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Research article

Metabarcoding assessment of arthropod diversity on green roofs in the metropolitan city of Hamburg

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Abstract

Cities have become valuable alternative habitats for many organisms, particularly arthropods, as they often offer more favourable environmental conditions, and greater resource availability compared to neighbouring intensive agroecosystems. However, urban biodiversity is threatened by habitat loss and fragmentation, driven mainly by urban development and densification. Green roofs are novel urban green spaces that may represent valuable stepping stones, supporting various taxa. However, so far, only few studies have evaluated the potential of green roofs to support the conservation of biodiversity in cities. Here, we assessed species richness and diversity of vascular plants and arthropods on eight extensive green roofs in the city of Hamburg in northern Germany to understand which local green roof parameters and landscape scale factors may support high arthropod richness on green roofs. Plant diversity varied between roofs, but none of the parameters explained the variance in plant diversity, with only age having a slightly negative effect. Arthropod richness was positively influenced by green roof size and arthropod composition by diversity of vascular plants on the green roofs. In addition, the amount of green land use types surrounding the location of the green roof had a positive effect on arthropod richness. Our results indicate that green roofs can harbor various arthropod species and could function as urban stepping stones for many species to enhance the connectivity of existing green spaces and, thereby, enhance urban biodiversity.

Key words: insect decline; urban ecology; connectivity; stepping stone habitats; plant diversity

Introduction

With a constantly growing global human population, agricultural practices in rural areas intensified to meet the growing global food demands (Tilman *et al.* 2011, Rosenzweig 2016). At the same time, animal and plant diversity continues to decline as a result of landscape alteration driven primarily by agricultural expansion and intensification (Díaz *et al.* 2019, Seibold *et al.* 2019, Eichenberg *et al.* 2020, Outhwaite *et al.* 2022). The unprecedented current rate of urban development poses an additional threat to biodiversity by fragmenting habitats, reducing green spaces and intensifying the impacts of pollution (Piano *et al.* 2020, Liang *et al.* 2023). Among the many groups affected, insects, the largest groups of animals, are experiencing rapid declines due to urban expansion. Their vulnerability is largely attributed to factors such as the body size, limited mobility and specific nesting requirements (Fenoglio *et al.* 2021, Vaz *et al.* 2023). Yet, paradoxically, cities can support a high number of plant and animal species and may harbor greater species diversity than rural areas (Aronson *et al.* 2014, Ives *et al.* 2016, Theodorou *et al.* 2020b). As such, recent studies argue that managing urban ecosystems through the development of green infrastructure – "strategically planned networks of natural and semi-natural areas" designed to deliver ecosystems services and enhance biodiversity (European Commission 2019, p. 1) - could be beneficial. By establishing interconnected green spaces with diverse habitat conditions, cities may act as refugia for plants and animals threatened by agricultural intensification (Madre *et al.* 2014, Baldock 2020, Theodorou *et al.* 2020b, Wenzel *et al.* 2020, Gentili *et al.* 2024).

A current and widely discussed approach to mitigate climate change and the negative effects of landscape alteration along with promoting biodiversity, particularly in urban areas, is the construction of green roofs (Knapp *et al.* 2019, Joshi *et al.* 2020). With an estimate of 20–25% of urban surfaces in the US being rooftops (Akbari and Rose 2008) and 14% of roofs being potentially suitable for greening (exemplified for the state of Brandenburg, Germany; Grunwald *et al.* 2017), there is great

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potential to establish green habitats within cities (Besir and Cuce 2018). Green roofs, characterized as roofs with vegetated surface and substrate (Oberndorfer et al. 2007), may provide multiple benefits in dense urban areas, such as storm and rainwater run-off management, mitigating the urban heat island (UHI) effect, providing insulation and therefore, decreasing energy consumption as well as air and water pollution (Oberndorfer et al. 2007, Berardi et al. 2014, Sutton 2015, Clar and Steurer 2021). They contribute to the sustainability, resilience and quality of life of cities and are relevant to the *Nature-based Solution* concept (NbS), which describes actions to preserve and enhance nature to mitigate and overcome societal challenges (Seddon et al. 2020). Furthermore, they have potential to improve urban biodiversity and represent important stepping stones for insects and other invertebrates by connecting (ground-level) habitats (Braaker et al. 2014).

