RESEARCH ARTICLE

Response of arthropod species richness and functional groups to urban habitat structure and management

T. Sattler · P. Duelli · M. K. Obrist · R. Arlettaz · M. Moretti

Abstract Urban areas are a particular landscape matrix characterized by a fine-grained spatial arrangement of very diverse habitats (urban mosaic). We investigated arthropods to analyse biodiversity-habitat associations along five environmental gradients (age, impervious area, management, configuration, composition) in three Swiss cities (96 study sites). We considered total species richness and species richness within different functional groups (zoophagous, phytophagous, pollinator, low mobility, and high mobility species). Information theoretical model selection procedures were applied and predictions were calculated based on weighted models. Urban areas yielded on average 284 arthropod species (range: 169–361), with species richness correlating mostly with heterogeneity indices (configuration and composition). Species richness also increased with age of urban settlement, while enlarged proportions of impervious area and intensified habitat management was negatively correlated. Functional groups showed contrasted, specific responses to environmental variables. Overall, we found surprisingly little variation in species richness along the gradients, which is possibly due to the fine-grained spatial interlinkage of good (heterogeneous) and bad (sealed) habitats. The highly fragmented nature of urban areas may not represent a major obstacle for the arthropods currently existing in cities because they have probably been selected for tolerance to fragmentation and for high colonisation potential. Given that built areas are becoming denser, increasing spatial heterogeneity of the urban green offers potential for counteracting the detrimental effects of densification upon urban biodiversity. By quantifying the expected effects along environmental gradients, this study provides guidance for managers to set priorities when enhancing urban arthropod species richness.

Keywords Rapid biodiversity assessment · Morphospecies · Insects · Spiders · Resilience · Switzerland

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Introduction

Recognition of cities as important environments for plants and animals has led to a recent increase in ecological studies in urban areas (McDonnell and Hahs 2008). This trend reflects the ecologists' appreciation of the growing importance of cities as a study object with particular characteristics. More than half of the human population worldwide lives in cities (United Nations 2008) on less than 3% of the global terrestrial area (Grimm et al. 2008). This proportion is substantially higher in some European regions with, for example, nearly 10% of the area of the United Kingdom (Fuller et al. 2002) and 15% of the Swiss lowlands (Bundesamt für Statistik 2005) are classified as urban. Urban areas are among the fastest growing land use types worldwide and the urban population is predicted to increase from 3.3 billion in 2007 to 6.4 billion in 2050 (United Nations 2008).

Urban nature provides benefits for a city's human inhabitants. Contact with nature contributes to human health (de Vries et al. 2003) and general human well being (Fuller et al. 2007). Contact with urban nature often constitutes the majority of first hand experience with nature for city residents (Miller 2005), which influences their general opinions on nature and specific views about nature conservation (Hunter and Rinner 2004). Due to the sheer number of urban residents, their experience with urban nature further influences political decisions on issues of biodiversity conservation outside cities (Dunn et al. 2006).

Increased species richness has been shown to stabilise ecosystems (Folke et al. 1996; Naeem and Li 1997) and generally increases the performance of geochemical ecosystem processes (Naeem et al. 1994). Diverse ecosystems with more species are usually more stable when exposed to external stressors such as invasive species or climatic warming (Folke et al. 2004). Ecological resilience is defined as the magnitude of stress/disturbance that an ecosystem can sustain before it shifts into a different state (Holling 1973; Folke et al. 2004). Ecosystem processes and functions are considered to be more secure in species rich than in impoverished environments (Duelli and Obrist 2003). We can conclude that species richness correlates with the resilience of an ecosystem and its ability to maintain its functions when faced with future, yet unknown impacts and threats.

Due to the inherent challenges of investigating abundant and species-rich systematic groups (McIntyre 2000) most studies on arthropods in urban areas concentrate on specific taxa or metrics of species diversity. The Rapid Biodiversity Assessment (RBA) method (Oliver and Beattie 1993), in which non-specialists with basic entomological training classify arthropod specimens to morphospecies level, is a procedure that includes many arthropod groups at feasible costs. RBA is useful for comparing species numbers in locations with similar land use types and it has been shown that the number of morphospecies strongly correlates with total richness of taxonomically determined species (Duelli and Obrist 2005; Obrist and Duelli, in press). If morphospecies are counted according to taxonomical groups that can be attributed to life history traits such as pollinators and zoophagous species, they additionally allow an assessment of the insurance value of arthropod specific ecosystem functions.

This study of arthropods in three Swiss cities evaluates total species richness and the richness of functional groups based on their diet (zoophagous, phytophagous species), pollination ability and mobility (low, high). We chose three quantified urban environmental variables, 'age of green area', 'management intensity', and 'fraction of impervious area' (= built and sealed area) to study their influence on species richness. With increasing age of green area, advancing succession creates more ecological niches. Additionally, the probability of successful stochastic local immigration of a species increases with increasing age (Rebele 1994; Niemela 1999). For arthropods, management intensity (Morris and Lakhani 1979; Helden and Leather 2004; Hartley et al. 2007) and the proportion of impervious area (Denys and Schmidt 1998; Smith et al. 2006b) are important human-made elements in urban ecosystems. We then contrasted these three urban variables with parameters for fine scale structural heterogeneity, as the urban mosaic is characterized by spatial heterogeneity of different habitat patches such as sealed area, monotonous ground vegetation, bushes and meadows (Rebele 1994). Heterogeneity is indicative of the number of ecological niches in that the more heterogeneous an area, the more niches and thus the more species can be expected to be found (Whittaker and Field 2001). Specifically, we analyse the effect sizes of the following environmental variables on arthropod

species richness and functional groups: (A) the three urban variables (1) age of green area, (2) management intensity of green area and (3) impervious area; (B) the heterogeneity of urban habitats by the indices for (4) configuration and (5) composition; finally we ask (C) how are the different response patterns of functional groups explained?

