarding microclimate, management) in a stochastic way in urban areas.

Our research design allowed the identification of major processes and their relative importance in shaping species assemblages in urban environments for at least two categories of animals: small, soil dwelling, and larger, more mobile. We strongly believe that our results go beyond the three studied taxonomic groups and the three cities and are applicable to many taxonomic groups in most urban areas. The near absence of pure spatial variance, which reflects neutral processes (apart from possible omissions of spatially structured environmental variables), suggests that processes such as nonstochastic dispersal and interspecific competition are insignificant to structure urban species assemblages. Environmental variables, reflecting niche processes, explained some variation in urban community composition, but usually remain lower than in seminatural and natural areas. Stochasticity, summarizing random events such as habitat destruction by human activity, anthropogenic transportation or the introduction of exotic species, seems more important in urban areas than in other habitat types. Species communities in urban areas are far from equilibrium and undergo constant change in adapting to the disturbances and changes that characterize their urban environments.

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APPENDIX A

Latin names of the 163 spider (Aranae) species, 139 bee (Apidae) species, and 63 bird (Aves) species, including their relative dominance and steadiness per city (*Ecological Archives* E091-236-A1).

APPENDIX B

Biplot of species community analysis of spiders (Araneae) for the three study cities (*Ecological Archives* E091-236-A2).

APPENDIX C

Biplot of species community analysis of birds (Aves) for the three study cities (*Ecological Archives* E091-236-A3).

Ecological Archives E091-236-A1

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Appendix A. Latin names of the163 spider (Aranae) species 139 bee (Apidae) species and 63 bird (Aves) species including their relative dominance and steadiness per city.

Table A1: Spider species (Aranae) collected in the three study cities. In total 21'048 spiders from 163 species were collected in the 96 locations (32 per city; for details per city see Table 2). Dominance indicates the percentage (%) of individuals of a single species on the total number of spider individuals. Steadiness expresses the percentage of sampling points with the presence of the species.

All figures in %		**Zurich**		**Lucerne**		**Lugano**	
Scientific name	**Abbreviations[1]**	**Dominance**	**Steadiness**	**Dominance**	**Steadiness**	**Dominance**	**Steadiness**
Achaearanea riparia	*Achrip*	0.017	3.1				
Achaearanea simulans	*Achsim*	0.017	3.1	0.039	9.4		
Achaearanea tepidariorum	*Achtep*	0.017	3.1				
Agelena gracilens	*Agegra*	0.033	6.3				
Agelena labyrinthica	*Agelab*			0.039	6.3		
Alopecosa cuneata	*Alocun*	0.017	3.1				
Alopecosa pulverulenta	*Alopul*	1.739	34.4	0.558	3.1	0.603	21.9
Alopecosa trabalis	*Alotra*					0.014	3.1
Anelosimus vittatus	*Anevit*			0.013	3.1		
Araeoncus humilis	*Arahum*	0.745	50.0	0.208	18.8	0.014	3.1
Araneus triguttatus	*Aratri*	0.017	3.1	0.013	3.1		
Araniella cucurbitina	*Aracuc*	0.066	12.5	0.130	25.0	0.055	12.5
Arctosa leopardus	*Arcleo*	0.066	6.3	10.056	78.1	2.492	28.1
Arctosa lutetiana	*Arclut*			0.026	3.1	0.110	15.6
Arctosa personata	*Arcper*					0.247	12.5
Atypus affinis	*Atyaff*	0.017	3.1	0.013	3.1	0.055	12.5
Aulonia albimana	*Aulalb*	0.066	6.3				
Bathyphantes gracilis	*Batgra*	0.017	3.1	0.013	3.1	0.055	9.4
Ceratinella brevis	*Cerbre*					0.219	3.1
Cheiracanthium mildei	*Chemil*	0.099	15.6	0.013	3.1	0.027	6.3
Clubiona brevipes	*Clubre*	0.066	12.5	0.013	3.1		
Clubiona comta	*Clucom*	0.017	3.1				
Clubiona genevensis	*Clugen*					0.014	3.1
Clubiona pallidula	*Clupal*			0.013	3.1		
Clubiona terrestris	*Cluter*	0.033	6.3				

Cnephalocotes obscurus	*Cneobs*	0.265	18.8	0.921	43.8	0.110	12.5
Cnephalocotes sanguinolentus	*Cnesan*	0.050	9.4			0.356	3.1
Collinsia inerrans	*Coline*	0.033	6.3				
Diaea dorsata	*Diador*			0.013	3.1		
Dictyna arundinacea	*Dicaru*	0.033	6.3				
Dictyna pusilla	*Dicpus*	0.017	3.1				
Dicymbium nigrum	*Dicnig*	0.480	34.4	0.221	25.0	0.014	3.1
Dicymbium tibiale	*Dictib*	0.033	3.1				
Diplocephalus cristatus	*Dipcri*	0.050	3.1	0.234	9.4		
Diplocephalus latifrons	*Diplat*	0.017	3.1	0.208	3.1	0.425	12.5
Diplostyla concolor	*Dipcon*	0.116	15.6	0.311	15.6		
Dipoena erythropus	*Dipery*					0.027	6.3
Dipoena melanogaster	*Dipmel*	0.033	6.3	0.013	3.1	0.027	6.3
Dipoena prona	*Dippro*					0.014	3.1
Drassyllus praeficus	*Drapra*					0.014	3.1
Drassyllus pumilus	*Drapum*					0.014	3.1
Drassyllus pusillus	*Drapus*	0.232	18.8			0.096	12.5
Drassyllus villicus	*Dravil*					0.027	3.1
Dysdera crocata	*Dyscro*					0.014	3.1
Dysdera erythrina	*Dysery*	0.050	3.1				
Enoplognatha latimana	*Enolat*	0.017	3.1	0.013	3.1		
Enoplognatha thoracica	*Enotho*	0.911	6.3	0.558	40.6	0.027	6.3
Entelecara acuminata	*Entacu*			0.026	6.3		
Entelecara congenera	*Entcon*			0.013	3.1		
Eperigone trilobata	*Epetri*	8.727	100.0	4.165	96.9	3.191	75.0
Episinus angulatus	*Epiang*			0.026	3.1		
Episinus truncatus	*Epitru*					0.014	3.1
Erigone atra	*Eriatr*	1.722	50.0	1.920	78.1		
Erigone autumnalis	*Eriaut*					10.942	9.4
Erigone dentipalpis	*Eriden*	34.112	9.4	20.293	9.4	16.872	87.5
Erigonella hiemalis	*Erihie*			0.026	3.1		
Ero aphana	*Eroaph*	0.033	6.3	0.026	6.3		
Euophrys erratica	*Euoerr*					0.014	3.1
Euophrys frontalis	*Euofro*	0.149	9.4			0.041	6.3
Euophrys lanigera	*Euolan*					0.014	3.1
Gongylidiellum latebricola	*Gonlat*			0.013	3.1		
Hahnia helveola	*Hahhel*	0.017	3.1				
Hahnia nava	*Hahnav*	0.348	18.8				
Heliophanus auratus	*Helaur*	0.033	6.3	0.013	3.1		
Heliophanus cupreus	*Helcup*					0.082	3.1
Heliophanus flavipes	*Helfla*	0.182	9.4	0.195	18.8	0.205	15.6
Heliophanus tribulosus	*Heltri*					0.014	3.1
Histopona torpida	*Histor*			0.052	9.4		
Icius subinermis	*Icisub*	0.017	3.1				
Keijia tincta	*Keitin*	0.033	6.3	0.013	3.1		
Larinioides patagiatus	*Larpat*	0.017	3.1				
Linyphia hortensis	*Linhor*			0.013	3.1		
Linyphia triangularis	*Lintri*			0.013	3.1		
Macaroeris nidicolens	*Macnid*	0.033	6.3			0.014	3.1
Maso sundevalli	*Massun*	0.017	3.1				
Meioneta fuscipalpa	*Meifus*					0.014	3.1
Meioneta mollis	*Meimol*					0.520	50.0
Meioneta rurestris	*Meirur*	4.537	9.4	2.219	78.1	10.189	100.0
Meioneta saxatilis	*Meisax*	0.017	3.1			0.041	9.4
Micaria pulicaria	*Micpul*	0.033	6.3	0.156	15.6	0.164	15.6