As green roofs are very variable in design and structure, ranging from simple extensive green roofs, which have a shallow substrate supporting simple sedum vegetation and low maintenance requirements, to complex intensive green roofs, having a deeper substrate (>20 cm) with complex vegetation and high maintenance costs (Oberndorfer et al. 2007), there are many different parameters that can determine their efficacy in supporting high species diversity. Substrate depth has an impact on plant diversity, since a deeper substrate can store more water and allows deeper root growth (Oberndorfer et al. 2007, Madre et al. 2013, 2014, Lönnqvist et al. 2021, Gonsalves et al. 2022). This allows a wider variety of species to persist, which may enhance the structural complexity of vegetation (Madre et al. 2013, Köhler and Kaiser 2021), thereby providing a feeding habitat for ground-dwelling species and pollinators (Haddad et al. 2011, Cook-Patton 2015, Bevk 2021). A comparison between simple green roofs (little structural diversity) and green roofs with more complexity, which have varying substrate depths, vegetation layers and woody debris, also showed that the higher habitat complexity of the latter supported a higher degree of insect diversity (Gonsalves et al. 2022). Another important factor is the size of the green roof. When investigating urban green spaces, Matthies et al. (2017) found that patch size positively influences plant and bird diversity. Similarly, Beninde et al. (2015) found patch size to be an important predictor for plant and insect diversity in an urban setting and Madre et al. (2013) found that patch size of green roofs has a positive influence on species richness. The results of these studies both align with the theory of island biogeography (MacArthur and Wilson 1967) and the species-area relationship concept, where larger green roofs host greater species diversity, similar to larger islands tending to support more species by offering more resources and diverse microhabitats (Lepczyk et al. 2017, Lönnqvist et al. 2021, Calheiros et al. 2022). Another factor that could influence the diversity on green roofs is the age of the roof (Madre et al. 2014, Beninde et al. 2015, Lönnqvist et al. 2021, Gonsalves et al. 2022). However, some studies found that older roofs have lower diversity, while others found no correlation between the age of the roof and species diversity. Additionally, the height of the roof can influence the abundance and species richness, since higher roofs may be harder to access and colonize or are more exposed to wind (Berardi et al. 2014, Madre et al. 2014, Williams et al. 2014, Lepczyk et al. 2017). In addition to the roof characteristics, the surroundings of green roofs influence their species diversity; urban areas with green land use types, such as parks, grassy areas, open unused spaces and small groves, in close proximity promote higher diversity on green roofs (Madre et al. 2014, Kyrö et al. 2018).

Here, we studied eight green roofs in the city of Hamburg, assessing vascular plant diversity, arthropod richness together with other local and landscape factors to identify key parameters influencing biodiversity on the selected green roofs in Hamburg and to answer the question: What are the primary determinants influencing arthropod richness on selected green roofs in Hamburg, and how do local roof parameters and surrounding landscape factors shape biodiversity patterns? The following hypotheses were tested: (1) A more diverse vegetation layer supports a higher richness of arthropods. (2) In addition to plant diversity and richness, the green roof size is an important predictor of arthropod species richness (we exclude age and height as factors as our setup shows too little variability between roofs) and (3) roofs embedded in a matrix of urban green land use types support a higher diversity of plant and arthropod species richness.

Materials and methods

Study area and selection of green roofs

This study was carried out on green roofs in the city of Hamburg in northern Germany (53° 33′ N, 10° 0′ E, 6 m a.s.l., Fig. 1).

Hamburg is located within the temperate climate zone and is, due to its proximity to the Baltic and North Sea, also characterized by an oceanic climate, with mild winters and temperate summers (Schmidt et al. 2014). Approximately 8% of Hamburg's surface area are bodies of water, vegetation cover accounts for 33% and settlement area accounts for 47% (Statistisches Amt für Hamburg und Schleswig-Holstein 2021). Being the second largest city in Germany with ∼1.8 million inhabitants, Hamburg faces several environmental and climatic challenges (Schlünzen et al. 2010, Four pillars to Hamburg's Green Roof Strategy 2016, Clar and Steurer 2021). However, Hamburg is often referred to as the main example of green roof implementation and was one of the first German cities to develop and implement a "green roof strategy" in 2015 (Four pillars to Hamburg's Green Roof Strategy 2016).

In total, we selected eight green roofs, evenly distributed across the area of the city of Hamburg (Fig. 1). The minimum distance between two roofs was 3.2 km (Exception "HPA BG1" and "HPA BG2" which were only 320 m apart), sufficient distance for the roofs to be considered independent. All green roofs are characterized as extensive green roofs, and one of them ("Lutterothstraße") has integrated rainwater retention mechanisms (Fig. 2). To describe the design characteristics of each roof, further parameters (roof type, age, height, total area, green roof size and maintenance) were recorded before sampling (Table 1). Additionally, we measured the substrate depth of the roofs, the cover of moss and lichens, cover and diversity of plants and surrounding land use types.

Since the architectural drawings were not accessible for all roofs, the total roof area and the green roof size (planted area on the roof excluding gravel areas and ventilation systems) were estimated using *QGIS* (Version 3.34.3-Prizren). Roof height data was mainly obtained from architectural drawings and in three cases, by personal communication with the person managing the roof.

All the eight roofs had parapet walls (low walls surrounding the rooftops), with three of them being higher than 70 cm, to protect the roofs from weather conditions and for human safety measures. Therefore, to minimize the effects of differential sun exposure, wind, and other weather parameters on the analyzed areas on the roofs, for the analyses, the green roof size was reduced by 1 m on each side using the "buffer" function in *QGIS*. For further analysis, random points were placed within the buffered roof area using the "random points in layer bounds" function

