

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

Received: 30 June 2009 / Accepted: 10 March 2010 / Published online: 4 April 2010
© Springer Science+Business Media B.V. 2010

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.

Electronic supplementary material The online version of this article (doi:[10.1007/s10980-010-9473-2](https://doi.org/10.1007/s10980-010-9473-2)) contains supplementary material, which is available to authorized users.

T. Sattler (✉) · M. Moretti
Ecosystem Boundaries, Swiss Federal Institute of Forest, Snow, and Landscape Research, Via Belsoggiorno 22, CH 6500 Bellinzona, Switzerland
e-mail: thomas.sattler@wsl.ch

T. Sattler · R. Arlettaz
Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, 3012 Bern, Switzerland

P. Duelli · M. K. Obrist
Biodiversity and Conservation Biology, Swiss Federal Institute of Forest, Snow, and Landscape Research, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

R. Arlettaz
Swiss Ornithological Institute, Valais Field Station, Nature Centre, 3970 Salgesch, Switzerland

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

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

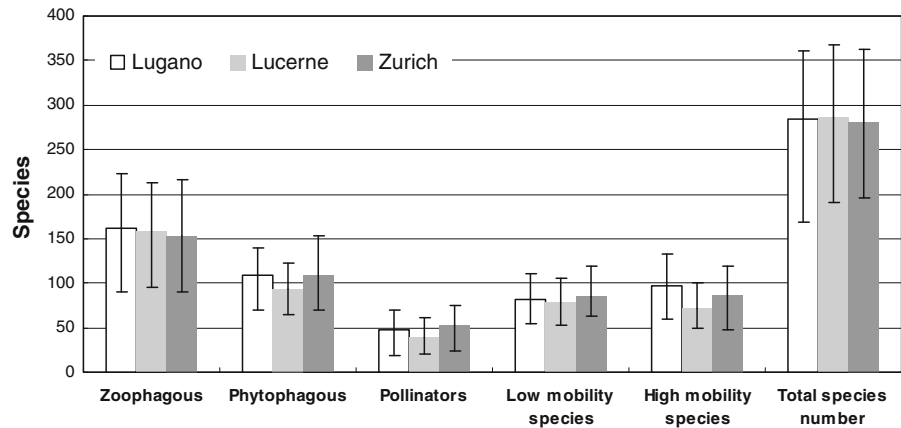
defined as the most parsimonious set of models. We predicted total species number and species numbers of the five functional groups for each of the five environmental variables based on the selected models. Species numbers were allowed to vary within the limits of the focal gradient, while the remaining 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

