



Research article

Green roofs harbor different and non-substituting invertebrate communities than surrounding ground-level habitats



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ABSTRACT

Green roofs are increasingly promoted to support urban biodiversity, potentially mitigating habitat loss from urban growth. Given their standardized design, however, green roofs are expected to differ ecologically from the ground-level habitats they are intended to substitute. Yet the extent of this divergence remains unclear, especially for taxa with varying dispersal abilities, including low-mobility invertebrates that are less often associated with green roofs. To quantify this divergence, we used environmental DNA metabarcoding to assess invertebrate diversity and identify environmental drivers affecting species with different dispersal abilities across 52 pairs of extensive green roof and ground-level sites in Zurich, Switzerland. We found that green roofs shared around 10 % of species with ground-level sites, regardless of how spatially isolated they were. Instead, green roofs harbored unique communities, albeit marginally poorer in number of species. However, this pattern varied by species mobility, with soil-dwelling species forming more heterogeneous communities, likely due to dispersal limitations between roofs. Additionally, green roof design choices, including substrate type and depth, as well as vegetation cover, emerged as key drivers of species richness, regardless of species dispersal abilities. Although green roofs do not structurally or ecologically replicate the ground-level habitats they would substitute, they provide complementary habitats that enhance urban biodiversity when designed with ecological considerations. While further research is required to evaluate the capacity of green roofs to sustain viable populations despite their spatial isolation, this study highlights practical design interventions, such as deepening the substrate, to improve their role as complementary habitats in cities.

1. Introduction

Biodiversity is declining at an alarming rate, with the elimination and fragmentation of habitats from urban sprawl and densification playing an important role (IPBES, 2019; Keck et al., 2025). Cities are called upon to restore biodiversity, offering novel environmental conditions that can support diverse species (Grimm et al., 2008; IPBES, 2019). One promising approach is the implementation of green roofs, which, beyond their well-documented benefits, such as stormwater

retention and thermal insulation, can support urban biodiversity (Brenneisen, 2006; Cook and Larsen, 2021).

In the context of ongoing urban expansion, green roofs are often promoted as compensatory measures intended to offset the loss of terrestrial habitats at the ground-level (Williams et al., 2014). However, green roofs can differ in many aspects from ground-level habitats (Cook and Larsen, 2021). Urban biodiversity requires space, connectivity, and time (Beninde et al., 2015; Nielsen et al., 2014; Ramalho and Hobbs, 2012), yet green roofs are relatively young, artificial, fragmented, and

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isolated. Nevertheless, they have been shown to provide habitats to several taxonomic groups, including spiders, beetles, bees, and birds (Brenneisen, 2006; Wang et al., 2022). They can also act as "stepping stones," supporting species movement between habitats, especially those with similar conditions to a green roof (e.g., dry, unmanaged, and highly disturbed) (Braaker et al., 2014; Williams et al., 2014).

Green roofs have also been found to share a significant number of species with similar habitat types on the ground (50 % (Braaker et al., 2014) to 74 % (Kyrö et al., 2022) of overlapping species) – although often in lower abundances (Dromgold et al., 2020; MacIvor and Lundholm, 2011). This high proportion of shared species with the ground might imply that green roofs could act as a replacement habitat for ground-level space lost during urban densification. However, most studies that evaluate green roof diversity focus on a comparison to ground-level habitats with similar environmental conditions, such as grasslands (Kyrö et al., 2022) or ruderal spaces (Braaker et al., 2014). While ecologically meaningful, such comparisons overlook the practical context in which green roofs are typically implemented—as compensatory measures for the loss of a broader and more heterogeneous array of habitats (e.g., private or shared gardens) due to urban development. In practice, green roof designs—predominantly extensive systems characterized by shallow substrates and minimal maintenance, in contrast to intensive systems with deeper soils and greater vegetation complexity—are rarely designed to replicate the ecological attributes of the habitats they substitute (Dunnett and Kingsbury, 2008; Losken et al., 2018). Instead, these systems typically adhere to standardized guidelines driven primarily by engineering requirements and cost-effectiveness (Dunnett and Kingsbury, 2008). Thus, while green roofs are unlikely to fully replicate ground-level habitats, we need to quantify the extent to which green roof communities diverge from those of nearby ground-level habitats—i.e., the spaces that they are intended to substitute.

Most studies comparing green roof and ground-level habitats have focused on highly mobile species, such as flying insects, in particular bees and ballooning spiders (Wang et al., 2022; Williams et al., 2014), which are generally well adapted to urban areas (Hahs et al., 2023). However, much less is known about the capacity of green roofs to support less mobile arthropods, including epigaeic (ground-dwelling) and edaphic (soil-living) invertebrates, such as ground beetles, springtails, and mites (Braaker et al., 2014; Rumble et al., 2018; Williams et al., 2014). Existing research indicates that the ability of green roofs to connect with ground-level habitats and support biodiversity depends on their spatial isolation, both horizontal (distance to the next green roof and to ground-level habitats) and vertical (building height) (Braaker et al., 2014), as well as their design factors such as age, vegetation diversity, and habitat heterogeneity (Gonsalves et al., 2021; Kyrö et al., 2018; Wang et al., 2022). Yet species with lower mobility may respond differently to vertical and horizontal isolation (Blank et al., 2017) and may depend on commonly overlooked design choices, such as substrate depth and type (Rumble et al., 2018), or the increased shade and moisture provided by solar panels (Cook and Larsen, 2021; Schindler et al., 2018). Thus, it remains unclear whether green roofs can effectively substitute ground-level habitats removed during construction, particularly for species with limited dispersal ability.

A key challenge in understanding the benefits of green roofs and their connection with ground-level habitats stems from the limited availability of green roofs (Blank et al., 2017). Green roofs remain relatively scarce, and access can be difficult to obtain. This scarcity often restricts studies to small sample sizes, limiting our ability to assess how spatial isolation and environmental factors jointly affect biodiversity across organisms with different dispersal abilities. However, recent advances in environmental DNA (eDNA) metabarcoding—i.e., the identification of species from DNA fragments left in the environment (e.g., soil) (Deiner et al., 2017; Pawłowski et al., 2020)—allow for more detailed biodiversity assessments in urban areas (e.g., Zhang et al., 2023), including of species with various mobility modes (e.g., flying,

walking, burrowing; Kirse et al., 2021).

In this study, we paired 52 green roofs with nearby ground-level sites to investigate whether green roofs can act as replacement habitats for ground-level species with different dispersal abilities. Specifically, we (1) compared species richness and composition within and between green roofs and ground-level habitats across species with different dispersal abilities, (2) identified key environmental drivers of species richness for each dispersal group, and (3) examined how vertical and horizontal spatial isolation influence species overlap between paired sites.