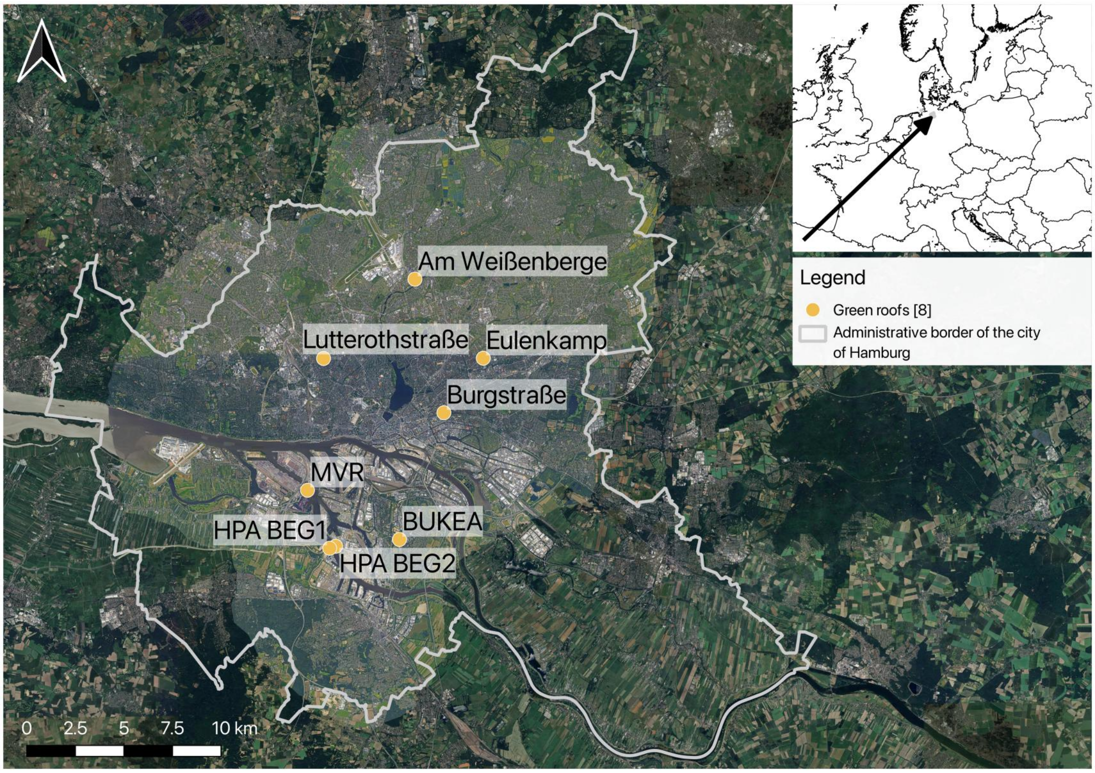

Figure 1. Overview map of the locations of the eight studied green roofs in Hamburg. The municipal boundary of Hamburg is shown with the grey line. The map was created using the current satellite imagery from Google Maps (Map data: ©2015 Google) and QGIS (Version 3.34.3-Prizren).

with a spacing of at least 1.5 m. These points were used as locations for arthropod traps, as well as the center of the 1 m^2 plots for the floristic analysis. Due to nesting seagulls, a limited part of the roof BUKEA was safely accessible. Traps and floristic analysis were placed randomly within this area. None of the roofs are accessible to the public.

Vegetation surveys and landscape variables

Each green roof was sampled with five plots of 1 m^2 size resulting in a total of 40 vegetation plots. To obtain standardized data, the plot size and number per roof were consistent across all roofs. This plot size has been shown to effectively capture typical vegetation characteristics on green roofs (Madre *et al.* 2014, Nash *et al.* 2016), and its size is small enough to allow for multiple repetitions across the roof, enabling the collection of data from various areas, ensuring a more comprehensive representation of the vegetation across the entire roof. Within the plot, plant species, their cover, growth height, substrate depth, stone coverage and percentage of litter were documented, and the Shannon diversity and Evenness calculated (Table 4 and Table S1). Moss and lichen cover was also estimated, and the presence of sandy areas or dead wood was noted for the entire green roof (Table S1).

Plant abundance was estimated using the semi-quantitative method of Braun-Blanquet (Reichelt and Wilmanns 1973, Tiemeyer *et al.* 2017, Tables S2 and S3). Most plants were identified on-site to minimize damage to the roof's vegetation. The species were identified using the following literature: Jäger *et al.* (2008), Parolly *et al.* (2016), Raabe, (1975) and Schauer *et al.* (2016). Information about originally planted species was obtained from roof manufacturing details. Unfortunately, the provided lists solely contain estimates of species and no detailed information. For two roofs the information was not available.

To estimate the composition of the surrounding landscape of a green roof, land use data provided by the Behörde für Umwelt, Klima, Energie und Agrarwirtschaft (BUKEA) was analyzed within a radius of 1 km of each site (BUKEA 2022). Using QGIS, land use types and their surface area were determined. Categories for describing land use types were chosen according to the land use classes predefined by the BUKEA and are as follows: "gray" for residential, commercial, industrial areas and roads and "green" for green spaces, parks, small groves, grassy areas and open unused vegetated spaces (Table 2).

Arthropod sampling and DNA metabarcoding

Arthropods were sampled from May to June 2022. The traps were installed on the 16^{th} and 17^{th} of May and controlled and emptied on a weekly basis. As the green roofs were spread throughout the city, they could not be visited all in one day, but in two consecutive days.