Micrargus herbigradus	*Micher*	0.017	3.1				
Micrargus subaequalis	*Micsub*	0.695	3.1	0.169	6.3		
Microlinyphia pusilla	*Micpus*	0.017	3.1			0.014	3.1
Misumena vatia	*Misvat*	0.017	3.1	0.013	3.1		
Monocephalus fuscipes	*Monfus*	0.017	3.1				
Myrmarachne formicaria	*Myrfor*			0.052	6.3	0.014	3.1
Neottiura bimaculata	*Neobim*	0.033	6.3	0.013	3.1		
Neriene clathrata	*Nercla*			0.026	3.1		
Nigma flavescens	*Nigfla*	0.017	3.1				
Oecobius maculatus	*Oecmac*					0.041	9.4
Oedothorax apicatus	*Oedapi*	0.679	12.5	0.039	9.4	0.082	9.4
Oedothorax fuscus	*Oedfus*	2.037	3.1	17.555	6.3	14.256	6.3
Ozyptila praticola	*Ozypra*	0.050	6.3				
Ozyptila sanctuaria	*Ozysan*					0.110	18.8
Ozyptila simplex	*Ozysim*					0.137	9.4
Ozyptila trux	*Ozytru*					0.014	3.1
Pachygnatha clercki	*Paccle*	0.033	3.1	0.026	6.3		
Pachygnatha degeeri	*Pacdeg*	18.480	81.3	17.322	90.6	4.232	59.4
Pachygnatha sp.	*Pacsp.*			1.518	3.1		
Pardosa agrestis	*Paragr*	0.828	12.5	0.013	3.1		
Pardosa amentata	*Parame*	0.348	15.6	2.855	37.5		
Pardosa hortensis	*Parhor*	1.888	53.1	0.804	21.9		
Pardosa palustris	*Parpal*	4.603	40.6	0.804	34.4		
Pardosa proxima	*Parpro*			0.039	3.1	16.954	71.9
Pardosa pullata	*Parpul*	0.629	6.3	0.519	6.3		
Pardosa saltans	*Parsal*	0.017	3.1	0.026	3.1		
Pelecopsis parallela	*Pelpar*			0.026	3.1		
Philodromus albidus	*Phialb*			0.065	9.4		
Philodromus aureolus	*Phiaur*	0.033	6.3	0.130	12.5		
Philodromus buxi	*Phibux*					0.014	3.1
Philodromus collinus	*Phicol*	0.033	3.1	0.065	12.5		
Philodromus praedatus	*Phipra*			0.013	3.1		
Philodromus rufus	*Phiruf*	0.017	3.1			0.027	6.3
Phlegra fasciata	*Phlfas*	0.149	12.5	0.039	3.1		
Phrurolithus festivus	*Phrfes*	1.904	6.3	0.311	3.1	0.055	12.5
Pirata hygrophilus	*Pirhyg*			0.026	3.1		
Pirata latitans	*Pirlat*	1.275	3.1	6.462	56.3		
Pisaura mirabilis	*Pismir*	0.066	6.3	0.013	3.1		
Pocadicnemis juncea	*Pocjun*			0.039	6.3	0.014	3.1
Porrhomma microphthalmum	*Pormic*			0.026	6.3		
Porrhomma pygmaeum	*Porpyg*	0.017	3.1				
Prinerigone sp.	*Prisp.*					0.520	28.1
Pseudomaro aenigmaticus	*Pseaen*			0.013	3.1		
Saaristoa abnormis	*Saaabn*			0.013	3.1		
Saloca diceros	*Saldic*			0.026	6.3		
Salticus cingulatus	*Salcin*					0.014	3.1
Salticus scenicus	*Salsce*	0.017	3.1			0.014	3.1
Scytodes thoracica	*Scytho*	0.017	3.1				
Sitticus distinguendus	*Sitdis*					0.041	3.1
Steatoda bipunctata	*Stebip*			0.013	3.1		
Steatoda italica	*Steita*					0.630	37.5
Steatoda phalerata	*Stepha*					0.247	21.9
Synema globosum	*Synglo*					0.041	9.4
Talavera aequipes	*Talaeq*					0.014	3.1
Tenuiphantes flavipes	*Tenfla*					0.027	6.3