2. Methods

2.1. Site selection and sampling

This study was conducted in Switzerland's largest city, Zurich (92 km², ~450,000 inhabitants). As a typical mid-sized European city, Zurich is a relevant model for studying urban growth, which is expected to occur mainly in small to mid-sized cities—although often in economically weaker regions (Seto et al., 2013). Although densely built, Zurich contains around 35 km² of green space and a substantial number of green roofs due to a 1991 mandate requiring the installation of green roofs on flat roofs of new and renovated buildings.

We selected 52 extensive, low-managed green roofs, each paired with a nearby ground-level site (as per Perrelet et al., 2025) along an urban densification (hereafter referred to as "urbanization") gradient (i.e., percentage of impervious surface in a 500m buffer) (Fig. 1). Ground-level sites consisted of a variety of urban green spaces all containing a pond, including private gardens, public parks, and vegetated areas owned by real estate entities – i.e., urban green spaces that are at risk of being developed in response to future urban densification. To ensure meaningful comparisons between habitat types, green roof sites were first selected based on their proximity to ground-level sites—i.e., horizontal isolation (mean distance = 155.2 m; range = 19.4–655.9 m). While not designed to mimic ground-level systems (e.g., no intensive green roofs with woody vegetation), this spatial pairing reflects frequently occurring scenarios where natural habitats are replaced by buildings, and subsequently offset through extensive green roof installation. To account for variability in roof design and environmental conditions, green roofs were selected to represent key predictive variables (Fig. 1), including vegetation cover, building height, roof age, area, and percentage of ground-level green spaces in a 50 and 500 m buffer around the building. These variables were selected based on their documented influence on invertebrate biodiversity (Wang et al., 2022), including species with different dispersal abilities (e.g., vegetation coverage for carabids (Braaker et al., 2014), building height for bees (MacIvor, 2016), and buffer sizes were chosen based on prior studies (e.g., from 100 up to 400 m, Braaker et al., 2014; 100 and 400 m, Kyrö et al., 2018; 500 m, Vergnes et al., 2017; 600 m, MacIvor, 2016). We also selected green roofs to minimize multicollinearity between predictive variables—as confirmed in Fig. S1. These variables were extracted using data provided by the city of Zurich, including: a high-resolution habitat map (Stadt Zürich, 2021), a 3D city model (Federal Office of Topography swisstopo, 2023b), and green roof map (including approximate vegetation cover (Stadt Zürich, 2014);), as well as a series of yearly orthophotos to determine age and identify green roofs that might have been built since the publication of the green roof map (Federal Office of Topography swisstopo, 2023a). Green roofs smaller than 30 m², lower than 3 m above ground-level, or with <25 % vegetation cover were excluded.

2.2. eDNA sampling

Green roofs were sampled in May 2023, while ground-level sampling took place in May 2022 (see Perrelet et al., 2025). To account for changes in community composition between years, we sampled four

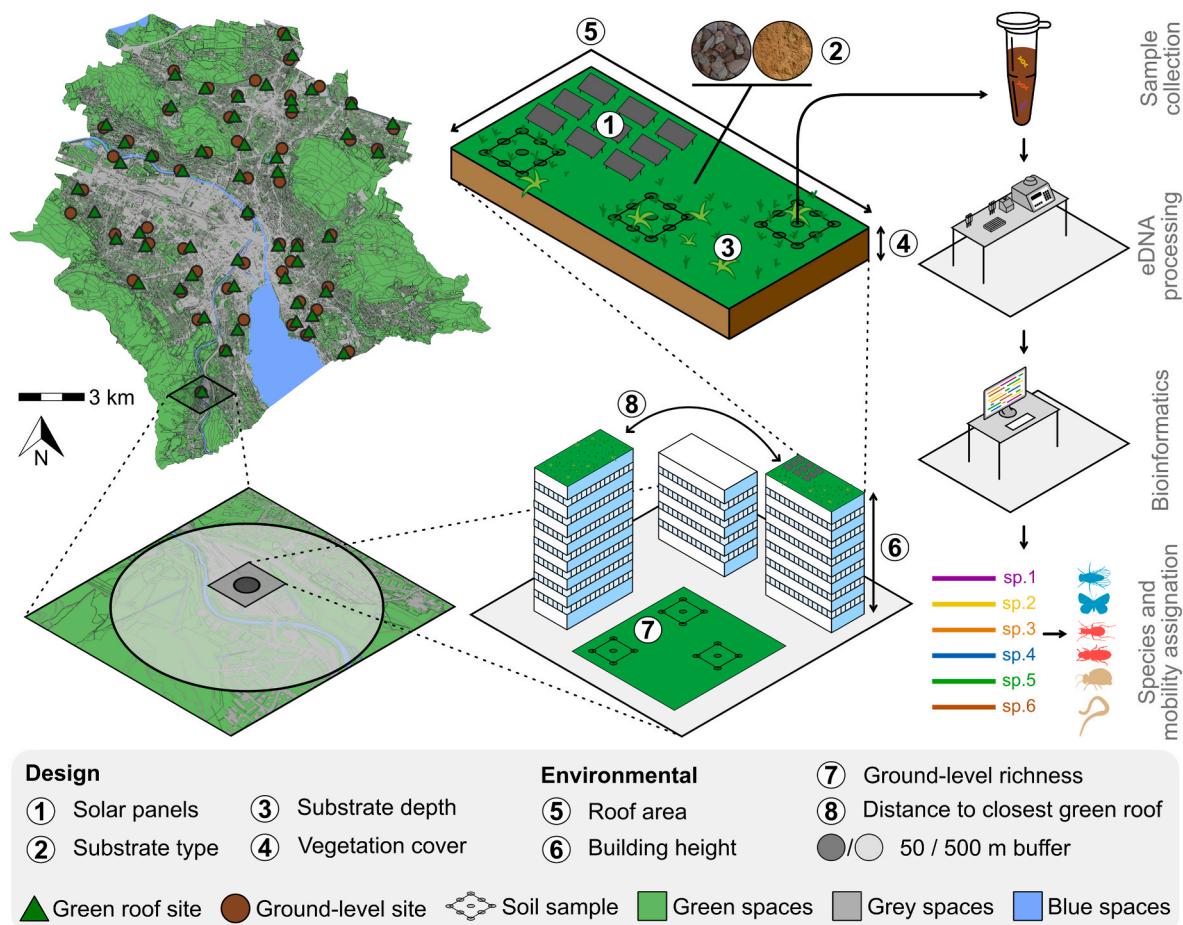


Fig. 1. Spatial distribution of green roof and ground-level sites within the city of Zurich and an overview of the sampling design, sample processing, predictive variables considered. Black squares indicate schematically where soil samples were collected from the most vegetated patches within each green roof. Green, grey, and blue spaces refer to urban green spaces (e.g., private gardens, public parks), impervious surfaces, and lakes and rivers, respectively.

green roof sites (hereafter referred to as “control”) in both 2022 and 2023, which confirmed minimal changes in community composition between years (Fig. S2).