Each green roof was sampled with five pitfall traps and three pan-traps (Fig. S1). At the first visit to the green roof, pitfall traps (plastic cups with an opening of 8.5 cm and a height of 10 cm) were placed according to the random points with at least 1.5 m distance. Holes were carefully dug into the substrate to fit the plastic cup and the edges were evened with the soil surface. To prevent the destruction of the pitfall and pan traps, wire enclosures were placed around them and fixed with stones. Unfortunately, on one green roof ("Lutterothstraße"), three of the five traps were emptied, presumably by birds, after the initial installation. Hence, the wire enclosures for the traps were hereafter fixed with tent pegs. This wire may influence capture of larger species (e.g. butterflies and bumblebees), yet, as all traps were treated similarly, comparability is not affected. As trapping solution, we used 200 ml of 99.5% propylene glycol, which is non-toxic, not flammable, evaporates slower than ethanol and has

Figure 2. Photographs of the vegetated areas of the eight analyzed green roofs (1 = MVR, 2 = HPA BG1, 3 = HPA BG2, 4 = BUKEA, 5 = Lutterothstraße, 6 = Am Weißenberge, 7 = Eulenkamp, 8 = Burgstraße).

Table 1. Green roof design characteristics (roof type, age, height, total area, green roof size and maintenance).

Roof	Roof type	Age [years]	Height [m]	Total area [m^2]	Green roof size [m^2]	Maintenance [1 = once a year]
MVR	Extensive	23	25.43	1496.89	1306.26	1
HPA BG1	Extensive	4	24.18	52.13	37.03	1
HPA BG2	Extensive	4	4.13	155.55	113.34	1
BUKEA	Extensive	9	20.10	1590.14	1364.81	1
Lutterothstraße	Extensive (retention)	6	17.85	440.36	339.03	1
Am Weißenberge	Extensive	7	12.20	107.11	72.18	1
Eulenkamp	Extensive	7	12.50	1015.16	620.16	1
Burgstraße	Extensive	7	18.91	1131.46	967.58	1

been proven to be effective in preserving insect DNA (Nakamura et al. 2020, Martoni et al. 2021). Traps were emptied and refilled with fresh medium every week, four times each.

Pan-traps were placed in the third week of the sampling period and emptied once a week for a period of two weeks. The traps themselves consisted of plastic bowls with an opening of 14.5 cm and a height of 5 cm and were filled with 200 ml of 99.5% propylene glycol. They were spray painted with UV-bright colors white, yellow and blue (Sparvar Leuchtfarbe, Spray-Color GmbH, Merzenich, Germany; Westphal et al. 2008). Colored UV-bright pan-traps have been shown to be more efficient, as they mimic the natural ability of flowers to reflect UV light (Westphal et al. 2008, Abrahamczyk et al. 2010, Nuttman et al. 2011, Saunders and Luck 2013). Each roof had a yellow, blue, and white trap placed in its center.

The sampled individuals were kept in fresh propylene glycol. As the trapping solution could also contain DNA fragments, 50 ml of each week's sample was kept and added to the final sample. The samples were pooled per green roof, resulting in eight samples for metabarcoding. DNA metabarcoding was chosen as a taxonomic classification method due to its high efficacy with mixed bulk samples from insect trapping (Piper *et al.* 2019, Svenningsen *et al.* 2021). DNA extraction, amplification and sequencing on an Illumina HiSeq 2000 were performed by Advanced Identification Methods (AIM, Leipzig, Germany). For bulk amplification of the CO1 mini barcode region, the primers (mlCOIintF/jgHCO2198) provided by Leray *et al.* (2013) were used.

The obtained sequences were quality filtered, cleaned, trimmed and clustered using Swarm 3.1.0 and the parameters -d 13—usearch-abundance. A cluster, also called a molecular operational taxonomic unit (mOTU), combines sequences that do not differ by more than 2%. The mOTUs can then be used to find hits in a reference database. To identify species, two databases (BOLD and NCBI) and one classifier (RDP Classifier = Ribosomal Database Project Classifier) were used. Some individuals could not be identified at the species level, as they may not be documented yet, or the databases and the classifier do not coincide with their species suggestion. Therefore, some mOTUs were only classified at the genus, family, or order levels. Subsequently, we only used arthropod species, that were unequivocally identified by the databases and those determined at the genus level after further manual checking. If at least two suggestions from the databases and the classifier were in concordance, the species were included in the final analysis and named as follows: *Psychoda* cf *satchelli*. Total arthropod richness was calculated from the metabarcoding data and used in our downstream statistical analysis.

Statistical analysis

The diversity of plant communities on the green roofs was estimated using the Shannon-Wiener index. The Shannon-Wiener index, denoted as H′, considers the number of species in the given habitat and their relative abundance. The higher the value of H′, the higher the diversity of species in the habitat. An H′ of 0 indicates that there is only a single or no species present.

To determine the most important predictors for plant diversity and richness on green roofs, we used a generalized linear model (GLM). The age of the roof, the green roof size, the amount of the surrounding green land use types at a radius of 1 km, the mean cover of vascular plants, the mean cover of moss and lichens and the substrate depth were used as predictors (Table 3). To determine the most important predictors of arthropod mOTU richness, we used generalized linear models (GLMs) with a negative binomial error structure. The Shannon diversity of plants, the green roof size, the amount of the surrounding green and gray land use types within a radius of 1 km and the height of the roof were used as predictors (Table 3). For all models, we used the "dredge"-function within the *MuMln R package* (Kamil Bartoń 2020) to find the best model(s) with up to two predictors to avoid overfitting. The models were ranked according to their AIC values (Akaike information criterion). We used a cut-off ΔAIC value of 2 (Burnham and Anderson 2004) and, if more than one model was retained, we used model averaging (function 'model.avg'; Barton 2020).

