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Local habitat characteristics have a stronger effect than the surrounding urban landscape on beetle communities on green roofs

Kukka Kyrö^{a,*}, Stephan Brenneisen^b, D. Johan Kotze^a, Alexander Szallies^b, Magdalena Gerner^b, Susanna Lehvävirta^{a,c}

^a Department of Environmental Sciences, University of Helsinki, P.O. Box 65, 00014, Finland

^b Institute of Natural Resources Sciences, University of Applied Sciences Zurich, Grüentalstrasse 14, Postfach 8820 Wädenswil, Switzerland

^c Department of Landscape Architecture, Planning and Management, Swedish University of Agricultural Sciences, PO Box 58, SE-23053, Alnarp, Sweden

Abstract

Green roofs are a promising tool to return nature to cities and mitigate biodiversity loss brought about by urbanization. Yet, we lack basic information on how green roofs contribute to biodiversity and how their placement in the urban landscape affects different taxa and community composition. We studied the effects of local and landscape variables on beetle communities on green roofs. We expected that both local roof characteristics and urban landscape composition shape beetle communities, but that their relative importance depends on species characteristics. Using pitfall traps, we collected beetles during two consecutive years from 17 green roofs in Basel, Switzerland. We evaluated the contribution of six local and six landscape variables to beetle community structure and to the responses of individual species. Communities on the roofs consisted of mobile and open dry-habitat beetle species, with both local and landscape variables playing a role in structuring these communities. At the individual species level, local roof variables were more important than characteristics of the surrounding urban landscape. The most influential factors affecting the abundances of beetle species were

vegetation, described as forb and grass cover (mainly positive), and roof age (mainly negative). Therefore, we suggest that the careful planning of green roofs with diverse vegetation is essential to increase their value as habitat for beetles. In addition, while beetle communities on green roofs can be diverse regardless of their placement in the urban landscape, the lack of wingless species indicates the need to increase the connectivity of green roofs to ground level habitats.

Keywords

Coleoptera; green infrastructure; landscape configuration; patch characteristics; pitfall traps; vegetated roofs

Introduction

Ecological resources and green infrastructure have historically been given minor roles in the development of urban landscapes (Benedict and McMahon 2006; Mell et al. 2013). This has allowed the shrinking of urban green areas with negative effects on biodiversity, ecosystem functioning and human well-being (Benedict and McMahon 2006; Tzoulas et al. 2007; Grimm et al. 2008). In order to halt and reverse the negative ecological and environmental effects brought about by urbanization, scientists, architects and urban planners are searching for solutions that add nature as part of the existing urban infrastructure (Francis and Lorimer 2011). Green (also called living or vegetated) roofs is one such solution that offers a multitude of ecological benefits without competing for economically valuable urban space (Oberndorfer et al. 2007). Therefore, they have a high potential for reconciliation ecology, i.e. modifying anthropogenic environments to support wildlife in a way that does not reduce the societal value of the area (Francis and Lorimer 2011; Rosenzweig 2016).

An additional advantage of green roofs is that they can be designed for specific purposes, such as the conservation of certain habitats and species (Landolt 2001; Kaupp et al. 2004; Kadas 2006; Brenneisen 2009). Results from studies on green roof biota have been encouraging and have shown that green roofs are able to harbour diverse plant and animal - especially invertebrate - communities (Brenneisen and Hänggi 2006; MacIvor and Lundholm 2011; Madre et al. 2013; Gabrych et al. 2015). In addition, they may increase connectivity of urban green space by acting as stepping stones (Braaker et al. 2014). Yet, there is a lack of basic information on factors affecting the biodiversity value of green roofs, which is of considerable importance if conservation benefits are to be realized.

An essential question that needs to be addressed regarding green roofs built for biodiversity purposes (Brenneisen 2006) is whether local roof characteristics (i.e., local

resources), the surrounding landscape (i.e., resources, source populations, dispersal and connectivity), or a combination of these are important in maintaining or promoting biodiversity in the city. Since the occurrence and abundance of species are defined by both local and landscape conditions (see Mazerolle and Villard 1999 for a review covering a wide array of habitat types and taxa; Soga and Koike 2012 for butterflies in urban forests; Zulka et al. 2014 for various invertebrate taxa in dry grasslands), the risk exists that green roofs designed for biodiversity may not function as such if located in an unfavourable urban milieu even when local roof characteristics are explicitly designed from the perspective of supporting biodiversity. Unfavourable landscape conditions may include, e.g., a lack of source habitat, or connectivity to such, due to a high proportion of impervious surfaces, water or other unsuitable environments for green roof fauna in the landscape. In this study, we aimed to identify and evaluate the relative contributions of local and landscape characteristics that shape green roof beetle communities and the abundances of individual species.

Based on previous green roof studies and widely acknowledged ecological theories, such as the island biogeography theory (MacArthur and Wilson 1967), we hypothesized that local characteristics related to habitat quality and accessibility, and landscape variables indicating such phenomena as the availability or lack of potential source populations and permeability of the landscape are influential in structuring beetle communities and individual species abundances. Previous studies have shown a positive effect of the amount of meadow type roof vegetation, i.e. vegetation dominated by forbs and grasses, on species richness and abundance of most invertebrate taxa on roofs (Brenneisen 2006; Kadas 2006; Madre et al. 2013). Thus, we expected the abundances of most species to be positively associated with the percentage cover of forbs and grasses on the roof. Additionally, we hypothesized that roof area has a positive effect (Rosenzweig 1995; Connor et al. 2000) and that the effect of roof height is negative due to increased isolation (MacArthur and Wilson 1967; Rosenzweig 1995) and the often strong

exposure to sun and wind on high roofs. Moreover, we expected the effect of roof age on beetle abundances to be either negative or peaking at intermediate roof age, because when roofs are constructed, populations increase with increased probability of colonization, but competition may limit species abundances on older roofs (Fahrig and Jonsen 1998; Bolger et al. 2000). Based on previous green roof studies, we expected substrate depth to have variable effects depending on the beetle species (Brenneisen 2009; Madre et al. 2013). Furthermore, we expected landscape variables, such as the proportions of various green space types and impervious surfaces of the urban landcover, to have positive and negative influences, respectively, based on their hypothesized value as habitat or contribution to connectivity (Braaker et al. 2014). Moreover, we expected the mobility of a species to affect the relative importance of local and landscape variables: we assumed that local roof characteristics will be important for sedentary species and landscape variables for highly mobile species (Öckinger et al. 2009; Braaker et al. 2014; Zulka et al. 2014). Finally, because of the complexity of phenomena at the community level, no directional hypotheses were put forth regarding the effects of the above independent variables on the beetle community composition - instead, the variables were simply hypothesised to affect the communities.

Material and Methods

Study area and sampling design

We performed this study in the city of Basel (47°34' N, 7°36' E), northwest Switzerland. Basel has promoted the building of new green roofs since 1996, and since 2002 all new developments with flat roofs were required by the building code of the city (§72) to have green roofs. Since 2006 even on existing buildings that needed to retrofit the roof membrane, green

roofs had to be installed as part of the obligation for ecological compensation in urban areas. Consequently, Basel has become one of world's hot spots for green roofs with up to a quarter of the flat roof area covered by vegetation (Kazmierczak and Carter 2010).

We sampled beetles from 17 green roofs (Fig. 1). The roofs varied in age, size, height, type of vegetation, and substrate depth and composition (Supplementary Material, Table S3). Vegetation on the roofs were either of meadow type (dominated by forbs and grasses), sedum dominated, or mixtures of meadow and sedum type vegetation. Five of the roofs were characterized by high within-roof variation in the characteristics of vegetation and amount of bare ground. Subsequently, these roofs were divided into two or three different habitat types (according to the number of recognized vegetation types) that were treated as separate trapping sites. Roofs that did not have notable within-roof variation in vegetation characteristics, had only one trapping site, regardless of roof size. Therefore, the total number of trapping sites on the 17 roofs was 24.

The main study was conducted in 2014, but we performed a pilot study in 2013. The beetles were collected in both years using pitfall traps (volume: 125 ml, diameter: 6 cm, depth: 6.8 cm, 10 % acetic acid solution with a trace of detergent) from the beginning of April until the end of October. Ten pitfall traps were set per trapping site. As explained above, the number of trapping sites did not depend on roof size, but varied from one to three according to the number of habitat types on a roof. Consequently, each roof had 10–30 pitfall traps. The roofs were visited every fortnight to empty and re-fill the traps. All samples were stored in 50% ethanol and later identified to species level, with the standard determination keys of “Die Käfer Mitteleuropas”, Vol 2-15 (Freude 1976). The catch was pooled per trapping site and year for statistical analyses.

Sampling was repeated in 2014 in a similar way as in 2013, but with a few essential improvements. Unlike the 2013 pilot study, the number of lost traps was recorded for each

trapping period in 2014, in order to define the actual trapping effort. In addition, all traps were carefully placed flush with the soil surface, which was sometimes a problem with the 2013 sample. Other initial problems in 2013 occurred caused by crows pulling out the traps from the substrate. Limitations of the pilot study were taken into account when interpreting the results.

Figure 1 approximately here

Environmental variables

To study the effects of local roof conditions on beetle communities and individual species, roof characteristics were described using six variables: roof age, size and height, substrate depth and the type of vegetation indicated by the covers of forbs and grasses (Table 1). For statistical analyses, we converted substrate depth into a categorical variable with three classes (1: < 10 cm, 2: 10-15 cm and 3: > 15 cm) because of an overrepresentation of shallow roofs (right-skewed distribution). The other local variables were continuous.

To evaluate effects of the surrounding landscape on the beetles, we classified the landscape into six land-use classes according to their hypothesised association (habitat value) with beetles on green roofs: 1) open urban green space and semi-open green space, where shrubs, single trees or groups of trees may grow, 2) forest, 3) railways, 4) buildings, 5) impervious surfaces, and 6) water (Table 1). We analysed the distribution of land cover classes for each roof using QGIS 2.10.1 Pisa (Quantum GIS Development Team 2015). Land use data were obtained from Geoportal Kanton Basel-Stadt (<http://www.geo.bs.ch/>). We calculated the proportions of different land-use classes adjacent to each green roof using 100 and 400 m buffer zones (referred to as landscape100 and landscape400 variables) to be able to study the importance of the immediate surroundings and the larger landscape on the beetle communities.