Methods

Study sites and sampling design

Data were collected in the three Swiss cities of Zurich, Lucerne (both North of the Alps) and Lugano (South of the Alps; Supplementary Material A), which are small to medium sized cities (Zurich 371,000 inhabitants/92 km², Lucerne 59,000/24 km², Lugano 53,000/26 km²) in the central European lowlands (273–436 m a.s.l.). All cities are composed of historical centres and residential areas (often >100 years), more recent apartment buildings and business quarters. All three cities border a lake and experience a temperate climate (North: average January temperature 1°C, July 17°C; South: January 3°C, July 20°C).

Within each city, 32 study locations were chosen (total 96) to include all possible combinations of the three gradients age of green area, impervious area, and management. The traps were installed on lawns and meadows (avoiding closed canopy; minimal distance of five meters to trees) of private gardens, semi-public spaces of apartment buildings, public parks and courtyards of industrial buildings (detailed locations in Germann et al. 2008). A minimum distance of 250 m was kept between study locations and towards the city fringe, thereby avoiding spatial auto-correlation of variables (tested with Moran's Index; Legendre and Legendre 1998).

Arthropod sampling and determination of species numbers

We applied the established, and strictly standardised, rapid biodiversity assessment (RBA) procedure for Switzerland, in which arthropods were collected during 7 weeks in the period of highest arthropod species richness (Duelli and Obrist 2005; Obrist and Duelli, in press). Methodological details and minor modifications to the original method RBA are specified in Supplementary Material B. Traps were opened between June 13th and 15th 2006 and then emptied weekly until closure between August 1st and 3rd 2006. At each of the 96 locations, surface dwelling arthropods were sampled using three pitfall traps (cups with diameter 7.5 cm; transparent roofs 10 cm above the cups provided rain protection), arranged in an isosceles triangle with a distance of one meter. Flying invertebrates were sampled using a non-directional window interception trap in combination with a yellow pan trap (diameter 44 cm) placed 1.5 m above ground (Duelli et al. 1999). Both, pitfall and combination traps, were filled with the same 0.2% Metatin (bactericide) solution. To reduce the effort and to prevent stochastic influences, such as bad weather or damaged traps, that could reduce the arthropod volume of the weekly samplings, the four weekly samples with the highest volume were subsequently chosen (see Supplementary Material B for exceptions). Higher volume usually corresponds to more species (Smith et al. 2006a), although there might be exceptions in cases of species outbreaks or swarming events. These four weekly catches per trap location were sorted into 29 taxonomic groups, within which morphospecies were counted. The allocation to 29 different taxonomic groups allowed expert classification of arthropod groups according to five functional groups within three life history traits (Table 1): trophic levels (zoophagous (including parasites), phytophagous), pollinator function, and mobility (low mobility was defined as <200 m per lifetime and high as >200 m). The attribution to functional groups is constrained by the fact that complete ecological information on diet or mobility at species level is not available for most arthropod groups. For this reason, and due to the morphospecies-approach, we were forced to make some generalisations with regard to the life history traits at broader taxonomic levels (Table 1). For instance, the threshold of 200 m to distinguish between low and high mobility groups is a somewhat arbitrary figure, which serves the distinction of two broad mobility classes. As a rather rough classification, these generalised functional groups include and may misclassify some species, so caution is needed when interpreting results. The arthropod groups Diptera, Collembola, Acari and juvenile spiders were excluded from the analysis because their morphospecies count has been found to

Table 1 Twenty-nine taxonomic arthropod groups, mean species number per study location and attribution to trophic level, pollinator function, mobility and the determination information available

