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Selection of Multiple Umbrella Species for Functional and Taxonomic Diversity to Represent Urban Biodiversity

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Abstract: *Surrogates, such as umbrella species, are commonly used to reduce the complexity of quantifying biodiversity for conservation purposes. The presence of umbrella species is often indicative of high taxonomic diversity; however, functional diversity is now recognized as an important metric for biodiversity and thus should be considered when choosing umbrella species. We identified umbrella species associated with high taxonomic and functional biodiversity in urban areas in Switzerland. We analyzed 39,752 individuals of 574 animal species from 96 study plots and 1397 presences of 262 plant species from 58 plots. Thirty-one biodiversity measures of 7 taxonomic groups (plants, spiders, bees, ground beetles, lady bugs, weevils and birds) were included in within- and across-taxa analyses. Sixteen measures were taxonomical (species richness and species diversity), whereas 15 were functional (species traits including mobility, resource use, and reproduction). We used indicator value analysis to identify umbrella species associated with single or multiple biodiversity measures. Many umbrella species were indicators of high biodiversity within their own taxonomic group (from 33.3% in weevils to 93.8% in birds), to a lesser extent they were indicators across taxa. Principal component analysis revealed that umbrella species for multiple measures of biodiversity represented different aspects of biodiversity, especially with respect to measures of taxonomic and functional diversity. Thus, even umbrella species for multiple measures of biodiversity were complementary in the biodiversity aspects they represented. Thus, the choice of umbrella species based solely on taxonomic diversity is questionable and may not represent biodiversity comprehensively. Our results suggest that, depending on conservation priorities, managers should choose multiple and complementary umbrella species to assess the state of biodiversity.*

Keywords: city, Complementarity of biodiversity, indicator value analysis, surrogate species, Switzerland

Selección de Múltiples Especies Paraguas para la Diversidad Funcional y Taxonómica para Representar la Biodiversidad Urbana

Resumen: *Los sustitutos como las especies paraguas comúnmente se usan para reducir la complejidad de la cuantificación de la biodiversidad por motivos de conservación. La presencia de una especie paraguas casi siempre es indicativa de una diversidad taxonómica alta; sin embargo, la diversidad funcional ahora se reconoce como una medida importante de la biodiversidad y por lo tanto debe considerarse al elegir especies paraguas. Identificamos especies paraguas asociadas con la biodiversidad taxonómica alta y funcional en áreas urbanas en Suiza. Analizamos 39, 752 individuos de 574 especies de animales de 96 parcelas de estudio y 1, 397 registros de 262 especies de plantas de 58 parcelas. Treinta y un medidas de biodiversidad de siete grupos taxonómicos (plantas, arañas, abejas, carábidos, catarinas, gorgojos y aves) se incluyeron en los análisis dentro de- y a lo largo de- taxones. Dieciséis medidas fueron taxonómicas (riqueza de especies y diversidad de especies), mientras que 15 fueron funcionales (características de especies incluyendo la movilidad,*

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uso de recursos y reproducción). Usamos el análisis del valor indicador para identificar especies paraguas asociadas con una o múltiples medidas de biodiversidad. Muchas especies paraguas fueron indicadoras de alta biodiversidad dentro de su grupo taxonómico (desde 33.3% en gorgojos hasta 93.8% en aves) y en menor medida fueron indicadoras a lo largo de taxones. El análisis de componentes principales reveló que las especies paraguas para medidas múltiples de la biodiversidad representaron diferentes aspectos de la biodiversidad, especialmente con respecto a las medidas de la diversidad taxonómica y funcional. Así, incluso las especies paraguas para medidas múltiples de la biodiversidad fueron complementarias en los aspectos de biodiversidad que representaron. Entonces, la elección de una especie paraguas basada únicamente en la diversidad taxonómica es cuestionable y puede no representar a la biodiversidad integralmente. Nuestros resultados sugieren que, dependiendo de las prioridades de conservación, los administradores deben elegir especies paraguas múltiples y complementarias para estudiar el estado de la biodiversidad.

Palabras Clave: Análisis del valor indicador, ciudad, complementación de la biodiversidad, especies sustitutas, Suiza

Introduction

Because biodiversity is complex (Gaston & Spicer 2004), multiple measures are required to approach quantitative studies of biodiversity comprehensively (Duelli & Obrist 2003; Fleishman et al. 2006). The motivations for conserving urban biodiversity are also manifold and include preservation of habitat specialists (usually rare species in secondary habitats), provision of ecosystem services (shade from trees) (Dearborn & Kark 2010), and human well-being (Luck et al. 2011). Species' functional traits are the characteristics of an organism that have demonstrable links to its ecological function, such as growth form, trophic level, and mobility (Violle et al. 2007). Recent studies show that functional diversity (FD), expressed as the magnitude of functional differences among the species in the community (Ricotta & Moretti 2011), is a better predictor of ecosystem functioning and connected services than is species diversity (Dìaz et al. 2007; Cadotte et al. 2011). Biodiversity studies based on functional traits allow the identification of general patterns across regions and ecosystems that are independent of species identities. Furthermore, the occurrence of species is influenced by factors that are often not related to the process being studied (here urbanization), such as biogeography, population dynamics, and sampling effort, whereas FD is less sensitive to these factors (Cadotte et al. 2011). Species with comparable life-history traits can respond similarly to environmental pressures, such as (human) disturbance regimes (e.g., Moretti et al. 2009; Öckinger et al. 2010; Vandewalle et al. 2010). Thus, assessment of FD may be a useful tool for monitoring and managing biodiversity in general (Cadotte et al. 2011) and urban biodiversity in particular (Lizée et al. 2011).

The urban population today is larger than the entire world population in 1900, and urbanization is predicted to continually increase during the next 100 years (United Nations 2009). Urban areas are recognized as novel ecosystems (Hobbs et al. 2006) with urban-specific processes that influence local species composition (Faeth et al. 2005; Sattler et al. 2010*a*) or pools of species within a landscape (Hobbs et al. 2006; Sattler et al. 2011). Thus, urban areas should be managed so as to maximize conservation of its biodiversity.