Shown in Fig. 1, three soil samples were collected from the most undisturbed vegetated patches at each green roof and ground-level site. Ground-level samples comprised five equidistant subsamples within a 1 m² area, whereas green roof samples comprised nine equidistant subsamples to achieve comparable soil volumes. This sampling protocol yielded a total of 312 soil samples—156 from green roofs and 156 from the ground—plus 24 “control” samples. All samples were kept cool during transport, sieved (2 mm mesh size), homogenized, and stored at -20 °C until analysis.

During green roof sampling, site-specific green roof design characteristics were recorded, including vegetation coverage, substrate type, substrate depth, and the presence of solar panels, based on their documented influence on biodiversity (Kyrö et al., 2018; Schindler et al., 2018; Schrader and Böning, 2006). Substrate types were classified as either stone-dominated or soil-dominated, with stone-dominated substrates defined as those containing more than 50 % coarse materials such as lava stones, pebbles, or gravel. Substrate depth was measured by inserting a ruler into the substrate until the drainage layer was reached, and solar panel presence was recorded as a binary variable (present = 1, absent = 0). For the purposes of subsequent analyses, we classified variables into “design” and “environmental” characteristics. Design characteristics were those directly associated with green roof construction—such as vegetation cover, substrate type, substrate depth, and the presence of solar panels. In contrast, environmental characteristics were those less amenable to modification during the design phase—such

as roof area, roof age, building height, proximity to the nearest green roofs, ground-level species richness, and the proportion of green space within 50 m and 500 m buffers surrounding the building (Fig. 1). While none of these variables were uniformly distributed across all study sites, each exhibited significant variation (Fig. S3).

2.3. eDNA processing and bioinformatics

For both green roof and ground-level samples, eDNA was extracted using the Qiagen PowerMax Soil Kit in a dedicated eDNA laboratory (see Deiner et al., 2015), following manufacturer’s instructions and including controls to account for contamination. We followed a two-step PCR amplicon sequencing workflow consisting of the amplification for each sample (five replicates) of a COI fragment using invertebrates-specific Terr_EPTDr2n primers (Perrelet et al., 2025), replicate pooling, purification with AMXBeads Pure beads, and indexing with Illumina Nextera XT (kits S and N). Following a second purification and quantification, samples were normalized, pooled to equimolar concentrations, and sequenced on an Illumina NovaSeq 6000 using an SP flowcell. Bioinformatics processing included quality control (FastQC v0.12.0 (Andrews, 2010);), primer removal (cutadapt v4.4 (Martin, 2011);), merging, dereplicating (VSEARCH v 2.22.1; (Rognes et al., 2016)), and clustering (SWARM v3.1.4, d = 1, fastidious (Mahé et al., 2021));. Sequence clusters (i.e., operational taxonomic units) were filtered in R v4.4.1 (R Core Team, 2024) to remove those deviating in length (max ±10 bp), high error rates (maxEE = 1), low abundance (<25 reads), containing “N”s, or identified as chimeras. To account for potential contaminations, we subtracted the ratio of each sequence

cluster found in negative controls from those in the samples. Remaining clusters were parsed using *lulu* v0.1.0 and rarefied to the 15th percentile to mitigate sequencing bias. For additional details on sample processing and bioinformatics, see Perrelet et al. (2025).

Taxonomic assignments were made using BLAST against the MIDORI2 database (Leray et al., 2022) with identity thresholds of 90 % for family, 95 % for genus, and 97 % for species levels (similar to Elbrecht et al., 2018), retaining matches with >90 % query coverage and selecting the one with the lowest E-value. Non-metazoan and unassigned sequence clusters were removed, and clusters matching the same taxon were aggregated. Species were categorized into mobility modes as flying, epigaeic, or edaphic based on their traits as adults. Flying species included those with wings (e.g., dipterans) and spiders capable of ballooning according to the BESTI database (Pey et al., 2014). Epigaeic species were wingless taxa that actively crawl (e.g., myriapods) or winged species documented as active walkers (e.g., carabids, rove beetles) in the BESTI database (Pey et al., 2014). Edaphic species were those primarily inhabiting the substrate (e.g., worms, springtails).

2.4. Statistical analysis

To compare green roof and ground-level habitats, we evaluated differences between individual samples from each habitat type as well as between sites (aggregating species found in the three samples per site). We assessed differences using several metrics, including alpha and beta diversity.

For the comparison of individual samples, alpha diversity was calculated as species richness per sample (i.e., number of species). As samples coming from the same site are not independent, differences in alpha diversity were evaluated using generalized mixed-effect models (negative binomial distribution) using habitat type (i.e., green roofs or ground-level) as a fixed effect and site ID as a random effect. Beta diversity (i.e., differences in the composition of species between the two habitat types) was calculated using Jaccard dissimilarity (Jaccard distances) – a dissimilarity index measuring the ratio of non-overlapping species between two samples. These dissimilarity values were then visualized using principal coordinate analysis (PCoA), and the significance of grouping patterns was evaluated through permutation-based multivariate analysis of variance (PERMANOVA), which assesses whether compositional differences between groups are greater than expected by chance. Thirdly, to compare sample homogeneity across all green roofs and ground-level samples, we performed dispersion tests with habitat type as the grouping factor, which compares the variability of Jaccard dissimilarities within each habitat type. Finally, to assess intra-site homogeneity—i.e., whether the three samples collected from the same site exhibit greater variability in green roof habitats compared to ground-level habitats—we repeated the dispersion test using site ID as the grouping factor.