Taxa	Mean species no	Trophic level	Pollinator function	Mobility	Species information for statistical analysis
Arthropoda: miscellaneous					
Aranae	12.6	Zoophagous		Low	Species
Remaining Arthropoda[a, b]	7.1	No attribution		No attribution	Morphospecies
Coleoptera					
Carabidae[a]	4.4	Zoophagous		Low	Species
Staphylinidae	13.1	Zoophagous		Low	Morphospecies
Silphidae	0.2	Zoophagous		Low	Morphospecies
Oedemeridae	2.8	Phytophagous	Pollinator	High	Morphospecies
Scarabeidae	1.9	Phytophagous	Pollinator	High	Morphospecies
Chrysomelidae	3.6	Phytophagous	Pollinator	High	Morphospecies
Curculionidae	6.9	Phytophagous	Pollinator	Low	Species
Cerambycidae[a]	0.8	Phytophagous	Pollinator	Low	Species
Buprestidae[a]	0.7	Phytophagous	Pollinator	High	Species
Coccinellidae	2.8	Zoophagous	Pollinator	High	Species
Cantharidae	0.6	Zoophagous	Pollinator	High	Morphospecies
Cleridae	0.9	Zoophagous	Pollinator	High	Morphospecies
Elateridae	1.5	Phytophagous		High	Morphospecies
Scolytinae	0.9	Phytophagous		High	Morphospecies
Remaining Coleoptera[a]	13.8	No attribution		No attribution	Morphospecies
Hymenoptera					
Formicidae worker	4.9	Zoophagous		Low	Morphospecies
Vespidae and Formicidae (winged)	15.7	Zoophagous		High	Morphospecies
Apiformes	17.9	Phytophagous	Pollinator	High	Morphospecies
Symphyta	1.2	No attribution	Pollinator	High	Morphospecies
Remaining Hymenoptera	94.4	Zoophagous		No attribution	Morphospecies
Hemiptera					
Zoophagous Heteroptera[c]	3.9	Zoophagous		Low	Morphospecies
Remaining Heteroptera	17.1	Phytophagous		Low	Morphospecies
Homoptera[a]	25.9	Phytophagous		High	Morphospecies
Insecta: miscellaneous					
Neuropterida[a]	1.9	Zoophagous		High	Species
Psocoptera[a]	3.6	Phytophagous		Low	Morphospecies
Thysanoptera[a]	13.8	Phytophagous		Low	Morphospecies
Lepidoptera[a]	7.4	Phytophagous	Pollinator	High	Morphospecies

[a] Represents the taxonomic groups of the original RBA (Obrist and Duelli, in press) whereas the remaining taxa are subgroups of former higher level groups

[b] Chilopoda, Diplopoda, Isopoda, Orthoptera, Ephemeroptera, Plecoptera, Odonata

[c] Reduviidae, Nabidae, Phymatidae, Anthocoridae, Saldidae, Hydrocorisae

produce unreliable estimates and exaggerated costs (Duelli and Obrist 2005; unpublished data). Seven arthropod groups were identified to species level (Table 1) and we used these 'true' species numbers for statistical analysis. Due to the high correlation between 'morphospecies' and 'species', and to simplify the text, we will use 'species' as a unified expression.

Environmental variables

The five environmental variables and their mean values are shown in Table 2 (values per study location in Supplementary Material C). We asked property owners to indicate the age of their green spaces, which we defined as the time since the last important structural modification or renewal of the green area (reflecting succession). To quantify the management variable, 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). Impervious area expresses the proportion of area within a 50 m radius around the trap locations (100% = 0.7854 ha) that is sealed or covered by buildings. Within the same 50 m radius, information on structural heterogeneity was obtained by mapping vegetation structures in the field, which were later digitized using Geographic Information Systems (ArcGIS 9.2, ESRI Redlands, USA). We assigned structural habitat patches to four categories: (1) hard cover area: impervious surfaces (built and sealed area), paving-stones and washed grit; (2) monotonous ground vegetation: meadows and lawns mown >3 times a year, ground-covering shrubs, vegetables, ornamental flowers, unwashed grit and open earth; (3) bushes and trees <3 m; (4) meadow: complex structured meadows (mown ≤3 times a year). All habitat patches sum to 100%. Trees >3 m have not been taken into account since previous studies showed that the trap types used (in top soil and 1.5 m above ground) do not adequately sample arboreal arthropods (Duelli et al. 2002; Bächli et al. 2006; Wermelinger et al. 2007). We calculated

the heterogeneity variables based on these four habitat categories. Heterogeneity of a landscape includes two concepts: (1) Composition refers to the area proportions of the different habitat types within the area of interest (here: 50 m radius), which we measured with the Shannon Index (McGarigal and Marks 1995; Jonsen and Fahrig 1997). (2) Configuration reflects the spatial distribution of individual habitat patches and includes information on their position relative to one another (McGarigal and Marks 1995). Ecotones feature characteristics that exert specific demands on biodiversity while also offering specific opportunities (Murcia 1995); the quantity and quality of ecotones between structural habitat patches are suspected to strongly influence arthropod species richness on a meter-scale (Dennis et al. 1998). Thus, the Mean Edge Contrast Index was chosen to represent configuration (McGarigal and Marks 1995), which often explains most variation among several potential measures for edge contrast (Cushman et al. 2008). The Mean Edge Contrast Index is calculated by summing the products of each of the perimeter segment lengths and their contrast weights, and dividing the total by the total perimeter length. We obtained contrast weights (between 0 and 1) by assigning values to ecotones to reflect the following expected habitat contrasts for arthropod species richness: ecotone 'hard cover area versus monotonous ground vegetation': contrast weight of 0.25; hard cover area versus bush and trees: 0.5; hard cover area versus meadow: 0.75; monotonous ground vegetation versus bush: 0.25; monotonous ground vegetation versus meadow: 0.5; bush versus meadow: 0.25. The digitised maps were rasterised in ARCGIS

Table 2 Mean and range (minimum and maximum) of the five environmental variables for each city separately and for the three cities summarised

Variable	Lugano		Lucerne		Zurich		3 cities	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Urban variables								
Management intensity[a]	7	1–20	6	0–16	5	1–13	6	0–20
Age of green area[b]	45	1–106	37	1–156	41	1–156	41	1–156
Impervious area[c]	48.7	10.6–85.2	48.3	6.5–86.3	50.2	2.5–91.8	49.1	2.5–91.8
Heterogeneity variables								
Configuration[d]	32.5	25.2–47.5	30.8	24.3–39.1	32.0	23.8–42.6	31.8	23.8–47.5
Composition[e]	1.02	0.47–1.32	1.03	0.49–1.31	0.96	0.34–1.29	1.01	0.34–1.32

