

Habitat connectivity and local conditions shape taxonomic and functional diversity of arthropods on green roofs

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Summary

1. Increasing development of urban environments creates high pressure on green spaces with potential negative impacts on biodiversity and ecosystem services. There is growing evidence that green roofs – rooftops covered with vegetation – can contribute mitigate the loss of urban green spaces by providing new habitats for numerous arthropod species.

2. Whether green roofs can contribute to enhance taxonomic and functional diversity and increase connectivity across urbanized areas remains, however, largely unknown. Furthermore, only limited information is available on how environmental conditions shape green roof arthropod communities.

3. We investigated the community composition of arthropods (Apidae, Curculionidae, Araneae and Carabidae) on 40 green roofs and 40 green sites at ground level in the city of Zurich, Switzerland. We assessed how the site's environmental variables (such as area, height, vegetation, substrate and connectivity among sites) affect species richness and functional diversity using generalized linear models. We used an extension of co-inertia analysis (RLQ) and fourth-corner analysis to highlight the mechanism underlying community assemblages across taxonomic groups on green roof and ground communities.

4. Species richness was higher at ground-level sites, while no difference in functional diversity was found between green roofs and ground sites. Green roof arthropod diversity increased with higher connectivity and plant species richness, irrespective of substrate depth, height and area of green roofs. The species trait analysis reviewed the mechanisms related to the environmental predictors that shape the species assemblages of the different taxa at ground and roof sites.

5. Our study shows the important contribution of green roofs in maintaining high functional diversity of arthropod communities across different taxonomic groups, despite their lower species richness compared with ground sites. Species communities on green roofs revealed to be characterized by specific trait assemblages. The study also provides details on the environmental conditions that influence arthropod diversity and gives new perspectives on how the design of green roofs can be improved to increase their ecological value. Furthermore, the study highlights the importance of integrating green roofs in planning policies which aim to enhance urban habitat connectivity.

Key-words: bees, brownfield, community assemblages, functional trait, ground beetles, insects, ruderal vegetation, spiders, vegetated roof, weevils

Introduction

Human population in urbanized areas is predicted to rise from 7 to over 10 billion by 2070 (United Nations, 2013).

The expected consequences of this drastic growth include urban sprawl into rural areas, the development of urban centres and increasing pressure on urban green space (Reginster & Rounsevell 2006; Dallimer *et al.* 2011). However, it is currently recognized that urban green spaces can provide valuable habitat for biodiversity (Sattler *et al.* 2010a), enhance important ecosystem services

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(Tratalos *et al.* 2007), foster the contact of people with nature close to where they work and live and they can contribute to human wellbeing (Fuller *et al.* 2007).

In the last decade green roofs, rooftops covered with vegetation, have been actively promoted to provide ecosystem services (Oberndorfer *et al.* 2007) but also to compensate for the loss of species habitat on ground level and to increase or maintain urban biodiversity (Francis & Lorimer 2011). Despite this general claim of green roof proponents there are currently only few studies with adequate design available, which demonstrate their ecological benefits. Therefore, no premature claims on the value of green roofs as compensation for ground-level habitat should be made (Williams, Lundholm & MacIvor 2014). We focus in this work on extensively managed green roofs (hereafter simply named green roofs) which are managed without irrigation systems, fertilizers and pesticides and require minimal maintenance (normally up to twice a year). In general, these green roofs have a shallow substrate with vegetation adapted to the extreme environmental conditions on green roofs (Köhler 2006). There is growing insight that extensively managed green roofs can harbour considerable abundance and diversity of arthropods, provided that they are designed with a diverse vegetation structure including high plant diversity (Brenneisen 2006; Madre *et al.* 2013). Comparison with ground-level habitats remain however rare. Braaker *et al.* (2014) showed that green roofs contribute to increasing habitat connectivity (*sensu* Fischer & Lindenmayer 2007) for different invertebrate groups across densely urbanized areas. Nevertheless, it is currently not well-understood how specific local environmental factors and habitat connectivity of green roofs influence taxonomic and functional diversity on green roofs and in surrounding urban green spaces (Francis & Lorimer 2011; Tonietto *et al.* 2011). This knowledge is however crucial for policymakers and green roof planners to promote the construction of biodiverse green roofs.

Community assembly rules predict that in a specific environment only species with adapted functional traits are able to survive (Keddy 1992; Grime 2006; Weiher *et al.* 2011). Green roof habitats are generally characterized by spatial isolation, limited size, large fluctuations in terms of temperature and water availability, high winds and strong insolation (MacIvor & Lundholm 2011). We expect that these harsh environmental conditions act as strong environmental filter leading to arthropod species communities with distinct functional traits related to dispersal, stress tolerance and resource requirements when compared to communities living in similar ground habitats (e.g. Moretti *et al.* 2009; Dziock *et al.* 2011; Gerisch *et al.* 2012; Fournier *et al.* 2015).