Tenuiphantes tenuis	*Tenten*	0.331	21.9	0.091	21.9	0.123	12.5
Tetragnatha montana	*Tetmon*	0.050	9.4	0.039	9.4		
Tetragnatha nigrita	*Tetnig*			0.013	3.1		
Tetragnatha obtusa	*Tetobt*	0.017	3.1	0.026	6.3		
Tetragnatha pinicola	*Tetpin*	0.083	3.1				
Theridion impressum	*Theimp*	0.099	15.6	0.013	3.1	0.014	3.1
Theridion nigrovariegatum	*Thenig*					0.096	15.6
Theridion pallens	*Thepal*	0.017	3.1	0.039	9.4		
Theridion pinastri	*Thepin*	0.116	18.8	0.597	21.9		
Theridion varians	*Thevar*	0.182	15.6	0.169	3.1	0.055	12.5
Tiso vagans	*Tisvag*	3.229	71.9	4.386	84.4	0.753	15.6
Trichopterna cito	*Tricit*					1.438	43.8
Trochosa ruricola	*Trorur*	3.444	71.9	1.336	56.3	1.411	65.6
Trochosa terricola	*Troter*	0.464	21.9	0.454	40.6		
Walckenaeria antica	*Walant*	0.331	28.1	0.208	25.0		
Walckenaeria vigilax	*Walvig*	0.116	3.1				
Xerolycosa miniata	*Xermin*	0.066	6.3			9.806	65.6
Xerolycosa nemoralis	*Xernem*					0.123	3.1
Xysticus cristatus	*Xyscri*	0.977	50.0	0.285	34.4		
Xysticus erraticus	*Xyserr*			0.013	3.1	0.301	15.6
Xysticus kochi	*Xyskoc*	0.298	25.0	0.156	15.6	0.452	28.1
Xysticus lanio	*Xyslan*					0.014	3.1
Zelotes exiguus	*Zelexi*					0.274	34.4
Zelotes hermani	*Zelher*					0.014	3.1
Zelotes petrensis	*Zelpet*					0.027	3.1
Zelotes tenuis	*Zelten*					0.014	3.1
Zodarion italicum	*Zodita*	0.845	6.3	0.285	28.1	0.110	12.5
Zodarion rubidum	*Zodrub*					0.068	15.6

[1] see Fig. S2 A, B, C

Table A2: Bee species (Apidae) sampled in the three study cities. In total 6’194 bees from 139 species were collected in the 96 locations (32 per city; for details per city see Table 2). Dominance indicates the percentage (%) of individuals of a single species on the total number of bee individuals. Steadiness expresses the percentage of sampling points with the presence of the species.

All figures in %	**Zurich**		**Lucerne**		**Lugano**	
Scientific name	**Dominance**	**Steadiness**	**Dominance**	**Steadiness**	**Dominance**	**Steadiness**
Andrena bicolor	0.19	12.50	0.25	12.50		
Andrena bimaculata					0.83	28.13
Andrena bucephala	0.05	3.13				
Andrena carantonica	0.05	3.13	0.13	6.25	0.16	12.50
Andrena chrysosceles	0.10	6.25			0.04	3.13
Andrena dorsata			0.06	3.13	0.40	25.00
Andrena flavipes	0.19	9.38	0.13	3.13	0.08	6.25
Andrena florea					0.04	3.13
Andrena fulvago	0.19	12.50	0.50	18.75	0.08	3.13
Andrena gelriae	0.05	3.13	0.13	3.13	0.32	12.50
Andrena gravida	0.05	3.13				
Andrena haemorrhoa			0.06	3.13		
Andrena hattorfiana					0.12	6.25
Andrena humilis			0.06	3.13		
Andrena minutula	0.29	15.63	0.31	12.50	0.24	15.63
Andrena minutuloides			0.06	3.13	0.04	3.13
Andrena nitidiuscula	0.05	3.13				
Andrena ovatula	0.34	15.63	0.50	18.75	0.99	31.25
Andrena pandellei	0.05	3.13				
Andrena rosae					0.36	15.63
Andrena tibialis					0.12	6.25
Andrena trimmerana					0.16	6.25
Andrena wilkella					0.04	3.13
Anthidium florentinum					0.04	3.13
Anthidium manicatum	0.43	28.13	0.56	21.88	0.28	21.88
Anthidium oblongatum			0.13	6.25	0.04	3.13
Anthidium scapulare					0.08	6.25
Anthidium septemspinosum					0.04	3.13
Anthidium strigatum					0.04	3.13
Bombus hortorum	0.86	34.38	1.88	50.00	0.44	28.13
Bombus humilis	0.38	21.88	0.38	9.38	0.08	6.25
Bombus hypnorum	0.96	34.38	0.38	12.50	0.12	9.38
Bombus lapidarius	7.24	87.50	3.01	46.88	2.39	75.00
Bombus lucorum	0.62	25.00	0.69	31.25	0.32	18.75
Bombus pascuorum	2.49	65.63	4.08	78.13	3.62	81.25
Bombus pratorum	0.34	15.63	0.63	25.00		
Bombus ruderarius	0.14	9.38				
Bombus terrestris	9.45	87.50	13.43	96.88	5.84	100.00
Bombus veteranus	0.05	3.13				
Ceratina cyanea					0.04	3.13
Chelostoma campanularum	0.19	3.13	0.06	3.13	0.12	9.38

Chelostoma distinctum	0.05	3.13	0.63	15.63	0.16	6.25
Chelostoma rapunculi	1.58	56.25	3.32	59.38	0.08	6.25
Coelioxys echinata					0.04	3.13
Coelioxys elongata					0.08	6.25
Colletes daviesanus			0.25	9.38		
Colletes similis	0.10	6.25	0.06	3.13		
Dasypoda hirtipes					0.04	3.13
Eucera longicornis			0.06	3.13		
Eucera nigrescens	0.10	6.25	0.06	3.13	0.04	3.13
Halictus confusus	0.24	12.50				
Halictus langobardicus	0.05	3.13			0.04	3.13
Halictus maculatus					0.32	18.75
Halictus rubicundus					0.80	40.63
Halictus scabiosae	0.62	12.50			0.04	3.13
Halictus sexcinctus					0.36	15.63
Halictus simplex	0.29	6.25			1.31	46.88
Halictus subauratus			0.06	3.13	2.74	71.88
Halictus tumulorum	2.35	65.63	1.25	37.50	0.12	9.38
Heriades crenulatus	0.10	6.25	0.31	15.63	0.48	6.25
Heriades truncorum	1.73	46.88	0.88	31.25	0.44	15.63
Hylaeus angustatus			0.13	3.13	0.04	3.13
Hylaeus annularis	0.05	3.13				
Hylaeus brevicornis			0.13	6.25		
Hylaeus communis	0.86	31.25	1.32	50.00	0.60	34.38
Hylaeus confusus	0.77	34.38	0.88	34.38	0.28	15.63
Hylaeus difformis	0.10	6.25			0.04	3.13
Hylaeus gredleri	0.19	12.50	0.13	6.25	0.04	3.13
Hylaeus hyalinatus	2.30	53.13	2.07	43.75	0.44	21.88
Hylaeus leptocephalus	0.14	9.38	0.06	3.13		
Hylaeus nigritus	2.11	56.25	2.45	59.38	0.40	25.00
Hylaeus pictipes	0.05	3.13			0.04	3.13
Hylaeus punctatus	0.34	12.50	0.50	15.63	1.47	40.63
Hylaeus punctulatissimus	0.10	6.25				
Hylaeus rinki			0.06	3.13		
Hylaeus signatus	0.05	3.13	0.69	15.63		
Hylaeus sinuatus	0.77	31.25	0.50	18.75	0.32	18.75
Hylaeus styriacus			0.06	3.13		
Lasioglossum calceatum	0.48	21.88	0.82	34.38	3.14	71.88
Lasioglossum fulvicorne	0.14	3.13	0.50	12.50	0.20	15.63
Lasioglossum glabriusculum					0.28	3.13
Lasioglossum interruptum			0.06	3.13		
Lasioglossum laticeps	18.13	93.75	23.02	93.75	24.02	96.88
Lasioglossum lativentre	0.14	9.38	0.25	12.50	0.04	3.13
Lasioglossum leucozonium	0.29	15.63	0.38	18.75	1.43	34.38
Lasioglossum malachurum	1.53	34.38	0.31	15.63		
Lasioglossum minutissimum					0.08	6.25
Lasioglossum morio	16.26	87.50	9.22	75.00	6.76	84.38
Lasioglossum nigripes					0.04	3.13
Lasioglossum nitidulum	2.45	59.38	3.95	40.63	1.31	40.63
Lasioglossum parvulum					0.04	3.13