To analyze species community composition, we used a canonical correspondence analysis (CCA) using the *vegan package* in R (Oksanen *et al.* 2022). To determine the main environmental factors influencing the composition of the community of arthropod and insect species, a full model including the amount of the green and gray land use types within a radius of 1 km, the Shannon diversity of plants, the green roof size and the roof height were used in CCA. Next, we carried out a forward and backward selection to identify the most important predictors.

Table 2. Percentage of green and grey land use types per green roof categorized according to their land use class as defined by the BUKEA (green = green spaces, parks, small groves, grassy areas and open unused spaces and gray = residential, commercial and industrial areas, including highways and track installations). Land use types were described in a 1 km circular radius measured from the center of the roof.

Roof	Sum green biotopes [%]	Sum grey biotopes [%]
MVR	2.32	50.64
HPA BG1	29.94	22.91
HPA BG2	24.53	34.82
BUKEA	15.37	53.44
Lutterothstraße	10.90	69.46
Am Weißenberge	3.09	69.45
Eulenkamp	8.09	76.92
Burgstraße	4.32	83.04

Table 3. Predictors influencing the species richness of vascular plants and arthropods using generalized linear models (GLMs). Significance levels are given for selected variables ($P \leq 0.05$*, $P \leq 0.01$**, $P \leq 0.001$***, ns = not significant, not relevant = no explanatory predictor in model according to AIC).

Response variable	Predictor	P-value
Vascular plant richness	Age	Not relevant
	Green roof size [m^2]	Not relevant
	Green land use types	0.225 ns
	Mean cover of vascular plants	Not relevant
	Mean cover of moss and lichens	0.967 ns
	Substrate depth	Not relevant
Arthropod richness	Green roof size [m^2]	3.19e-07***
	Green land use types	< 2e-16***
	Gray land use types	Not relevant
	Shannon diversity of plants	Not relevant
	Height of the roof	Not relevant

Analyses were performed using the *R Statistical Software* and *RStudio* (v4.1.2, R Core Team 2021, RStudio Team 2022) including the following packages: *MASS* (Venables *et al.* 2002), *effects and car* (Fox and Weisberg 2018). All predictors were standardized to a mean of 0 and a standard deviation of 1 prior to analysis. We used variance inflation factors with a cut-off value of 3 to check for multicollinearity (Zuur *et al.* 2009). No major effects of collinearity were found (VIF was lower than 3 for all predictors). All model (GLM and LM) assumptions were checked visually and were found to conform to expectations (e.g. normality of the distribution of residuals, homoscedasticity, linearity, no outliers). The residuals of all regression models were tested for spatial autocorrelation using Moran's *I* implemented in the R package 'ape' (Paradis and Schliep 2019). The residuals were not found to be autocorrelated ($P > 0.05$ for all models).

Results

Environmental characteristics of the green roofs

Substrate depth varied between green roofs with a maximum of 17 cm and a minimum of 7.4 cm (Table S1). The mean cover of mosses and lichens varied between 84% and 6% and the maximum of the mean vascular plant cover was 57% with a minimum of 38% (Table S1).

In total, 61 vascular plant species (min. 8 on Burgstraße and max. 28 on Lutterothstraße) were found across all green roofs (Table S4). These species belonged to 16 families (Fig. 3). With 14 species, Asteraceae was the plant family with most species, followed by Crassulaceae with 11 and Caryophyllaceae with seven species. Three species, all belonging to the family of Crassulaceae, occurred on each green roof: *Phedimus kamtschaticus*, *Sedum sexangulare* and *Phedimus spurius*. All roofs were designed as sedum-roofs, however the number of species found on the roofs differed (Table 4). Model selection identified the null model to be the best model and none of our predictors influenced plant richness (Table 3). Green roofs originally contained between 50–55 species and at the time of this study supported an average of 11.33 ± 6.13 species of the originally sown ones (Table S5). Am Weißenberge only contained 10% (5 out of 50 species) of the original ones, while Lutterothstraße still supported 41% (23 out of 55 species).

Arthropod richness and community composition

Illumina sequencing of arthropods captured in traps on the eight green roofs resulted in 633 mOTUs. After removing all mOTUs not attributed to Arthropoda, our total metabarcoding dataset contained 621 mOTUs. The majority of mOTUs (354 out of 621, 57.0%) were successfully assigned at species level (Table S6) and can be divided into the following classes: 306 species (86.44%) belonged to Insecta, followed by Arachnida with 26 species (7.34%), Collembola (8 species, 2.26%), Chilopoda (6 species, 1.69%) and Malacostraca and Diplopoda both with 4 species (1.13%). The Arthropoda included 18 orders which are displayed in Fig. 3.

On average, each green roof harbored 75.5 ± 32.35 SD arthropod species (Table 5). No species occurred on all roofs, but the domestic honeybee, *Apis mellifera*, was the only one present on most roofs, except for the green roof "HPA BG1".