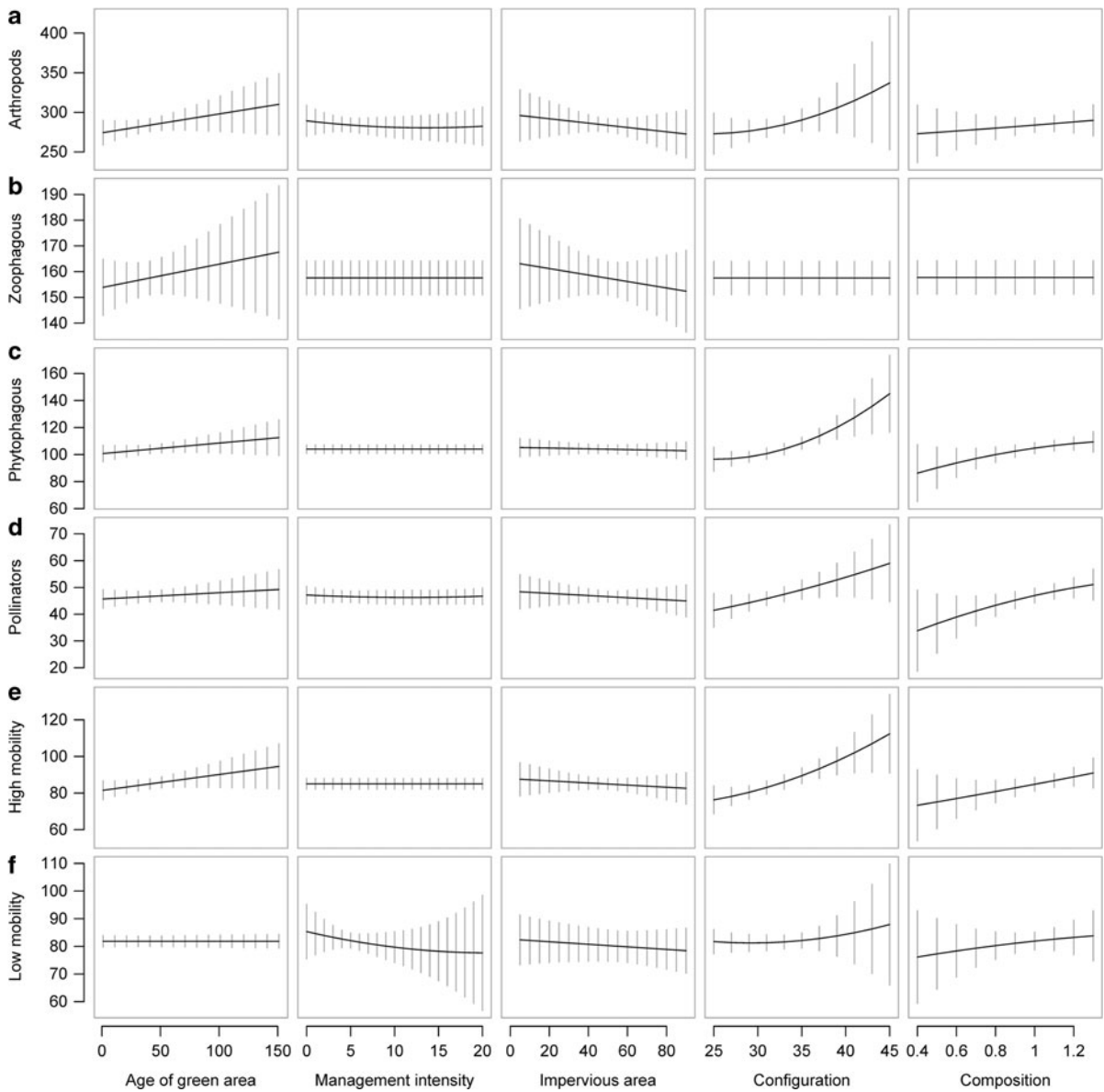


Fig. 2 Model averaged predictions (mean \pm SD) for total species richness and the five functional groups across the five environmental gradients within their respective minimum and maximum. Predictions resulted by averaging selected models (Table 3) based on their AIC_c weights (for more information

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 heterogeneous 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 m² to 10000 m². 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.

Acknowledgements We thank the house owners that provided access to their properties and the authorities of Lucerne, Lugano and Zurich for their support of the project. We are grateful to V. Albin, J. Ambrosini, J. Bolliger, F. Bontadina, T. Fabbro, B. Fecker, F. Fibbioli, S. Fontana, F. Gebreselassie, D. Häring, R. Home, W. Kastenholz, F. Kienast, M. Cooke Kindermann, S. Klopstein, L. Milani, A. Niederer, J. Pellet, M. Ryf, M. Schaub, A. Schulz, R. Siegwart, R. Tester and P. Wirz who helped in the field, in the lab, with statistical questions or the organization of the project. The following arthropod specialists supported us by determining the species: C. Canepari (Coccinellidae), Y. Chittaro (Carabidae), P. Duelli (Neuroptera), C. Germann (Curculionidae), X. Heer (Araneae), C. Pradella (Lucanidae, Buprestidae, Cerambycidae). F. Bontadina, R. Home and M. Schaub and two anonymous reviewers improved earlier versions of the manuscript. Special thanks go to M. Lehmann. This study forms part of the interdisciplinary project 'BiodiverCity' (www.biodivercity.ch) which aims at the identification, maintenance and enhancement of biodiversity and their acceptance in the urban development process. BiodiverCity was funded by the Swiss National Science Foundation as a project of NRP54 'Sustainable development of the built environment' (www.nrp54.ch).