In this study, we compare the impact of environmental factors related to area, height, vegetation, substrate and connectivity on species richness (taxonomic diversity) and species trait diversity (functional diversity) of four distinct arthropod groups (Apidae, Curculionidae, Araneae and

Carabidae) by investigating extensively managed 40 green roofs and 40 ground sites in the city of Zurich, Switzerland. The selected environmental variables are expected to influence diversity of arthropods judging from previous studies on green roofs (Schindler, Griffiths & Jones 2011; Madre *et al.* 2013). The four model arthropod groups were selected because of their sensitivity to changes in environmental conditions and their use of resources over different spatial scales (e.g. Eyre *et al.* 1989; Cane *et al.* 2006; da Silva *et al.* 2008; Kovács-Hostyánszki *et al.* 2013). They are therefore expected to respond to both, local habitat conditions and landscape features in different ways. Specifically, we ask the following questions: (i) Does taxonomic and functional diversity differ between green roofs and ground sites? (ii) Which environmental factors impact taxonomic and functional diversity on green roofs and on ground sites? (iii) Are arthropod communities on green roofs characterized by species with specific traits? (iv) What species traits are associated with specific environmental variables on green roofs and ground sites?

Materials and methods

STUDY AREA AND STUDY SITES

The city of Zurich, Switzerland, covers a surface of 91.9 km² and has approximately 400 000 inhabitants (2014 census data). Zurich has neighbourhoods of densely built-up residential and industrial areas, but also contains a large number of historical and recently established public and private green spaces (Hennig & Ghazoul 2011). Many buildings support intensively or extensively managed vegetated rooftops (87 ha vegetated roofs in 2007, i.e. 23% of the surface that could be potentially vegetated; Tschander 2007). We selected 40 extensively managed green roofs (hereafter green roofs) with ages ranging between 2 and 45 years (mean = 13) and substrate depths between 5 cm (50% of all green roofs) and 13 cm, with one exception with a substrate depth of 200 cm. The single roof with deep substrate layer was retained in our analyses since the site was not an outlier in any of the other environmental variables or in arthropod abundance or number of taxa.

We also chose 40 extensively managed green sites at ground level (hereafter ground sites) such as road verges, brownfields and dry meadows, representing the best possible analogues to green roof vegetation. Similar to the investigated green roofs, the extensively managed ground sites are managed without irrigation system, fertilizers and pesticides and require little to no maintenance. The ages of the ground site vegetation ranged between 0 and 86 years (mean = 12). Equipment vandalism forced us to exclude two study sites at the ground from the analyses. All study sites were well-distributed over the city with a median distance between adjacent study sites of 242 m (25% quartile = 109 m; 75% quartile = 479 m).

ARTHROPOD SPECIES AND SPECIES TRAITS

Flying arthropods were captured using a non-directional window interception trap in combination with a yellow pan trap (diameter 44 cm) placed at 1.5 m above ground (Duelli, Obrist & Schmatz

1999). Surface-dwelling arthropods were sampled using pitfall traps (diameter 72 mm), covered with transparent roofs 10 cm above the cups. At each site, six pitfall traps were arranged in groups of three with a minimum of 20 m distance between tri-plets. Traps were filled with 0.2% Rocima solution (bactericide-fungicide; Acima, Buchs, Switzerland). Specimens were collected weekly during two sampling periods from May 24th to July 4th and from August 2nd to September 5th in 2010 resulting in a total of 11 visits. Specialists (see Acknowledgements) counted and identified bees (Apidae), weevils (Curculionidae), spiders (Araneae) and ground beetles (Carabidae) to the species level. Honey bees (*Apis mellifera*) were excluded from the analysis since they are dependent on the location of apiaries and it is expected that the determinants of honeybee distribution is confounded by the locations of the bee hives. Voucher specimens of each species were deposited in the private collections of the specialists.

From the literature, we compiled a broad set of species traits relevant for survival and fitness of the species (*sensu* Violle *et al.* 2007). The species traits describe aspects considered to be sensitive to urbanization including life history, mobility and foraging behaviour (see Table 1 and Appendix S1, Supporting Information for references for the selected traits). Pearson correlation coefficients between species traits revealed to be all below 0.6 (data not shown).

ENVIRONMENTAL PREDICTORS

At each study site, we measured ten environmental variables: age of vegetation in years (*Age*), study site area in m² (*Area*), proportion of bare ground (*Bare Ground*), mean flower abundance (*FlwAb*), number of plant species (*No. plant sp.*), proportion of *Sedum* plants and other Crassulaceae (*Crassulaceae*), substrate depth (*SubDepth*), substrate type (*SubType*), site height class (*HeightCl*) and site connectedness (*Connectivity*) (Table 2). We used land-cover types from a GIS habitat map of Zurich with a precision of 10 m (Biotoptypenkartierung der Stadt Zürich 2010), in combination with GIS layers of buildings and streets from the Swiss Federal Office of Topography (Vector25 Swisstopo 2011) to measure habitat connectivity of the sites. Since different arthropod groups have different mobility and depend on different