The choice of the size of buffer zones followed Braaker et al. (2014), but instead of using four buffers (100, 200, 300 and 400 m), we decided to include only the smallest and largest one. For one roof, approximately 5% of the 400 m buffer zone extended outside the Swiss border and we did not have land-use data for that part but we considered that a minor shortcoming. Semi-open and open green space and railways were considered possible habitat for the green roof beetle fauna. Forests were considered as non-habitat, together with impervious surfaces and water, because green roofs are open and semi-open habitats that should not support communities of forest species. Buildings could either be considered as habitat or non-habitat, because part of some of the buildings had green roofs, but the land-use data did not distinguish between vegetated and non-vegetated roofs. However, because green roofs are rather equally distributed in Basel, buildings could be considered coherent as a land-use class.

Table 1 approximately here

Statistical analyses

We used R version 3.2.2 (R Core Team 2015) to perform the statistical analyses. We applied non-metric multidimensional scaling (NMDS) with stable solutions from random starts and the Bray-Curtis dissimilarity index (metaMDS in the vegan-package ver. 2.3.-1.; Oksanen et al. 2015) to describe the beetle community structure on the roofs and to determine the role of the measured environmental variables. We included all local and landscape variables in the ordinations, except Forest100, which was zero for all roofs, and used the *envfit* function to fit environmental variables onto the ordination and to assess the statistical significance of the results. For year 2014, the beetle catch (i.e., all beetles collected) was standardized for trapping effort by dividing the number of individuals collected by the number of days that traps were active on the roofs, then multiplied by 100 to give individuals collected per 100 trapping days.

The 2013 dataset was standardized in a similar way, except instead of number of days that the traps were active, we used the total number of days from the installation of traps to their removal at the end of the trapping season. We also performed an ordination for the combined 2013 and 2014 datasets to determine whether samples from the same sampling sites grouped together between the years. This combined ordination revealed large differences in community structure between years, and since the 2013 dataset is deemed less reliable, we used this year's data only for descriptive purposes.

We modelled the responses of individual species to local and landscape variables with generalised linear mixed models (GLMM, function `glmer` in the `lme4` package) (Bates et al. 2015). We analysed individual species only from the 2014 dataset, beginning with the most abundant species and continued until the models returned unstable results, the total number of individuals caught was < 20 , or the species was caught from less than seven trapping sites (45 species in total were analysed). If the model failed to converge, we excluded roofs with zero catch and reran the model (4 species). Two species were removed from the original choice of analysed species, because of problematic distributions, i.e. the species had very high numbers of individual at one or two sampling sites compared to the other sites.

The response variable (number of individuals) was modelled following a Poisson error distribution, and overdispersion, typical for count data, was taken into account by including an individual level random effect (Harrison 2014). Because of multiple trapping sites on five of the roofs, we needed to include roof identity as a random term in the models to avoid pseudoreplication and to allow for roof-specific random variation. We excluded some of the local and regional predictor variables used in the NMDS's because of strong correlations or very low values. For instance, we excluded the cover of mosses and sedums as it was highly correlated ($r = -0.88$) with the cover of forbs and grasses. Furthermore, the proportion of forest and water within both the 100 and 400 m buffer zones and the proportion of railway within the

100 m buffer were excluded because of very low values. All predictor variables, except substrate depth, were centered to zero mean and unit variation in order to improve the interpretation of the effects of variables with different original scales (Schielzeth 2010).

Because of the high number of potential explanatory variables, we ran five different models for each species: I) local variables only, II) landscape100 variables, III) landscape400 variables, and based on these first results, using IV) statistically significant local and landscape100 variables and V) statistically significant local and landscape400 variables. We performed model selection based on p- and AIC-values. Variables were removed sequentially based on two criteria: the p-value of the variable had to be > 0.2 (starting with the variable with the highest p-value), and once the variable was removed, the AIC-value of the subsequent model had to be smaller than the previous one. We continued model selection until all variables in the model had p-values < 0.2 . To determine whether models IV or V (i.e. local variables with landscape100 or landscape400 variables) were superior, we compared them using the *anova* function in R and selected the model with the lower AIC value. If depth (a categorical variable), was retained in the final model, we performed an ANOVA-comparison between models with and without depth and retained depth in the model if that model had a smaller AIC and a p-value below 0.2. The 20% risk of a type I-error in the model selection procedure was taken into account by considering important only those variables that were statistically significant at $p < 0.05$ in more than 20% of the final models.

Results

We captured 161 beetle species (21 families) represented by 3137 individuals in 2013 and 237 species (32 families) and 7433 individuals in 2014. Altogether 42/70 (2013/2014) species were represented by singletons. The most abundant family in both years was the Carabidae with

56% of individuals and 31% of species in 2013 and 55% of individuals and 19% of species in 2014, respectively. In addition, rove beetles (Staphylinidae), weevils (Curculinidae) and leaf beetles (Chrysomelidae) formed a substantial part of the number of individuals and species collected in both years. Other families were typically caught in low numbers (Supplementary Material, Table S1). Some species were red listed in Switzerland or Germany. Since the study area of Basel is located close to the south-western border of Germany, and being in the south of the Oberrheingraben as a biogeographically warm area, we present the red list status of beetles collected from both countries; 4 species in 2013 and 3 species in 2014 (Table 2).

Table 2 approximately here

Community structure

Ordination results for the 2014 data showed that both local and landscape variables affected beetle community structure on the green roofs (Fig. 2). Beetle community structure differed significantly between years ($r^2 = 0.717$, $p < 0.001$). Because of limitations in the 2013 data (described in the Materials and Methods section), we could not evaluate whether this difference is real, suggesting a high turnover rate of roof communities, or whether it is a consequence of differences in trapping effort between years. Therefore, below, we focus on results based on the main dataset, 2014. Landscape variables were more influential than local ones. We present results only for the 400 m buffer zone since the 100 m buffer results reflected those at 400 m. Statistically significant landscape variables within the 400 m buffer included open and semi-open green areas ($r^2 = 0.432$, $p = 0.003$), the proportion of forest ($r^2 = 0.415$, $p = 0.006$) and the proportion of impervious surfaces ($r^2 = 0.331$, $p = 0.014$). The proportion of forest within the selected 400 m buffer zone was low ($< 10\%$) for all the roofs and correlated

with the proportion of green areas ($r = 0.72$). Because the low amount of forest around all the studied roofs made the ecological interpretation of the role of forest impossible, it is not presented in the figure. Of the local variables, only roof size was statistically significant ($r^2 = 0.331$, $p = 0.014$), but because the proportion of forb and grass cover ($r^2 = 0.237$, $p = 0.059$) was close to significance, we decided to include it in Fig. 2.

Information about species ecologies is limited or non-existing for most beetle species we collected, except the Carabidae. According to information we retrieved from the carabid beetle database by Homburg et al. (2013), the species in our dataset were open dry habitat specialists or habitat generalists, and their wing forms were either macropterous or dimorphic, indicating good dispersal ability. The majority of carabid beetles collected in 2014 were facultative herbivores (75% of the individuals, 55% of the species). Predators accounted for 19% of the individuals and 35% of the species and omnivores 1% of the individuals and 11% the species, respectively (Homburg et al. 2013).

Figure 2 approximately here

Responses of individual species to local and landscape variables

Forty-three species from the 2014 dataset were analysed individually using GLMMs. Local roof characteristics were most frequently retained in the models (Table 3, see Supplementary material Table S2 for landscape variables). The most influential variables that were statistically significant ($p < 0.05$) in at least 20% of the models were cover of forbs and grasses (remained in the final model for 24 species), with a predominantly positive effect (23 species, statistically significant in 15 models), roof age (18 species) that showed a negative effect in most species (15 species, statistically significant in 9 models) and roof size (11 species) that was either

positive (6 species, statistically significant in 6 models) or negative (5 species, statistically significant in 3 models), depending on the species (Fig. 3). Substrate depth also appeared to be important to a number of species (Fig. 3). Intermediate substrate depth (10-15 cm) had a predominantly positive effect (14/19 species, statistically significant in 3), while the effect of the deepest substrate (> 15 cm) varied and did not differ from the thin substrate for any of the species (positive: 10/19 species). Roof height was statistically significant in less than 20% of the models and was thus considered an unimportant variable. None of the landscape variables occurred in the final models in sufficient numbers to be considered important in explaining species abundance.

Table 3 approximately here

Figure 3 approximately here

Discussion

We showed that green roofs in urban areas harbour a large number of beetle species (161 beetle species in 2013 and 237 species in 2014), including a few dry open habitat species of conservation interest. Using similar methods in 1999, Brenneisen (2009) collected 175 species from 11 green roofs in Basel, also including rare and endangered dry open habitat species. Thus, our results support the suggestion of Brenneisen (2009) that stenoeccious species requiring open habitats can benefit from green roofs.

Furthermore, we showed that both local roof conditions and landscape configuration are important in structuring beetle communities. This is well in line with the argument presented by Kotze et al. (2011) that beetle communities consist of species with highly variable

ecologies, which indicates that at the community level, both local habitat conditions as well as characteristics of the surrounding landscape are important to beetles in fragmented environments. The numbers of individuals of a particular species, those abundant enough to be analysed singly, were primarily influenced by local roof conditions, mainly plant cover, roof age and roof size, which is in agreement with Mazerolle and Villard (1999) and Brenneisen (2009). Below, we first discuss the implications of local roof features on beetles on green roofs, after which we elaborate on the ramifications of the urban landscape on the beetle fauna.