The automated model selection approach to explore the potential of multiple factors influencing arthropod and insect richness, revealed strong effects of the green roof size as well as the surface area of the surrounding green land use types on richness. We found a positive relationship between the green roof size and arthropod richness (GLM; $z = 5.11$, $P < 0.001$; Fig. 4). In addition, the amount of green land use types in the surroundings of the roof had a positive effect on arthropod richness (GLM; $z = 9.33$, $P < 0.001$; Fig. 4), especially on the orders Diptera, Coleoptera and Lepidoptera (GLM; $z = 6.49$, $P < 0.001$; $z = 4.12$, $P < 0.001$; $z = 2.44$, $P < 0.01$, respectively).

A canonical correspondence analysis was carried out for arthropods to examine the most important predictors of their community composition. Important predictors for each response variable are shown in Table 6. The composition of arthropods was significantly influenced by the amount of green land use types ($P < 0.01$) and the amount of gray land use types (i.e. residential, commercial, industrial areas and roads) ($P < 0.05$), the green roof size (m^2) ($P < 0.01$) and the Shannon diversity of plants ($P < 0.05$; Table 6 and Fig. S2).

Discussion

Our study shows the potential of green roofs as resources for supporting and enhancing urban biodiversity. Interestingly, plant species diversity on the roofs could not be explained by any of the measured variables. In contrast, arthropod richness was strongly positively related to the green roof size and the proportion of green land use types in the surrounding area. A smaller positive effect on the arthropod composition was detected for plant diversity. In the following section, we discuss these findings in relation to our research aims and explore their implications for urban biodiversity conservation.

Effects of local roof characteristics on arthropod communities

Firstly, we tested the effects of different green roof characteristics on arthropod richness. Contrary to our expectations and other studies, plant richness and diversity on green roofs did not affect arthropod richness in our study, but only arthropod community composition (Ollerton 2017, Drukker *et al.* 2018, Theodorou *et al.* 2020a).

While we do not see a relationship between arthropod richness and the plant species richness and diversity, we detected a weak, positive relationship of plant species diversity on arthropod composition. This indicates that vegetation contributes to shaping the composition of arthropod communities, but not necessarily determines their richness in this system, suggesting that while certain arthropod groups (e.g. pollinators and surface-dwelling species) respond to plant diversity, the full extent of the interaction may depend on the inclusion of phytophagous species, which were likely underrepresented and therefore probably

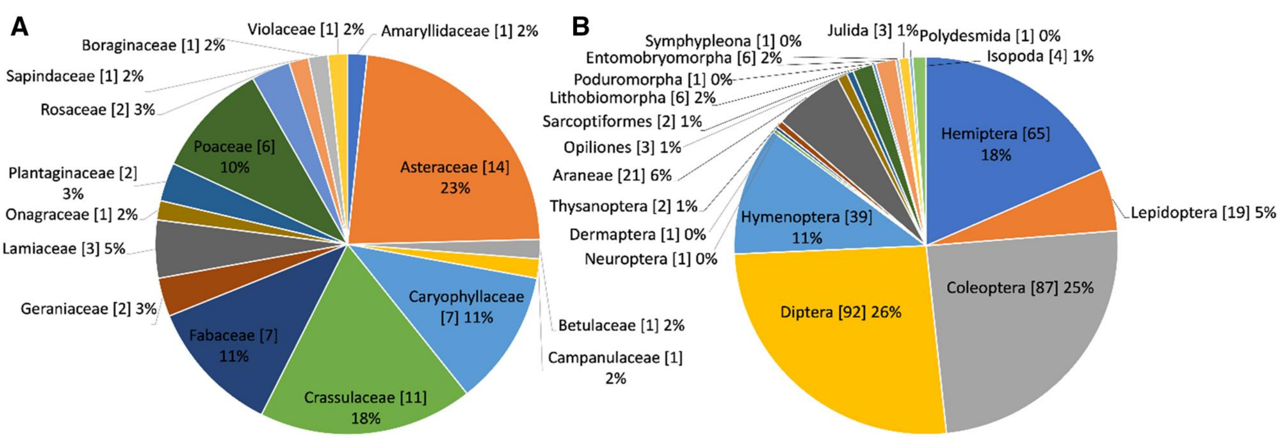

Figure 3. Pie chart showing the vascular plant composition found across all green roofs (A). The absolute number of species per plant family is displayed in square brackets followed by the percentage. Pie chart showing the arthropod composition found across all green roofs (B). The absolute number of species per arthropod order (mOTU reads) is displayed in square brackets followed by the percentage

underestimated in the current sampling campaign. However, environmental factors (plant diversity, substrate depth, water availability, nesting and feeding grounds, etc) potentially influencing arthropod richness vary over time, showing that green roofs are dynamic ecological systems (Thuring and Dunnett 2014) and not all relationships can be analysed in small scale experiments.

While the plant species diversity did not influence the arthropod richness, our results show that the green roof size does strongly, confirming our second hypothesis. The concept of the species-area relationship describes, similar to the island biogeography theory, how habitat size correlates with species richness and diversity (Connor and McCoy 1979), mainly due to more diverse microhabitats and greater resource availability, both of which promote species richness and diversity (Fabián *et al.* 2021). Accordingly, green roof size appears to be a key predictor of arthropod richness, as supported by findings from several other studies (Berthon *et al.* 2015, Ksiazek-Mikenas *et al.* 2018, Sánchez Domínguez *et al.* 2020). Green roofs, appearing in fragmented urban environments with limited habitat availability, may act as "green islands", in line with the island biogeography theory; the green land use types surrounding the roofs likely represent the source populations.