Lasioglossum pauxillum	18.03	93.75	14.62	87.50	10.22	96.88
Lasioglossum politum	0.19	3.13			15.94	93.75
Lasioglossum punctatissimum					0.04	3.13
Lasioglossum pygmaeum					0.04	3.13
Lasioglossum sabulosum			0.06	3.13		
Lasioglossum semilucens			0.06	3.13		
Lasioglossum tricinctum					0.04	3.13
Lasioglossum villosulum	0.14	9.38	0.13	6.25	0.16	6.25
Lasioglossum zonulum			0.56	15.63	0.20	12.50
Lithurgus chrysurus					0.64	28.13
Macropis fulvipes			0.44	12.50		
Megachile centuncularis	0.29	18.75			0.08	6.25
Megachile ericetorum	0.05	3.13			0.20	12.50
Megachile flabellipes					0.04	3.13
Megachile maritima					0.04	3.13
Megachile nigriventris	0.05	3.13	0.13	6.25		
Megachile pilicrus					0.08	6.25
Megachile rotundata					0.40	28.13
Megachile willoughbiella	0.14	6.25	0.31	9.38	1.03	53.13
Nomada fabriciana	0.10	6.25	0.13	6.25	0.04	3.13
Nomada flavoguttata					0.04	3.13
Nomada flavopicta					0.12	6.25
Osmia adunca			0.06	3.13		
Osmia bicornis	0.05	3.13				
Osmia caerulescens	0.19	9.38	0.31	15.63	0.16	12.50
Osmia leaiana	0.10	6.25				
Osmia leucomelana	0.05	3.13	0.13	6.25	0.04	3.13
Osmia mustelina					0.04	3.13
Osmia niveata					0.04	3.13
Panurgus calcaratus					3.78	65.63
Psithyrus barbutellus	0.34	21.88	0.31	15.63		
Psithyrus bohemicus			0.13	6.25		
Psithyrus campestris	0.14	9.38	0.31	12.50		
Psithyrus norwegicus	0.05	3.13				
Psithyrus rupestris	0.19	9.38				
Psithyrus vestalis	0.14	9.38			0.12	6.25
Sphecodes crassus	0.05	3.13			0.04	3.13
Sphecodes ephippius			0.19	9.38	0.16	12.50
Sphecodes ferruginatus	0.24	12.50			0.20	12.50
Sphecodes gibbus					0.04	3.13
Sphecodes hyalinatus	0.05	3.13			0.04	3.13
Sphecodes monilicornis	0.05	3.13			0.20	15.63
Sphecodes niger	0.05	3.13				
Sphecodes reticulatus			0.06	3.13	0.04	3.13
Stelis breviuscula	0.05	3.13	0.13	6.25	0.04	3.13
Stelis punctulatissima	0.10	6.25	0.13	6.25		
Stelis simillima					0.08	6.25
Xylocopa violacea					0.08	6.25

Table A3: Bird species (Aves) recorded in the three study cities. In total 4’120 birds from 63 species were recorded at the 96 locations (32 per city; for details per city see Table 2). Dominance indicates the percentage (%) of individuals of a single species on the total number of bird individuals. Steadiness expresses the percentage of sampling points with the presence of the species.

All figures in %		**Zurich**		**Lucerne**		**Lugano**	
Scientific name	**Abbreviations[1]**	**Dominance**	**Steadiness**	**Dominance**	**Steadiness**	**Dominance**	**Steadiness**
Accipiter nisus	*Accnis*	0.1	3.1%	0.1	3.1%		
Acrocephalus scirpaceus	*Acrsci*			0.1	3.1%		
Aegithalos caudatus	*Aegcau*	0.9	15.6%	2.3	43.8%	1.9	31.3%
Anas platyrhynchos	*Anapla*	0.1	3.1%	0.8	15.6%		
Apus apus	*Apuapu*	18.4	87.5%	12.2	90.6%	7	78.1%
Apus melba	*Apumel*	0.4	6.3%	0.7	6.3%	0.1	3.1%
Ardea cinerea	*Ardcin*			0.1	3.1%		
Buteo buteo	*Butbut*			0.1	3.1%		
Carduelis cannabina	*Carcan*					0.1	3.1%
Carduelis carduelis	*Carcar*	1.7	46.9%	2.5	59.4%	3.7	78.1%
Carduelis chloris	*Carchl*	4.6	93.8%	3.1	81.3%	4.5	93.8%
Certhia brachydactyla	*Cerbra*	0.3	12.5%	0.4	15.6%	0.1	6.3%
Coccothraustes coccothraustes	*Coccoc*	0.1	3.1%				
Columba livia f. *domestica*	*Colliv*	3.3	37.5%	1.8	25.0%	5.6	68.8%
Columba palumbus	*Colpal*	0.2	9.4%	1	31.3%		
Corvus corone	*Corcor*	4.9	87.5%	5	87.5%	6.9	100.0%
Corvus monedula	*Cormon*	0.3	3.1%	0.7	15.6%		
Delichon urbica	*Delurb*	0.1	3.1%			2.4	28.1%
Dendrocopos major	*Denmaj*	0.6	21.9%	0.6	21.9%	0.1	6.3%
Emberiza cirlus	*Embcir*			0.1	3.1%		
Erithacus rubecula	*Erirub*	1.1	37.5%	0.9	34.4%	1.2	43.8%
Fringilla coelebs	*Fricoe*	3.6	81.3%	4.8	93.8%	3.7	87.5%
Garrulus glandarius	*Gargla*	0.4	9.4%	0.5	15.6%		
Hippolais polyglotta	*Hippol*					0.1	3.1%
Hirundo rustica	*Hirrus*	0.2	3.1%	0.1	3.1%	0.4	12.5%
Jynx torquilla	*Jyntor*					0.1	3.1%
Larus michahellis	*Larmic*			0.1	3.1%		
Locustella naevia	*Locnae*			0.1	3.1%		
Loxia curvirostra	*Loxcur*					0.1	3.1%
Mergus merganser	*Mermer*			0.1	6.3%		
Milvus migrans	*Milmig*	0.2	6.3%	0.2	6.3%		
Motacilla alba	*Motalb*	0.7	21.9%	1	31.3%	0.9	34.4%
Muscicapa striata	*Musstr*	0.6	21.9%	1.5	46.9%	1	31.3%
Oenanthe oenanthe	*Oenoen*					0.1	3.1%
Parus ater	*Parate*	0.2	9.4%	0.6	18.8%	0.7	21.9%
Parus caeruleus	*Parcae*	3.9	87.5%	4.3	81.3%	1.4	50.0%
Parus cristatus	*Parcri*			0.2	6.3%		
Parus major	*Parmaj*	5.9	90.6%	6.4	100.0%	3	75.0%
Parus palustris	*Parpal*	0.1	3.1%	0.3	9.4%		