We repeated similar steps of alpha and beta diversity calculation for the comparison of green roof and ground-level sites. We calculated and compared species richness using a Wilcoxon test, with Benjamini-Hochberg correction to account for multiple comparisons. To account for potential species that may have been overlooked during sampling, we generated species accumulation curves—i.e., curves based on rarefied or extrapolated richness estimates derived from bootstrapping of sites. Beta diversity was again calculated as Jaccard dissimilarity and visualized via PCoA, with differences in composition between site types tested through permutation tests. To further assess inter-site homogeneity within each habitat type, we calculated pairwise Jaccard dissimilarity within green roof sites and within ground-level sites and compared the dissimilarity value using a Wilcoxon test (Benjamini-Hochberg correction). These steps were then repeated by subsetting the entire dataset based on species mobility modes: flying species, epigaeic, and edaphic species-only.

2.5. Modelling of community drivers and overlap

To evaluate variation in species distribution across green roofs, we quantified the number of sites where individual species occurred for each mobility mode. Moreover, to identify drivers of species richness across mobility modes, we considered 11 local and landscape variables known to influence green roof biodiversity (reviewed in Wang et al., 2022). These predictors include: roof age, area, building height, distance to the closest green roof, percentage of green spaces in both a 50 and 500 m buffer around the building (i.e., environmental predictors, all determined using existing maps and orthophotos, see *Site selection*), vegetation cover, substrate depth and type, and presence of solar panels (i.e., design predictors, all determined during the site visit, see *eDNA sampling*), as well as species richness of the paired ground-level site. Generalized linear models (Poisson distribution) were used to test the effect of each predictor on species richness for all species and for each mobility mode. Coefficients and 95 % confidence intervals were reported using coefficient plots. Predictor importance and non-linear relationships were further evaluated with random forest models, consisting of an ensemble tree averaging 50,000 decision trees, with each tree trained on a random subset of the data (~2/3) and each split considering a single random predictive variable. Predictor importance was ranked based on mean decrease in accuracy (measured as the Mean Squared Error) of the ensemble tree when omitted.

Finally, to investigate community overlap between green roofs and ground-level habitats, we calculated shared species counts and Jaccard dissimilarity for paired sites (i.e., proximate green roof and ground-level sites; see Fig. 1). To assess whether these metrics between paired sites differed from random expectations, we designed two null model randomization scenarios to evaluate whether observed patterns (e.g., correlations between species richness at one site and the number of shared species with its paired site) reflected non-random processes in species assembly (scenario 1) or inherent compositional similarities between paired habitats (scenario 2). In the first randomization scenario, the total species richness at each site was fixed, but species were randomly selected from either the green roof or ground-level species pool according to site type (hereafter, “semi-randomization”). In the second scenario, the species composition of either the green roof or ground-level site was fixed, but was randomly paired with a site of the opposite habitat type (hereafter, “random pairing”). Fixing either the green roof or the ground-level sites yielded comparable results, thus only the results from the version where green roof sites were fixed are reported in subsequent analyses.

All analyses were conducted using R v4.4.1 (R Core Team, 2024). The following packages were used in the analysis: *exactextractr* v0.10.0 for covariates calculations (Baston & ISciences, 2023); *vegan* v2.6-8 for alpha and beta diversity metric calculations (Oksanen et al., 2024); and *randomForest* v4.7-1.2 for modeling (Breiman et al., 2024).

3. Results

Green roof sites exhibited significantly lower species richness compared to ground-level sites, with an average of 62 ± 14 species detected versus 74.2 ± 12.7 species, respectively (Wilcoxon test with Benjamini-Hochberg correction, $p < 0.0001$; Fig. 2B, S4). Green roof sites were also more homogeneous, although the difference was small (Wilcoxon test with Benjamini-Hochberg correction, $p < 0.05$; Fig. 2C). These patterns were mirrored at the sample level, where green roof samples had lower species richness than ground-level samples (37.7 ± 9.8 and 33.4 ± 10.9 species detected on average, respectively; GLMM, $p = 0.0002$). Green roof samples also exhibited slightly greater overall homogeneity (GLMM, $p = 0.002$) but showed a much stronger pattern of intra-site homogeneity compared to ground-level samples (Fig. S4).

Alpha and beta diversity patterns varied depending on species mobility. Green roofs hosted slightly richer but more homogeneous flying species and epigaeic assemblages than ground-level sites (Fig. 2B