resources we first created four alternative binary landscape maps with different *a priori* designation of certain land-cover types being habitat or matrix (Table S1). Habitat was defined as either *Brown* (ruderal vegetation, gravel sites, green roofs), *Urbangreen* (homogeneous and structured green land cover), *Vegetation* (all land-cover types having some vegetation including woody plants and gravel dominated sites) or as *Nonvertical* (all land cover types except buildings and woody plants) while all other land cover types were defined as hostile matrix respectively (Table S1). For each study site, connectivity was calculated as edge density (ED), mean proximity (MP) and mean nearest neighbour distance (MNN) based on each of the four habitat-matrix landscapes at four different scales around the study site (100, 200, 300 and 400 m radius) resulting in 16 measures of ED, MP and MNN respectively. For each diversity measure (species richness and functional diversity) of each arthropod group we subsequently selected the optimal scale and landscape matrix (Schweiger *et al.* 2005) for ED, MP and MNN separately based on the spearman correlation coefficient ρ_{ho} . As final step a principal component analysis (PCA) was performed with the optimal measures of ED, MP and MNN. The first PCA axes (one per arthropod group and diversity measure) were used as connectivity variables in the subsequent analyses (for details see Appendix S2, Tables S1 and S2).

STATISTICAL ANALYSES

Statistical analyses were performed in R Version 2.13.1 (R Development Core Team, 2011) separately for the four arthropod groups. We measured biodiversity in terms of species richness (SR) and of functional diversity (FD_Q). Species richness was inferred as the number of species per site. Functional diversity was measured using Rao's index of quadratic entropy FD_Q (Rao 2004), a widely used metric of functional diversity which has been shown to be independent of species richness (Mouchet *et al.* 2010). FD_Q, calculated using the R-package FD_Q (Laliberté & Shipley 2011), equals the sum of pairwise distances between species weighted by their relative abundance and can be interpreted as the mean functional distance between two randomly selected individuals (Botta-Dukat 2005). Species occurring in one single site, were excluded from the calculation and a log(x + 1) transformation was applied on abundance to reduce the influence of very

Table 1. Species traits of bees, weevils, spiders and carabids related to mobility (size, wing size and flying or ballooning ability), foraging behaviour (sociality, parasitism and hunting strategy) and resource selection (diet breadth, nesting habitat, habitat specialization). Sources for species traits are listed in Appendix S1

Group	Trait	Type	Description
Bees	Size	Continuous	Inter-tegula distance in mm
	Sociality	Nominal	Solitary/Social (including primitive eusocial and social species)
	Cleptoparasitic	Nominal	Non-parasitic/Parasitic
	Diet breadth	Nominal	Oligolectic/Polylectic
	Nesting habitat	Nominal	Cavity-nesting/Ground-nesting (not exclusive)
Weevils	Flying	Nominal	Non-flying/Flying
	Diet breadth	Nominal	Monophagous/Oligophagous/Polyphagous
Spiders	Size	Continuous	Body size in mm
	Ballooning	Nominal	Not ballooning, ballooning
	Hunting strategy	Nominal	Web builders: sheet web, space or orb web (SpaceOrb web) Hunters: running, ambushing or stalking (AmbushStalk)
Carabids	Size	Continuous	Body size in mm
	Wing size	Ordinal	Brachypterous (0), polymorphic (0.5), macropterous (1)
	Habitat specialization (Habitat spec.)	Ordinal	Little habitat specialist (1), medium specialist (2), high specialist (3)

Table 2. Environmental variables measured at each site

Env. variables	Description
<i>Age</i>	Years since last structural modification (e.g., ploughing, building demolition)
<i>Area</i>	Area of site in m ²
<i>Bare ground</i>	Proportion of study site covered by bare soil
<i>FlowAb</i>	Mean flower abundance at site*
<i>No. plant sp.</i>	Number of plant species [†]
<i>Crassulaceae</i>	Proportion of study site surface covered by Crassulaceae (mainly <i>Sedum</i> species)
<i>SubDepth</i>	Depth of substrate divided in two classes: 1 (≤5 cm), 2 (>5 cm)
<i>SubType</i>	Substrate type in 4 categories: soil; coarse gravel; mixed gravel, volcanic substrate [‡]
<i>HeightCl</i>	Height of site divided in three classes: 1 (<5 m), 2 (5–14 m), 3 (≥15 m)
<i>Connectivity</i>	First axis of PCA of three habitat connectivity metrics (see Appendix S1)

*Flower units were counted within three square meters with a stratified distribution at each site every second week May 24th to July 4th and from August 2nd to September 5th 2010. Densely clustered floral heads such as Apiaceae, Asteraceae and Fabaceae were counted as single flower units. Flower abundance per site was averaged across the whole sampling period.

[†]Assessed once by identifying all plant species in a five meter radius around each pitfall trap triplet, summed up for each site (grasses of the order Poales were not identified to species level).

[‡]Substrate type was recorded but was then excluded from analyses as it showed collinearity with other variables (VIF >3).

abundant species and approximate a normal distribution (de Bello *et al.* 2007).