Passer domesticus	*Pasdom*	24.1	100.0%	16.7	90.6%		
Passer hispaniolensis italiae	*Pashis*					29.4	100.0%
Passer montanus	*Pasmon*	0.2	3.1%	0.1	3.1%	0.4	6.3%
Phalacrocorax carbo	*Phacar*			0.1	3.1%		
Phoenicurus ochruros	*Phooch*	1.8	59.4%	3.3	87.5%	1.2	43.8%
Phoenicurus phoenicurus	*Phopho*	0.2	6.3%	0.1	3.1%	1.8	56.3%
Phylloscopus collybita	*Phycol*	0.5	15.6%	0.9	31.3%	0.1	6.3%
Phylloscopus trochilus	*Phytro*					0.1	3.1%
Pica pica	*Picpic*	2.3	59.4%	1.4	34.4%		
Picus viridis	*Picvir*	0.1	3.1%	0.1	3.1%	0.1	6.3%
Ptyonoprogne rupestris	*Ptyrup*					0.4	6.3%
Pyrrhula pyrrhula	*Pyrpyr*			0.1	3.1%		
Regulus ignicapillus	*Regign*	0.6	18.8%	1.6	46.9%	0.8	28.1%
Regulus regulus	*Regreg*	0.2	3.1%				
Saxicola rubetra	*Saxrub*					0.1	3.1%
Serinus serinus	*Serser*	0.6	25.0%	1.5	46.9%	2.7	75.0%
Sitta europaea	*Siteur*	0.7	25.0%	1	31.3%	0.6	21.9%
Streptopelia decaocto	*Strdec*	1.9	43.8%	0.6	15.6%	2.7	59.4%
Sturnus vulgaris	*Stuvul*	3.4	62.5%	3.3	59.4%	1.4	31.3%
Sylvia atricapilla	*Sylatr*	3.2	65.6%	3.3	84.4%	4.8	87.5%
Troglodytes troglodytes	*Trotro*	0.4	9.4%	0.4	15.6%	0.4	12.5%
Turdus merula	*Turmer*	7.1	96.9%	12.5	100.0%	8.1	96.9%
Turdus philomelos	*Turphi*			0.1	6.3%		
Turdus viscivorus	*Turvis*			0.1	3.1%		

[1] see Fig. S3 A, B, C

Ecological Archives E091-236-A2

Sattler T., D. Borcard, R. Arlettaz, F. Bontadina, P. Legendre, M.K. Obrist and M. Moretti. 2010. Spider, bee and bird communities in cities are shaped by environmental control and high stochasticity. *Ecology* 91:3343–3353.

Appendix B. Biplot of species community analysis of spiders (Araneae) for the three study cities.

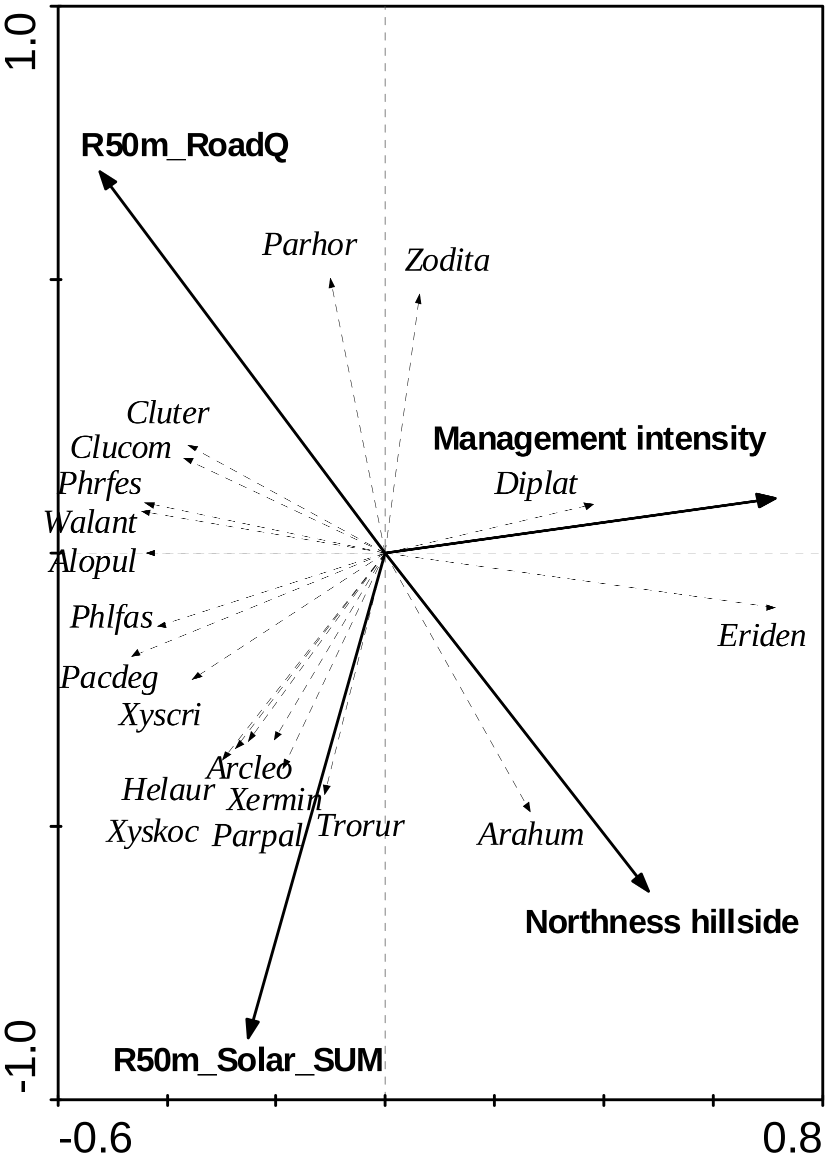

Fig. B1: Biplot of species community analysis of spiders (Araneae) in Zurich (RDA, for details see methods) showing the first canonical axis on the x-axis and the second on the y-axis (n = 32). Selected environmental variables in bold arrows; for visibility only the species most correlated to the first two canonical axes are shown (dashed arrows); abbreviated species names (i.e. 3 letters of the genus and 3 letters of the species) see Table A1. Q = squared variable.