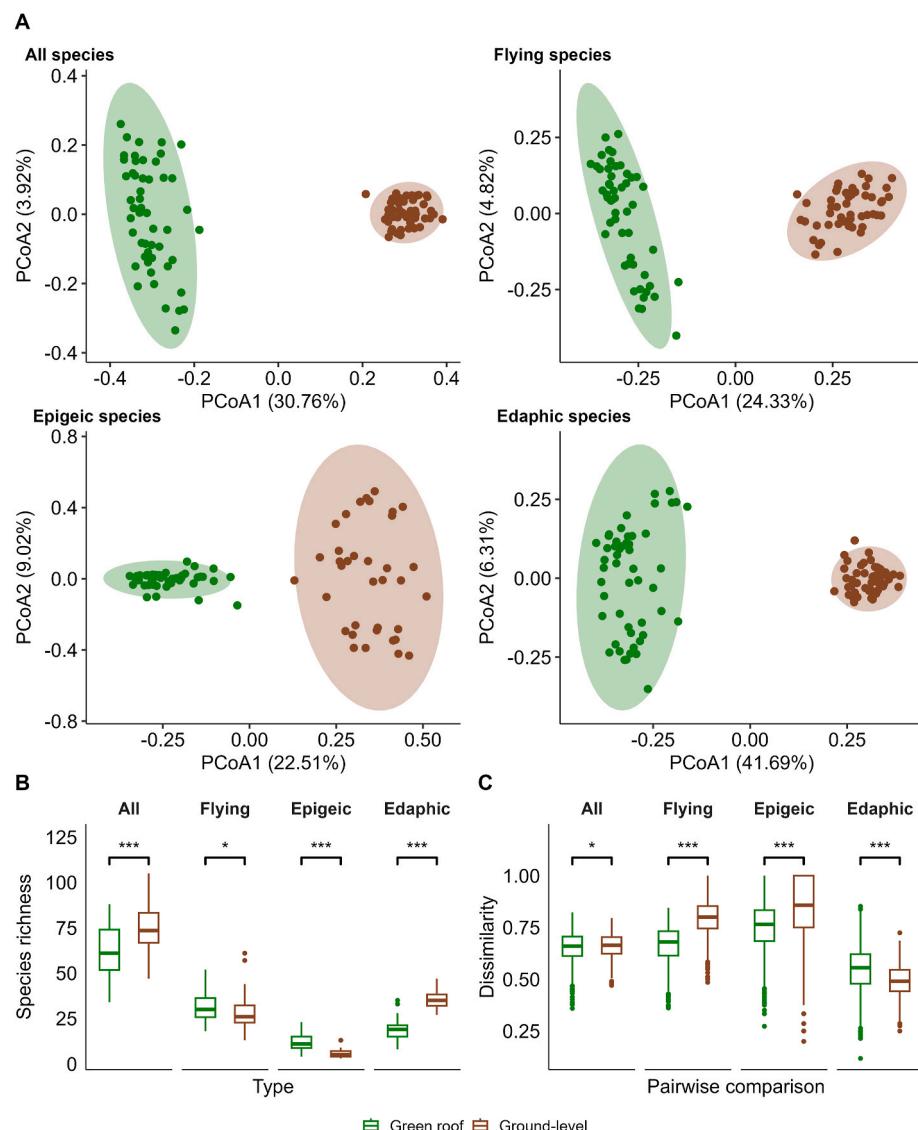


Fig. 2. Diversity and composition of assemblages of various mobility modes. (A) PCoA plots representing all sites (dots) and 95 % confidence ellipses, both color-coded based on type, and replicated for the complete dataset (All species), flying species, epigeic, and edaphic species only. (B) Violin plots showing species richness of green roof (green) and ground-level (brown) sites for all mobility modes. (C) Boxplots showing the pairwise Jaccard dissimilarity between pairs of green roof sites (green) and pairs of ground-level sites (brown) for all mobility modes. Stars indicate levels of significance (Wilcoxon tests with Benjamini-Hochberg correction: * ≤ 0.05 , *** ≤ 0.0001).

and C). Conversely, green roofs featured fewer edaphic species, but showed higher heterogeneity in their assemblages than ground-level sites. However, regardless of the mobility mode, green roof and ground-level communities differed greatly and clearly aggregated based on site habitat type (permutation test; $R^2 = 0.06$, p-value < 0.001 ; Fig. 2A). While the separation of ground-level and green roof sites remained for all mobility modes, it was especially evident for edaphic species, as illustrated by the higher values along the first PCoA axis—24.33 %, 22.51 %, and 41.69 % for flying, epigeic, and edaphic species, respectively (Fig. 2A).

Although communities at the species-level differed greatly between green roof and ground-level sites, both habitats contained similar taxa at higher taxonomic levels and in similar proportion (Fig. 3). Both green roof and ground-level sites were dominated by worms, springtails, and insects (mainly dipterans), though with notable differences: green roofs featured tardigrades and higher insect prevalence, particularly butterflies and beetles, whereas ground-level sites included more crustaceans, worms, and myriapods (Fig. 3, S5). Although both habitats shared broad taxonomic representation, ground-level sites detected more species

across most taxonomic groups, except coleopterans, lepidopterans, arachnids, and tardigrades (Fig. 3, S6). Increased sampling effort would have accentuated this trend, except for coleopterans (Fig. S6). These differences in composition were reflected in differences in the proportion of mobility modes; epigeic species were more prevalent on green roofs, while ground-level sites included a small proportion of taxa associated with aquatic habitats. These ratios between the mobility modes remained stable with increasing level of urbanization at green roof sites, although ground-level communities were increasingly dominated by edaphic species, to the partial detriment of flying species (Fig. S7).

Species assemblages on green roofs exhibited marked spatial heterogeneity, with the majority of species—irrespective of mobility mode—restricted to a limited number of sites (Fig. S8). Nevertheless, a subset of species, particularly edaphic species, were consistently present across all green roofs.

Biodiversity on green roofs was positively associated with several design characteristics, including substrate depth, vegetation cover, and soil-dominated substrates (Fig. 4A and B). Environmental characteristics

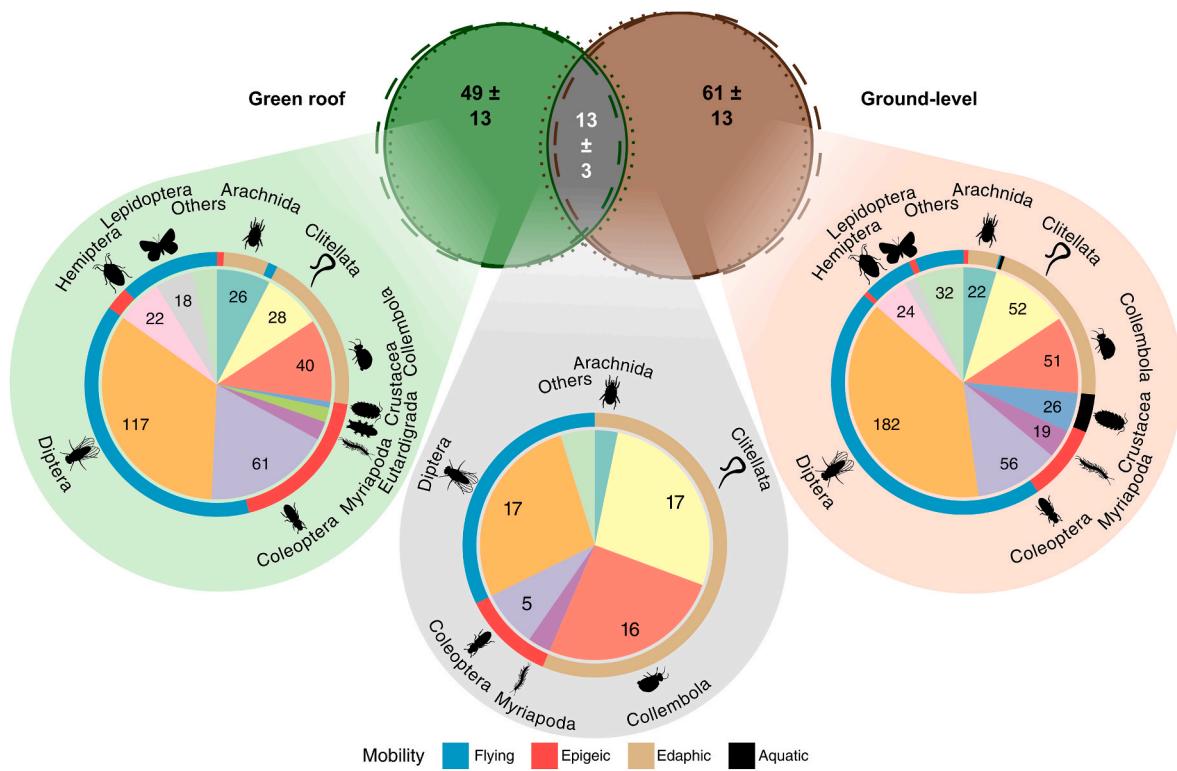


Fig. 3. Composition of green roof and ground-level samples, as well as their degree of overlap. Venn-Diagram (top) showing ground-level only (brown), green roof only (green), and shared (grey) mean species richness per site, with solid lines indicating the mean and dashed lines indicating the standard deviation. For each part of the Venn-Diagram, a pie-donut chart (bottom) is provided, depicting the ratio and total number of species identified (inner circle), as well as their mobility modes (outer circle).