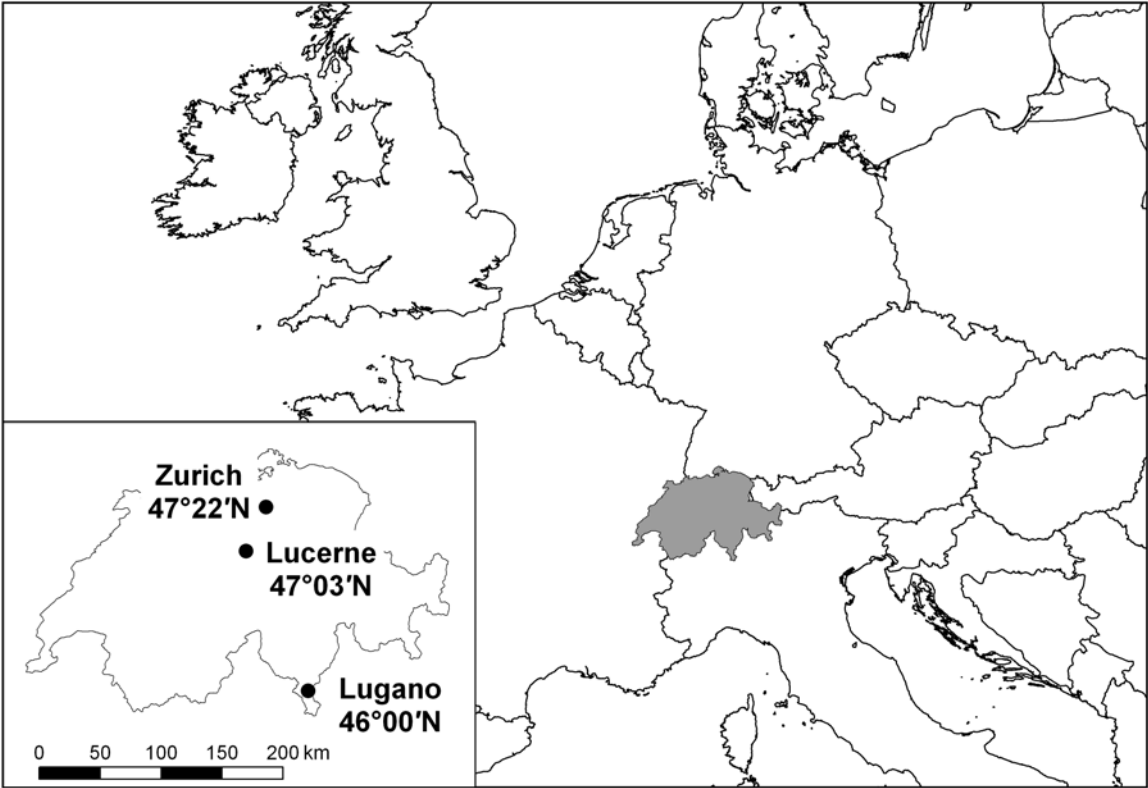
References

- Angold PG, Sadler JP, Hill MO, Pullin A, Rushton S, Austin K, Small E, Wood B, Wadsworth R, Sanderson R, Thompson K (2006) Biodiversity in urban habitat patches. *Sci Total Environ* 360:196–204
- Bächli G, Flückiger PF, Obrist MK, Duelli P (2006) On the microdistribution of species of Drosophilidae and some other Diptera across a forest edge. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 79:117–126
- Bornstein RD (1968) Observations of the urban heat island effect in New York City. *J Appl Meteorol* 7:575–582
- Bundesamt für Statistik (2005) Arealstatistik Schweiz: Zahlen—Fakten—Analysen, Neuchâtel, p 99
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310
- Crawley MJ (2007) *The R book*. John Wiley & Sons Ltd, Chichester
- Cushman SA, McGarriyal K, Neel MC (2008) Parsimony in landscape metrics: strength, universality, and consistency. *Ecol Indic* 8:691–703
- de Vries S, Verheij RA, Groenewegen PP, Spreeuwenberg P (2003) Natural environments—healthy environments? An exploratory analysis of the relationship between greenspace and health. *Environ Plan A* 35:1717–1731
- Dennis P, Young MR, Gordon IJ (1998) Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. *Ecol Entomol* 23:253–264
- Denys C, Schmidt H (1998) Insect communities on experimental mugwort (*Artemisia vulgaris* L.) plots along an urban gradient. *Oecologia* 113:269–277
- Duelli P (1997) Biodiversity evaluation in agricultural landscapes: an approach at two different scales. *Agric Ecosyst Environ* 62:81–91
- Duelli P, Obrist MK (2003) Biodiversity indicators: the choice of values and measures. *Agric Ecosyst Environ* 98:87–98
- Duelli P, Obrist MK (2005) Eine preiswerte Methode zur Abschätzung der lokalen Arthropodenfauna: "rapid biodiversity assessment" (RBA). *Schriftenreihe der Forschungsanstalt Reckenholz* 56:132–138