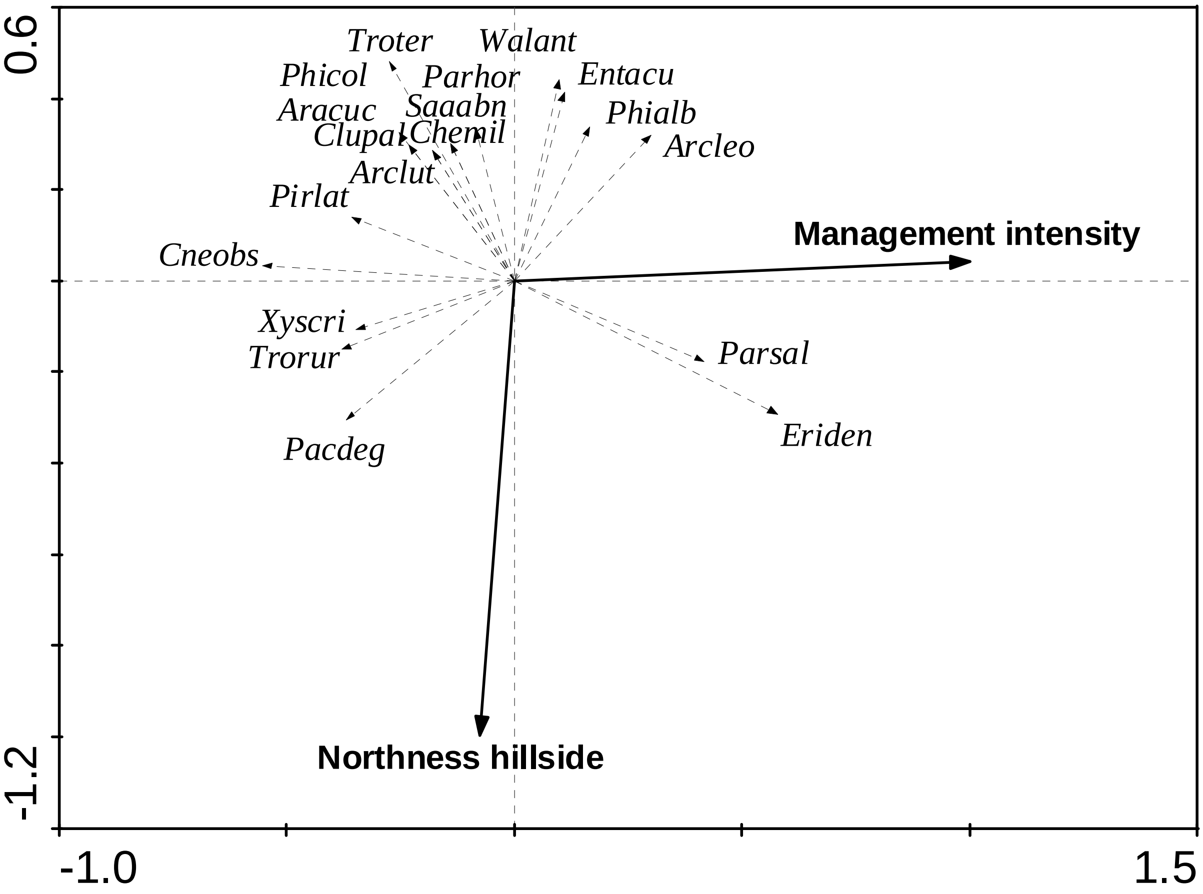

Fig. B2: Biplot of species community analysis of spiders (Araneae) in Lucerne (RDA, for details see methods) showing the first canonical axis on the x-axis and the second on the y-axis (n = 32). Selected environmental variables in bold arrows; for visibility only the species most correlated to the first two canonical axes are shown (dashed arrows); abbreviated species names (i.e. 3 letters of the genus and 3 letters of the species) see Table A1.