Local roof characteristics

The carabid species captured were highly dispersive open habitat generalists associated with xeric habitats, which is in line with earlier studies on green roof invertebrate fauna (Klausnitzer 1988; Hirschfelder and Zucchi 1992; Kaupp et al. 2004; Brenneisen and Hänggi 2006; Brenneisen 2009, Madre et al. 2013; Rumble and Gange 2013). Such a result is expected given that the vegetation on green roofs typically resembles dry meadows or other kinds of open or semi-open habitats (Madre et al. 2014; Gabrych et al. 2016). With the expansion of urban building integrated greening comprised of woody habitats (arbustive and arboreous, sensu Madre et al. 2014), an interesting question would be to what extent the variety of habitats on the “roof islands” can expand the species pool of beetles found on roofs. For example, dispersal capability may remain a limiting factor as green roofs form a highly fragmented habitat network that is both vertically and horizontally isolated from the surroundings. We did not collect wingless species at all and while this is a strong indication of the need for effective dispersal for access to these habitats, with no data we were unable to evaluate whether and to what extent the relative importance of local conditions and landscape composition for species depends on mobility.

Vegetation composition best explained the abundances of individual species. The positive effect of forbs and grasses on the abundance of beetles is similar to earlier findings concerning green roof arthropod fauna that showed that meadow roofs harbour more diverse arthropod communities than sedum roofs (Brenneisen 2006; Kadas 2006; Madre et al. 2013). The proportion of forbs and grasses reflects structural and even taxonomic diversity of vegetation on the studied roofs, because a low proportion of forbs and grasses typically means a high abundance of mosses and a few sedum species. The positive relationship between forb and grass cover, and the abundances of beetle species supports the habitat heterogeneity hypothesis (MacArthur and Wilson 1967; Rosenzweig 1995; Tews et al. 2004) and suggests bottom up control in these arthropod communities (Hunter and Price 1992). However, the cover of forbs and grasses is a very coarse characterisation of the vegetation and the relative importance of structural diversity and plant species diversity or productivity on the abundance of beetles cannot be inferred from our data.

The negative effect of roof age was very consistent in our data. Only two xerophilous carabid species showed a statistically significant positive response to roof age: *Calathus melanocephalus* and *Harpalus anxius*. The negative effect of age is in accordance with the suggestion by Brenneisen (2006) based on a spider survey (Brenneisen & Hänggi 2006) that new green roofs have a strong influx of mobile pioneer species. These pioneer species typically prefer dry open habitats with sparse vegetation, and thus require early successional habitats. During later successional stages, changes in vegetation towards communities dominated by stress-tolerant and ruderal plant species (Catalano et al. 2016) and an increase in competition (Benes et al. 2003) lead to a decrease or disappearance of the pioneer arthropod species.

Substrate depth was not important in the structuring of communities or the abundances of individual species. Depth was retained in the final models for many of the species, but its effect was statistically significant in only a few, and the direction of the effect varied between

species. Substrate depth often correlates with the type of vegetation, which makes it difficult to distinguish between effects of substrate depth and the composition of vegetation on species (Madre et al. 2013). Contrary to Madre et al. (2013), our data did not show strong correlations between substrate depth and characteristics of the vegetation. This is likely to be explained by the highly variable composition of the substrate and especially of the amount of organic material in the substrate: the composition of which was unique for almost all studied roofs (see Supplementary Material, Table S3).

Roof size was an important predictor in explaining species abundance. Contrary to expectation however, we did not find an overwhelming positive relationship between roof size and species abundance, but the effect was either positive or negative. In fact, previous studies have found only a weak connection between green roof size and species abundance or diversity (Madre et al. 2013; Braaker et al. 2014; and Gabrych et al. 2016 for plant species). A positive abundance-area relationship is predicted by the island biogeography theory (MacArthur and Wilson 1967; Rosenzweig 1995) and has received wide support (Connor et al. 2000). However, contradictory evidence has also shown that small habitat patches benefit species abundance, while species richness decreases with decreasing patch size (Cameron and Leather 2012). As urban areas are characterised by high fragmentation and small habitat patches, species that are not sensitive to fragmentation and reduced patch size typically benefit, whereas species that require large continuous habitat suffer from urbanisation (McIntyre 2000). Furthermore, highly dispersive species with wide habitat tolerances, i.e., generalists, which are typical for green roofs, and also for our data, are less affected by patch size than species of low mobility and specialized to certain habitat types (Halme and Niemelä 1993; de Vries et al. 1996).

Height was not an important predictor at either the community or individual species level. Thus, it appears that the overall high dispersal ability of species inhabiting green roofs

allows them to colonise even the highest of roofs. However, according to the GLMM models, height had a predominantly positive effect when it was retained, which was opposite to Madre et al. (2013), and MacIvor (2016) and to what we had expected. Blank et al. (2017) made a similar observation from the data of Kadas (2006), but suggested that a positive relationship between height and species diversity is likely explained by other roof variables that are connected to height, for example mediated by the plant community that may respond to height (Gabrych et al. 2016) or solar radiation (Getter et al. 2009; Buckland-Nicks et al. 2016) and high wind speeds.

Landscape effects

Landscape composition was important in explaining community structure, but not the abundances of individual beetle species on these roofs. This possibly indicates that the landscape acts as a filter for species to get to the roofs, but once they have successfully established on a roof, the landscape is of little consequence. Furthermore, the community analysis included information about rare species while the single species analysis only focused on abundant species. Therefore, a plausible explanation is that landscape characteristics are important to species that have not yet been able to establish abundant populations on the roofs. For those species that have been able to establish abundant populations on the roofs, it is rather a matter of habitat characteristics on the roof than the landscape that is of importance.

Moreover, contrary to our expectations, the amount of non-habitat, i.e. impervious surfaces, appeared to have a positive effect on species, whereas the effect of open and semi-open green areas was sometimes negative. In previous studies, the effect of the amount of possible source habitats has been positive (MacIvor 2016), but often weak (Tonietto et al. 2010; Madre et al. 2013; Braaker et al. 2014). These studies partly examined different taxa (bees, ants, spiders,

true bugs and weevils), which may explain differences in the importance of potential source habitats. A possible explanation for the positive relationship between impervious surface and the abundances of beetle species is to escape avian predation; densely built areas have lower abundances of insectivorous birds compared to urban areas with more vegetation cover (White et al. 2005; Máthé and Batáry 2015) and, thus, species colonising green roofs in the city centre benefit from decreased predation.

Conclusions

Results of this study provide support to the notion that green roofs can be efficient in adding nature to cities, and even contribute to nature conservation (Landolt 2001; Brenneisen 2009; Williams et al. 2013). We showed that both local habitat characteristics and the immediate urban landscape surrounding these roofs affect the community structure of beetles, but species abundance is mainly influenced by local roof characteristics. Thus, in cities such as Basel, where green roofs are common, the placement of green roofs should be less important than the, primarily, vegetative characteristics on the roofs. However, this may not apply to cities where green roofs and other green infrastructure is scarce; if the potential source habitats are few and isolated, the location of vegetated roofs might be important.

Furthermore, the lack of wingless species shows a weak point in the suitability of green roofs in species conservation and supports the assumption that, although green roofs may be a good addition to the variety of habitats in the urban setting, they do not compensate for the lack of ground level space. Moreover, the lack of wingless species on the roofs also points out a need for connecting green roofs better with other green infrastructure. This could be done with green walls and facades or other solutions that directly connect the roofs tops to ground level green infrastructure. Furthermore, our results attest to the key role of meadow type vegetation

in adding urban biodiversity via green roofs. Interestingly, roof age affected almost all species negatively. As we have pointed out, this should, to some extent, reflect high colonisation rates of early successional species when new habitats are provided in the urban matrix. However, the negative relationship between roof age and species abundances also raises the question about the suitability of green roofs as habitat in the long term and the role of maintenance of vegetation in the suitability of green roofs as habitat. This highlights the need for studies on temporal changes in green roof community composition. The effect of roof size varied among species, indicating low sensitivity of these beetle species to small patch size. High dispersal ability was a common feature of the carabid species collected, suggesting on the one hand, that vertical isolation of the roof tops efficiently excludes species with low mobility and, on the other hand, that species able to colonize green roofs are likely to occur on them regardless of connectivity to the rest of the green infrastructure. Based on these results, we suggest that green roofs, also small and isolated ones, can be efficient tools to increase habitat availability and support biodiversity even in densely built urban cores, but their benefits are likely to be restricted only for species with good dispersal abilities.

As Blank et al. (2017) stated, the difficulty in green roof research lies in the variety of green roofs. Each roof is typically a unique combination of both abiotic and biotic conditions. Thus, it is difficult to perform studies with a sufficient number of replicates for statistical analyses, and large-scale hypothesis-driven studies on green roofs are still rare. This problem has led to a situation where our knowledge from green roofs as habitats is largely based on small observational studies that cannot reveal causal relationships between green roof characteristics and species or communities. Therefore, in order to better understand what shapes green roof communities and, further, what are the potential and limitations of green roofs as artificial habitats, we need large-scale studies with study designs that allow for proper hypotheses testing. Our data indicated a potentially high yearly turnover in green roof beetle

communities. Because of small differences in the trapping procedure and a lack of information on exact trapping effort in the first year's data, we cannot reliably infer whether turnover was high between the years or a consequence of methodological differences. However, this issue identifies a need for long-term studies on population and/or community dynamics on green roofs in order to reveal source-sink dynamics of green roof communities.

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Fig. 1. Locations of sampled green roofs in the city of Basel and 400 m buffer zones used to calculate landscape variables. The six land use types for the area are indicated in Supplementary material, Fig. S2.

Figure 2. NMDS ordination plots presenting the most important roof and landscape characteristics within a 400 m buffer that structured the beetle community: roof size (a), the proportion of open and semi-open green areas (b), the proportion of impervious surfaces (c) and the proportion of forb and grass cover (d). The local and landscape variables in the plots are measured at roof level, not the sampling site level. The symbols represent catches per site per year and are labelled according to roof characteristic (b–d). Ordiellipses represent standard deviations around the sampling sites from the lowest category of the roof characteristic (dotted lines) to intermediate (dashed lines), and the highest category (solid lines).