[a] Number of cuts; [b] years; [c] % in 50 m radius; [d] FRAGSTATS Mean Edge Contrast Index; [e] FRAGSTATS Shannon-Index

9.2. The size of the grid cells chosen to calculate these indices is critical for spatial pattern detection (Wu 2004). We chose a 1×1 m grid size (7854 cells per sampling location) to represent the appropriate scale for arthropods in urban areas, because (a) most arthropods are fine-scale oriented and (b) habitat types in urban context change within small distances due to varied human uses. Mean Edge Contrast Index and Shannon Index (referred to as 'heterogeneity variables') were both calculated with the software FRAGSTATS (McGarigal et al. 2002).

Statistical analysis

Linear mixed-effects models with a normal error distribution were used to analyse the relationship between species richness and the environmental variables. This modelling technique was chosen since the residuals were found to conform to the assumptions of homoscedasticity and normality (Crawley 2007), which is expected for count data with a mean >30. Study locations are geographically aggregated within cities, so 'city' was treated as a random factor in the models. All explanatory variables were continuous and were tested for pair-wise correlation. Correlations between explanatory variables are low and remained below $r = 0.2$ with one exception (sealed area − composition $r = 0.41$). Hump-shaped relationships were expected for management based on the Intermediate Disturbance Hypothesis (Connell 1978) and for the heterogeneity indices configuration and composition based on habitat area requirements for minimum viable population size (Shaffer 1981). These terms were a-priori included as linear and quadratic terms into the modelling.

For model selection, we followed an information-theoretic approach (Burnham and Anderson 2002; Johnson and Omland 2004) in which a-priori models were ranked according to their support by the data using Akaike weights obtained from the Akaike's Information Criterion corrected for small sample size (AIC_c). We defined 32 candidate models (Supplementary Material D), resulting from all possible combinations of the five variables (three urban and two heterogeneity variables) and the Null model (no environmental variables included, assuming random distribution). Linear and quadratic functions were simultaneously added/withdrawn from a-priori models. The models with AIC_c weights above 5% were
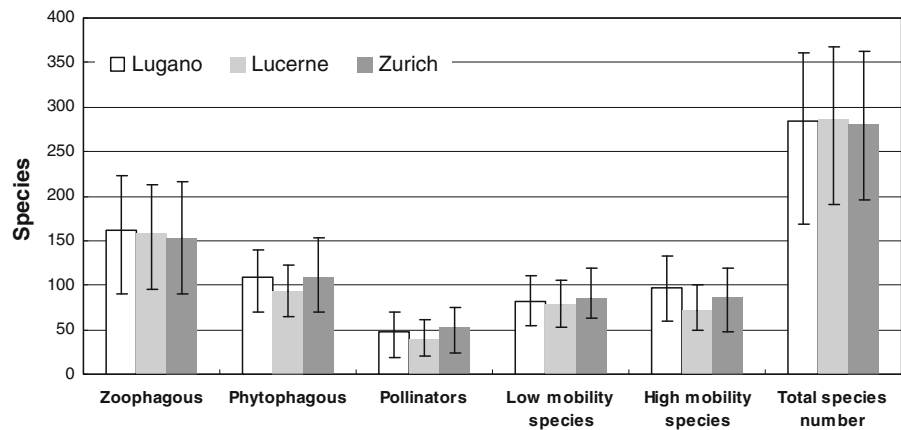
defined as the most parsimonious set of models. We predicted total species number and species numbers of the five functional groups for each of the five environmental variables based on the selected models. Species numbers were allowed to vary within the limits of the focal gradient, while the remaining variables in the model were held at their respective mean values. We based each prediction on 1000 bootstrap samples of equal size to the original data set by random sampling with replacement. For each bootstrap sample, we recalculated the model parameter estimates. Finally, the predictions for each model were averaged based on their AIC_c weights (Burnham and Anderson 2002), estimating coefficients, and standard deviations (SD). The advantages of these new modelling and prediction techniques are that the effect size and a related error term of the gradients can be illustrated directly. In this way, the effect size estimate is not based on only one single best model but on an average effect of several good models. We calculated an estimate for Goodness-of-fit for the selected linear mixed effect models, which takes into account that study locations are aggregated in cities (Xu 2003).

Based on their content of environmental predictors and as illustrated in Supplementary Material D, the 32 possible a-priori models were attributed to one of the four model sets URBAN VARIABLES (models consisting of the variables age, impervious area and management), HETEROGENEITY VARIABLES (models with composition, configuration), URBAN AND HETEROGENEITY VARIABLES (including combination of variables from both model sets) and NULL MODEL (equal to random distribution). Summarising single models in such model sets allows a comparison of their relative importance, i.e. urban variables versus heterogeneity variables. All statistical calculations were carried out with the program R v2.6.0 (R Development Core Team 2007) using library nlme (Pinheiro et al. 2008).

Results

Approximately 310,000 arthropod specimens were included in the analysis with an average of 284 (SD = 45) species found per location (range 169–361) with little variation between cities (Fig. 1). Little variation between cities was similarly found in

Fig. 1 Mean number and range (minimum/maximum) of total arthropod species and five functional groups in the three Swiss cities of Lugano, Lucerne and Zurich

the five functional groups (Fig. 1). The mean species number of the 96 locations was 158 zoophagous, 104 phytophagous, 47 pollinator, 82 low mobility and 85 high mobility species.