The importance of urban biodiversity is recognized by planners and managers, and many local authorities protect their biodiversity for direct and indirect benefits to residents. The Convention on Biological Diversity developed the City Biodiversity Index in the frame of an action plan (Secretariat of the Convention on Biological Diversity 2012). Plants, birds, and butterflies were selected as core indicators. The selection of these taxa as indicators reflects convenience because data on them are available. However, these data are often used to generalize the requisites for all biodiversity. Taxa recognized as indicators become important in policy making and guide implementation efforts. When indicators are selected on the basis of convenience rather than scientific study, it is unclear whether they are indeed representative of other biodiversity components. We believe indicator taxa and species needs to be adequately and rigorously tested, especially when they are applied across taxa.

Monitoring programs or efforts to prioritize areas for conservation are typically restricted by a lack of time, financial support, or adequate methods. To counter incomplete biodiversity surveys, surrogate species indicative of states of populations, species, communities or ecosystems are a common shortcut (Landres et al. 1988; Andelman & Fagan 2000; Fleishman et al. 2005). Caro (2010) clarified the different meanings and uses of surrogate species including indicator, umbrella, and keystone species. He also introduced the concept of local umbrella species to complement the classic umbrella species concept (Wilcox 1984). The latter focuses on space-demanding species that, when protected, guarantee the survival of other sympatric species as opposed to local umbrella species that co-inhabit a spatially limited area with high biodiversity (Caro 2010). Empirical studies show umbrella species are both successful (e.g., Fleishman et al. 2000; Suter et al. 2002; Roth & Weber 2008) and unsuccessful (Launer & Murphy 1994; Ozaki et al. 2006) surrogates of, for example, species richness of a co-occurring taxonomic group. The utility of umbrella species as surrogates often depends on the spatial scale of the study area; broad geographic analysis hinders their general applicability (Andelman & Fagan 2000). The mosaic structure of cities (different habitat types within close spatial distances, Sattler et al. 2010*b*) suggests that the umbrella species concept should be applied on a local scale in the urban environment.

For urban biodiversity in Switzerland, we sought to identify umbrella species for both taxonomic diversity and FD in within- and across-taxa analyses of 7 taxonomic groups; to determine which species, from among identified umbrella species, are complementary and associated with multiple measures of urban biodiversity; and to characterize the general geographic distribution of umbrella species.

Methods

Study Area

We studied urban areas in the Central Swiss Plateau and lowland areas of southern Switzerland. The Swiss Plateau is about 30% of the surface of Switzerland (approximately12,500 km^2) and is characterized by intensive agriculture, managed forests, and densely populated urban areas (380 people/km^2). On the plateau, 15% of the area is urban (Swiss Federal Statistical Office 2005). Southern Switzerland is dominated by forested mountains interspersed by lowland areas that are as heavily populated as those on the plateau.

Species Data and Trait Information

We studied 7 taxonomic groups (hereafter taxa): vascular plants (Plantae), spiders (Aranae), bees (Apiformes), ground beetles (Carabidae), lady bugs (Coccinelidae), weevils (Curculionidae), and birds (Aves). These taxa occupy different trophic levels and spatial extents and are widely assessed in biodiversity surveys. Urban areas are often closely interlinked with other ecosystems so care needs to be taken to identify local umbrella species that reflect urban biodiversity and not that of neighboring ecosystems. Therefore taxa were sampled in circular plots of various sizes appropriate to assess taxa-specific local species assemblages. We obtained vascular plant data from circular plots of 1.78-m radius and bird data from 50-m radius plots. Arthropod data were collected with interception traps. The area of sampled plots depended on the mobility of the taxa (Niemela et al. 1996; Zurbuchen et al. 2010) (Supporting Information). Plots of approximately 1.78-m radius were sampled for low-mobility surface-dwelling arthropods. Plots of approximately 500-m radius were sampled for large flying insects. Study plots included private gardens, semipublic spaces between apartment buildings, public parks, and courtyards of industrial buildings.

Urban plant data originated from the Species Diversity in Habitats program, which is part of the Biodiversity Monitoring of Switzerland (BDM) scheme (Weber et al. 2004). We selected all 58 study plots in the BDM database located in urban environments. Data were collected from 2005–2009. All plots were surveyed once and contained a total of 1397 presences of 262 plant species.

Data for arthropods and birds were collected in Lucerne, Zurich, and Lugano. For details on data collection see Supporting Information. In each city, we selected 32 study plots (total 96) with a minimal distance of 250 m between plots (Sattler et al. 2010*b*). Fauna data were obtained on the same plots. Surface-dwelling arthropods were sampled with 3 pitfall traps, and flying invertebrates were sampled with a nondirectional window trap combined with a yellow pan trap (Duelli et al. 1999). Traps were deployed for 7 weeks between mid-June and the beginning of August and were emptied weekly (Sattler et al. 2010*a*, 2010*b*). Spiders, ground beetles, weevils, lady bugs, and bees were identified by specialists (see Acknowledgments). We surveyed birds in the early morning with the point count method (Bibby et al. 2000). Each of the 96 plots was visited 6 times between mid-April and mid-June (breeding season), and bird species were surveyed in a plot with a radius of 50 m for 15 min (=90 min/sampling plot, Fontana et al. 2011). The abundance for each species in a sampling plot was the maximum number of individuals present during any of the 6 visits. For the fauna, we analyzed 39,752 individuals from 574 species (Table 1) (96 plots specified above).

For vascular plants, ground beetles, bees, and birds, we obtained nutrition, mobility, reproduction, and life-form information (Table 2 & Supporting Information), which link traits with the species' fitness and ecological function and which we expected to respond to changes in urban environmental conditions (Vandewalle et al. 2010; Lizée et al. 2011). These traits were used to calculate corresponding FD. No trait information was available for spiders, weevils, or lady bugs.

Biodiversity Measures

To identify single species that indicate multiple measures of biodiversity, we calculated several properties of taxonomic and FD for each of the selected taxa. We defined *species richness* as the total number of species recorded in each plot and *species diversity* on the basis of the Simpson index (Simpson 1949). The Simpson index emphasizes the evenness of a community and can be interpreted as the probability that 2 randomly chosen individuals belong to the same species. The Simpson index was calculated for all taxa except plants, for which only presence–absence data were available.