Figure 3. Predicted number of individuals for selected species in relation to cover of forbs and grasses, roof age, roof size and substrate depth. For continuous variables (forb and grass cover, age and size), substrate depth was set at the intermediate level (10-15 cm) and the number of trap days was set to its mean (1584 trapdays) for all variables. No random effects were included in the predictions. Categories for substrate depth are 1: <10 cm, 2: 10-15 cm, 3: >15 cm.

Table 1. Summary statistics of local roof characteristics and landscape variables used in the analyses. Roof size was measured from aerial images as the size of the vegetated part and not the whole roof. For local variables, the units of measure are stated in parenthesis. All landscape variables are given as percentage cover inside a 100 or 400 m buffer. Green100/400 = semi-open and open green space. Forest and Water 100 and 400 were not used in the analysis because of low values. The hypothesised associations of the landscape variables are indicated after the variable.

Variable	Minimum	Mean	Median	Maximum
Local				
Age (years)	1	8.75	6	26
Size (m ²)	370	4739	3640	11960
Height (m)	2	12	13	18.5
Substrate depth (cm)	3.6	12	10.3	48
Forb and grass cover (%)	5	49.2	48	100
Landscape				
Railway100 +/-	0	5.3	0	33.2
Green100 +	4.6	18.3	12.8	52
Forest100 -	0	0	0	0
Buildings100 -	11.4	31	25.4	61.9
Impervious100 -	25.1	43.3	38.7	82.4
Water100 -	0	2.2	0	37.4
Railway400 +/-	0	5.2	3.7	15.2
Green400 +	10.8	20.8	16.5	50.5
Forest400 -	0	0.6	0	9.4
Buildings400 -	10.9	26.4	27.6	42.5

Impervious400 -	24.4	40.4	37.1	57.4
Water400 -	0	6.5	2	30.4

Table 2. Red listed species data per year for those trapping sites where the species was captured: Red list (RL) status of Switzerland / Germany, median (minimum, maximum) values for roof age, vegetated area, roof height, forb and grass cover, substrate depth, number of individuals and the number of occurrences on roofs and trapping sites are provided. 1= threatened by extinction, 2 = severely threatened, V = species with rapid loss of abundance, potentially threatened, R = “restricted”, very rare species, but there is no acute threat to it, n = non-threatened, - = category not available (Geiser 1998; Huber and Marggi 2005; Schmidt et al. 2016).

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Species	Family	RL status	Year	Age (years)	Area (m ²)	Height (m)	Forb and grass cover (%)	Substrate depth (cm)	Nr. indiv.	Occur. (roofs)	Occur. (sites)
<i>Amara cursitans</i>	Carabidae	R / V	2013	14 (14)	11200 (11200-11200)	15 (15-15)	33 (25-40)	8 (6-10)	2	1	2
<i>Amara tibialis</i>	Carabidae	1 / n	2013	6 (2-26)	5350 (370-11960)	15 (2-22)	52 (5-100)	11 (4-25)	66	11	17
			2014	5 (2-16)	3000 (370-11960)	13.5 (2-22)	60 (5-100)	11 (4-25)	180	14	18
<i>Harpalus progreiens</i>	Carabidae	R / 2	2013	9 (4-14)	6275 (1350-11200)	18.5 (15-22)	89 (77-100)	10 (6-14)	4	2	2

<i>Rabigus pullus</i>	Staphylinidae	- / 2	2014	9 (1–14)	6275 (480–11200)	15 (10–22)	64 (25–100)	9 (6–15)	44	4	4
			2013	13 (10–15)	2150 (1300–3000)	16 (14–18)	81 (73–88)	16 (13–19)	8	2	2
			2014	4 (1–15)	2270 (480–11960)	13 (3.5–18)	62 (5–100)	9 (4–25)	50	8	10

Table 3. Generalised linear mixed effect model results of the individually analysed species. Statistically significant coefficients for local roof variables ($p < 0.05$) are indicated in bold. Est. = coefficient, SE = standard error. Landscape (LS) variables are indicated as “+” if they were retained in the model, and with “++” if they were statistically significant. Coefficients and standard errors for landscape variables are listed in the Supplementary Material, Table S2. Species that were analysed after removing roofs with zero occurrences are denoted with *. Family information for the species listed here are presented in the Supplementary Material, Table S1.

Species	Intercept		Age (years)		Area (m ²)		Depth (10-15 cm)		Depth (>15cm)		Forbs and grass cover (%)		Height (m)		LS 100 (%)	LS 400 (%)
	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE		
<i>Protapion fulvipes</i>	-8.25	0.50					1.04	0.61	0.99	0.65						++
<i>Cytilus sericeus</i>	-7.99	0.60									0.65	0.45				++
<i>Amara aenea</i> *	-5.12	0.29														++
<i>Amara tibialis</i>	-6.35	0.33	-0.51	0.31							0.66	0.34				+
<i>Anisodactylus binotatus</i>	-9.71	0.80	-1.70	0.41	1.05	0.43	3.30	0.81	-0.50	0.88			-1.59	0.40	++	
<i>Bembidion</i>	-6.04	0.34					-1.74	0.62	0.08	0.62	0.61	0.25			++	

<i>quadrимaculatum</i>															
<i>Calathus</i>															
<i>melanocephalus</i>	-8.45	0.52	0.76	0.27	1.22	0.22	0.78	0.48	-1.39	1.09	0.76	0.21			
<i>Elaphropus parvulus</i>	-5.29	0.20			0.48	0.20					-0.46	0.21	0.34	0.21	
<i>Harpalus affinis</i>	-5.63	0.40					1.24	0.57	1.16	0.67			0.75	0.26	
<i>Harpalus anxius*</i>	-8.26	0.83	0.84	0.39			1.85	0.97	2.03	1.06	0.67	0.45			
<i>Harpalus attenuatus</i>	-8.03	0.51	-1.58	0.59	1.87	0.41					0.98	0.16	-0.68	0.47	
<i>Harpalus rubripes</i>	-4.89	0.24	-0.41	0.16	0.90	0.17	1.39	0.38	-0.08	0.38	0.27	0.17			++
<i>Harpalus tardus</i>	-9.65	1.54									0.98	0.23			+
<i>Parophonus</i>															
<i>maculicornis</i>	-7.37	0.33			-0.76	0.30	-1.38	0.51	-0.93	0.65	0.97	0.26			
<i>Poecilus cupreus</i>	-8.13	0.47	-0.60	0.39			-0.67	0.69	-1.76	1.09	1.05	0.32	1.44	0.30	++
<i>Pseudoophonus rufipes</i>	-8.10	0.52	-0.93	0.46			-1.82	1.06	0.61	0.58					++
<i>Pterostichus vernalis*</i>	-6.34	0.24			-0.97	0.34							0.84	0.48	++
<i>Syntomus foveatus</i>	-7.60	0.34			0.83	0.22	0.46	0.26	-1.28	0.64	0.65	0.12			++
<i>Chaetocnema hortensis</i>	-4.37	0.25	-0.42	0.23											

<i>Longitarsus</i>															
<i>melanocephalus</i>	-6.94	0.45			-1.59	0.55	-3.27	1.14	-1.69	1.02	0.72	0.38			++
<i>Longitarsus pratensis</i>	-6.73	0.28													++
<i>Coccinella</i>															
<i>septempunctata</i>	-7.75	0.43													++
<i>Tytthaspis</i>															
<i>sedecimpunctata</i>	-9.58	1.09	-1.21	0.91							1.30	0.69			
<i>Hypera miles</i>	-7.96	0.63									0.89	0.24			
<i>Sitona cylindricolis</i>	-7.64	0.38									0.84	0.33			+
<i>Sitona humeralis</i>	-8.25	0.45					0.35	0.61	1.42	0.54					++
<i>Corticarina truncatella</i>	-8.39	0.49					1.27	0.55	0.91	0.59					++
<i>Melanophthalma</i>															
<i>distinguenda</i>	-7.39	0.46	-1.17	0.48							0.69	0.19			
<i>Atheta fungi</i>	-7.39	0.30	-0.55	0.21	-0.31	0.24	0.73	0.38	0.46	0.51					
<i>Aleochara bipustulata</i>	-8.29	0.44													++
<i>Amischa decipiens</i>	-6.82	0.27	-0.29	0.16	-0.33	0.22	0.57	0.36	-0.42	0.55	0.27	0.20	-0.25	0.17	

<i>Carpelimus corticinus</i>	-7.06	0.51	-1.05	0.41	0.12	0.74	-1.98	1.13				
<i>Oxypoda praecox</i>	-8.82	0.73	-1.74	0.81								++
<i>Philonthus</i>												
<i>carbonarius</i>	-7.26	0.32							0.67	0.28	0.77	0.29
<i>Platydracus</i>												
<i>stercorarius</i>	-9.39	1.05							1.06	0.22		+
<i>Quedius levicollis</i>	-8.12	0.52							0.61	0.21		++
<i>Quedius nitipennis</i>	-6.90	0.24							0.33	0.22		
<i>Rabigus pullus</i>	-8.92	0.88										++
<i>Scopaeus laevigatus</i>	-6.37	0.22	-0.31	0.21								
<i>Stenus ater</i>	-9.64	0.97			0.74	1.12	1.81	0.80			-0.85	0.66
<i>Stenus atratulus</i>	-8.22	0.46	0.65	0.34								++
<i>Tachyporus pusillus*</i>	-7.76	0.42	-1.20	0.45					0.47	0.22		++
<i>Xantholinus linearis</i>	-7.65	0.43	-0.48	0.27	1.18	0.47	0.52	0.55	0.61	0.23		

Supplementary Material, Table S1. Full list of species and number of individuals caught in the study (total, mean, minimum and maximum per trapping site and number of occurrences on roofs and trapping sites). 2013 data are in parenthesis if the species was collected both years.