To compare SR and FD_Q on roof and ground sites (question *i*), we performed generalized linear models (GLM) with Poisson distribution for SR and Gaussian distribution for FD_Q (Zuur *et al.* 2009) using the binary variable *Roof* (ground = 0, roof = 1) as the predictor variable (predictor variables all in capitals and italics). To identify the environmental variables influencing roof and ground communities (question *ii*) we applied univariate and multivariate GLMs with Poisson distribution for SR and Gaussian distribution for FD_Q. Since on ground sites *Crassulaceae* were almost not present, and there was little or no variation in respect to substrate depth (*SubDepth*) and site height (*HeightCl*), we assessed the impact of these variables on SR and FD_Q for roof communities only. We performed three univariate regressions, one for each predictor, with Holm's correction for multiple testing (Holm 1979). Multivariate regressions were used to identify the combined effect for the remaining seven variables: *Age*, *Area*, *Bare Ground*, *FlowAb*, *No. plant sp.*, *Substrate type* and *Connectivity*. For *Bare Ground* and *Connectivity* we also included quadratic terms as predictors (*a priori*, only included in models with linear terms). Predictors were ensured to be non-collinear by checking that their variance inflation factor VIF – i.e. the proportion of variance in one predictor explained by all the other predictors in the model – was lower than three (Zuur, Ieno & Elphick 2010). *Substrate type* showed a VIF >3 and was consequently excluded from the analyses. We calculated multivariate regressions (R-package MuMIn; Barton 2012) for all possible combinations of predictor variables and performed AICc-based model averaging (AICc: Akaike's Information Criterion with correction for small sample size; Burnham & Anderson 2002) using

only top models with an AICc weight ≤6 (Richards, Whittingham & Stephens 2011). Model averaging calculates averaged coefficients for each predictor variable and the relative importance of a predictor as the sum of AICc weights of all top models containing that variable (Burnham & Anderson 2002). The relative importance of a predictor (the maximum importance of the predictor is one if it is present in all top models) can be interpreted as its contribution to the explanatory power of the models in which it is present. We validated the models with visualization tools to check the assumptions of normality, homogeneity and independence of residuals. Where we detected violation of the assumptions, predictor variables were transformed and/or outliers removed. We used arcsine transformation for all proportions p (\sqrt{p}) log10 transformation for area and flower abundance and log10 transformation for age ($Age + 1$) as the ages of some ground sites were less than 1 year. To facilitate the comparison of parameter estimates, we standardized all variables (mean = 0; SD = 1) before model analysis. A Mantel test between model residuals and the pairwise Euclidean distance matrix of coordinates of study sites revealed no spatial autocorrelation (Mantel test: P -value >0.05, based on 9999 permutations; Legendre & Legendre 1998). Since model averaging and interpreting the relative importance of variables is only meaningful if model fit is reasonably high (Symonds & Moussalli 2011), we calculated model fit of the full model using Cox & Snell's (1989) Pseudo- R^2 (abbreviated as R^2).

We investigated species trait-environment associations including green roof as a binary environmental variable (questions *iii* and *iv*) with the fourth-corner method (Dray *et al.* 2014) and RLQ analysis (Doledec *et al.* 1996). Both methods enable the simultaneous linking of a table containing environmental variables (R), a community table with log-transformed species abundances (L) and a species traits table (Q). The fourth-corner method assesses the statistical significance of bivariate trait-environment relationships, while the RLQ analysis provides a multidimensional summary of the multivariate association. We first ran the fourth-corner method to investigate the link between species abundance and species traits, and between species abundance and environmental variables (according Dray & Legendre 2008). The null hypothesis of an absence of a link was tested at a significance level of $\alpha = 0.05$, after applying Holm's correction (Holm 1979) to the P -value for multiple testing (ter Braak, Cormont & Dray 2012), and was rejected. Second, we performed an RLQ analysis (Doledec *et al.* 1996) to check for overall associations between species traits and environmental variables. RLQ analysis is an extension of co-inertia analysis in which the L table is analysed by a correspondence analysis (CA-L) and then R and Q tables are analysed by a Hill-Smith analysis (Hill & Smith 1976) with site-scores from CA-L as row weights for R and as column weights for L. Finally, RLQ maximises the covariance between the ordination of the R and Q tables via the species table (L).

Results

In total, we captured and identified 48 086 specimens (21 240 on green roofs) of 480 species (321 on green roofs; 253 occurred at both green roofs and ground sites; Table S3). Univariate regressions of species richness (SR) showed significant differences between ground and roof sites for all taxonomic groups (Table 3a), with 1.28–1.5 times higher mean species richness at ground sites

compared with green roofs (Table S3). No significant difference was found for FD_Q for any arthropod group (Table 3b). Environmental variables specific to roof sites (substrate depth, height of the building or proportion of Crassulaceae) did not impact either SR or FD_Q of green

roofs based on univariate regressions (Table S4). The effect on SR or FD_Q of the environmental variables occurring at both ground and roof sites was evaluated by the direction (positive or negative) and the relative importance of the explanatory variables in model averaging.