We calculated FD using R package FD, which yielded an index of functional dispersion (FDis) (Laliberté & Legendre 2010). For each plot, we calculated FDis for

Table 1. Nos. and types of biodiversity measures obtained per taxonomic group.

Taxa	Records[a]	Total no. of species	Biodiversity measure[b]: Species richness	Species diversity	FD nutrition	FD mobility	FD reproduction	FD life form	Total biodiversity measures applied
Flora									
Plants	1397	262	1	-	2	1	1	1	6
Fauna									
Spiders	20,893	161	1	1	-	-	-	-	2
Ground beetles	3088	60	1	1	1	1	-	1	5
Lady bugs	2242	32	1	1	-	-	-	-	2
Weevils	3215	120	1	1	-	-	-	-	2
Bees	6194	139	1	1	1	1	1	-	5
Birds	4120	62	1	1	1	1	1	1	6
Total fauna[c]	39,752	574	1	1	-	-	-	-	2
RBA Index[d]	Approximately 310,000	-	1	-	-	-	-	-	1
Total measures for fauna			8	7	3	3	2	2	25
Total measures			9	7	5	4	3	3	31

[a] *For plants, records refer to species occurrences (presence–absence data), for all animal taxa to number of individuals.*
[b] *FD, functional diversity.*
[c] *Sum of the 6 fauna taxa identified to the species level.*
[d] *Morphospecies including additional taxonomic groups included in the rapid biodiversity assessment. Total number of species cannot be indicated for methodological reasons (Methods and Supporting Information).*

15 traits (continuous values) within the 4 trait categories (nutrition, mobility, reproduction, and life form of plants, ground beetles, bees, and birds) (Table 2). The FDis is the mean distance in multidimensional trait space of individual species to the centroid of all species and is the multivariate analogue of the weighted mean absolute deviation, which means the index is unaffected by species richness (Laliberté & Legendre 2010). We calculated FDis for both, presence–absence data (flora data) and species abundances in which the species traits were weighted by the relative abundance of each species in the communities (fauna data).

Following Fleishman et al. (2005), we complemented the biodiversity measures for the individual taxa with 3 additional measures for all fauna taxa together to identify local umbrella species that are indicative for overall taxonomic aspects. We calculated species richness and Simpson diversity of spiders, ground beetles, weevils, lady bugs, bees, and birds in one group and called them total fauna richness and total fauna diversity. To identify umbrella species for an even broader measure of taxonomic diversity, we included species richness of 29 arthropod groups obtained with a rapid biodiversity assessment (RBA) approach in which arthropod specimens were classified to morphospecies level at the same 96 plots (Obrist & Duelli 2010; Sattler et al. 2010*b*). We took the morphospecies data (RBA index) as a measure of overall arthropod species richness. The index was based on approximately 310,000 arthropod specimens with an average of 284 morphospecies (SD 45) per plot (range 169–361) (Sattler et al. 2010*b*) (Supporting Information).

In summary, we measured urban biodiversity with total fauna, the RBA index, and 6 indexes (species richness, species diversity, and FD in the 4 trait categories nutrition, mobility, reproduction, and life form) in 7 taxonomic groups. Not all combinations of indexes and taxonomic groups were possible because of lack of data. We obtained and analyzed 31 combinations (6 for flora, 25 for fauna), which we called *biodiversity measures* (Table 1).

Statistical Analyses

An overview of the steps of analyses is given in Fig. 1. We applied the indicator value method (IndVal analysis, Dufrêne & Legendre 1997) to identify umbrella species for the different measures of biodiversity. We chose this statistical approach with discrete categories to reduce the effect of extreme values, which often occur with (incomplete) count data. The IndVal analysis assesses the association between species and plot groups (often habitat or community types) with nonnegative indicator value indexes, which examines the relationship between the plots of the target plot group and the plots where the species are found (Dufrêne & Legendre 1997; De Cáceres et al. 2010; De Cáceres et al. 2012). The IndVal analysis

Table 2. Description of functional traits of vascular plants, ground beetles, bees, and birds and the values of these traits used to calculate functional diversity as a biodiversity measure.

Taxa	*Trait category*	*Trait*	*Description*	*Type*
Plants	Nutrition	Light value	Indicates the average light quantity attained by the species	Ordinal (1–5)
		Nutrient value	Characterizes the average nutrient content in the soil attained by the species	Ordinal (1–5)
	Mobility	Dispersal of diasporas	7 categories (anthropochorous, autochorous, boleochorous, dysochorous, endochorous, epichorous, meteorochorous, myrmecochorous)[a] reflecting different mobility types	Nominal[b]
	Reproduction	Reproduction strategy	2 categories (sexual and vegetative reproduction); 0.5 describing the presence of both types	Nominal
	Life form	Growth form	6 categories (herbaceous chamaephyte, geophytes, hemicryptophyte, nanophanerophyte, phanerophyte, therophyte)[c]	Nominal
Ground beetles[d]	Nutrition	Trophic level	2 categories (herbivorous, carnivorous) reflecting feeding preference	Nominal
	Mobility	Flight ability	2 categories (brachipter, macropter) reflecting wing form[e]	Nominal
	Life form	Body size	In millimeter	Continuous
Bees[f]	Nutrition	Trophic specialization	2 categories (oligolectic, polylectic) reflecting the number of families of plants visited for nectar[g]	Nominal
	Mobility	Intertegula distance	Distance between the 2 insertion points (tegula) of the wings (in millimeter)	Continuous
	Reproduction	Breeding grounds	4 categories (miner-carder, renter, carpenter, mason)[h]	Nominal
Birds	Nutrition	Trophic specialization	Fraction per 3 categories (vertebrates, invertebrates, vegetal)	Nominal
	Mobility	Migration	3 categories (short-distance migration, partial migration, long-distance migration)	Nominal
	Reproduction	Nesting habits	Fraction per 5 categories (buildings, tree, bush, ground, cavity)	Nominal
	Life form	Body mass	In grams	Continuous