Family	Species	Nr. of individuals	Mean (sites)	Minimum (sites)	Maximum (sites)	Occurrences (sites)	Occurrences (sites)
Anthicidae	<i>Anthicus antherinus</i>	45 (14)	1.9 (0.6)	0 (0)	39 (14)	4 (1)	4 (1)
	<i>Hirticomus hispidus</i>	1	0.0	0	1	1	1
	<i>Omonadus floralis</i>	1	0.0	0	1	1	1
Anthribidae	<i>Anthribus albinus</i>	1 (6)	0.0 (0.3)	0 (0)	1(6)	1(1)	1 (1)
	<i>Plathyrinus resinosus</i>	1	0.0	0	1	1	1
Apionidae	<i>Ceratapion onopordi</i>	1	0.0	0	1	1	1
	<i>Cyanapion columbinum</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (1)	0 (1)
	<i>Cyanapion spencii</i>	1 (1)	0.0 (0.0)	0 (0)	1 (1)	1 (1)	1 (1)
	<i>Eutrichapion punctigerum</i>	1	0.0	0	1	1	1

	<i>Hemitrichapion lanigerum</i>	0 (4)	0.0 (0.2)	0 (0)	0 (3)	0 (2)	0 (2)
	<i>Hemitrichapion pavidum</i>	0 (3)	0.0 (0.1)	0 (0)	0 (3)	0 (1)	0 (1)
	<i>Holotrichapion pisi</i>	1 (2)	0.0 (0.1)	0 (0)	1 (1)	1 (1)	1 (2)
	<i>Ischnopterapion virens</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (1)	0 (1)
	<i>Oxystoma cracca</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (1)	0 (1)
	<i>Protapion filirostre</i>	3	0.1	0	2	2	2
	<i>Protapion fulvipes</i>	22 (8)	0.9 (0.3)	0 (0)	5 (4)	11 (3)	13 (4)
	<i>Protapion nigrিতarse</i>	2	0.1	0	1	2	2
	<i>Protapion trifolii</i>	4 (1)	0.2 (0.0)	0 (0)	2 (1)	3 (1)	3 (1)
	<i>Stenopterapion tenue</i>	2	0.1	0	1	2	2
Byrrhidae	<i>Byrrhus fasciatus</i>	5	0.2	0	3	2	2
	<i>Cytilus sericeus</i>	47 (104)	2.0 (4.3)	0 (0)	9 (20)	10 (12)	10 (14)

	<i>Simplocaria semistriata</i>	4 (6)	0.2 (0.3)	0 (0)	1 (2)	4 (5)	4 (5)
Cantharidae	<i>Cantharis rustica</i>	1	0.0	0	1	1	1
Carabidae	<i>Acupalpus flavicollis</i>	5	0.2	0	3	2	2
	<i>Agonum muelleri</i>	0 (3)	0.0 (0.1)	0 (0)	0 (3)	0 (1)	0 (1)
	<i>Agonum sexpunctatum</i>	0 (3)	0.0 (0.1)	0 (0)	0 (3)	0 (1)	0 (1)
	<i>Amara aenea</i>	377 (309)	15.7 (12.9)	0 (0)	101 (69)	14 (11)	19 (16)
	<i>Amara bifrons</i>	2 (1)	0.1 (0.0)	0 (0)	1 (1)	2 (1)	2 (1)
	<i>Amara convexior</i>	19	0.8	0	13	4	4
	<i>Amara cursitans</i>	0 (2)	0.0 (0.1)	0 (0)	0 (1)	0 (1)	0 (2)
	<i>Amara eurynota</i>	0 (7)	0.0 (0.3)	0 (0)	0 (4)	0 (4)	0 (4)
	<i>Amara familiaris</i>	5 (4)	0.2 (0.2)	0 (0)	2 (2)	4 (2)	4 (2)
	<i>Amara fulvipes</i>	1	0.0	0	1	1	1
	<i>Amara montivaga</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (1)	0 (1)

<i>Amara ovata</i>	8 (3)	0.3 (0.1)	0 (0)	6 (3)	3 (1)	3 (1)
<i>Amara plebeja</i>	1 (1)	0.0 (0.0)	0 (0)	1 (1)	1 (1)	1 (1)
<i>Amara similata</i>	2	0.1	0	2	1	1
<i>Amara tibialis</i>	180 (66)	7.5 (2.8)	0 (0)	41 (14)	14 (11)	18 (17)
<i>Anisodactylus binotatus</i>	53 (98)	2.2 (4.1)	0 (0)	16 (28)	8 (16)	9 (15)
<i>Anisodactylus signatus</i>	1 (21)	0.0 (0.9)	0 (0)	1 (18)	1 (2)	1 (3)
<i>Badister bullatus</i>	8 (4)	0.3 (0.2)	0 (0)	3 (2)	4 (3)	5 (3)
<i>Bembidion femoratum</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (1)	0 (1)
<i>Bembidion lampros</i>	13 (4)	0.5 (0.2)	0 (0)	4 (2)	5 (2)	7 (3)
<i>Bembidion quadrimaculatum</i>	151 (18)	6.3 (0.8)	0 (0)	60 (10)	15 (7)	19 (7)
<i>Bembidion tetracolum</i>	0 (6)	0.0 (0.3)	0 (0)	0 (4)	0 (3)	0 (3)
<i>Bradycellus csikii</i>	0 (2)	0.0 (0.1)	0 (0)	0 (1)	0 (2)	0 (2)

<i>Bradycellus harpalinus</i>	5	0.2	0	2	4	4
<i>Calathus melanocephalus</i>	33 (17)	1.4 (0.7)	0 (0)	15 (13)	5 (3)	7 (4)
<i>Calathus mollis</i>	0 (18)	0.0 (0.8)	0 (0)	0 (10)	0 (3)	0 (5)
<i>Elaphropus parvulus</i>	390 (19)	16.3 (0.8)	0 (0)	104 (2)	16 (8)	23 (11)
<i>Elaphropus quadrisignatus</i>	51 (24)	2.1 (1.0)	0 (0)	24 (15)	3 (2)	4 (3)
<i>Harpalus affinis</i>	588 (641)	24.5 (26.7)	0 (0)	99 (167)	14 (14)	21(21)
<i>Harpalus anxius</i>	127 (46)	5.3 (1.9)	0 (0)	76 (23)	9 (7)	11 (9)
<i>Harpalus atratus</i>	3	0.1	0	3	1	1
<i>Harpalus attenuatus</i>	194 (15)	8.1 (0.6)	0 (0)	126 (8)	9 (4)	12 (5)
<i>Harpalus dimidiatus</i>	185 (23)	7.7 (1.0)	0 (0)	165 (20)	1 (1)	2 (2)
<i>Harpalus distinguendus</i>	8 (15)	0.3 (0.6)	0 (0)	6 (6)	2 (7)	3 (8)
<i>Harpalus honestus</i>	0 (7)	0.0 (0.3)	0 (0)	0 (5)	0 (3)	0 (3)

<i>Harpalus latus</i>	0 (2)	0.0 (0.1)	0 (0)	0 (2)	0 (1)	0 (1)
<i>Harpalus luteicornis</i>	0 (4)	0.0 (0.2)	0 (0)	0 (2)	0 (2)	0 (3)
<i>Harpalus progreiens</i>	44	1.8	0	25	4	6
<i>Harpalus progreiens</i>	0 (4)	0.0 (0.2)	0 (0)	3 (0)	2 (0)	2 (0)
<i>Harpalus pumilus</i>	3 (5)	0.1 (0.2)	0 (0)	3 (5)	1 (1)	1 (1)
<i>Harpalus rubripes</i>	971 (168)	40.5 (7.0)	0 (0)	203 (25)	15 (12)	22 (17)
<i>Harpalus rufipes</i>	0 (13)	0.0 (0.5)	0 (0)	0 (5)	0 (4)	0 (5)
<i>Harpalus serripes</i>	11 (7)	0.5 (0.3)	0 (0)	5 (2)	4 (4)	5 (5)
<i>Harpalus signaticornis</i>	5	0.2	0	3	3	3
<i>Harpalus tardus</i>	132 (51)	5.5 (2.1)	0 (0)	48 (19)	6 (6)	8 (7)
<i>Lionychus quadrillum</i>	0 (2)	0.0 (0.1)	0 (0)	0 (2)	0 (1)	0 (1)
<i>Loricera pilicornis</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (1)	0 (1)

<i>Microlestes minutulus</i>	209 (3)	8.7 (0.1)	0 (0)	165 (1)	9 (3)	12 (3)
<i>Nebria brevicollis</i>	1	0.0	0	1	1	1
<i>Nebria salina</i>	3 (11)	0.1 (0.5)	0 (0)	2 (4)	2 (4)	2 (4)
<i>Ophonus azureus</i>	25 (13)	1.0 (0.5)	0 (0)	14 (7)	3 (3)	4 (4)
<i>Ophonus puncticeps</i>	1	0.0	0	1	1	1
<i>Parophonus maculicornis</i>	23 (9)	1.0 (0.4)	0 (0)	6 (4)	7 (3)	9 (4)
<i>Poecilus cupreus</i>	32 (48)	1.3 (2.0)	0 (0)	12 (16)	8 (9)	9 (10)
<i>Pseudoophonus griseus</i>	18	0.8	0	12	3	4
<i>Pseudoophonus rufipes</i>	24	1.0	0	7	7	9
<i>Pterostichus nigrata</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (1)	0 (1)
<i>Pterostichus vernalis</i>	25 (26)	1.0 (1.1)	0 (0)	11 (7)	8 (6)	10 (9)
<i>Stenolophus teutonus</i>	10 (5)	0.4 (0.2)	0 (0)	6 (2)	4 (4)	4 (4)