Table 4. Number of vascular plant species, Shannon diversity and Evenness per GR. Mean values are displayed with the standard deviation.

Roof	Plant species [total number]	Shannon diversity	Evenness
MVR	11	0.996 ± 0.13	0.536 ± 0.07
HPA BG1	22	1.502 ± 0.30	0.645 ± 0.13
HPA BG2	21	1.747 ± 0.13	0.705 ± 0.05
BUKEA	19	1.588 ± 0.19	0.691 ± 0.07
Lutterothstraße	28	1.492 ± 0.48	0.639 ± 0.22
Am Weißenberge	13	1.096 ± 0.23	0.544 ± 0.11
Eulenkamp	13	1.169 ± 0.38	0.633 ± 0.13
Burgstraße	8	0.869 ± 0.44	0.493 ± 0.24

Table 5. Species richness of arthropods per roof. * marks the roof with the trap loss.

Roof	Arthropod species
MVR	56
HPA BG1	118
HPA BG2	98
BUKEA	122
Lutterothstraße*	56
Am Weißenberge	39
Eulenkamp	64
Burgstraße	51

Landscape scale effects on green roof arthropod richness and plant diversity

Findings from our study suggest that the presence of green land use types surrounding roofs significantly enhances arthropod richness, but not plant diversity, only partly supporting our third hypothesis.

The colonization of green roofs is likely to depend on patches of green habitat in the matrix between the green roofs representing the source populations. The permeability of the gray matrix, the presence of adjacent green spaces providing movement corridors, and the species traits determine the dispersal capacity. As a result, green roofs enhance the connectivity of existing green spaces in urban areas (Braaker *et al.* 2014, Mayrand and Clergeau 2018), functioning as stepping stones, enhancing migration and distribution. Consequently, a higher proportion of green land use types in the surroundings of a green roof affected the richness and composition of arthropods. As Braaker *et al.* (2014) and MacIvor and Lundholm (2011) suggest, highly mobile insects are generally more strongly affected by the connectivity to surrounding green land use types, whereas the composition of immobile species tends to be more affected by local environmental conditions.

As stepping stones, green roofs can provide essential feeding and, in some cases, nesting habitats, serving as alternative habitats and thereby counteract these negative effects and promote biodiversity conservation in cities (Blank *et al.* 2017, Ksiazek-Mikenas *et al.* 2018). However, these benefits vary depending on the taxa. Epigaeic arthropods are more likely to complete their

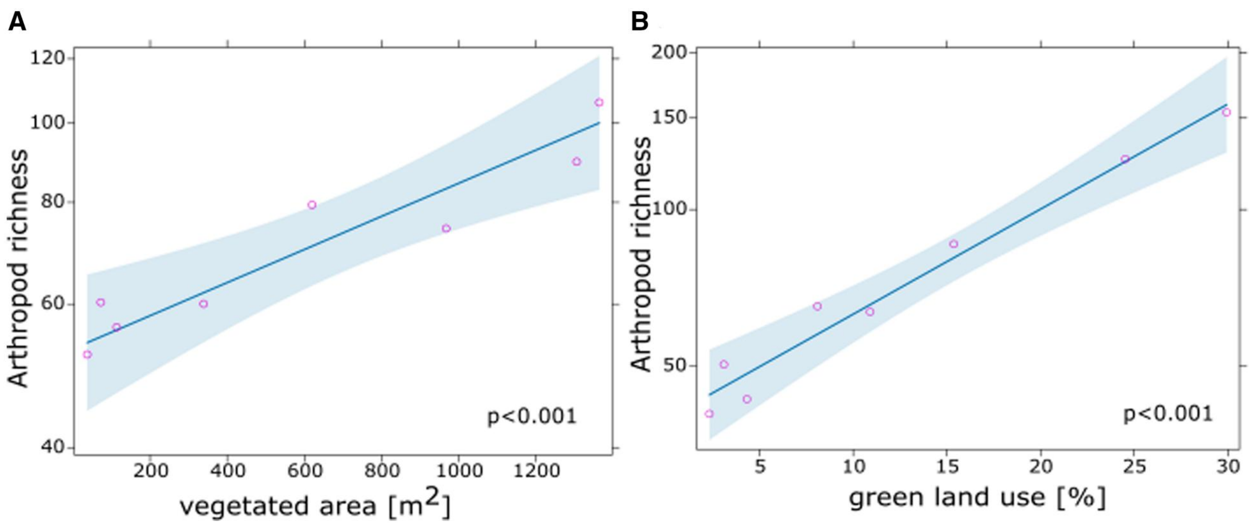

Figure 4. Effects of the green roof size (m2) (A) and the percentage (%) of green land use types in the surrounding area (B) on arthropod richness across all green roofs (*n* = 8). Blue lines correspond to the predicted relationships and shaded areas correspond to 95% confidence intervals. Partial residuals are shown.