[a] *Definitions: anthropochorous, dispersal by humans; autochorous, self-dispersal; boleochorous, dispersal by wind gusts (no morphologic adaptation); dysochorous, animals cache; endochorous, dispersal by animals (seeds passing through the gut); epichorous, dispersal by animals (seeds clinging to animals); meteorochorous, dispersal by air currents (with morphologic adaptation); myrmecochorous, dispersal by ants.*
[b] *Continuous variables are included as their absolute values in the distance matrix to calculate functional diversity values; nominal variables were booleanized into dummy variables, each with presence (1) or absence (0) of each category (except for reproduction and diet in birds for which the fraction per category is known). See methods and Laliberté & Legendre (2010) for more information.*
[c] *Definitions: herbaceous chamaephyte, herbaceous plant with resting buds on persistent shoots; geophytes, plant with resting buds below the ground; hemicryptophyte, plant with resting buds on or directly below the ground; nanophanerophyte, woody plant growing as a shrub, 0.4–4 m tall; phanerophyte, woody plant >4 m growing as a shrub or tree; therophyte, plant thriving during only one vegetation period.*
[d] *Because of data paucity no functional traits for reproduction.*
[e] *Definitions: brachiptera, short wings or without wings (low flight ability); macroptera, long wings (high flight ability).*
[f] *Because of data paucity no functional traits for body size.*
[g] *Definitions: oligolectic, pollen collecting restricted to plants within the same plant family; polylectic, pollen collecting on a number of species from different plant families.*
[h] *Definitions: miner-carder, excavator in the ground; renter, occupies existing cavities in the ground, shells, wood, and walls; carpenter, excavator in woody substrate; mason, builds nest with mud.*

is based on specificity, which is the conditional probability of a positive predictive value of a given species as an indicator of the target plot group and sensitivity (or fidelity), which is the conditional probability that the given species will be found in a newly surveyed plot belonging to the same plot group (Dufrêne & Legendre 1997; De Cáceres & Legendre 2009; De Cáceres et al. 2012). Following Dufrêne and Legendre (1997), a good indicator species should be both ecologically restricted to the target plot group and frequent within it. They define the IndVal index of a species in a plot group as the product of specificity and sensitivity. We estimated sensitivity of the species as the relative frequency of the species in plots belonging to the target plot group. In contrast, specificity could be calculated from either presence–absence or abundance data. De Cáceres and Legendre (2009) further developed IndVal analysis to include occurrence data to calculate sensitivity, and De Cáceres et al. (2010) expanded the method to associate species with any combination of site groups (here, plot

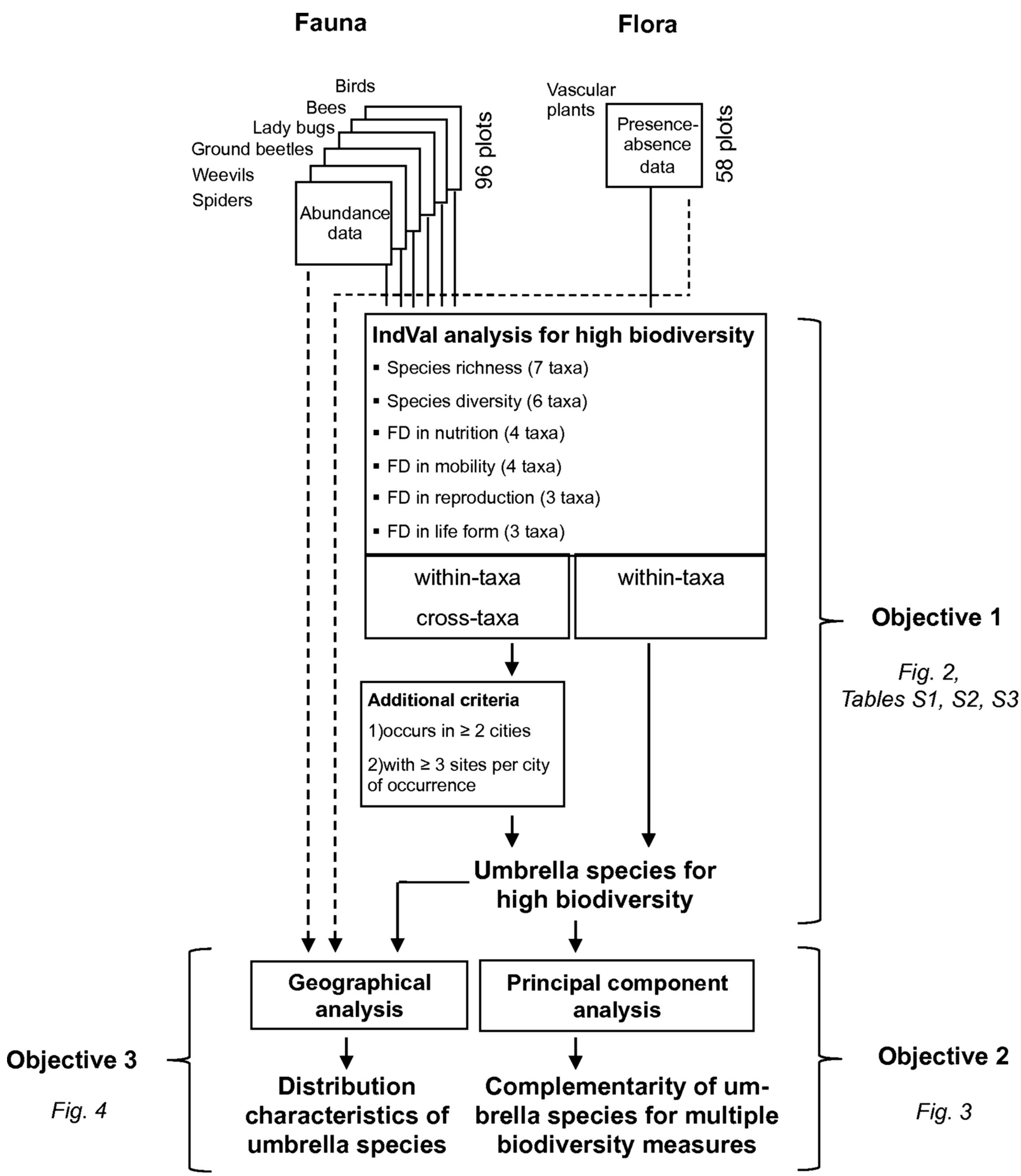

Figure 1. Six faunistic groups and one flora group and steps used to identify umbrella species that are indicators of high urban biodiversity in Switzerland (italics, results of the corresponding analysis; IndVal, indicator value; FD, functional diversity).

groups) instead of each single group individually. Thus, IndVal analysis needs 2 kinds of input that can be either occurrence or abundance values: plot-by-species table containing the presence–absence data or abundance values of species at plots (Fig. 1) and partition of the plots into a set of plot groups (nonoverlapping classes).