	<i>Syntomus foveatus</i>	114 (10)	4.8 (0.4)	0 (0)	60 (8)	8 (2)	11 (3)
	<i>Syntomus truncatellus</i>	3 (1)	0.1 (0.0)	0 (0)	1 (1)	3 (1)	3 (1)
	<i>Trechus quadristriatus</i>	10 (2)	0.4 (0.1)	0 (0)	3 (1)	7 (2)	8 (2)
Chrysomelidae	<i>Altica oleracea</i>	2 (1)	0.1 (0.0)	0 (0)	1 (1)	2 (1)	2 (1)
	<i>Asiolestia ferruginea</i>	0 (14)	0.0 (0.6)	0 (0)	0 (14)	0 (1)	0 (1)
	<i>Asiolestia transversa</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (1)	0 (1)
	<i>Bruchus luteicornis</i>	2	0.1	0	1	2	2
	<i>Cassida nobilis</i>	1	0.0	0	1	1	1
	<i>Chaetocnema concinna</i>	21	0.9	0	14	6	6
	<i>Chaetocnema hortensis</i>	779 (243)	32.5 (10.1)	1 (0)	142 (141)	17 (13)	24 (16)
	<i>Chrysolina hyperici</i>	0 (11)	0.0 (0.5)	0 (0)	0 (10)	0 (2)	0 (2)

<i>Cryptocephalus moraei</i>	0 (4)	0.0 (0.2)	0 (0)	0 (3)	0 (2)	0 (2)
<i>Cryptocephalus pygmaeus</i>	0 (3)	0.0 (0.1)	0 (0)	0 (1)	0 (3)	0 (3)
<i>Cryptocephalus sericeus</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (1)	0 (1)
<i>Cryptophagus lycoperdi</i>	1	0.0	0	1	1	1
<i>Cryptopleurum minutum</i>	2	0.1	0	1	1	2
<i>Diabolia cynoglossi</i>	1	0.0	0	1	1	1
<i>Diabolia femoralis</i>	1	0.0	0	1	1	1
<i>Galeruca pomonae</i>	3 (94)	0.1 (3.9)	0 (0)	3 (27)	1 (8)	1 (9)
<i>Galeruca tanaceti</i>	5 (9)	0.2 (0.4)	0 (0)	4 (4)	2 (4)	2 (5)
<i>Gastrophysa viridula</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (1)	0 (1)
<i>Hispa atra</i>	12	0.5	0	12	1	1

<i>Longitarsus anchusae</i>	1	0.0	0	1	1	1
<i>Longitarsus atricillus</i>	0 (5)	0.0 (0.2)	0 (0)	0 (3)	0 (2)	0 (2)
<i>Longitarsus exoletus</i>	5	0.2	0	4	2	2
<i>Longitarsus holsaticus</i>	3	0.1	0	1	3	3
<i>Longitarsus luridus</i>	2 (1)	0.1 (0.0)	0 (0)	2 (1)	1 (1)	1 (1)
<i>Longitarsus melanocephalus</i>	42	1.8	0	15	9	11
<i>Longitarsus nasturtii</i>	13	0.5	0	6	8	8
<i>Longitarsus ochroleucus</i>	7 (5)	0.3 (0.2)	0 (0)	3 (2)	4 (4)	5 (4)
<i>Longitarsus pellucidus</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (1)	0 (1)
<i>Longitarsus pratensis</i>	75	3.1	0	11	12	17
<i>Longitarsus rubiginosus</i>	0 (2)	0.0 (0.1)	0 (0)	0 (2)	0 (1)	0 (1)

	<i>Longitarsus suturellus</i>	0 (2)	0.0 (0.1)	0 (0)	0 (2)	0 (1)	0 (1)
	<i>Oulema melanopus</i>	2	0.1	0	1	2	2
	<i>Phyllotreta atra</i>	7	0.3	0	4	2	2
	<i>Phyllotreta cruciferae</i>	1 (2)	0.0 (0.1)	0 (0)	1 (2)	1 (1)	1 (1)
	<i>Phyllotreta nomorum</i>	2	0.1	0	2	1	1
	<i>Phyllotreta striolata</i>	172	7.2	0	99	9	10
	<i>Psylliodes chrysocephala</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (1)	0 (1)
	<i>Psylliodes napi</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (1)	0 (1)
	<i>Timarcha goettingensis</i>	0 (2)	0.0 (0.1)	0 (0)	0 (2)	0 (1)	0 (1)
Ciidae	<i>Cis boleti</i>	1	0.0	0	1	1	1
	<i>Ennearthron pruinolum</i>	1	0.0	0	1	1	1
Coccinellidae	<i>Coccinella septempunctata</i>	41 (14)	1.7 (0.6)	0 (0)	9 (2)	9 (9)	13 (10)

	<i>Cynegetis impunctata</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (1)	0 (1)
	<i>Halyzia sedecimpunctata</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (1)	0 (1)
	<i>Harmonia axiridis</i>	2 (2)	0.1 (0.1)	0 (0)	1 (2)	2 (1)	2 (1)
	<i>Hippodamia variegata</i>	11 (18)	0.5 (0.8)	0 (0)	3 (3)	6 (9)	7 (10)
	<i>Platynaspis luteorubra</i>	0 (2)	0.0 (0.1)	0 (0)	0 (2)	0 (1)	0 (1)
	<i>Propylea quatuordecimpunctata</i>	4 (12)	0.2 (0.5)	0 (0)	2 (5)	3 (6)	3 (6)
	<i>Psyllobora vigintiduopunctata</i>	0 (9)	0.0 (0.4)	0 (0)	0 (9)	0 (1)	0 (1)
	<i>Rhyzobius chrysomeloides</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (1)	0 (1)
	<i>Tytthaspis sedecimpunctata</i>	32 (67)	1.3 (2.8)	0 (0)	17 (43)	7 (6)	7 (6)
Corylophidae	<i>Arthrolips obscurus</i>	1	0.0	0	1	1	1
Cryptophagidae	<i>Atomaria fuscata</i>	3	0.1	0	3	1	1

	<i>Atomaria lewisi</i>	1	0.0	0	1	1	1
	<i>Atomaria linearis</i>	1	0.0	0	1	1	1
	<i>Ephistemus globulus</i>	2	0.1	0	2	1	1
Curculionidae	<i>Baris coerulescens</i>	0 (1)	0.0 (0)	0 (0)	0 (1)	0 (1)	0 (1)
	<i>Brachypera zoilus</i>	6	0.3	0	1	4	6
	<i>Ceutorhynchus contractus</i>	1	0.0	0	1	1	1
	<i>Ceutorhynchus erysimi</i>	2	0.1	0	1	2	2
	<i>Gymnetron veronicae</i>	1	0.0	0	1	1	1
	<i>Hypera meles</i>	17 (7)	0.7 (0.3)	0 (0)	5 (2)	7 (4)	7 (4)
	<i>Hypera miles</i>	58 (30)	2.4 (1.3)	0 (0)	24 (9)	9 (10)	11 (12)
	<i>Hypera nigrirostris</i>	5 (1)	0.2 (0.0)	0 (0)	2 (1)	4 (1)	4 (1)
	<i>Hypera postica</i>	1	0.0	0	1	1	1
	<i>Hypera striata</i>	1 (2)	0.0 (0.1)	0 (0)	1 (1)	1 (2)	1 (2)

<i>Mecinus pyraister</i>	1	0.0	0	1	1	1
<i>Orchestes fagi</i>	12 (3)	0.5 (0.1)	0 (0)	2 (1)	7 (3)	10 (3)
<i>Otiorhynchus sulcatus</i>	27 (18)	1.1 (0.8)	0 (0)	14 (14)	2 (2)	4 (3)
<i>Pityogenes chalcographus</i>	0 (1)	0.0 (0)	0 (0)	0 (1)	0 (1)	0 (1)
<i>Rhinusa antirrhini</i>	1	0.0	0	1	1	1
<i>Sibinia viscaria</i>	5 (11)	0.2 (0.5)	0 (0)	5 (11)	1 (1)	1 (1)
<i>Sitona ambiguus</i>	1	0.0	0	1	1	1
<i>Sitona cylindricolis</i>	38	1.6	0	7	11	12
<i>Sitona hispidulus</i>	4 (15)	0.2 (0.6)	0 (0)	2 (4)	3 (7)	3 (7)
<i>Sitona humeralis</i>	20 (93)	0.8 (3.9)	0 (0)	5 (22)	10 (10)	11 (12)
<i>Sitona inops</i>	1	0.0	0	1	1	1
<i>Sitona languidus</i>	5 (166)	0.2 (6.9)	0 (0)	2 (124)	4 (7)	4 (7)
<i>Sitona lepidus</i>	8	0.3	0	2	5	6

<i>Sitona lineatus</i>	3	0.1	0	2	2	2
<i>Sitona puncticollis</i>	0 (1)	0.0 (0)	0 (0)	0 (1)	0 (1)	0 (1)
<i>Sitona striatellus</i>	1	0.0	0	1	1	1
<i>Stenocarus ruficornis</i>	1	0.0	0	1	1	1
<i>Teretriorhynchites cineraceum</i>	0 (1)	0.0 (0)	0 (0)	0 (1)	0 (1)	0 (1)
<i>Trichopterapion holosericeum</i>	1	0.0	0	1	1	1
<i>Trichosirocalus troglodytes</i>	5 (4)	0.2 (0.2)	0 (0)	3 (1)	2 (4)	3 (4)
<i>Tychius brevisculus</i>	1 (3)	0.0 (0.1)	0 (0)	1 (2)	1 (2)	1 (2)
<i>Tychius picirostris</i>	17	0.7	0	9	5	6
<i>Tychius squamulatus</i>	1	0.0	0	1	1	1
<i>Xyleborus saxeseni</i>	1	0.0	0	1	1	1