were also influential, with roof age emerging as the strongest predictor (positive correlation), but building height (negative correlation), although this variable had low predictive importance. Moreover, while roof age correlated with species richness across all mobility modes, the influence and importance of other environmental drivers varied. Epigaeic species richness was most strongly influenced by substrate type, with stone-dominated substrate having the largest standardized coefficient and ranked as the most important design factor for this group. Epigaeic species richness was also positively associated with roof age, substrate depth, and vegetation coverage, although the latter contributed minimally to random forest regression accuracy compared to other factors. Similarly, edaphic species richness was also positively associated with roof age and substrate depth but showed a negative relationship with surrounding landscape greenness, which had a minor impact on model accuracy relative to roof age or depth. In contrast, flying species richness positively correlated and was best predicted by soil-dominated substrates, followed by the proportion of surrounding green space within a 50 m buffer and vegetation cover. Flying species richness was also associated with roof age and building height, but their inclusion reduced random forest regression accuracy. Finally, while none of the mobility modes correlated with ground-level richness (Fig. 4A), this variable was frequently selected by the random forest regression for all groups except epigaeic species, although often with a relatively low importance (Fig. 4B).

Species richness between paired ground-level and green roof sites showed no significant correlation (linear model; $p = 0.467$) (Fig. S9). However, these paired sites consistently shared a relatively stable number of species, usually around 15–20 % of species found at either site. The shared taxa, predominantly worms and springtails, with insects comprising approximately 30 % of shared taxa, were largely edaphic or, to a lesser extent, flying, with few ground-dwelling species (Fig. 3), a pattern that stayed consistent regardless of urbanization intensity (Fig. S7). Not only was the number of shared species in pairs of sites

relatively stable (Fig. 3), but most shared species only occurred in a limited number of sites (Fig. S10) and—along with Jaccard dissimilarity—were unaffected by neither height nor distance between paired sites (Fig. 5). Interestingly, the number of shared species correlated with green roof species richness (GLM; $p\text{-value} < 0.001$), but not with ground-level species richness ($p\text{-value} = 0.264$). Null model analyses indicated that these patterns—or lack thereof—between shared species richness and species richness at green roof and ground-level sites, respectively, were consistent with expectations under random pairings of green roof and ground-level sites. However, the models also indicated that randomly assembled communities shared fewer species and exhibited greater dissimilarity than observed (Fig. 5). Furthermore, in the random assembly scenario, Jaccard dissimilarity decreased (i.e., communities became increasingly similar) with increasing green roof species richness—a pattern that was not reflected in the empirical data.

4. Discussion

The goal of this study was to compare species diversity and composition between green roofs and ground-level sites and to identify the key drivers shaping these patterns across a gradient of species mobility. We found that green roofs hosted lower alpha and beta diversity than ground-level sites, although these patterns were significantly shaped by species mobility. We also found that green roofs and ground-level sites shared a limited number of species, regardless of the degree of spatial isolation between sites.

While green roofs did support similar major taxonomic groups as ground-level habitats, at finer taxonomic levels, these habitats harbored distinct communities, as reflected in the clear clustering patterns separating green roof and ground-level communities. This separation underscores the capacity of green roofs to host unique assemblages (Braaker et al., 2014, 2017; MacIvor and Lundholm, 2011). Furthermore, while some species were shared between green roofs and