For the definition of the plot groups, we conceptually broadened the classical application of IndVal analysis by using habitat or community types to determine indicator species. We sought to identify species indicative of plot groups characterized by high biodiversity instead of habitat or community types. The a priori definition of plot groups depends on the study question, so despite this new way of defining plot groups, our IndVal analysis followed the regular calculation principles. To apply the IndVal method, for each biodiversity measure, we grouped plots according to 3 equally sized biodiversity levels (quantiles in 3 levels = tertiles): high, medium, and low biodiversity. To identify umbrella species for the fauna data, we defined the 3 biodiversity levels of the IndVal analysis for each city and ended up with 9 biodiversity level groups (3 biodiversity levels × 3 cities). We analyzed the fauna data per city to account for a substantial proportion of the species only occurring in one or 2 cities.

As an association measure for the IndVal calculation, we used the indicator value statistic (Dufrêne & Legendre 1997; De Cáceres & Legendre 2009) on log-transformed abundance data (except for plants). In this way, we selected any combination of plot groups with a given biodiversity level that was most associated with the observed species. We used group-equalized indexes, which assume the ecological variability of each site-group combination is proportional to the number of site groups it contains (De Cáceres et al. 2010). Species that correlated most with any combination of biodiversity levels had high indicator values and were assessed for their statistical significance (rejection of the null hypothesis that negates the association between species and plot groups). Following De Cáceres and Legendre (2009) and De Cáceres et al. (2010), we identified species that showed significant indicator values ($P < 0.05$) after 9999 random permutations and Holm correction for multiple tests. An *indicator event* was when a species significantly indicated high biodiversity for any biodiversity measure.

Plant species that had at least one indicator event for any of the 6 plant biodiversity measures were defined as umbrella species and were analyzed further. The same within-taxa analysis was also done for each of the 6 fauna taxa, for which we were also able to perform an across-taxa indicator analysis because they were sampled at identical plots. Across-taxa IndVal analysis revealed species from one taxa that indicated a particular biodiversity measure of another taxa, resulting in additional possible indicator events. For fauna, an indicator event had to fulfil 2 additional criteria for it to be useful as an umbrella species: occur in ≥2 cities and at ≥3 plots/city. This was because the IndVal analysis for fauna was performed individually in the 3 cities, and we were interested in umbrella species with a general applicability.

To identify the complementarity of detected umbrella species, we performed a principal component analysis (PCA) based on the biodiversity measures that define a space of 6 dimensions for the flora (6 biodiversity measures) and 25 for the fauna (25 biodiversity measures). Umbrella species are considered complementary when they are distant in the multidimensional space of biodiversity measures and to be related when they are clustered.

Statistical analyses were performed in R version 2.11.1 (R Development Core Team 2011) with the libraries indicspecies 1.4.0 (De Cáceres & Legendre 2009) and vegan 1.17.3 (Oksanen et al. 2010).

Umbrella Species and Geographical Distribution

To determine whether urban umbrella species showed distribution patterns that could be a general characteristic across taxa, we calculated the relative occurrence of all urban species (umbrella and nonumbrella species) in Switzerland in all environment types and plotted them with respect to their number of different biodiversity measures in 3 taxonomic groups: umbrella plant species were compared with the median occurrence of nonumbrella species in all 1650 10 m^2 plots of the systematic grid of the Biodiversity Monitoring Switzerland (Bühler & Roth 2011); umbrella birds were compared with the median occurrence of nonumbrella species in all 396 plots of the Biodiversity Monitoring Switzerland (Kéry & Schmid 2006); and spiders, ground beetles, weevils, lady bugs, and bees were compared with the median occurrence of nonumbrella species throughout Switzerland (42,851 km^2), as listed in the national database of the Swiss Biological Records Center.

Results

From the 1572 indicator tests for the 6 flora biodiversity measures (262 plant species by 6 biodiversity measures), 97 indicator events (6.2% of all tests) for 63 species (24.0%) were associated with one of the 6 biodiversity measures for plants. For the fauna, we ran 14,350 indicator tests (574 species by 25 biodiversity measures; Table 1) and identified 78 indicator events (0.5% of all tests) for 50 species (8.7%) associated with one of the 25 biodiversity measures for animals. The proportion of umbrella species to the total number of species ranged from 3.1% for lady bugs to 15% for ground bugs (weevils 5.0%, bees 7.9%, spiders 8.7%, birds 14.5%).

Within- and Across-Taxa Indications

Individual species were generally good indicators of biodiversity measures of their own taxa (Fig. 2); proportions of indicator events associated with the species' own taxa ranged from 33.3% for weevils to 93.8% for birds (spiders 34.5%, bees 46.2%, ground beetles 61.5%; lady bugs had only one indicator event which was not included). The 3 taxa with the most indicator species (spiders, bees, weevils) were best associated with the 3 measures for total species biodiversity (i.e., species richness, species diversity, and RBA index) (Supporting Information).