Predictions of environmental variables

Table 3 shows the details of the a-priori models for each of the six species numbers, which we considered as the most parsimonious model set (models with AIC_c weights >5%) and the corresponding fraction of explained variance R^2. Based on these selected models we predict total species number and the species number of the five functional groups (Fig. 2). Increasing age and increasing configuration exhibit a noticeable and positive effect on total species number (Fig. 2a). For the age gradient, the absolute number of total species richness is predicted to increase from 274 for a one year old urban area to 310 species for an area that is 150 years old, even though SD increases rapidly for locations >90 years (Fig. 2a). For configuration, species richness is predicted to increase from 273 species for an area with limited ecotones to 337 species for the most heterogeneous area with many ecotones, but high prediction uncertainty is shown by large SD for Edge Contrast Mean Index >38 (Fig. 2a). Composition also had a positive, but less pronounced, effect with species numbers rising from 273 for an area with only few habitat types (high SD for low Shannon Diversity values) to 290 species with several habitat types. Increasing the proportion of impervious area from 3 to 92% means a reduction from 296 to 273 species, whereas increasing management intensity from zero meadow cuts to 20 lawn cuts accounts for a marginal decrease from 289 to 282 species. The negative effect

of increasing management, however, levels off after approximately six cuts, and prediction insecurity increases. Poorly predicted species numbers, shown by an increasing SD, were mainly due to small sample numbers in this range of the gradient or, more rarely, to true high variability in species numbers. The selected models for total species richness explained, on average, 13.5% of the total variance. The selected models for zoophagous species numbers (Table 3) include the Null model, which reflects random distribution of the samples. Therefore it is not surprising that predictions for zoophagous species richness (Fig. 2b) had high standard deviations when showing positive (age of the green area) or negative correlations (impervious area). Zoophagous species numbers showed no correlation with management, configuration, and composition. Accordingly, the selected models for this functional group explained on average 3.9% of the total variance, which was the least amount of variance explained for any of the functional groups. Phytophagous species richness is predicted quite precisely (Fig. 2c). Increasing age and configuration have pronounced positive effects, while habitat composition seems to reach a plateau above a Shannon Diversity Index of ca. 1.1 (min. 0.34–max. 1.32). The selected models for phytophagous species richness explained on average 24.5% of the total variance, which was the greatest amount of variance explained for any of the functional groups. Pollinator species numbers (Fig. 2d) are also positively influenced by the two heterogeneity variables. No influence of the three urban variables, namely age, management intensity, and impervious area on pollinators was found. The similar response curves of pollinators and phytophagous species is partly explained by the fact that 88.4% of the

Table 3 Selected linear mixed-effects models for species numbers of total arthropod species and five functional groups (out of 32 models)

	Model no.	Age of green area	Impervious area	Management intensity	Configuration	Composition	k	Delta AIC$_c$	AIC$_c$ Weight (%)	R^2 (%)
Total species number	21	X			X	X	8	0.00	17.0	22.3
	17	X	X		X		7	0.16	15.7	18.5
	11		X		X		6	1.65	7.5	13.4
	7	X		X			6	1.99	6.3	13.1
	1	X					4	2.16	5.8	4.9
	3			X			5	2.31	5.3	8.8
Zoophagous	1	X					4	0.00	23.8	4.3
	0						3	0.04	23.3	0.0
	2		X				4	0.79	16.0	3.5
	6	X	X				5	0.90	15.2	7.6
Phytophagous	21	X			X	X	8	0.00	51.1	29.1
	15				X	X	7	2.02	18.6	24.3
	11		X		X		6	4.20	6.3	18.4
	28	X	X		X	X	9	4.25	6.1	29.3
	17	X	X		X		7	4.63	5.1	21.5
Pollinator	21	X			X	X	8	0.00	26.3	27.7
	15				X	X	7	0.45	21.0	24.0
	11		X		X		6	1.57	12.0	18.8
	5					X	5	3.11	5.6	14.7
	14			X		X	7	3.14	5.5	22.0
High mobility	21	X			X	X	8	0.00	52.1	28.6
	17	X	X		X		7	2.85	12.5	22.6
	15				X	X	7	3.17	10.7	22.8
	11		X		X		6	3.82	7.7	18.3
	28	X	X		X	X	9	4.39	5.8	28.6
Low mobility	10		X	X			6	0.00	18.7	17.4
	15				X	X	7	0.37	15.6	21.7
	14			X		X	7	0.87	12.1	21.0
	25			X	X	X	9	1.17	10.4	27.7
	3			X			5	1.94	7.1	11.4
	21	X			X	X	8	2.63	5.0	23.4