Table 3. Results of the univariate regression of species richness (a) and functional diversity (b) with the binary predictor *Roof* (ground = 0 and roof = 1). Estimates, standard errors (SE), test statistics (Wald z , t -value) and P -values are given. Significant differences between ground and roof diversity are highlighted with bold values. Species richness, but not functional diversity, of ground communities is significantly higher than that of green roof communities

(a) Species richness				
Group	β	\pm SE	Wald z	P -value
Bees	-0.424	0.053	-7.965	0.000
Weevils	-0.494	0.061	-8.054	0.000
Spiders	-0.243	0.051	-4.774	0.000
Carabids	-0.566	0.068	-8.367	0.000
(b) Functional diversity				
Group	β	\pm SE	t -value	P -value
Bees	-0.066	0.103	-0.642	0.521
Weevils	0.128	0.128	0.998	0.318
Spiders	-0.060	0.104	-0.572	0.567
Carabids	0.052	0.166	0.316	0.752

Species richness (SR; results shown in Fig. 1): Full models of multivariate regression analyses showed model fits (R^2) of 0.37–0.62 for green roofs and of 0.57–0.93 for ground sites (Fig. 1, Table S5), with highest variance explained for carabids (93%). Connectivity had a strong effect (relative importance >0.6) on all arthropod groups on roof and ground sites, except for weevils at ground sites. The effect of connectivity on SR was mainly positive, whereas carabids showed a hump-shaped response (negative quadratic term). On green roofs, flower abundance increased the SR of bees, while the number of plant species had a strong positive effect on the SR of weevils and spiders. At ground level, the age of the sites had a prominent negative effect on SR of carabids. Site area increased the SR of weevils and spiders. The proportion of bare ground decreased the species richness of weevils, while a hump-shaped relationship was found for carabids. Further, at ground sites, flower abundance was important for the SR of weevils and the number of plant species for weevils and spiders.

Functional diversity (FD_Q ; results shown in Fig. 2): Full models of multivariate regression analyses showed model fits (R^2) of 0.22–0.42 for green roofs and of 0.46–0.70 for ground sites (Fig. 2, Table S6). On green roofs,

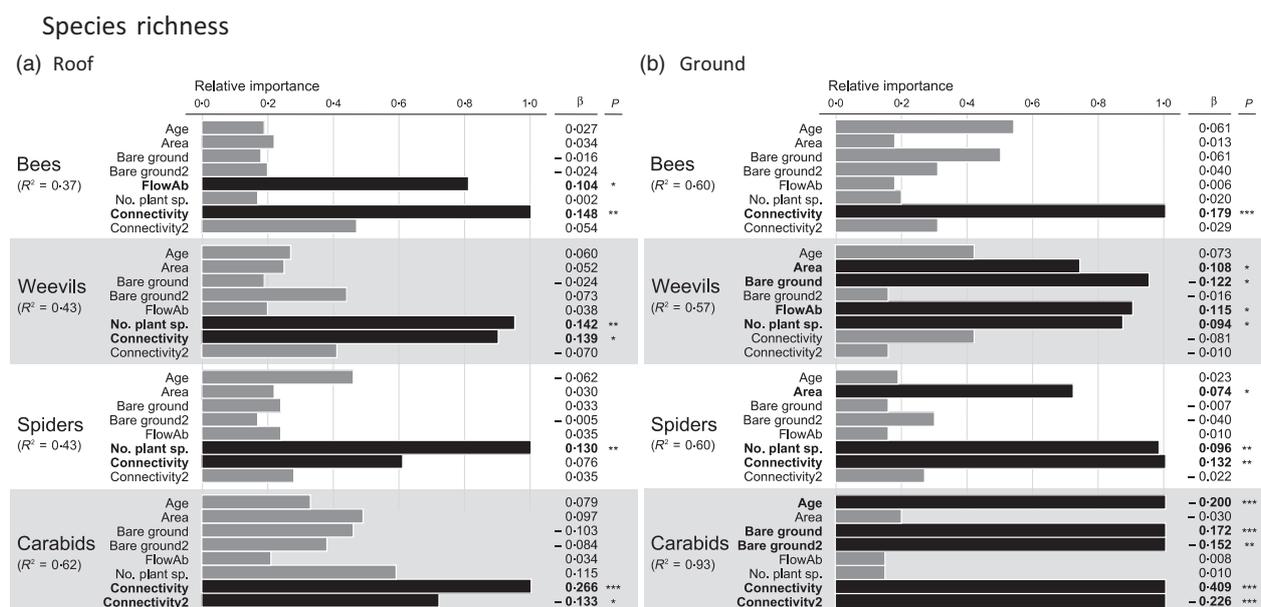


Fig. 1. Relative importance (bar length), estimates (β) and significance ($*P < 0.05$; $**P < 0.01$; $***P < 0.001$) of model-averaged multiple regressions for species richness analysed for green roofs (a) and ground sites (b) separately. Relative importance of predictor variables indicates the individual contribution of the variable to the explanatory power of the models (a value of 1 indicates its presence in all top models; bars in black if >0.6). R^2 is measured as Pseudo- R^2 based on Cox & Snell (1989). P -values are only provided for comparison of the model averaging approach with null hypothesis testing. Predictor variables are listed in Table 2, while the number 2 following the variable name indicates quadratic terms.