Table 6. Predictors influencing the species composition of arthropods using a canonical correspondence analysis (CCA). Significance levels are given for selected variables ($P \leq 0.05$*, $P \leq 0.01$**, ns = not significant).

Response variable	Predictor	P-value
Arthropod community composition	Green land use types	0.005**
	Gray land use types	0.005**
	Green roof size [m^2]	0.010**
	Shannon diversity of plants	0.025*
	Height of the roof	0.600 ns

life cycle on green roofs, whereas for many pollinating insects, such as butterflies and ground-nesting or cavity-nesting bees which have very specific requirements, green roofs may not offer suitable conditions. Additionally, green roofs alone, without the presence of adjacent green spaces and their connectivity, are unlikely to play a significant role in sustaining arthropod diversity within urban environments, as existing green habitats play a crucial role in sustaining diverse and stable populations.

The diversity of plants on green roofs might not be affected by surrounding green land use types in our study, because seed dispersal may be limited by height and plant survival could be limited by substrate composition and depth (Kiehl et al. 2021). Instead, the plant diversity may be more closely related to the originally planted species and their suitability to the challenging conditions found on green roofs; ecological sorting likely plays an important role (e.g. Braaker et al. 2014). Hence, the originally planted community on the roofs may be a determining factor. However, it has to be noted that the results of this study only capture a single, short moment in time. With advancing age, the plant species diversity and composition will develop gradually from the originally seeded plants and presumably a more characteristic plant species assemblage will establish. Angold et al. (2006) and Madre et al. (2014) obtained similar results regarding plant diversity and later posed the question to which extent plants seeded on green roofs might also migrate to ground level habitats. Seven documented plant species in our study were classified as neophytes for Germany (Poppendieck 2010, Metzing et al. 2018), but four of them were included in the originally seeded plant list. If these species migrate to ground-level habitats, it becomes crucial to prioritize the use of native plants on green roofs to prevent the spread of alien species. Using non-native or neophyte species on green roofs has been common practice as these species tend to be more robust against harsh roof environments, but they can have negative implications for biodiversity, potentially leading to the displacement of native plants and a loss of ecosystem balance. Recent studies, however, also found a suite of native species to persist on green roofs making them more suitable and environmentally friendly alternatives (Kiehl et al. 2021, Esfahani et al. 2022, Fenoglio et al. 2023).

While our findings provide valuable insights into the factors influencing the value of green roofs for various arthropod species, our analysis is based on a limited number of roofs in a single city in Germany. Our analysis demonstrates that some local roof parameters influence the arthropod composition, suggesting that these effects may be further amplified when accounting for diverse geographic regions and varying local arthropod communities. Other parameters, such as age and height did not display effects on plant or arthropod richness, likely because the green roofs exhibited similar characteristics regarding these parameters (e.g. all roofs had similar heights, so the effect of height could not be explored with our data). Therefore, our results will have to be validated at a larger geographic scale with wider ranges for certain parameters. Moreover, we applied metabarcoding to identify species. This method has the advantage of objectively allowing identification of large numbers of organisms, but it still has some limitations (Förster et al. 2023). It strongly depends on the primers used and may partially have biases as some taxa amplify better than others. Furthermore, species identifications are closely tied to database completeness; therefore, we focused solely on mOTU-level analyses to ensure comparability of diversity across locations. When considering these limitations, the advantage of getting more general insight into arthropod communities compared to studies based on single groups of insects with potentially higher resolution and confidence outweighs the disadvantages.

Conclusion

This work shows the potential of green roofs to serve as stepping stones or alternative habitats for supporting arthropod diversity in urban environments. The success of a roof largely depends on the diversity and abundance of the surrounding green infrastructure, which provides source populations and essential resources, and on the green roof size. To optimize their benefits, it is crucial to design green roofs that incorporate diverse microhabitats using native plant species, which are strategically placed to enhance connectivity with surrounding green land uses and prioritize larger roof areas. Future research should investigate various types of green roofs across different urban settings while examining the impact of controlled variables on biodiversity outcomes. By understanding and optimizing the multidimensional benefits of green roofs—including stormwater management, biodiversity conservation, urban heat island mitigation and improved human well-being—their role as essential components of urban green infrastructure can be strengthened, enhancing both environmental resilience and social impacts.

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Author contributions

Stella Nevermann (Conceptualization [lead], Data curation [equal], Formal analysis [equal], Investigation [lead], Methodology [equal], Project administration [lead], Resources [equal], Validation [equal], Visualization [equal], Writing—original draft [lead], Writing—review & editing [equal]), Hannes Hoffmann (Conceptualization [equal], Investigation [equal], Methodology [equal], Supervision [equal], Validation [equal], Writing—review & editing [equal]), Panagiotis Theodorou (Data curation [equal], Formal analysis [equal], Methodology [equal], Validation [equal], Visualization [equal], Writing—review & editing [equal]), Irene Peters (Conceptualization [equal], Supervision [supporting], Writing—review & editing [equal]), and Martin Husemann (Conceptualization [equal], Data curation [equal], Funding acquisition [lead], Investigation [equal], Methodology [equal], Project administration [equal], Resources [equal], Supervision [lead], Validation [equal], Visualization [equal], Writing—review & editing [equal])

Supplementary data

Supplementary data are available at *JUECOL* online.

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Data availability

All data used in this study are available as supplementary materials.

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