Environmental variables included in models are shown with X. Per explained species number, models are ranked according to AIC$_c$ weights. k is the number of parameters in the model. The minimum of three parameters for the Null model (no. 0 assuming random distribution of species numbers) comprises intercept, random factor city and unexplained variance

pollinators are also phytophagous species. The selected models for species richness of pollinators explained, on average, 21.4% of the total variance. Richness of highly mobile species (Fig. 2e) clearly augments with increasing age, configuration and composition, while it decreases with increasing impervious area. Management intensity does not have an effect. On average, the selected models for richness of

highly mobile species explained 24.2% of the total variance, which was the greatest amount of variance explained for any of the functional groups. Low mobility species (Fig. 2f) is the only functional group whose richness is negatively affected by management, however the predictions become unreliable above approximately ten cuts. While the richness of low mobility species increases with configuration and
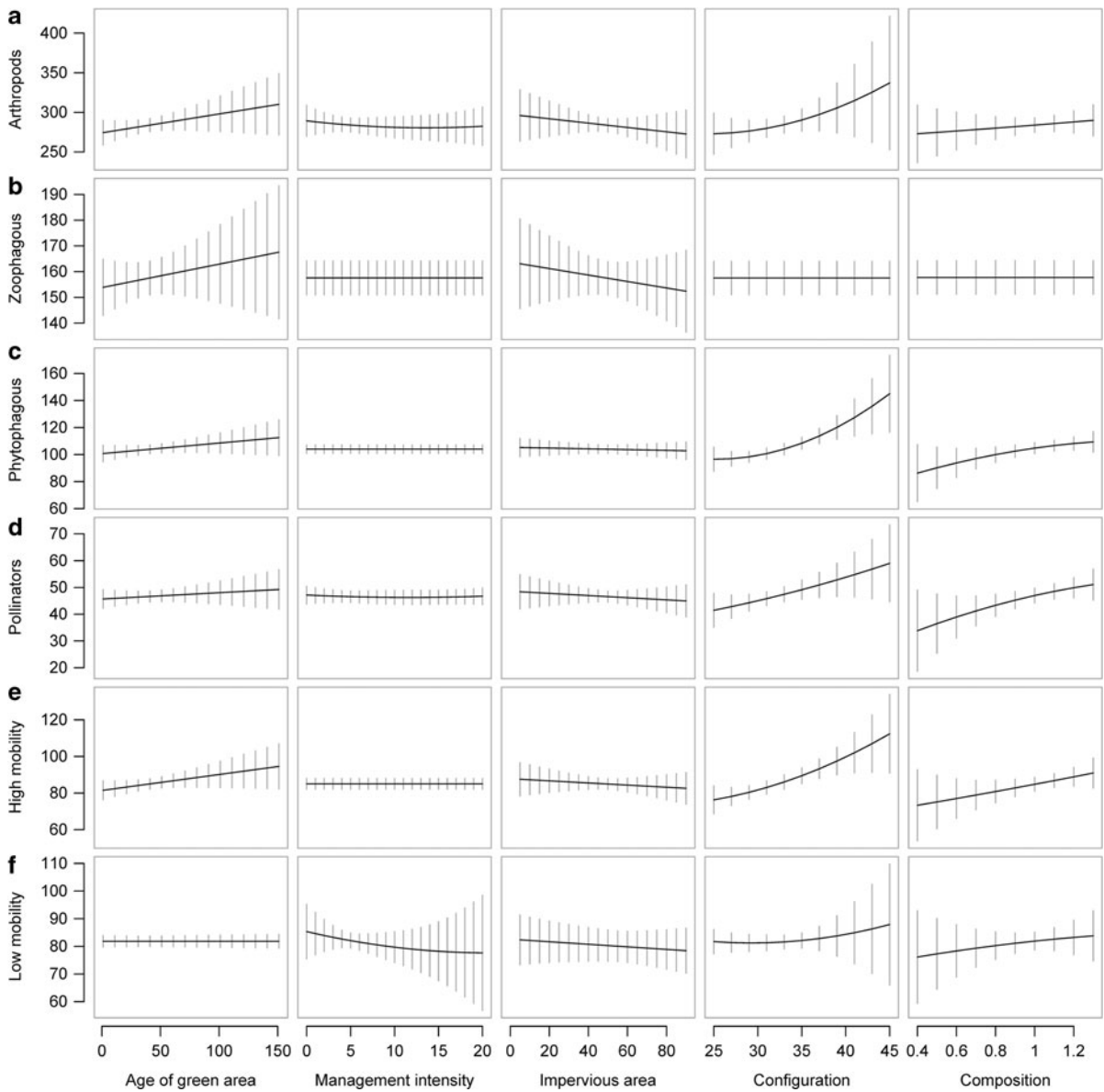
Fig. 2 Model averaged predictions (mean ± SD) for total species richness and the five functional groups across the five environmental gradients within their respective minimum and maximum. Predictions resulted by averaging selected models (Table 3) based on their AIC$_c$ weights (for more information

see methods). For methodological reasons (single taxonomic groups can count in several functional groups; Table 1), direct comparison of predictions is only allowed for total species number and within functional categories, which are trophic (**b**, **c**), pollinator (**d**) and mobility (**e**, **f**) guilds

composition, it slightly decreases with increasing impervious area and shows no correlation with age of green area. The selected models for richness of low mobility species explained on average 20.4% of the total variance.