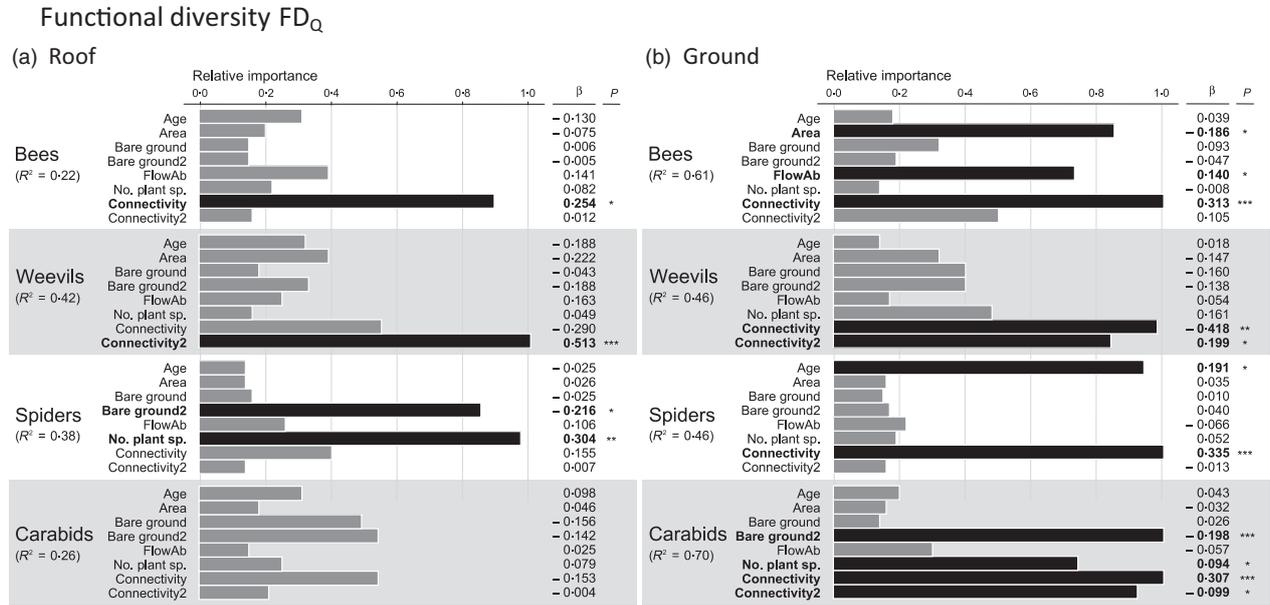


Fig. 2. Results of model-averaged multiple regressions for functional diversity (FD_Q). Figure description as for Fig. 1.

connectivity strongly increased the FD_Q of bees and showed a U-shaped relationship (positive quadratic term) for weevils. The FD_Q of spiders revealed a hump-shaped relationship with bare ground and strongly increased with the number of plant species. At ground sites, connectivity was very important for the FD_Q of all arthropod groups although uniform relationships were not found (positive: bees and spiders, U-shaped: weevils and hump-shaped:

carabids). The effects of the other variables on the FD_Q of ground sites varied considerably between arthropod groups.

Investigating the association between community species traits and environmental variables, fourth-corner analyses revealed several significant relationships (Table 4). Green roofs were positively linked with social

Table 4. Results of the fourth-corner analysis testing the relationships between species traits (rows; see Table 1) and environmental variables (columns; see Table 2). Significant positive relationships are indicated by + signs, significant negative relationships by – signs

Env. variables		Age	Area	Bare Ground	FlowAb	No. Plant sp.	Connectivity	Roof
Bees	Size							
	Social				+			+
Weevils	Oligolectic						+	
	Cleptoparasitic							
	Ground-nesting		+					+
	Cavity-nesting							
	Flying			+				
Spiders	Monophagous							
	Oligophagous						–	
	Polyphagous							+
	Running		+			+	+	–
Carabids	Size							
	Wing size			+				
	Habitat specialization					+		

and ground-nesting bees as well as with polyphagous weevils, while negatively associated with running spiders. Connectivity was positively related to cleptoparasitic bees and running spiders and negatively with polyphagous weevils. The global test of association between species traits and environmental variables in RLQ analyses were found to be significant ($P < 0.001$; permutation test with 999 replicates). The first RLQ axis accounted for 73.8% (bees) to 81.7% (weevils) of the total co-inertia between species traits and environmental variables, and was mainly associated to the binary variable *Roof* (roof = 1, ground = 0, see Fig. S1). The graphical representations of RLQ analyses provide a summary of the multivariate structure of the trait-environment relationship which was revealed to be highly consistent with the results of the fourth-corner analyses (Fig. S1). Additional relationships complementing the results from the fourth-corner analyses were inferred from the RLQ graph. In particular, large bees and small carabids as well as ballooning spiders hunting on sheet-webs correlated positively with green roofs in addition to the traits already identified by the fourth-corner analysis.