- Duelli P, Obrist MK, Schmatz DR (1999) Biodiversity evaluation in agricultural landscapes: above-ground insects. *Agric Ecosyst Environ* 74:33–64
- Duelli P, Obrist MK, Flückiger PF (2002) Forest edges are biodiversity hotspots—also for neuroptera. *Acta Zoologica Academiae Scientiarum Hungaricae* 48:75–87
- Dunn RR, Gavin MC, Sanchez MC, Solomon JN (2006) The pigeon paradox: dependence of global conservation on urban nature. *Conserv Biol* 20:1814–1816
- Folke C, Holling CS, Perrings C (1996) Biological diversity, ecosystems, and the human scale. *Ecol Appl* 6:1018–1024
- Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling CS (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annu Rev Ecol Evol Syst* 35:557–581
- Fuller RM, Smith GM, Sanderson JM, Hill RA, Thomson AG, Cox R, Brown NJ, Clarke RT, Rothery P, Gerard FF (2002) Countryside survey 2000 module 7. Land cover map 2000. Final report CSLCM. Centre for Ecology and Hydrology, Monks Wood, UK
- Fuller RA, Irvine KN, Devine-Wright P, Warren PH, Gaston KJ (2007) Psychological benefits of greenspace increase with biodiversity. *Biol Lett* 3:390–394
- Germann C, Sattler T, Obrist MK, Moretti M (2008) Xerothermophilous and grassland ubiquitous species dominate the weevil fauna of Swiss cities (Coleoptera, Curculionoidea). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 81:141–154
- Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu JG, Bai XM, Briggs JM (2008) Global change and the ecology of cities. *Science* 319:756–760
- Hartley DJ, Koivula MJ, Spence JR, Pelletier R, Ball GE (2007) Effects of urbanization on ground beetle assemblages (Coleoptera, Carabidae) of grassland habitats in western Canada. *Ecography* 30:673–684
- Helden AJ, Leather SR (2004) Biodiversity on urban roundabouts—Hemiptera, management and the species-area relationship. *Basic Appl Ecol* 5:367–377