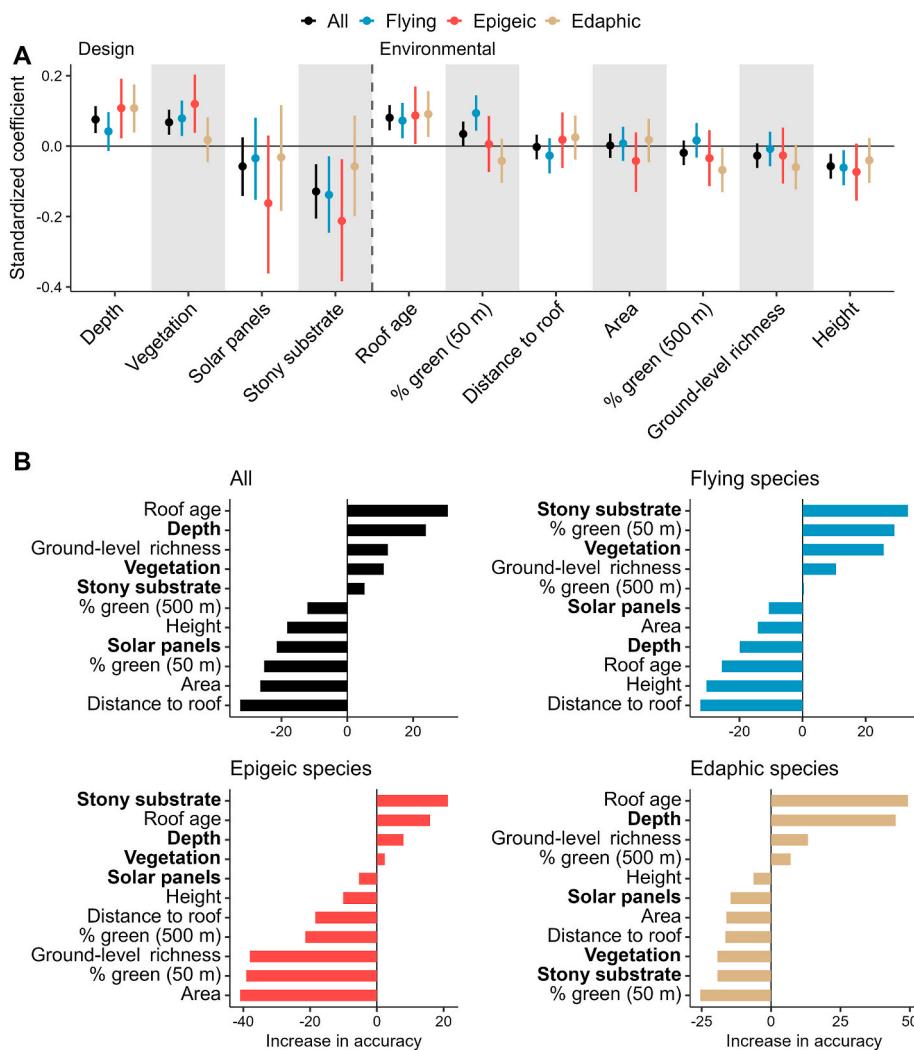


Fig. 4. Variable effect and importance based on mobility modes. (A) Coefficient plot showing the standardized coefficients and 95 % confidence intervals of multiple design parameters on the species richness of various mobility groups (color-coded), including: substrate depth, roof age, vegetation, fraction of green spaces (50 m buffer), distance to closest green roof (distance to roof), roof area, fraction of green spaces (500 m buffer), ground-level richness, building height, presence of solar panels, and substrate type. A correlation is considered significant if the error bars do not cross zero (black line). (B) Random forest model classification of variable importance for all mobility modes, with variables ranked based on the mean increase in accuracy (mean squared error, MSE) across of mobility modes. Higher MSE values indicate stronger predictive importance, while lower values suggest limited or no contribution.

ground-level sites, most shared species were edaphic (Joimel et al., 2018; Rumble et al., 2018). For these low-mobility species, dispersal on a green roof is mostly passive, driven by human-mediated measures (e.g., substrate addition from different providers and locations) or stochastic means (e.g., through wind or other animals) (Joimel et al., 2018). The prevalence of passive dispersers over more actively flying species indicates predominantly stochastic dispersal and minimal functional connections between the two habitat types. This was further supported by the absence of significant correlations between shared species richness as well as Jaccard dissimilarity and vertical (building height) or horizontal (distance to ground-level) isolation. Although paired sites were more similar than expected by chance, green roofs were as dissimilar to their paired ground-level sites as to any other ground-level site. Moreover, while increasing species richness on green roofs did raise the number of shared taxa with paired ground-level sites, overall dissimilarity remained stable, suggesting that green roofs do accumulate some shared taxa but mostly host different communities. Our results thus suggest that green roofs further function as isolated ecological compartments that tend to develop into distinct ecosystems, underscoring their potential as complementary habitats (Fournier et al., 2020; Kyrö et al., 2022; MacIvor and Lundholm, 2011).

Green roof communities contained fewer species and were slightly more homogeneous than ground-level samples. This trend was mirrored at the sample level, where green roof samples showed higher intra-site homogeneity. These patterns likely stem from the unique environmental conditions (e.g., dry, shallow soil, high and sun wind exposure) and the standardized nature of extensive green roof designs (Brenneisen, 2006; Dunnett and Kingsbury, 2008), which often lacks the microhabitat diversity present in urban ground-level environments, such as trees, shrubs, and water bodies (Beninde et al., 2015). This suggests that green roofs impose stricter environmental constraints on species establishment and survival (Braaker et al., 2014). Additionally, stormwater drainage systems on green roofs, although typically located below the substrate, may have promoted lateral water transport across the substrate during heavy rainfall, enabling horizontal eDNA transport across the roof and thereby increasing sample homogeneity. In contrast, given the lack of a drainage layer, rainfall is more likely to drive vertical transport of eDNA on the ground-level sites (Valentin et al., 2021).

Despite the lower species richness and slightly higher homogeneity on green roofs, these patterns varied depending on species mobility. Green roofs supported greater richness of flying and epigeic species relative to ground-level sites, in contrast with previous studies (Kyrö

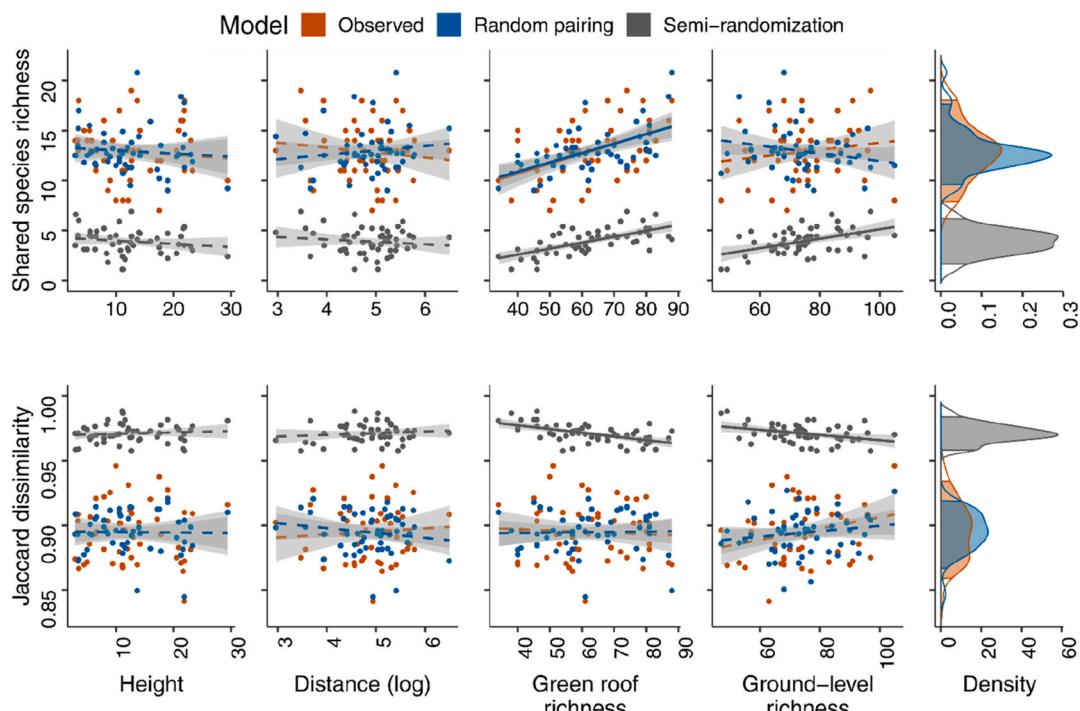


Fig. 5. The influence of height, distance, green roof, and ground-level richness on shared species richness (top) and Jaccard dissimilarity (bottom) for observed and null model data (color-coded). Solid lines represent significant relationships, while dashed lines indicate non-significant ones. Density plots (far right) show data distributions, with shaded areas representing the 95 % confidence interval.