Discussion

COMPARISON OF ARTHROPOD DIVERSITY ON ROOF AND GROUND SITES

The first objective of our study on four distinct arthropod groups on 40 green roofs and 38 extensively managed urban ground sites was to investigate whether taxonomic and functional diversity differ between green roofs and ground sites (question *i*). Indeed, species richness (SR) was found to be 1.5 times higher at ground sites compared with green roofs. However, functional diversity (FD_Q) did not differ between ground and roof sites. Higher species richness at ground sites compared with green roofs was also found by Tonietto *et al.* (2011), while similar functional diversity of pollinators at green roofs and ground sites was revealed by Ksiazek, Fant & Skogen (2012), showing that green roofs did not suffer from higher pollen limitation than ground sites. A possible explanation for the similar functional diversity on roof and ground sites is that functional traits on green roofs are more evenly distributed compared with ground sites. The harsh environmental conditions of green roofs may reduce the competitive exclusion of a few highly dominant species at ground sites, leading to a more even distribution among species and traits on roof sites compared with ground sites.

ENVIRONMENTAL VARIABLES IMPACTING GREEN ROOF ARTHROPOD DIVERSITY

This study further aimed to identify which environmental factors impact taxonomic and functional diversity on green roofs compared with ground sites (question *ii*).

Habitat connectivity of the landscape surrounding the study sites had the most consistent effect (high coefficient and relative importance) on species richness on roof and ground sites and on functional diversity at ground sites. Our results are in line with the other studies demonstrating that landscape composition and configuration enhance species richness and composition of urban green space at ground level (Sattler *et al.* 2010b; Vergnes, Le Viol & Clergeau 2012). In a previous study on green roofs in the city of Zurich, Switzerland, Braaker *et al.* (2014) investigated community composition as the ensemble of species sampled with their abundance at a given site (β -diversity, species by sites matrix with abundances). They showed that green roof β -diversity of low-mobile species (carabids and spiders) was predominantly shaped by local processes (local environmental variables and species interactions) while β -diversity of high-mobile species (bees and weevils) was rather shaped by dispersal processes (immigration and emigration). Further their study demonstrated that connectivity variables strongly shaped arthropod communities on green roofs and showed indications of an exchange of individuals between green roofs and ground-level sites.

In complementing the study of Braaker *et al.* (2014) which evaluated the overall impact of local processes on community composition, we investigated in this study the impact of specific environmental variables on species richness and functional diversity. Functionally diverse vegetation on green roofs has been shown to improve several ecosystem services such as storm water retention and building cooling (Lundholm *et al.* 2010). Our study demonstrates that diverse green roof vegetation additionally enhances arthropod diversity. The number of plant species on green roofs had a strong positive effect on the species richness of spiders and weevils. Although a positive relationship between plant diversity and animal diversity seems self-evident especially for phytophagous taxa (Siemann *et al.* 1998), this hypothesis has rarely been verified on green roofs (MacIvor & Lundholm 2011; Schindler, Griffiths & Jones 2011; Madre *et al.* 2013).

Our data did not show an effect of the substrate depth and the proportion of *Sedum* plants (Crassulaceae) on arthropod species richness or on functional diversity. Shallow substrate and large proportion of the roof surfaces covered by *Sedum* plants are expected to be characterized by low plant and low arthropod species richness mainly on newly installed green roofs (Gedge & Kadas 2005; Brenneisen 2006; Oberndorfer *et al.* 2007), while this relationship likely changes on older green roofs. Extensively managed green roofs are dynamic systems in which it has been shown that, over the long term, biomass and taxonomic and functional diversity of colonized plant species change considerably (Dunnett, Nagase & Hallam 2008; Catalano *et al.* 2016). The green roofs in our study had a mean age of 13 years and consequently were mature enough, that spontaneous colonization of plants increased species richness (Brenneisen 2006; Catalano

et al. 2016). Further, spontaneous colonization has been shown to be facilitated on green roofs with shallow substrates as more open space is available (Dunnett, Nagase & Hallam 2008), but of course such spontaneous colonization will only influence plant species richness if management of green roofs is kept minimal. An additional variable influencing arthropod diversity mainly on ground sites is the proportion of vegetation and bare ground. The highest carabid species richness was found at old ground sites with intermediate levels of bare ground and landscape connectivity (explaining 93% of the variance). Carabid species richness on ground sites in our study is in line with the intermediate heterogeneity hypothesis (Duelli 1997), according to which increasing small-scale heterogeneity will positively affect biodiversity up to the point where edge density becomes too high and patch size too small, resulting in a decline in biodiversity (Fahrig *et al.* 2011). This hump-shaped pattern of connectivity could also be caused by the competitive disadvantage at intermediate connectivity levels of a few otherwise dominant species, thereby the survival of other species is facilitated and consequently leads to higher species diversity (Mouquet & Loreau 2003).