	<i>Zacladus exiguus</i>	4	0.2	0	4	1	1
Dermestidae	<i>Anthrenus pimpinellae</i>	0 (1)	0.0 (0)	0 (0)	0 (1)	0 (1)	0 (1)
Dryopidae	<i>Dryops ernesti</i>	4	0.2	0	4	1	1
Elateridae	<i>Agriotes lineatus</i>	5 (4)	0.2 (0.2)	0 (0)	3 (3)	3 (2)	3 (2)
	<i>Agriotes sputator</i>	55 (9)	2.3 (0.4)	0 (0)	51 (6)	4 (4)	4 (4)
	<i>Agriotes ustulatus</i>	1 (6)	0.0 (0.3)	0 (0)	1 (4)	1 (3)	1 (3)
	<i>Agrypnus murina</i>	2 (2)	0.1 (0.1)	0 (0)	1 (1)	2 (2)	2 (2)
	<i>Cidnopus pilosus</i>	2	0.1	0	1	2	2
	<i>Zorochros meridionalis</i>	93 (20)	3.9 (0.8)	0 (0)	36 (9)	4 (2)	5 (3)
Erotylidae	<i>Tritoma bipustulata</i>	4 (2)	0.2 (0.1)	0 (0)	3 (1)	1 (1)	2 (2)
Eucinetidae	<i>Eucinetus haemorrhoidalis</i>	35 (3)	1.5 (0.1)	0 (0)	11 (2)	5 (2)	6 (2)
Helophoridae	<i>Helophorus nubilus</i>	2	0.1	0	2	1	1

Histeridae	<i>Hister quadrimaculatus</i>	26 (13)	1.1 (0.5)	0 (0)	22 (7)	4 (5)	4 (6)
	<i>Margarinotus neglectus</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (1)	0 (1)
	<i>Margarinotus purpurascens</i>	4 (17)	0.2 (0.7)	0 (0)	2 (12)	2 (5)	2 (5)
Hydrophilidae	<i>Anacaena globulus</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (1)	0 (1)
	<i>Cercyon convexiusculus</i>	1	0.0	0	1	1	1
	<i>Megasternum obscurum</i>	1	0.0	0	1	1	1
Hyperidae	<i>Brachypera zoilus</i>	0 (22)	0.0 (0.9)	0 (0)	0 (6)	0 (5)	0 (8)
Lathridiidae	<i>Cartodere constricta</i>	1	0.0	0	1	1	1
	<i>Corticaria elongata</i>	1	0.0	0	1	1	1
	<i>Corticarina fuscula</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (1)	0 (1)
	<i>Corticarina truncatella</i>	27	1.1	0	6	10	12

	<i>Corticicara gibbosa</i>	2	0.1	0	1	2	2
	<i>Corticicara gibbosa</i>	0 (2)	0.0 (0.1)	0 (0)	0 (1)	0 (2)	0 (2)
	<i>Enicmus transversus</i>	3	0.1	0	1	3	3
	<i>Melanophthalma curticolis</i>	1	0.0	0	1	1	1
	<i>Melanophthalma distinguenda</i>	92	3.8	0	23	11	13
Lucanidae	<i>Dorcus parallelipipedus</i>	3 (3)	0.1 (0.1)	0 (0)	1 (3)	1 (1)	3 (1)
Malachiidae	<i>Clanoptilus elegans</i>	1	0.0	0	1	1	1
Melyridae	<i>Dolichosoma lineare</i>	4	0.2	0	1	4	4
Monotomidae	<i>Monotoma brevicollis</i>	1	0.0	0	1	1	1
	<i>Monotoma picipes</i>	1	0.0	0	1	1	1
Mordellidae	<i>Curtimorda maculosa</i>	1	0.0	0	1	1	1
	<i>Variimorda villosa</i>	1	0.0	0	1	1	1

Nitidulidae	<i>Epuraea melanocephala</i>	2	0.1	0	1	2	2
	<i>Epuraea unicolor</i>	1	0.0	0	1	1	1
	<i>Stelidota geminata</i>	7	0.3	0	3	3	3
Oedemeridae	<i>Oedemera lurida</i>	0 (3)	0.0 (0.1)	0 (0)	0 (1)	0 (3)	0 (3)
	<i>Oedemera virescens</i>	8	0.3	0	5	3	3
Phalacridae	<i>Olibrus corticalis</i>	2	0.1	0	2	1	1
Ptinidae	<i>Stegobium paniceum</i>	2	0.1	0	1	1	2
Scarabaeidae	<i>Amphimallon ochraceum</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (1)	0 (1)
	<i>Amphimallon sostitiale</i>	0 (3)	0.0 (0.1)	0 (0)	0 (3)	0 (1)	0 (1)
	<i>Aphodius niger</i>	1	0.0	0	1	1	1
	<i>Hoplia philanthus</i>	1	0.0	0	1	1	1
	<i>Onthophagus coenobita</i>	1	0.0	0	1	1	1

	<i>Onthophagus joannae</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (1)	0 (1)
	<i>Oxyomus sylvestris</i>	0 (2)	0.0 (0.1)	0 (0)	0 (1)	0 (2)	0 (2)
	<i>Psammodius asper</i>	1	0.0	0	1	1	1
	<i>Valgus hemipterus</i>	9 (4)	0.4 (0.2)	0 (0)	7 (4)	2 (1)	3 (1)
Scraptiidae	<i>Anaspis brunnipes</i>	1	0.0	0	1	1	1
Silphidae	<i>Ablattaria laevigata</i>	21 (42)	0.9 (1.8)	0 (0)	12 (13)	5 (6)	5 (7)
	<i>Necrophorus investigator</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (1)	0 (1)
Staphylinidae	<i>Acrotona consanguinea</i>	1	0.0	0	1	1	1
	<i>Aleochara bilineata</i>	0 (1)	0.0 (0.1)	0 (0)	0 (1)	0 (1)	0 (1)
	<i>Aleochara bipustulata</i>	35	1.5	0	16	8	11
	<i>Aleochara haematodes</i>	4 (1)	0.2 (0.0)	0 (0)	3 (1)	2 (1)	2 (1)
	<i>Aleochara lanuginosa</i>	1	0.0	0	1	1	1

<i>Aloconota gregaria</i>	1	0.0	0	1	1	1
<i>Amarochara umbrosa</i>	1	0.0	0	1	1	1
<i>Amischa analis</i>	10	0.4	0	4	5	5
<i>Amischa decipiens</i>	64	2.7	0	12	15	18
<i>Anotylus tetracarinatus</i>	7	0.3	0	3	4	4
<i>Arpedium quadrum</i>	2	0.1	0	1	1	2
<i>Astenus gracilis</i>	3	0.1	0	2	2	2
<i>Atheta britanniae</i>	1	0.0	0	1	1	1
<i>Atheta coriaria</i>	1	0.0	0	1	1	1
<i>Atheta crassicornis</i>	1	0.0	0	1	1	1
<i>Atheta flavipes</i>	2	0.1	0	2	1	1
<i>Atheta fungi</i>	42	1.8	0	9	14	16
<i>Atheta glivicollis</i>	15	0.6	0	5	7	9

<i>Bledius erraticus</i>	4	0.2	0	3	1	2
<i>Bledius fontinalis</i>	0 (2)	0.0 (0.1)	0 (0)	0 (2)	0 (1)	0 (1)
<i>Carpelimus corticinus</i>	77	3.2	0	20	12	14
<i>Carpelimus punctatellus</i>	4	0.2	0	1	3	4
<i>Dinaraea angustula</i>	32	1.3	0	29	3	3
<i>Gabrius breviventer</i>	11	0.5	0	3	7	7
<i>Gabrius coxalus</i>	0 (1)	0.0 (0.1)	0 (0)	0 (1)	0 (1)	0 (1)
<i>Gabrius nigrutilus</i>	5	0.2	0	1	5	5
<i>Gauropterus fulgidus</i>	8	0.3	0	5	4	4
<i>Gyrophypnus angustatus</i>	30	1.3	0	28	2	2
<i>Ischnosoma splendidus</i>	10	0.4	0	3	5	6
<i>Lithocharis nigriceps</i>	1	0.0	0	1	1	1

<i>Metopsia clypeata</i>	1	0.0	0	1	1	1
<i>Mycetoporus longulus</i>	0 (1)	0.0 (0.0)	0 (0)	0 (1)	0 (2)	0 (1)
<i>Neobisnius villosulus</i>	1	0.0	0	1	1	1
<i>Ocypus olens</i>	48 (39)	2.0 (1.6)	0 (0)	31 (31)	4 (2)	5 (2)
<i>Ocypus ophthalmicus</i>	132 (5)	5.5 (0.2)	0 (0)	109 (3)	2 (1)	3 (2)
<i>Ocyusa nigrata</i>	12	0.5	0	3	7	7
<i>Omalius caesum</i>	0 (18)	0.0 (0.8)	0 (0)	0 (10)	0 (2)	0 (2)
<i>Othius laeviusculus</i>	0 (1)	0.0 (0.1)	0 (0)	0 (1)	0 (1)	0 (1)
<i>Othius subuliformis</i>	9	0.4	0	2	6	7
<i>Oxypoda praecox</i>	34 (1)	1.4 (0.0)	0 (0)	14 (1)	7 (1)	9 (1)
<i>Parocyusa rubicunda</i>	2	0.1	0	1	2	2
<i>Philonthus carbonarius</i>	54	2.3	0	12	12	14

<i>Philonthus cognatus</i>	6 (10)	0.3 (0.4)	0 (0)	3 (7)	4 (3)	4 (3)
<i>Philonthus quisquiliarius</i>	16	0.7	0	8	6	6
<i>Philonthus tenuicornis</i>	1	0.0	0	1	1	1
<i>Philonthus varians</i>	0 (9)	0.0 (0.4)	0 (0)	0 (2)	0 (7)	0 (7)
<i>Platydacus latebricola</i>	0 (3)	0.0 (0.1)	0 (0)	0 (2)	0 (2)	0 (2)
<i>Platydacus stercorarius</i>	89 (9)	3.7 (0.4)	0 (0)	43 (3)	6 (5)	8 (5)
<i>Platystethus alutaceus</i>	2	0.1	0	1	2	2
<i>Platystethus capito</i>	3	0.1	0	2	2	2
<i>Platystethus nitens</i>	6	0.3	0	3	4	4
<i>Proteinus laevigatus</i>	0 (2)	0.0 (0.1)	0 (0)	0 (1)	0 (2)	0 (2)
<i>Quedius boops</i>	11	0.5	0	4	5	6
<i>Quedius fuliginosus</i>	0 (1)	0.0 (0.1)	0 (0)	0 (1)	0 (1)	0 (1)