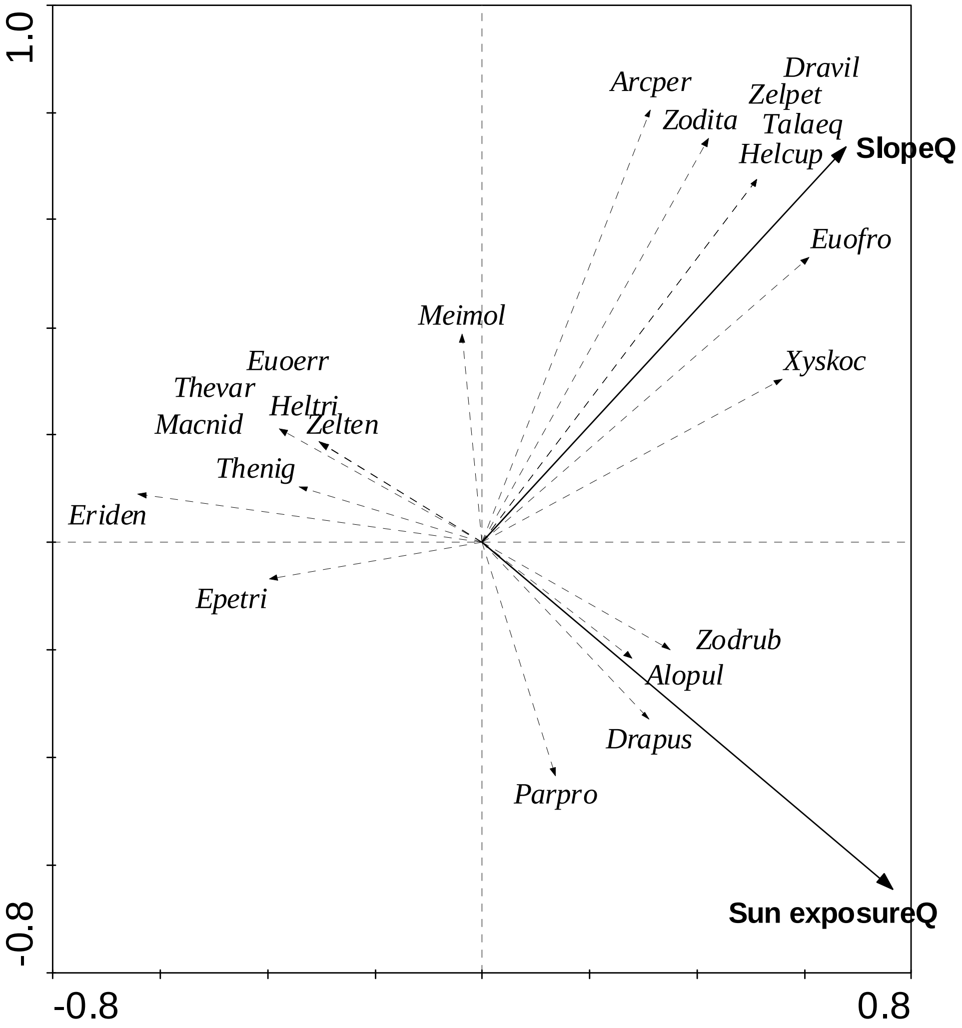

Fig. B3: Biplot of species community analysis of spiders (Araneae) in Lugano (RDA, for details see methods) showing the first canonical axis on the x-axis and the second on the y-axis (n = 32). Selected environmental variables in bold arrows; for visibility only the species most correlated to the first two canonical axes are shown (dashed arrows); abbreviated species names (i.e. 3 letters of the genus and 3 letters of the species) see Table A1. Q = squared variable.

Ecological Archives E091-236-A3

Sattler T., D. Borcard, R. Arlettaz, F. Bontadina, P. Legendre, M.K. Obrist and M. Moretti. 2010. Spider, bee and bird communities in cities are shaped by environmental control and high stochasticity. *Ecology* 91:3343–3353.

Appendix C. Biplot of species community analysis of birds (Aves) for the three study cities.

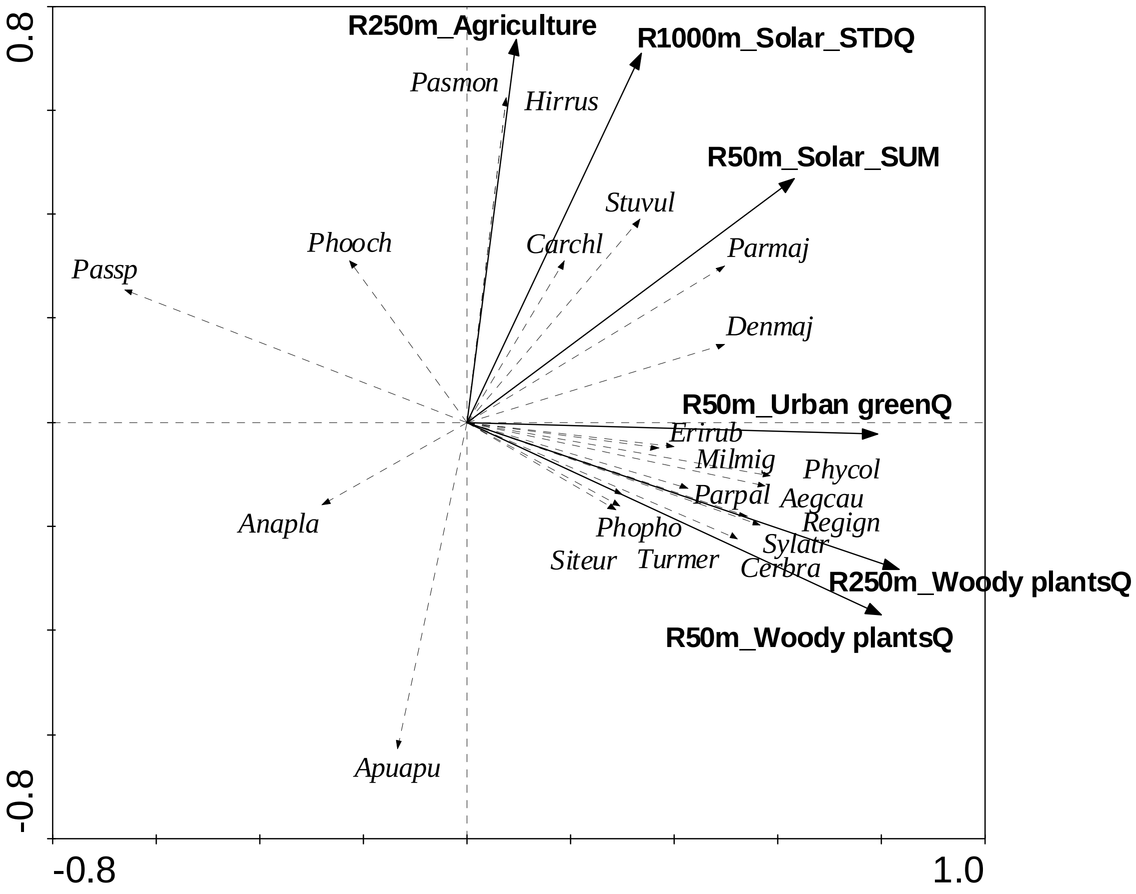

Fig. C1: Biplot of species community analysis of birds (Aves) in Zurich (RDA, for details see methods) showing the first canonical axis on the x-axis and the second on the y-axis (n = 32). Selected environmental variables in bold arrows; for visibility only the species most correlated to the first two canonical axes are shown (dashed arrows); abbreviated species names (i.e. 3 letters of the genus and 3 letters of the species) see Table A3. Q = squared variable.