TRAIT-ENVIRONMENT RELATIONSHIPS

We identified several arthropod species traits, which showed a significant positive association with green roofs, i.e., traits that were more likely to be found at green roof than ground sites (question *iii*). Social bees, which were positively associated with green roofs and with flower abundance (Table 4), have been reported to be more flexible in terms of resource exploitation than solitary bees (Michener 2000; Westphal, Steffan-Dewenter & Tscharnke 2003). This might enable them to use the limited peak flowering time of *Sedum* plants on green roofs more efficiently (Dunnett, Nagase & Hallam 2008; MacIvor, Ruttan & Salehi 2015). In this study, ground-nesting bees (Table 4) and less pronounced also large bees (Fig. S1) were positively linked to green roofs and large study sites. In cities, ground-nesting bees are usually less frequent than cavity-nesting bees because of limited nesting resources, disturbance by humans, and high sensitivity to fragmentation and habitat loss (Zanette, Martins & Ribeiro 2005; Cane *et al.* 2006; McFrederick & LeBuhn 2006). One hypothesis to explain the positive association of ground-nesting bees with green roofs is that the stony and sandy, partially bare soil, of green roofs might provide suitable undisturbed nesting habitat for ground-nesting bees, while at the same time offering sufficient flowering plants as foraging resources in proximity. Indeed, bees nesting in the substrate could be observed on some of the monitored green roofs during the field work (S. Braaker, pers. obs.). However, further research is needed to investigate the suitability of green roofs as nesting habitat for bees. Consistent with our study small bees were observed to be less common on green roofs

compared with larger bees by MacIvor, Ruttan & Salehi (2015). Polyphagous weevils were also significantly positively associated with green roofs (Table 4). As generalist species they likely find the required foraging resources on green roofs. Moreover, at poorly connected sites, polyphagous weevils likely experience reduced competition with the more specialized oligo- and monophagous species. This hypothesis is supported by the positive, although not significant, correlation of the more specialized oligophagous species with well-connected ground sites rich in plant species (Fig. S1).

Furthermore, we identified a few environment-trait relationships which are not directly linked to green roofs (question *iv*). The link between cleptoparasitic bees and well-connected sites can be explained by their dependence on large populations of their specific host species. They are reported to be rare in fragmented urban ecosystems, likely because of their highly specialized diet (Matteson, Ascher & Langelotto 2008; Banaszak-Cibicka & Zmihorski 2012). The positive association of running spiders with large and well-connected sites, but negative relationship with green roofs is consistent with the description of running spiders as specialized species (K-strategists) of later succession stages (Nentwig 1988). Given their hunting strategy they need large foraging areas to find enough prey and are thus also more affected by connectivity than web building spiders (Bonte *et al.* 2003). In contrast, ballooning species are more likely to colonize roof sites since, as pioneer organisms (r-strategists), they are adapted to early successional stages and temporary habitats (Samu & Szinetár 2002).

The physical isolation at the horizontal and vertical plane of green roofs is generally assumed to limit arthropod colonization to highly mobile species (Brenneisen 2006; MacIvor 2015). Surprisingly, we found no clear link between mobility-related traits and connectivity or green roofs (Fig. S1). It is possible that urbanization acts as a strong filter leading to a convergence of mobility traits so that only highly mobile species survive in cities (Crocini *et al.* 2008; Knapp *et al.* 2008). However, Lizée *et al.* (2011) could not confirm this hypothesis for urban butterflies. Alternatively, the ability to move may not be a single trait, but a complex of several related phenotypic and other life-history traits each affecting the movement of an individual (Bowler & Benton 2005; Clobert *et al.* 2009). Testing of these alternative hypotheses is beyond the scope of the present study and we suggest that further urban-rural gradient analyses will be necessary to test an overall increased mobility of arthropod species in cities.

CONCLUSION AND MANAGEMENT IMPLICATIONS

To the best of our knowledge, this is the first time that – in addition to recognizing the value of green roofs as species habitat – the role of green roofs in maintaining high functional diversity of arthropod communities has been clearly demonstrated for different taxonomic groups. Our study has shown that urban green roofs host not merely

an impoverished subset of ground communities but are characterized by species communities with specific trait assemblages, despite their lower species richness compared with ground sites. To enhance arthropod species richness and functional diversity of the investigated taxonomic groups, green roof design should focus on increasing vegetation diversity, spatial heterogeneity and resource abundance. Especially spontaneous colonization of plant species should be fostered since this process is a natural way towards achieving higher plant diversity on green roofs. If the objective is to favour the presence of pollinators on green roofs, planners should increase the proportion of flowering plants. Further, we demonstrated that habitat connectivity (i.e. a dense network of urban green areas) is essential to increase α - and β - taxonomic and functional diversity on and among green roofs. For these reasons, policy makers should strive to promote an ecological design of green roofs to increase their biodiversity but should additionally enhance the integration of green roofs in urban planning strategies.

Authors' contributions

M.M., M.O. and S.B. conceived the ideas and designed methodology; S.B. collected and analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.ps657> (Braaker *et al.* 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Sources for species traits.

Appendix S2. Measuring habitat connectivity.

Table S1. Description of land-cover types and derived connectivity metrics.

Table S2. List of the best connectivity measures retained for PCA analysis.

Table S3. Number of species captured on roof and ground sites.

Table S4. Estimates of univariate regressions to predict species richness and functional diversity on roof sites.

Table S5. Estimates of multivariate regressions to predict species richness on roof and ground sites.

Table S6. Estimates of multivariate regressions to predict functional diversity on roof and ground sites.

Fig. S1. Graphical representation of RLQ analysis.