et al., 2022; MacIvor and Lundholm, 2011). This discrepancy could stem from the higher levels of anthropogenic disturbance (e.g., mowing, pesticide, trampling) experienced by our ground-level habitats compared to those usually studied in the literature (e.g., unmanaged, open grasslands; Kyrö et al., 2022). Green roofs, however, harbored many fewer edaphic species – although still in notable proportion (~30 %), challenging the idea that green roofs are mostly home to highly mobile species (Dunnett and Kingsbury, 2008; Lepczyk et al., 2017). This reduced species richness likely reflects the low moisture or organic matter in green roof substrates, crucial for edaphic species such as springtails (Jacobs et al., 2022; Rumble et al., 2018). Additionally, green roof edaphic communities were more heterogeneous than those found at ground-level sites. Given the stochastic and often human-mediated dispersal of these low-mobility species (Joimel et al., 2018), dispersal limitations may have resulted in dissimilar assemblages across green roofs, raising concerns that green roofs could act as ecological traps for these low-mobility taxa (Brenneisen, 2006; Lepczyk et al., 2017; MacIvor, 2015). However, most green roof species were confined to a limited number of sites, while a few edaphic species were consistently present across all roofs. This suggests that, despite environmental filtering and dispersal constraints, some species may remain well adapted to green roof habitats. Given the uncertainties surrounding the suitability of green roofs to support low-mobility species, future studies should aim to directly measure species traits, as this study relied on trait inferences from taxonomic and functional databases (e.g., BETSI; Pey et al., 2014) due to the limitations of eDNA metabarcoding. Nonetheless, the clear patterns in alpha and beta diversity based on species dispersal modes (i.e., flying, crawling, digging) highlight that green roofs do not benefit all taxa equally.

This inequality across mobility types is confirmed by their differing sensitivities to environmental factors (e.g., building height, roof age, surrounding land-use). This also hints at why green roofs differed so significantly from ground-level habitats. Biodiversity needs space, time, and connectivity (Beninde et al., 2015; Nielsen et al., 2014; Ramalho and Hobbs, 2012), yet green roofs are recently built, artificial, and

isolated structures. Interestingly, roof age emerged as a stronger predictor of species richness than degree of vertical isolation. This suggests that the longer colonization and resource accumulation period on older roofs (Fabián et al., 2021; Kyrö et al., 2020) outweighs the dispersal challenges posed by taller buildings (Blank et al., 2017). Regardless, these results suggest that newer green roofs on taller buildings—increasingly common in the face of urban densification (Chen et al., 2023)—may host poorer communities. Further studies are needed to investigate whether green roof design can offset inherent constraints, including building height and surrounding land-use.

While environmental variables cannot be changed, our findings underscore that local design choices are key to increasing available resources for species and supporting biodiversity across varying dispersal abilities (Kyrö et al., 2018; Wang et al., 2022). Some drivers were specific to certain mobility modes—for example, vegetation coverage positively correlated with epigaeic but not edaphic species richness—and contributed to the diverging alpha and beta diversity patterns observed for each mobility mode. However, we did not identify any trade-offs where a single variable benefited one mode while disadvantaging another. Specifically, roofs with higher vegetation coverage and deeper, soil-dominated substrates supported greater biodiversity across mobility modes. Increasing plant coverage and using deeper substrates with higher organic content can also lead to synergies and cascading ecological benefits. These factors have been shown to improve stormwater retention (Cook and Larsen, 2021; VanWoert et al., 2005) and create additional microhabitats (Muller et al., 2014), which can trigger increasing plant diversity that in turn supports a broader range of taxa (Aloisio et al., 2020; Wang et al., 2022).

However, even with incremental design improvements such as deeper substrates or increased vegetation cover, green roofs remained significantly different from ground-level habitats. This highlights that extensive green roof designs may not fully replicate the structure and function of the habitats they often substitute. Achieving closer ecological convergence would require a shift towards intensive green roofs, e.g., deeper substrates, introducing woody vegetation, and potentially

even integrating water features (Cook and Larsen, 2021). Whether such interventions can fully replicate the biodiversity and ecological dynamics of ground-level habitats, however, remains uncertain. In the absence of such redesign, it is important to acknowledge that green roofs cannot serve as direct substitutes for the ground-level habitats they are built upon. Rather, their implementation in place of ground-level green spaces results in the creation of novel habitats that support distinct communities, while simultaneously leading to the loss of the original ground-level biodiversity.

5. Conclusion

Green roofs could represent a promising strategy to mitigate the loss of ground-level habitats, yet their effectiveness is constrained by the diverse ecological requirements of urban biodiversity. Through a paired-sampling approach along an urbanization gradient, our study demonstrates that green roofs differ significantly from the ground-level habitats they would substitute. Instead, they support diverse communities, although poorer in species and slightly more homogeneous compared to ground-level sites, likely due to the unique environmental conditions (i.e., high temperatures, water stress) and standardized design of green roofs.

Green roofs can support a surprisingly high diversity of flying and ground-dwelling (i.e., epigaeic) species, yet they consistently harbor significantly fewer soil-living (i.e., edaphic) species, even though these communities were surprisingly heterogeneous. The lack of soil-living species could be due to dispersal barriers and unsuitable environmental conditions, which calls into question whether green roofs act as sustainable habitats or serve as ecological traps for such low-mobility species. Given that species with limited dispersal abilities may only sporadically colonize green roofs, it is unclear whether green roofs end up hosting stable and self-sustaining communities or whether they primarily support "opportunistic" assemblages of non-interacting species. Nonetheless, targeted design factors, such as increasing vegetation coverage, substrate depth, or the organic content of the substrate, could support biodiversity across taxa with varying mobility modes.

Future studies are needed to assess whether intensive green roofs with deeper substrates, woody vegetation, or water features enable green roofs to more closely replicate the biodiversity and ecological function of the ground-level habitats they often substitute. In particular, future research should focus on the ecological dynamics within green roofs, exploring how species forage, interact, and form food webs, ideally across multiple trophic levels, to determine how networks of species react to the addition (e.g., green roof colonization) or removal (e.g., competitive exclusion, environmental filtering) of species. Additionally, studies should foster collaboration with architects and engineers to address inherent constraints (e.g., roof area, height) and enhance connectivity with ground-level habitats—such as via ramps or terraces—while considering factors such as substrate origin to optimize biodiversity conservation.

CRediT authorship contribution statement

Kilian Perrelet: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Marco Moretti:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Océane Ingland:** Writing – review & editing, Investigation, Formal analysis. **Florian Altermatt:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization. **Lauren M. Cook:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2025.126630>.

Data availability

Sequencing data generated during this study is available on the European Nucleotide Archive under accession project number PRJEB94011. Code is available on github at https://github.com/KPerrelet/Green_Roof_eDNA.

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