Umbrella Species and Complementarity of Biodiversity Indications

Although most species were indicative of only one particular measure of biodiversity, some species indicated multiple measures. Six of the 63 flora umbrella species

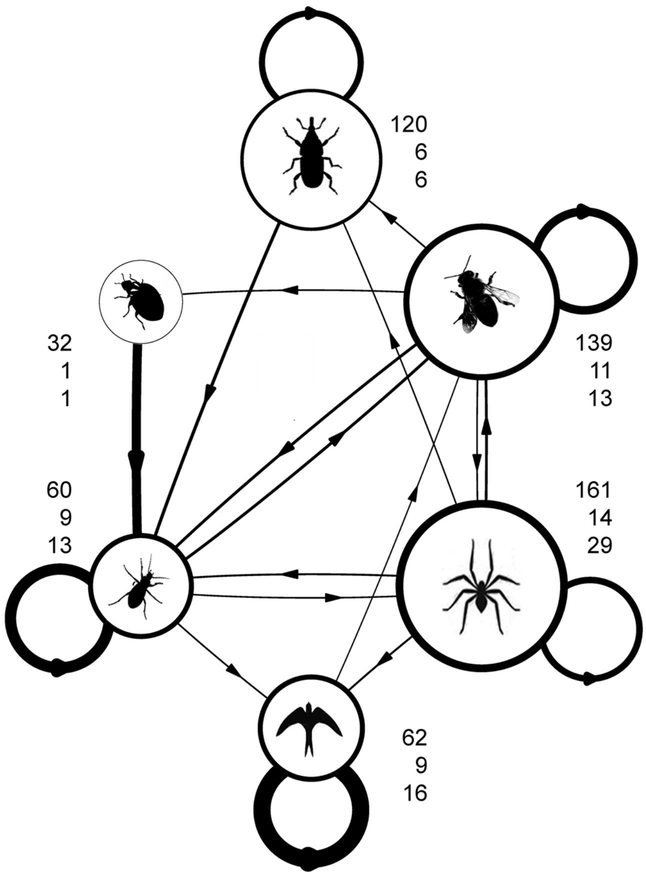

Figure 2. Indicator strength of fauna species (spider, bee, ground beetle, lady bug, weevil, and bird taxonomic groups) within and across taxa. Size of the individual circle is relative to the absolute number of species in that taxa. Thickness of the circle line indicates the number of umbrella species relative to the number of species in that taxa. Circular arrows indicate within-taxa indications, straight arrows indicate across-taxa indicators. Thickness of the arrows indicates the percentage of all indicator events (i.e., indicator value analysis identified a species that indicates high biodiversity for any measure) that indicated the other taxa or itself (effective numbers in Supporting Information). Numbers next to taxa symbols refer to number of species (top), number of umbrella species (middle), and number of indicator events (bottom) of each taxa.

indicated $\geq$3 biodiversity measures, whereas 57 species were associated with one or 2 measures (Supporting Information). Of the 50 fauna umbrella species, 5 spiders, 2 birds, and one ground bug species were associated with $\geq$3 biodiversity measures, which was the minimum number to represent our criteria of multiple measures of biodiversity (Supporting Information).

As the different biodiversity measures are not independent, umbrella species clustered in the multidimensional space of biodiversity measures. For flora umbrella species, most measures of FD did not correlate with species richness (Fig. 3a), whereas FD for reproduction was negatively correlated with richness. The umbrella species *Veronica persica, Veronica hederifolia, Glechoma hederacea* s.l., and *Vicia sepium* indicated high FD for light, mobility, and life form traits whereas *Bellis perennis* indicated biodiversity aspects; however, these aspects were not differentiated according to the first 2 PCA axes. For the fauna umbrella species, the pattern was more complex (Fig. 3b). Bird species such as *Columba palumbus* and *Regulus ignicapilla* corresponded to bird species richness and Simpson index. These biodiversity measures also seemed to be (partially) represented by the spiders *Drassyllus pusillus* and *Trochosa terricola*. Other spiders, such as *Walckenaeria antica* and *Xysticus kochi*, clearly represented other aspects of urban biodiversity, correlating with species richness of spiders and with species richness of all 6 taxa.

Umbrella Species and Geographical Distribution

Umbrella species were more widely distributed than nonindicator species (Fig. 4a-c). Fifty-four of 63 plant umbrella species (median = 1.65% occurrence), 6 of 9 bird umbrella species (median = 36.0%), and 31 of 41 arthropod umbrella species (median = 0.15%) occurred in more places than the median of all recorded species. For umbrella species associated with more than one measure of biodiversity, all species in all 3 taxa were above the median distribution.

Discussion

We identified local umbrella species for urban biodiversity in 7 taxa on the basis of 31 biodiversity measures (15 FD measures in 4 trait categories). Most umbrella species (57 of 63 flora, 42 of 50 fauna) indicated one or 2 biodiversity measures, whereas the remaining 6 and 8 species respectively were associated with multiple measures of biodiversity. In cases where conservation decisions are based on broad aspects of biodiversity, these latter species are especially well-suited for interventions. Following Caro (2010), they could be called management umbrella species that can be used to monitor populations of sympatric species or associated biodiversity measures. However, even these species clustered in groups (Fig. 3) that represented different aspects of biodiversity. This implies that umbrella species from different clusters provide complementary information on biodiversity. Thus, multiple and complementary umbrella species ought to be applied to preserve broad taxonomic and functional aspects of urban biodiversity.

The use of multiple umbrella species to maximize biodiversity coverage is promoted by others who have