<i>Quedius levicollis</i>	52 (16)	2.2 (0.7)	0 (0)	17 (4)	9 (8)	11 (9)
<i>Quedius nitipennis</i>	49	2.0	0	8	16	18
<i>Quedius semiaeneus</i>	6 (4)	0.3 (0.2)	0 (0)	2 (1)	5 (4)	5 (4)
<i>Rabigus pullus</i>	50 (8)	2.1 (0.3)	0 (0)	11 (7)	8 (2)	10 (2)
<i>Scopaeus laevigatus</i>	92 (1)	3.8 (0.0)	0 (0)	12 (1)	15 (1)	20 (1)
<i>Scopaeus minutus</i>	7	0.3	0	3	4	5
<i>Sepedophilus pedicularis</i>	2	0.1	0	1	2	2
<i>Stenus ater</i>	21 (3)	0.9 (0.1)	0 (0)	12 (2)	7 (2)	8 (2)
<i>Stenus atratulus</i>	32	1.3	0	15	9	10
<i>Stenus junco</i>	0 (1)	0.0 (0.1)	0 (0)	0 (1)	0 (1)	0 (1)
<i>Tachyporus chrysomelinus</i>	6	0.3	0	4	3	3
<i>Tachyporus hypnorum</i>	10 (1)	0.4 (0.0)	0 (0)	3 (1)	5 (1)	5 (1)
<i>Tachyporus nitidulus</i>	14	0.6	0	8	5	6

	<i>Tachyporus obtusus</i>	2	0.1	0	1	2	2
	<i>Tachyporus pusillus</i>	30 (1)	1.3 (0.0)	0 (0)	6 (1)	11 (1)	15 (1)
	<i>Tasgius ater</i>	1	0.0	0	1	1	1
	<i>Tasgius melanarius</i>	0 (1)	0.0 (0.1)	0 (0)	0 (1)	0 (1)	0 (1)
	<i>Thanatophilus sinuatus</i>	0 (14)	0.0 (0.6)	0 (0)	0 (3)	0 (6)	0 (7)
	<i>Tinotus morion</i>	1	0.0	0	1	1	1
	<i>Xantholinus linearis</i>	60 (11)	2.5 (0.5)	0 (0)	11 (4)	11 (7)	15 (7)
	<i>Xantholinus semirufus</i>	23	1.0	0	12	2	3
	<i>Zoosetha prociua</i>	15	0.6	0	6	2	3
Tenebrionidae	<i>Cteniopus flavus</i>	0 (2)	0.0 (0.1)	0 (0)	0 (2)	0 (1)	0 (1)
Zopheridae	<i>Bitoma crenata</i>	1	0.0	0	1	1	1

Supplementary Material, Table S2. Generalized linear mixed model results for landscape variables. Statistically significant coefficients ($p < 0.05$) are indicated in bold. Est. = coefficient, SE = standard error. Species that were analysed after removing roofs with zero occurrences are denoted with *.

Species	Intercept		Imp100		Green100		Build100		Imp400		Build400		Green400		Rail400S	
	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE
<i>Protapion fulvipes</i>	-8.25	0.50							0.48	0.24						
<i>Cytilus sericeus</i>	-7.99	0.60							0.98	0.45						
<i>Amara aenea</i> *	-5.12	0.29									0.65	0.28				
<i>Amara tibialis</i>	-6.35	0.33											-0.51	0.34		
<i>Anisodactylus binotatus</i>	-9.71	0.80	0.85	0.20												
<i>Bembidion quadrimaculatum</i>	-6.04	0.34			0.74	0.23										
<i>Calathus melanocephalus</i>	-8.45	0.52														
<i>Elaphropus parvulus</i>	-5.29	0.20														
<i>Harpalus affinis</i>	-5.63	0.40														
<i>Harpalus anxius</i> *	-8.26	0.83														
<i>Harpalus attenuatus</i>	-8.03	0.51														

<i>Harpalus rubripes</i>	-4.89	0.24								-0.55	0.21
<i>Harpalus tardus</i>	-9.65	1.54									-1.56 1.11
<i>Parophonus maculicornis</i>	-7.37	0.33									
<i>Poecilus cupreus</i>	-8.13	0.47					1.91	0.54		2.27	0.50
<i>Pseudoophonus rufipes</i>	-8.10	0.52		0.84	0.33	1.34	0.49				
<i>Pterostichus vernalis</i> *	-6.34	0.24					1.99	0.62		0.60	0.46
<i>Syntomus foveatus</i>	-7.60	0.34				1.07	0.28				
<i>Chaetocnema hortensis</i>	-4.37	0.25									
<i>Longitarsus melanocephalus</i>	-6.94	0.45								-1.72	0.52
<i>Longitarsus pratensis</i>	-6.73	0.28						0.57	0.29		0.58 0.27
<i>Coccinella septempunctata</i>	-7.75	0.43								-1.32	0.57 0.67 0.34
<i>Tytthaspis sedecimpunctata</i>	-9.58	1.09									
<i>Hypera miles</i>	-7.96	0.63									
<i>Sitona cylindricolis</i>	-7.64	0.38				0.46	0.30				
<i>Sitona humeralis</i>	-8.25	0.45				0.55	0.24				
<i>Corticarina truncatella</i>	-8.39	0.49				0.79	0.30				

<i>Melanophthalma distinguenda</i>	-7.39	0.46							
<i>Atheta fungi</i>	-7.39	0.30							
<i>Aleochara bipustulata</i>	-8.29	0.44	1.64	0.39	1.42	0.48			
<i>Amischa decipiens</i>	-6.82	0.27							
<i>Carpelimus corticinus</i>	-7.06	0.51							
<i>Oxypoda praecox</i>	-8.82	0.73			1.62	0.73		0.80	0.38
<i>Philonthus carbonarius</i>	-7.26	0.32							
<i>Platydracus stercorarius</i>	-9.39	1.05						-1.45	0.91
<i>Quedius levicollis</i>	-8.12	0.52	1.30	0.48	1.40	0.61			
<i>Quedius nitipennis</i>	-6.90	0.24							
<i>Rabigus pullus</i>	-8.92	0.88	3.73	1.84	4.36	2.10			
<i>Scopaeus laevigatus</i>	-6.37	0.22							
<i>Stenus ater</i>	-9.64	0.97							
<i>Stenus atratulus</i>	-8.22	0.46	0.81	0.27					
<i>Tachyporus pusillus*</i>	-7.76	0.42			1.42	0.44			
<i>Xantholinus linearis</i>	-7.65	0.43							

Supplementary Material, Table S3. Descriptive data of the 24 trapping sites on the 17 green roofs in Basel, Switzerland.

Site	Age (years)	Area (m ²)	Height (m)	Substrate depth (cm)	Substrate contents
BVB Bus garage Rank, upper roof level	3	1540	7.5	3.6	Lava-pumice
BVB Bus garage Rank, lower roof level	3	370	6.0	10.6	Sandy gravel (grain size 0-30 mm) with Crushed tiles and compost
BVB Tram depot Wiesenplatz, roof level with varying slope conditions	2	6220	8.0	7.4	Crushed tiles, lava-pumice, compost
BVB Tram depot Wiesenplatz, roof level without slope	2	930	6.5	10.6	Crushed tiles, lava-pumice, compost
Erlenmatt upper roof level	4	1350	22.0	13.6	Sandy gravel (grain size 0-30 mm), compost, lava-pumice
Erlenmatt lower roof level	4	480	10.0	14.6	Sandy gravel (grain size 0-30 mm), compost, lava-pumice
Felix Platter Hospital, lower roof level	3	1260	3.5	7.8	Crushed tiles, lava-pumice, compost and

					straw
Jacob Burckhardt-Haus, Roof part west	6	5350	18.5	16.0	Lava-pumice, sand, compost, sandy gravel (grain size 0-200 mm)
Jacob Burckhardt-Haus, Roof part north	6	5350	18.5	4.2	Lava-pumice
Jacob Burckhardt-Haus, Roof part east	6	5350	18.5	11.4	Lava-pumice, topsoil, sandy gravel (grain size 0-200 mm)
University Hospital Klinikum 2, substrate level 8 - 12 cm	10	3000	18.0	7.8	Sandy topsoil
University Hospital Klinikum 2, substrate level 12 - 20 cm	10	3000	18.0	19.2	Sandy topsoil, topsoil
Exhibition hall 1, shallow substrate area	14	11200	15.0	6.0	Lava-pumice
Exhibition hall 1, higher substrate level area with added wood	14	11200	15.0	6.4	Lava-pumice, compost, wood
Exhibition hall 1, part mixed with fotovoltaic panels	14	11200	15.0	10.0	Lava-pumice

Migros Eglisee	17	860	5.0	7.8	Lava-pumice
Nordtangente, gravel part	14	7050	2.0	16.6	Sandy gravel (grain size 0-200 mm)
Nordtangente, soil part	14	7050	2.0	48.0	Sandy gravel (grain size 0-200 mm), topped with topsoil
Pirelli	1	650	11.0	8.3	Sandy gravel (grain size 0-30 mm), compost, lava-pumice, straw
Rhypark	26	830	2.0	11.2	Sandy gravel (grain size 0-30 mm), topsoil
Rossetti-Building	15	1300	14.0	13.4	Loamy gravel (grain size 0-200 mm)
Stücki Shopping Center, gravel part	4	11960	13.0	9.6	Sandy-loamy gravel (grain size 0-30 mm)
Stücki Shopping Center, meadow part	4	11960	13.0	24.8	Sandy-loamy gravel (grain size 0-30 mm), topsoil
University Hospital for children	14	4280	16.0	9.0	sandy gravel (grain size 0-30 mm), compost, lava-pumice

25 Supplementary Material, Figure S4. Rarefaction curves for the beetle data from the 24 sampling sites.