- Holling CS (1973) Resilience and stability of ecological systems. *Annu Rev Ecol Syst* 4:1–23
- Home R, Keller C, Nagel P, Bauer N, Hunziker M (2009) Selection criteria for species as representatives of conservation organizations. *Environ Conserv* 36:139–148
- Hunter L, Rinner L (2004) The association between environmental perspective and knowledge and concern with species diversity. *Soc Nat Resour* 17:517–532
- Johnson JB, Omland KS (2004) Model selection in ecology and evolution. *Trends Ecol Evol* 19:101–108
- Jonsen ID, Fahrig L (1997) Response of generalist and specialist insect herbivores to landscape spatial structure. *Landscape Ecol* 12:185–197
- Kouakou D, Sattler T, Obrist MK, Duelli P, Moretti M (2008) Recent Swiss records of rare bee species (Hymenoptera, Apidae) with two species new to Switzerland. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 81:191–198
- Legendre P, Legendre L (1998) *Numerical ecology*. Elsevier Science PV, Amsterdam
- Marzluff JM (2005) Island biogeography for an urbanizing world: how extinction and colonization may determine biological diversity in human-dominated landscapes. *Urban Ecosyst* 8:157–177
- Matteson KC, Ascher JS, Langellotto GA (2008) Bee richness and abundance in New York city urban gardens. *Ann Entomol Soc Am* 101:140–150
- McDonnell MJ, Hahs AK (2008) The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions. *Landscape Ecol* 23:1143–1155
- McGarigal K, Marks BJ (1995) FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. General technical report PNW-GTR-351. USDA Forest Service, Pacific North West Research Station 351, Portland, OR, p 141
- McGarigal K, Cushman SA, Neel MC, Ene E (2002) FRAGSTATS: spatial pattern analysis program for categorical maps. University of Massachusetts, Amherst
- McIntyre NE (2000) Ecology of urban arthropods: a review and a call to action. *Ann Entomol Soc Am* 93:825–835
- McIntyre NE, Rango J, Fagan WF, Faeth SH (2001) Ground arthropod community structure in a heterogeneous urban environment. *Landscape Urban Plan* 52:257–274
- McKinney ML (2006) Urbanization as a major cause of biotic homogenization. *Biol Conserv* 127:247–260
- Miller JR (2005) Biodiversity conservation and the extinction of experience. *Trends Ecol Evol* 20:430–434
- Morris MG, Lakhani KH (1979) Responses of grassland invertebrates to management by cutting: 1. species-diversity of Hemiptera. *J Appl Ecol* 16:77–98
- Murcia C (1995) Edge effects in fragmented forests: implications for conservation. *Trends Ecol Evol* 10:58–62
- Naeem S, Li SB (1997) Biodiversity enhances ecosystem reliability. *Nature* 390:507–509
- Naeem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM (1994) Declining biodiversity can alter the performance of ecosystems. *Nature* 368:734–737
- Niemela J (1999) Is there a need for a theory of urban ecology? *Urban Ecosyst* 3:57–65
- Niemela J, Haila Y, Punttila P (1996) The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. *Ecography* 19:352–368
- Obrist MK, Duelli P (in press) Rapid biodiversity assessment of arthropods for monitoring average local species richness and related ecosystem services. *Biodivers Conserv*. doi:10.1007/s10531-010-9832-y
- Oliver I, Beattie AJ (1993) A possible method for the rapid assessment of biodiversity. *Conserv Biol* 7:562–568
- Peres-Neto PR, Legendre P, Dray S, Borcard D (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87:2614–2625
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core team (2008) nlme: linear and nonlinear mixed effects models
- R Development Core Team (2007) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rebele F (1994) Urban ecology and special features of urban ecosystems. *Glob Ecol Biogeogr Lett* 4:173–187
- Sattler T, Borcard D, Arlettaz R, Bontadina F, Legendre P, Obrist M, Moretti M (in press) Spider, bee and bird communities in cities are shaped by environmental control and high stochasticity. *Ecology*. doi:10.1890/09-1810
- Shaffer ML (1981) Minimum population sizes for species conservation. *Bioscience* 31:131–134
- Smith RM, Gaston KJ, Warren PH, Thompson K (2006a) Urban domestic gardens (VIII): environmental correlates of invertebrate abundance. *Biodivers Conserv* 15:2515–2545
- Smith RM, Warren PH, Thompson K, Gaston KJ (2006b) Urban domestic gardens (VI): environmental correlates of invertebrate species richness. *Biodivers Conserv* 15:2415–2438
- United Nations (2008) World urbanization prospects: the 2007 revision. United Nations, New York
- Ward DF, Harris RJ (2005) Invasibility of native habitats by argentine ants, *Linepithema humile*, in New Zealand. *N Z J Ecol* 29:215–219
- Wermelinger B, Flückiger PF, Obrist MK, Duelli P (2007) Horizontal and vertical distribution of saproxylic beetles (Col., Buprestidae, Cerambycidae, Scolytinae) across sections of forest edges. *J Appl Entomol* 131:104–114
- Whittaker RJJWK, Field R (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *J Biogeogr* 28:453–470
- Wu JG (2004) Effects of changing scale on landscape pattern analysis: scaling relations. *Landscape Ecol* 19:125–138
- Xu RH (2003) Measuring explained variation in linear mixed effects models. *Stat Med* 22:3527–3541
- Zanette LRS, Martins RP, Ribeiro SP (2005) Effects of urbanization on Neotropical wasp and bee assemblages in a Brazilian metropolis. *Landscape Urban Plan* 71:105–121

Supplementary material A:

Figure: Location of the three study sites, the cities of Zurich, Lucerne and Lugano in Switzerland.



Supplementary material B:

Information on method Rapid Biodiversity Assessment (RBA)

In previous publications the method Rapid Biodiversity Assessment (RBA), as applied in Switzerland, is explained in great detail (Duelli and Obrist 2005; Obrist and Duelli in press). Here we summarise the most important information. RBA samples arthropods during seven weeks in the period of highest arthropod abundance and subsequently selects the four weeks with largest volume for the count of morphospecies.