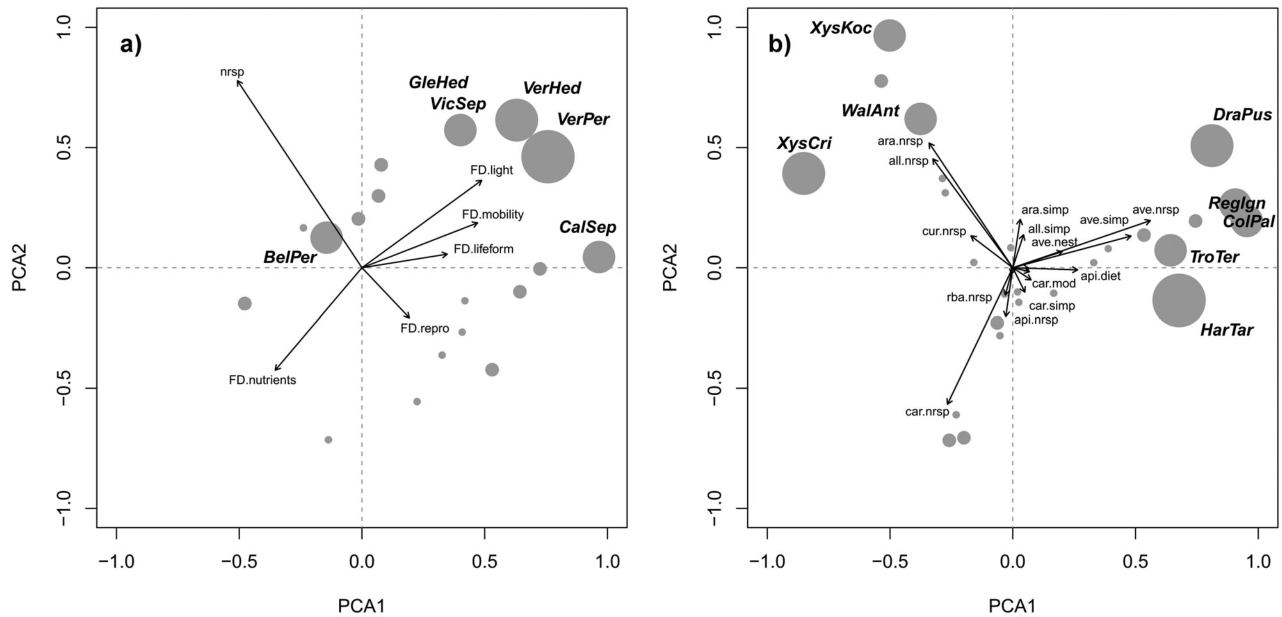

Figure 3. Results of principal component analysis illustrating the similarity (species are clustered) or the complementarity (species are distant) of umbrella species. (a) Flora umbrella species (63 species) associated with the 6 plant biodiversity measures (arrows) (first axis explains 30.1% and second axis explains 24.6% of variation in indicator events, i.e., indicator value analysis identified a species to indicate high biodiversity for any measure). (b) Fauna umbrella species (50 species) associated with the 25 biodiversity measures for the fauna (first axis explains 19.5% and second axis explains13.4% of the information). Point size is relative to number of significant indicator events for the respective species. Species abbreviations are provided for species associated with ≥3 biodiversity measures (Supporting Information for full names). In (a) Glechoma hederacea and Vicia sepium are represented by the same point because their points are close together. In (b) names for very short arrows are omitted.

analyzed many species to test their appropriateness for use as umbrella species (e.g., Fleishman et al. 2005; Maes & Dyck 2005; Caro 2010). In addition to representing different aspects of biodiversity, the identification of a single umbrella species is inevitably limited by factors such as stochasticity, demography, phenology, and sampling effort. Thus, habitat patches supporting high biodiversity may remain unoccupied by a single umbrella species (Fleishman et al. 2000), which provides an additional argument for choosing multiple umbrella species.

Increasing urbanization is often associated with a loss of FD (Vandewalle et al. 2010; Lizée et al. 2011). Functional diversity, however, is fundamental to ensure long term ecosystem functioning and services, especially when traits are directly linked with specific ecosystem processes (Dìaz et al. 2007; Cadotte et al. 2011). We found evidence that the identification of umbrella species for FD in fundamental trait categories covered additional aspects of urban biodiversity that would be missed when if one were to consider purely taxonomic measures.

Ecological Characteristics of Umbrella Species

The high score of some umbrella species (Fig. 3) may be explained by their preference for similar habitat structures. The plant species *Calystegia sepium, G. hederacea* s.l., *V. hederifolia, V. persica,* and *V. sepium* often occur along hedges or fences or on extensively or unmanaged open areas (waste grounds). In such habitats many species with different traits coexisted. Thus, these plant species, which indicated high biodiversity for different measures, live in semidisturbed places, which is consistent with Connell's (1978) intermediate disturbance hypothesis. The daisy *B. perennis* indicated complementary aspects of biodiversity and was a common species in mown or trampled grassland. The 8 fauna umbrella species clustered mainly in 2 groups: 3 spiders (*W. antica*, *X. cristatus*, and *X. kochi*) that are thermophile ambush hunters in open habitats such as meadows and the spiders *D. pusillus* and *T. terricola* and the birds *C. palumbus* and *R. ignicapilla* that inhabit urban tree groves. While the 2 spiders in the latter group hunt on the ground and prefer moist and shaded conditions, the birds