Environmental variables according to model groups

On average, a-priori models of the model set URBAN AND HETEROGENEITY VARIABLES consist of

more variables than the remaining model sets. Models with more variables always explain more of the total variation by chance alone and thus reach higher goodness of fit values (Peres-Neto et al. 2006). In order to avoid this problem, the mean AIC_c weight, which is corrected for the number of parameters, is preferred to the mean R^2 to compare the different model sets. Table 4 summarises all 32 a-priori models in model sets to compare their AIC_c weights. Mean weight values per model set need to be compared with the mean of all models (=3.1%). The set URBAN VARIABLES (age, impervious area, management) is most important for total species numbers (mean model weight of 4.3%). An average model of the model set HETEROGENEITY VARIABLES (configuration, composition) attains a higher mean model weight for phytophagous (7.4%), pollinator (8.9%), and high mobility species numbers (4.2%) while the URBAN VARIABLES are now negligible. Low mobility species richness is also best explained with models from the set HETEROGENEITY VARIABLES (6.3%), but in this case models from the set URBAN VARIABLES are also of some importance (4.4%). For the species numbers of these four functional groups the models of the set HETEROGENEITY VARIABLES are thus more important than the remaining models and, as models are selected based on this weight value, they affect their respective predictions more. The large value for the Null model for zoophagous species numbers (23.3%) leads to the conclusion that none of the present model sets explains the variation in this group sufficiently.

Discussion

We investigated the effect size of five local environmental gradients (age, impervious area, management, configuration, composition) on total arthropod species numbers and on species numbers within functional categories representing trophic, pollinator, and mobility guilds. Total species richness of urban arthropods correlated mostly with two heterogeneity indices that characterise the urban mosaic, namely configuration (Mean Edge Contrast Index) and composition (Shannon Diversity Index). This generally positive correlation of species richness with increasing urban heterogeneity was also observed for the functional groups phytophagous, pollinator, low mobility, and high mobility species richness but not for zoophagous species numbers. Total species richness increased with the age of the urban settlement, while enlarged proportions of impervious area and intensified habitat management exerted negative effects. Functional groups usually showed contrasted, specific responses to these environmental variables. Overall, we found surprisingly little variation in richness of all species as well as for the functional species groups. Species numbers seem to be quite robust along the age of urban area, impervious area and management gradients. However, due to the lack of ecological information for many arthropods and the morphospecies approach (see methods for details), the attribution to functional groups based on expert knowledge still contains some generalisations. This implies that we should proceed with

Table 4 Mean AIC_c weight of all 32 a-priori models (Supplementary Material D) within the four model groups explaining the species numbers of the six functional groups

	Total species number	Zoophagous	Phytophagous	Pollinator	High mobility	Low mobility
Model group (numbers of models in group)	Mean weight	Mean weight	Mean weight	Mean weight	Mean weight	Mean weight
URBAN VARIABLES ($n = 7$)	4.3%	9.0%	0.1%	0.8%	0.3%	4.4%
HETEROGENEITY VARIABLES ($n = 3$)	2.2%	1.2%	7.4%	8.9%	4.2%	6.3%
URBAN AND HETEROGENEITY VARIABLES ($n = 21$)	2.8%	0.5%	3.6%	3.2%	4.1%	2.3%
NULL MODEL ($n = 1$)	4.2%	23.3%	0.2%	0.3%	0.3%	1.3%
Mean of all models ($n = 32$)	3.1%	3.1%	3.1%	3.1%	3.1%	3.1%

Mean AIC_c weight values per model set need to be compared with the mean of all models (=3.1%; all models add to 100%)

caution when interpreting and generalizing mechanisms.

The average arthropod species number sampled in our urban study locations is 284 (range 169–361). These values are within the figures obtained for non-urban environments where the same method was applied (Duelli and Obrist 2005; Obrist and Duelli, in press): an average forest sampling location yielded 232 species (69–473), while an average agricultural area resulted in 317 species (161–470). We conclude that urban areas host many arthropod species and cannot be regarded as species-poor environments. However, we also need to note that species number is in no means an appraisal of the conservation value of the species present. Urban fauna may include generalist and/or exotic species that are not considered to be of interest for conservation (Duelli and Obrist 2003).

Reasons for high species richness

The reasons for the high species numbers in urban areas, despite continuous habitat loss through increasing impervious area, are multifaceted. We suspect that historical, climatic and human-made structural causes, some embedded in our five variables, may play a role. Some species survive in small grassland patches that previously formed part of wider meadowland. The generally warmer climate in cities allows the survival and/or immigration of arthropod fauna from seminatural dry-meadows (Germann et al. 2008). In addition, and again due to the urban heat island effect (Bornstein 1968), Mediterranean species have invaded cities and exotic species are able to survive (or even thrive) in urban areas after accidental introduction by man (Ward and Harris 2005; Germann et al. 2008; Kouakou et al. 2008; Matteson et al. 2008). The urban mosaic is characterised by the many different habitat types, which are spatially close (Rebele 1994). Furthermore, abundant habitat boundaries create ecotones that offer additional resources and micro-habitat conditions (Murcia 1995). The spatial proximity, the habitat mix and the ecotones combine to deliver resources that meet the various needs of many species at different life cycle stages (egg and larval development, reproduction). Additionally, patch dynamics induced by human activity is high in urban areas, provoking a high dynamic in local extinctions and recolonisations, which in turn

enables the coexistence of many species (Holling 1973; Rebele 1994; Marzluff 2005).