Every study location is established with two trap types. Surface dwelling arthropods were sampled using pitfall traps, whereas flying invertebrates were sampled using so called combination traps (Duelli et al. 1999). Pitfall traps consisted of three plastic cups recessed into the soil (opening diameter 75 mm; arranged in an isosceles triangle with a distance of one meter). Transparent roofs installed approximately 10 cm above the cups provided protection from the rain. This contrasts the original method, where only one funnel trap (150 mm diameter x 400mm depth) had been used, the cause being restrictions by property owners. But as shown by Obrist and Duelli (1996) these two methods are near equal with respect to their trapping efficiency. The interception traps combine a non-directional window trap and a yellow water pan (diameter of 0.44 m) placed at a height of 1.5 m above ground. At each of the 96 locations, three cup traps and one combination trap were installed on a meadow or lawn plot (homogeneous within at least a radius of 5 m). Both, pitfall and combination traps, were filled with 0.2% Metatin (bactericide) solution. For both trap types, the probability of s species being caught is a function of their abundance and their activity (Duelli et al. 1999).

Duelli et al. (1999) identified the optimal time period for assessing terrestrial arthropod species richness, which still allows a reliable assessment of species numbers despite of reduced effort. The selection of seven sampling weeks with the highest species richness from mid-June to beginning of August corresponds to the warmest period in the Swiss summer. Thus, traps of the present study were opened between June 13th and 15th (depending

on cities) and then emptied weekly during seven weeks until closure between August 1st and 3rd 2006. Insects were stored per location and trap type in vials containing 70 % alcohol. After the seven sampling weeks and to prevent stochastic influences like bad weather, loss or damage of traps, which accidentally reduced the arthropod volume of the weekly samplings, four weekly samples per trap type were selected: In the beginning, the first vial (mid-June) and the last vial (early August) of both trap types were selected to cover as much as possible the seasonal spectrum of the changing species composition. If, however, the volume (measured with a measuring jug in ml, without alcohol) was less than two thirds of the second or the second-last weeks, respectively, the latter were chosen instead. Of the remaining five weekly samples, the two with the highest volume were chosen, independently for the two trap types. Higher volume corresponds to more species (Smith et al. 2006), although there might be exceptions to that in cases of species outbreaks or swarming events. Only the material from the selected four weeks was processed further. This selection procedure guarantees a high correlation of the samples with the species richness of the whole year ($R^2 = 0.92$; Obrist and Duelli in press). These four weekly catches per trap location were sorted in 29 taxonomic groups (Table 1). This was a further refinement of the original RBA method (Duelli and Obrist in press) which attributed arthropods into 14 taxonomic groups. The refinement allowed improved expert classification of arthropod groups according to five functional groups in three categories: trophic levels (zoophagous (including parasites), phytophagous species), pollinator function and mobility (low means < 200m per lifetime, high means > 200m; Table 1). If a taxonomic group was ecologically heterogeneous with respect to the five functional groups, the group was not attributed (i.e. remaining Coleoptera, remaining Arthropoda). Morphospecies were counted in each of these 29 taxonomic groups. Two specimens were assigned to different morphospecies, if an entomologically trained but non-specialist processor could distinguish external morphological differences. With such a definition, many species with sexual dimorphism or juvenile stages could split into multiple morphospecies, whereas cryptic species were lumped into one morphospecies. Despite these constraints, species numbers obtained in this way showed for most taxa high corre-

lation with 'true' species numbers (Obrist and Duelli in press). Seven arthropod groups were identified to named species (Table 1). We used these 'true' species numbers for statistical analysis. The sorting of Diptera, Collembola, Acari and juvenile spiders to morphospecies resulted in unreliable counts and exaggerated costs (Duelli and Obrist 2005; unpublished data), while accounting for an average volume of only 5.1 % (1.5% - 10.6%) of a study locations catch. Therefore these groups were omitted from this study. Due to their high correlation of 'morphospecies' and 'species', and to simplify the text, we use 'species' as a unified expression.

Supplementary material C:

Table: Specifications of the city and the five variables (Management intensity, Age of green area, Impervious area, Configuration, Composition) investigated for each of the 96 study locations.