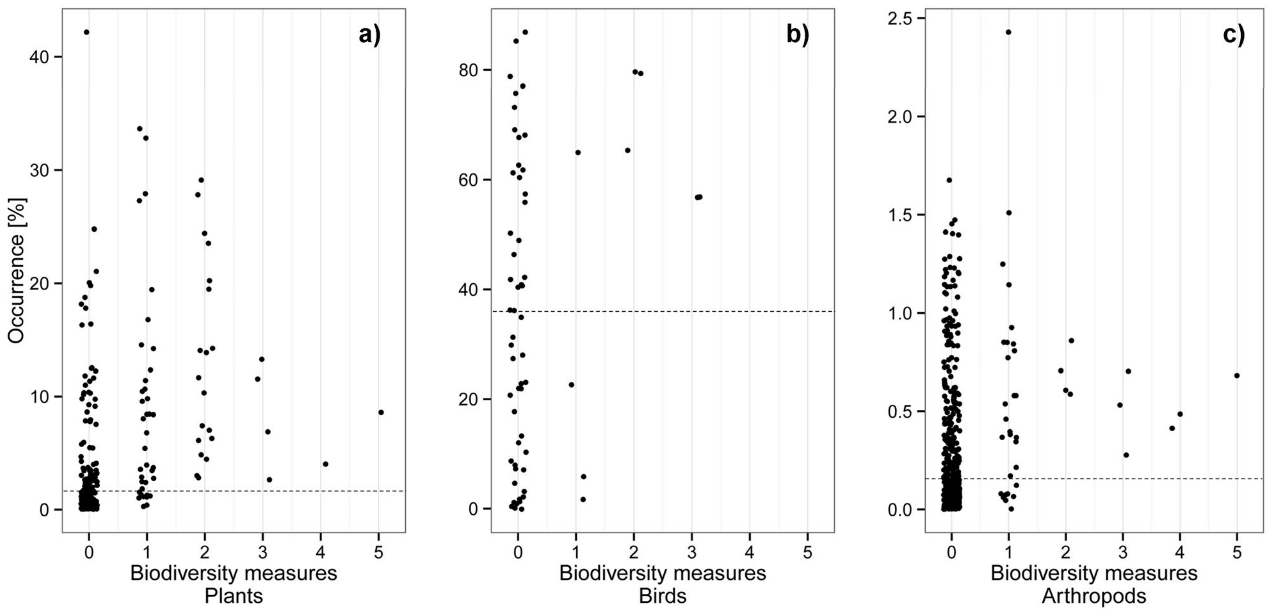

Figure 4. Overall occurrence in all environments, including urban environments, of plant, bird, and arthropod species (points) in Switzerland relative to the number of significant biodiversity measures (umbrella species, indicator species indicative of ≥3 biodiversity measures). The distribution of (a) 262 plant species with respect to their relative occurrence in the Biodiversity Monitoring of Switzerland (100% occurrence = 1481 study plots), (b) 62 bird species with respect to their relative occurrence in the Biodiversity Monitoring of Switzerland (100% occurrence = 396 km^2); (c) 512 arthropod species with respect to their relative occurrence throughout Switzerland on the basis of the national database of the Swiss Biological Records Center (100% occurrence = 42,851 km^2). Species are displaced from the exact line to illustrate their density at certain occurrence levels (minimizing point overlap). Dotted line indicates median. The scale on the y-axis differs among graphs.

prefer a mixture of coniferous and broad-leaved trees. The latter habitat conditions maximize species richness and species diversity of urban birds (Fontana et al. 2011).

Studying different taxonomic groups that are influenced by habitat composition on different spatial scales (plants and ground-dwelling arthropods on fine scales versus birds and flying insects on broad scales) ensures that selected umbrella species also reflect environmental factors acting at different scales (focal species sensu Lambeck 1997). In Central European cities, dimensions of managed areas usually refer to the local scale (square meters to hectares), so plants may be the preferred taxa when working on very fine scales, and birds may be preferred at the hectare scale. Invertebrates are rarely used as umbrella species and plants hardly ever (Caro 2010). Among the reasons for the marginal use of invertebrates and plants as umbrella species are their limited spatial requirements, which conflicts with the definition of the classical umbrella species concept (large home ranges encompassing viable populations of background species, Caro 2010). Becuse of the mosaic structure of urban areas, the identification of classical umbrella species for urban biodiversity is neither feasible nor desirable. Management actions in favor of biodiversity mainly occur on private property, which means at fine scales, so plants and arthropods may function well as local umbrella species in the urban context. Spatial auto correlation, a factor that could affect such analyses, is virtually nonexistent in urban areas (Sattler et al. 2010*a*). The influence by humans on biodiversity in urban areas seems to disrupt spatial structure in urban species assemblages.

Our results suggest umbrella species that indicate high urban biodiversity are widely distributed species inside and outside urban areas. This is also the case for umbrella species associated with multiple measures of biodiversity, which were found to be of intermediate or even wide distribution in Switzerland. These results corroborate findings of previous studies for classical umbrella species (Caro 2010; Fleishman et al. 2000) and suggests that wide geographic distribution is also a key characteristic of local umbrella species.

Within- and Across-Taxa Umbrella Species

Most fauna umbrella species indicated high levels of within-taxa biodiversity, whereas across-taxa indications were rare (Fig. 2). This is predicted by theory; life-history characteristics that affect interaction with the environment are likely to be more similar within taxonomic groups than between them (Betrus et al. 2005). This premise is supported by Fleishman et al. (2005). Although birds and carabids, 2 taxa that are often used as surrogates for other taxonomic groups, mainly predicted measures of biodiversity for their own groups (6.2% and 38.5%, respectively, of indicator events were across-taxa), bees and especially spiders were good indicators of high biodiversity levels in other groups (53.8% and 65.5%, respectively, of indicator events were across taxa). The fact that birds were less suitable as umbrella species of arthropod biodiversity may not be surprising considering the different spatial scales they use.

We did not account for the fact that detection probability might be quite different between (or among) taxa and thus affect the outcome of IndVal analysis. Even for species within a given taxa, detection probability can vary considerably. For example, detection probability can range from 0.08 to 0.99 for birds, a taxa with assumed high detection probability (Kéry & Royle 2008). However, it remains unknown how these different detection probabilities affect the identification of indicator species with the IndVal method.

The identification of surrogate species, including umbrella species, often remains an academic exercise without application in the real world (Caro 2010). However, most quests for umbrella species originate from a conservation perspective and thus call for implementation. This is also true for our study in urban areas. One of the issues that constrains the application of umbrella species concepts in management is that single species have been chosen for singular aspects of biodiversity. Although biodiversity can never be captured in its entirety, we argue that the selection of several umbrella species associated with multiple aspects of biodiversity provide a convincing argument for their application. We therefore suggest that the local umbrella species for multiple measures of urban biodiversity in central Europe that we identified may provide a useful tool for managers wishing to promote urban biodiversity. We recommend biodiversity managers use a complementary set of local umbrella species from those identified in this study when they want to identify areas that protect broad biodiversity aspects or monitor the effects of human interventions on general biodiversity over time. Because these umbrella species for biodiversity are broadly supported, they could also potentially be used in conflict mitigation. Furthermore, our general approach on how to identify local umbrella species that serve as management tools is not limited to cities and could easily be expanded by managers and scientists to nonurban environments.

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Supporting Information

Details on species data and trait information complementing the methods (Appendix S1); a cross-tabulation with relative numbers of total indicator events of indicating taxa per indicated taxa (Appendix S2); species identity of flora umbrella species and related biodiversity measures (Appendix S3); and identity of fauna umbrella species and related biodiversity measures (Appendix S4) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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