The observation that different habitat types in the urban mosaic are spatially close leads to the speculation that arthropods, in their quest for good foraging and breeding conditions, often cross the boundaries of their characteristic native habitat, thus being more prone to explore new territories. In doing so, they are expected to regularly occur in suboptimal habitats. This process may explain why species numbers in 'good' and 'bad' study locations (i.e. old and heterogenous vs young and monotonous plots) did not differ as much as expected, assuming that isolation and fragmentation through impervious areas do not represent major barriers to movements (Angold et al. 2006). Actually, species occurring in cities must have been selected because of the ability to overcome obstacles. This hypothesis needs further investigations.

Urban variables

We suspect that the positive correlation between total species richness and age of the green area is based on the combined effects of species accumulation through stochastic local immigration over time and gradual species-specific occupation of ecological niches that appear with vegetation succession (Rebele 1994).

Increasing management had a minor negative influence on total species richness. We expected to observe a higher negative influence of increased management as found by previous studies (Morris and Lakhani 1979; Helden and Leather 2004; Hartley et al. 2007). This may be due to potential methodological biases. In our study, management intensity (i.e. the number of grass cuts) was measured within a radius of 5 m around the traps, whereas sampled grass and meadow plot sizes ranged from 20 m^2 to 10000 m^2. Small intensively managed plots are likely to be invaded from surrounding, less intensively managed areas and in this way a negative effect of intensive management might be masked. These views are supported by the results on heterogeneity (see below). Despite these limitations a negative effect of increasing management on low mobile species richness was found, which is a result that underlines the negative impact of local high-intensity management. Note that we did not find support for a peak in species richness at intermediate cutting frequencies, which was one of our main predictions.

Sealed and built areas are generally regarded as hostile environments that prevent high biodiversity, because they harbour reduced vegetation cover. Smith et al. (2006b) documented the expected negative effect of impervious area on total arthropod richness. Even more pronounced are the negative effects of urbanisation in broad-scale rural–urban gradients (McDonnell and Hahs 2008). At our finer scale (0.79 ha) and within cities, we also found a negative influence of impervious area on total species richness, but with a narrow average range between 296 and 273 species along a gradient from 3 to 92% impervious area. We conclude that a sealed radius of 50 m does not represent a major barrier for flying insects in general. Yet, for zoophagous species in particular, the negative effect of sealing was much stronger, thus corroborating findings of Denys and Schmidt (1998) who found a pronounced negative effect of urbanisation on parasitoid species. Finally, phytophagous species in our study experienced a less pronounced negative effect than that found by Denys and Schmidt (1998) in both polyphagous and monophagous species.

Heterogeneity variables

Our two indices for structural heterogeneity (Edge Contrast Mean Index for configuration and Shannon Index for composition) represent good metrics for the urban mosaic. We found that total urban arthropod species richness and most species richness measures for functional groups (all but zoophagous species numbers) are positively linked to both heterogeneity measures (composition and configuration). This result is similar to the findings of previous studies on arthropods inside (McIntyre et al. 2001; Zanette et al. 2005) and outside urban areas (Niemela et al. 1996; Duelli 1997; Jonsen and Fahrig 1997). Overall, the sheer diversity and quantity of ecotones in the urban area seem to be very important for urban arthropod diversity.

Grouping the statistical models into model sets (URBAN VARIABLES, HETEROGENEITY VARIABLES, URBAN AND HETEROGENEITY VARIABLES) and considering the mean AIC_c weight allows the identification of important variable sets. Among the functional groups, the heterogeneity variables (configuration, composition) were most important for phytophagous, pollinator, and high

mobility species numbers (Table 4), whereas both the urban variables (age, impervious area, management) and the heterogeneity variables were important for low mobility species numbers. However, none of these model sets seems to explain the variance in zoophagous species richness.

Conclusions

Urban areas offer unique opportunities (warmer climate, fine grained urban mosaic) that are readily exploited by a variety of arthropods. Local species richness does not appear to be vitally threatened by the extent of urbanisation within the three investigated Swiss cities. Total species numbers of urban areas (average 284 species) are comparable to values of other semi-natural areas (232 morphospecies in forest, 317 in farmland; Obrist and Duelli, in press). At least some urban habitat patches seem to support many species. Species richness, however, is one among several metrics of biodiversity, with others possibly being just as important (e.g. species composition, Sattler et al., in press; species of conservation concern, McKinney 2006). Species richness is a baseline measure for a relative comparison of the insurance value of a present community with respect to future disturbances of ecosystem functions. Urban arthropod species richness as a part of a diverse urban biodiversity must be protected for various reasons; we explicitly mention two: (1) high arthropod richness is expected to guarantee that ecosystem functions are 'better insured' against future disturbances; (2) high biodiversity offers a wealth of experience and a source of relaxation for city dwellers and is therefore beneficial to humans in general. In the face of current and future densification of urban areas, we propose actions to maintain or even improve arthropod species richness in urban areas. By estimating the effect sizes for different environmental gradients that can be affected by human activities, our study offers some guidelines for choosing actions to promote arthropod species richness in urban areas. Based on the pre-eminent role of both configuration and composition for total species richness and most functional groups, we recommend designing the remaining urban green as heterogeneous habitats. We thereby should never forget that urban areas are built for humans and thus

actions in favour of biodiversity will only persist if they consider the use and perceptions of their human inhabitants. Studies on human preferences of landscapes show that city inhabitants prefer heterogeneous landscapes (Home et al. 2009), indicating that arthropod and human requirements for good urban habitats may be largely aligned. These are important messages for city planners and managers willing to positively influence urban biodiversity.

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