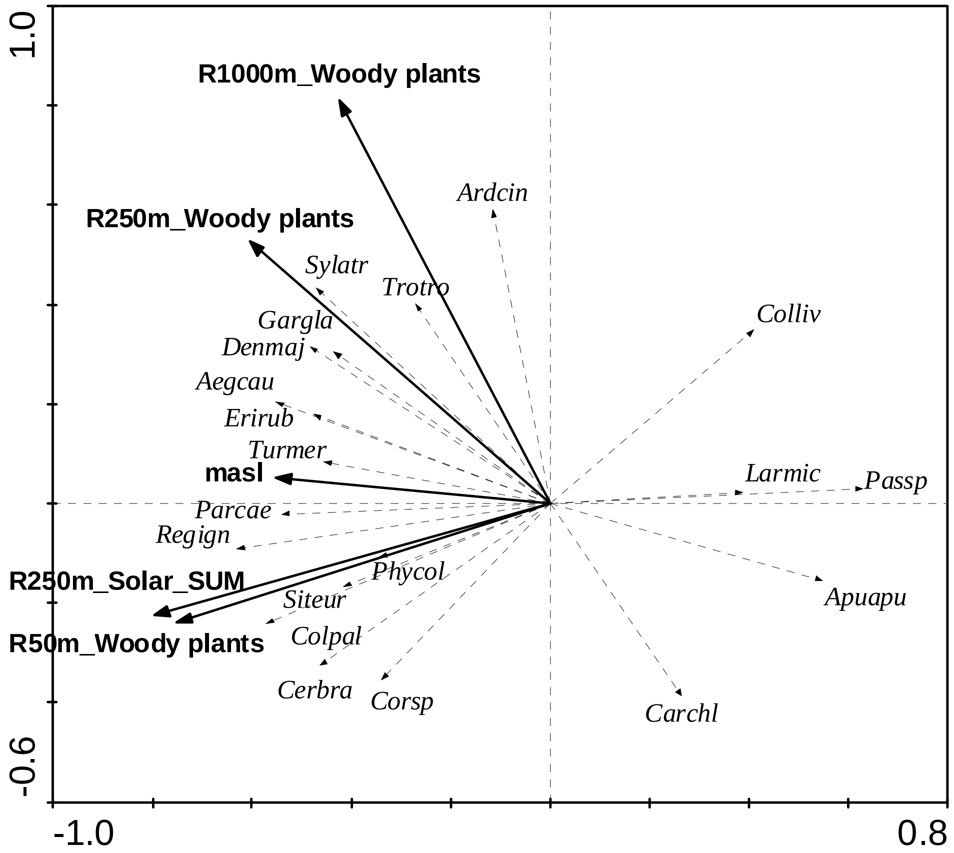

Fig. C2: Biplot of species community analysis of birds (Aves) in Lucerne (RDA, for details see methods) showing the first canonical axis on the x-axis and the second on the y-axis (n = 32). Selected environmental variables in bold arrows; for visibility only the species most correlated to the first two canonical axes are shown (dashed arrows); abbreviated species names (i.e. 3 letters of the genus and 3 letters of the species) see Table A3.

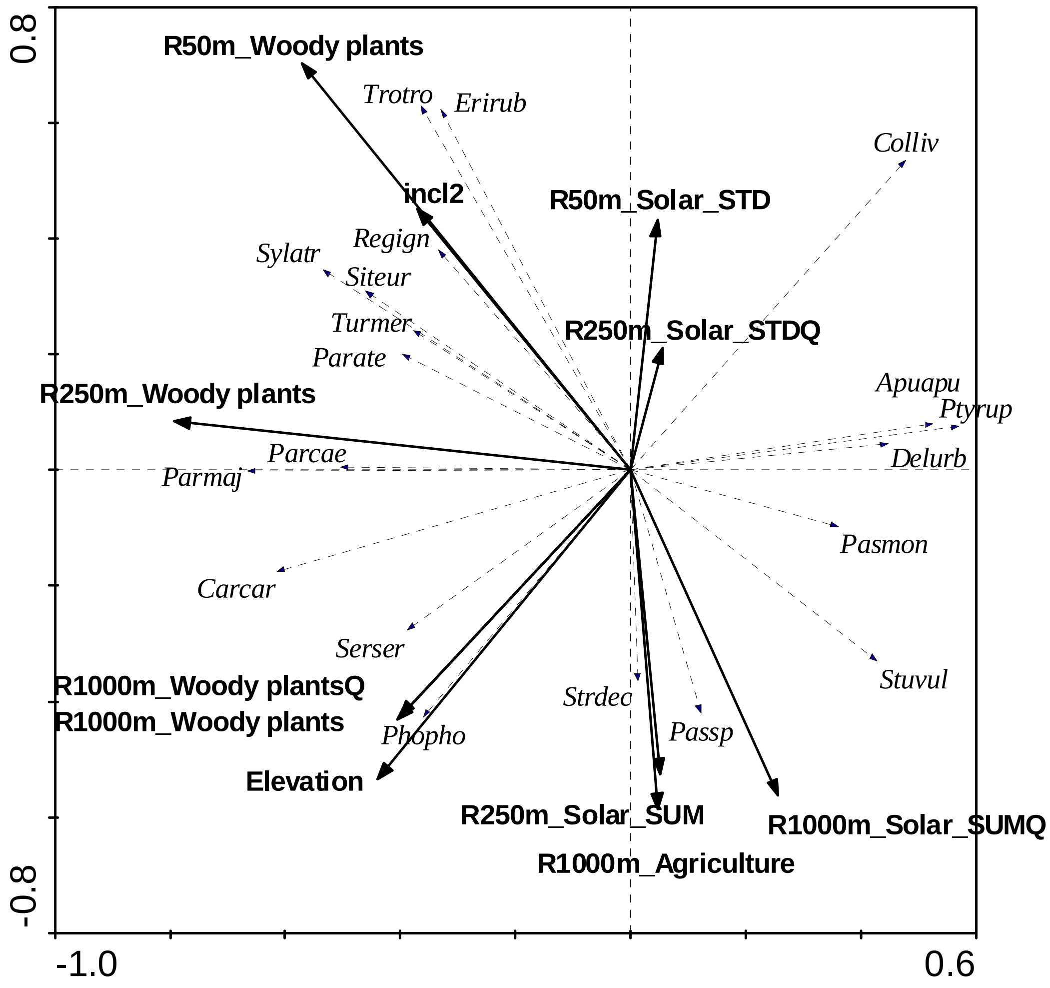

Fig. C3: Biplot of species community analysis of birds (Aves) in Lugano (RDA, for details see methods) showing the first canonical axis on the x-axis and the second on the y-axis (n = 32). Selected environmental variables in bold arrows; for visibility only the species most correlated to the first two canonical axes are shown (dashed arrows); abbreviated species names (i.e. 3 letters of the genus and 3 letters of the species) see Table A3 (*Passp* = *Passer spec.* = *P. domesticus* and *P. hispaniolensis italiae*). Q = squared variable. The influence of solar radiation at fine scales, reflecting microclimatic conditions, is not uniform. This Figure shows that the standard deviation of solar radiation on R50m and R250m points in the opposite direction of the sum of solar radiation on R250m and R1000m. Standard deviation of solar radiation reflects a structurally highly diversified habitat. So the opposing directions point at the fact that places with highest solar radiation at ground level tend to be less structurally diversified. Highest solar radiation therefore means absence of woody plants or houses, which in turn means more homogeneous habitats.