Study locations	City	Management intensity ^a	Age of green area ^b	Impervious area ^c	Configuration ^d	Composition ^e
101	Zurich	3	6	78.46	42.57	0.64
102	Zurich	8	2	77.6	29.61	0.58
103	Zurich	1	3	60.23	27.34	1.02
104	Zurich	3	1	67.48	30.55	0.87
105	Zurich	11	49	58.9	28.51	0.81
106	Zurich	2	20	2.49	31.17	0.95
107	Zurich	9	44	22.85	23.75	0.95
108	Zurich	11	55	47.71	30.32	1
109	Zurich	5	54	48.1	29.61	0.9
110	Zurich	12	36	23.57	28.9	0.83
111	Zurich	9	36	44.33	32.06	1.07
112	Zurich	6	3	41.65	25.24	1.04
113	Zurich	6	12	53.53	28.85	0.93
114	Zurich	2	16	36.31	37.21	1.19
115	Zurich	7	22	59.71	30.33	0.89
116	Zurich	1	11	33.55	39.93	1.17
117	Zurich	13	140	9.87	25.81	1.19
118	Zurich	6	129	64.58	29.66	0.7
119	Zurich	3	66	79.15	31.18	0.57
120	Zurich	3	107	75.34	35.74	0.69
121	Zurich	2	156	43.78	36.67	1.14
122	Zurich	11	11	47.92	30.39	1.16
123	Zurich	1	58	50.49	32.59	1.17
124	Zurich	1	24	53.21	33.78	1.14
125	Zurich	13	4	39.88	32.11	1.24
126	Zurich	2	34	52.84	32.93	1.07
127	Zurich	6	66	91.82	35.56	0.34
128	Zurich	8	63	66.09	36.15	0.87
129	Zurich	3	54	26.9	31.34	1.29
130	Zurich	4	34	46.51	36.19	1.24
131	Zurich	1	6	49.16	29.91	1.2
132	Zurich	2	5	51.88	39.35	0.99
201	Lucerne	12	34	42.03	26.15	1.05
202	Lucerne	8	10	58.88	30.67	0.86
203	Lucerne	3	3	62.23	37.44	0.93
204	Lucerne	7	46	55.33	27.77	0.96
205	Lucerne	9	86	7.72	25.18	1.19
206	Lucerne	9	49	42.13	30.91	1.25
207	Lucerne	10	12	39.22	25.2	1.16
208	Lucerne	2	21	15.03	33.46	0.95
209	Lucerne	6	4	70.16	31.24	0.85
210	Lucerne	6	71	78.45	28.78	0.57
211	Lucerne	0	66	86.26	34.84	0.5
212	Lucerne	2	31	25.53	27.77	1.31
213	Lucerne	6	34	52.98	25.28	0.93

214	Lucerne	2	41	85.58	35.48	0.51
215	Lucerne	2	106	51.72	31.08	1.06
216	Lucerne	12	11	49.46	30.22	1.23
217	Lucerne	13	6	55.65	29.2	1.01
218	Lucerne	2	75	48.95	30.47	1.2
219	Lucerne	16	10	65.72	27.53	0.77
220	Lucerne	2	10	54.15	32.57	1.13
221	Lucerne	6	53	80.71	35.1	0.67
222	Lucerne	3	46	43.46	29.37	1.28
223	Lucerne	4	156	32.09	29.04	1.31
224	Lucerne	9	2	35.09	27.57	1.16
225	Lucerne	9	3	38.18	30.41	1.26
226	Lucerne	2	1	38.87	39.08	1.24
227	Lucerne	16	106	6.51	24.33	0.86
228	Lucerne	2	7	40.31	32.29	1.23
229	Lucerne	2	9	41.03	34.79	1.18
230	Lucerne	7	58	50.91	30.77	1.09
231	Lucerne	2	18	46.1	37.21	1.26
232	Lucerne	3	3	45.95	33.35	1.17
301	Lugano	6	31	73.64	32.9	0.71
302	Lugano	11	36	69.7	32.84	0.74
303	Lugano	12	20	56.42	28.4	0.9
304	Lugano	20	13	47.55	30.33	1.2
305	Lugano	12	14	61.13	33.67	0.94
306	Lugano	12	1	47.9	30.13	1.09
307	Lugano	9	30	42.68	25.21	0.85
308	Lugano	12	16	31.73	28.2	1.14
309	Lugano	5	36	80.45	30.13	0.6
310	Lugano	2	71	64.24	29.74	0.93
311	Lugano	3	34	48.59	37.18	1.14
312	Lugano	2	46	85.24	47.54	0.47
313	Lugano	3	35	40.13	33.64	1.31
314	Lugano	1	16	35.67	34.06	1.21
315	Lugano	4	106	37.79	32.92	1.3
316	Lugano	2	16	33.93	31.46	1.25
317	Lugano	10	11	59.96	36.03	1.1
318	Lugano	8	96	67.94	33.83	0.79
319	Lugano	16	53	48.37	36.85	1.12
320	Lugano	6	85	61.25	37.63	1.06
321	Lugano	10	106	48.21	27.32	0.92
322	Lugano	8	46	18.92	29.74	0.97
323	Lugano	10	26	24.29	27.54	0.81
324	Lugano	12	26	10.6	27.63	1
325	Lugano	5	26	39.91	29.9	1.24
326	Lugano	2	71	73.78	37.86	0.84
327	Lugano	1	80	66.56	38.29	0.95
328	Lugano	1	46	50.33	35.97	1.23
329	Lugano	3	86	33.86	29.9	1.24
330	Lugano	4	54	47.72	29.75	1.25
331	Lugano	4	71	11.57	32.16	1.02
332	Lugano	2	50	39.59	30.43	1.32

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

Shannon-Index

Supplementary material D:

Table: Overview on all 32 linear mixed-effects models formulated a-priori which were evaluated for all six explained variables (total, zoophagous, phytophagous, pollinator, high mobility, low mobility species richness). Model set indicates whether the respective models consist of urban variables or of heterogeneity variables only or of combination of both variable types. Selected models are shown in Table 3. Abbreviations: age = Age of green area; impervious = Impervious area; cut+cut² (linear and quadratic function) = Management; ECON+ECON² = Configuration (Edge Contrast Mean Index (heterogeneity)); SHDI+SHDI² = Composition (Shannon diversity Index (heterogeneity)). See methods for definition of explaining variables. Variables are aggregated within random factor 'city' (explicit formulation not shown).

Model set	Model - No.	Candidate Models
Urban variables	1	age
	2	impervious
	3	cut+cut2
	6	age+impervious
	7	age+cut+cut2
	10	impervious+cut+cut2
	16	age+impervious+cut+cut2
Heterogeneity variables	4	ECON+ECON2
	5	SHDI+SHDI2
	15	ECON+ECON2+SHDI+SHDI2
Urban and heterogeneity variables	8	age+ECON+ECON2
	9	age+SHDI+SHDI2
	11	impervious+ECON+ECON2
	12	impervious+SHDI+SHDI2
	13	cut+cut2+ECON+ECON2
	14	cut+cut2+SHDI+SHDI2
	17	age+impervious+ECON+ECON2
	18	age+impervious+SHDI+SHDI2
	19	age+cut+cut2+ECON+ECON2
	20	age+cut+cut2+SHDI+SHDI2
	21	age+ECON+ECON2+SHDI+SHDI2
	22	impervious+cut+cut2+ECON+ECON2
	23	impervious+cut+cut2+SHDI+SHDI2
	24	impervious+ECON+ECON2+SHDI+SHDI2
	25	cut+cut2+ECON+ECON2+SHDI+SHDI2
26	age+impervious+cut+cut2+ECON+ECON2	
27	age+impervious+cut+cut2+SHDI+SHDI2	
28	age+impervious+ECON+ECON2+SHDI+SHDI2	
29	age+cut+cut2+ECON+ECON2+SHDI+SHDI2	
30	impervious+cut+cut2+ECON+ECON2+SHDI+SHDI2	
31	age+impervious+cut+cut2+ECON+ECON2+SHDI+SHDI2	
Null model	0	

References cited in Supplementary Material

Duelli P. and Obrist M.K. (2005) Eine preiswerte Methode zur Abschätzung der lokalen Arthropodenfauna: "Rapid biodiversity assessment" (RBA). Schriftenreihe der Forschungsanstalt Reckenholz 56: 132-138.

Duelli P., Obrist M.K. and Schmatz D.R. (1999) Biodiversity evaluation in agricultural landscapes: above-ground insects. *Agriculture Ecosystems & Environment* 74: 33-64.

Obrist M.K. and Duelli P. (1996) Trapping efficiency of funnel- and cup-traps for epigeal arthropods. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 69: 367-369.

Obrist M.K. and Duelli P. (in press) Rapid Biodiversity Assessment (RBA) of arthropods for monitoring average local species richness and related ecosystem services. *Biodiversity and Conservation*. doi: 10.1007/s10531-010-9832-y

Smith R.M., Gaston K.J., Warren P.H. and Thompson K. (2006) Urban domestic gardens (VIII): environmental correlates of invertebrate abundance. *Biodiversity and Conservation* 15: 2515-2545.