Biodiversity of collembola on green roofs

Jacobs, Jeffrey; Berg, Matty; Beenaerts, Natalie; Artois, Tom

published in
Ecological Engineering
2022

DOI (link to publisher)
10.1016/j.ecoleng.2022.106572

document version
Publisher's PDF, also known as Version of record

document license
Article 25fa Dutch Copyright Act

citation for published version (APA)
Jacobs, J., Berg, M., Beenaerts, N., & Artois, T. (2022). Biodiversity of collembola on green roofs: A case study of three cities in Belgium. *Ecological Engineering*, *177*, 1-15. Article 106572. https://doi.org/10.1016/j.ecoleng.2022.106572

Ecological Engineering 177 (2022) 106572

Contents lists available at ScienceDirect

Ecological Engineering

journal homepage: www.elsevier.com/locate/ecoleng

Biodiversity of collembola on green roofs: A case study of three cities in Belgium

Jeffrey Jacobs [a,*], Matty Berg [b,c], Natalie Beenaerts [a], Tom Artois [a]

[a] UHasselt, Centre for Environmental Sciences, Agoralaan Gebouw-D, 3590 Diepenbeek, Belgium
[b] Department of Ecological Science, Vrije Universiteit, De Boelelaan 1085, 1081, HV, Amsterdam, the Netherlands
[c] Community and Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences, University of Groningen, 9700, CC, Groningen, the Netherlands

ARTICLE INFO

Keywords:
Green roofs
Collembola
Biodiversity
Urbanization
Functional trait diversity
Soil fauna

ABSTRACT

Green roofs are often promoted as a mean to counter the negative environmental effects of urbanization on nature and to increase the amount of green space in cities. Green roofs often enhance aboveground biodiversity, especially herbivores and pollinators. However, if and in what way they support belowground biodiversity, and more specifically soil fauna, is rarely studied. Therefore, we evaluated the diversity of a dominant group of soil fauna, Collembola (springtails), on twelve extensive green roofs in three cities in Belgium (Antwerp, Ghent and Hasselt), over a one year period. The roofs differed in height above the ground, surface area, vegetation type, and age, i.e. time since construction. We analysed if these roof characteristics influenced species richness, abundance or diversity of Collembola. In total we found ten species of Collembola. Species richness was not higher on roofs that were larger (habitat area) or closer to the ground (isolation to surrounding soil), indicating that island-biogeographic theory is not applicable to species richness in our study system. However, significant differences in the mean number of individuals (abundance) were found between different months. Collembola taxonomical composition also varied between the roofs, but this variation could not be related to any of the measured roof variables. Roof communities were characterised by hemiedaphic life forms, preferring neutral to semi-moist conditions. Apart from the age of the roof that showed a positive significant impact on the abundance of Collembola present, our results suggested that the collembolan fauna showed no significant differences in abundance, species richness or diversity between roofs with different characteristics. However, we suggest that future studies are needed to investigate whether our findings are applicable to other groups of soil-living arthropods.

1. Introduction

Recent projections indicate that the percentage of the human population living in urban areas worldwide will reach nearly 70% by 2050 (United Nations Development Programme, 2014). This trend towards urbanization has several consequences, one of which is a major threat to biodiversity on a global level (Faeth et al., 2011; Elmqvist et al., 2016). Furthermore, urbanization is known as one of the main land-use changes behind the global insect collapse (Fenoglio et al., 2021). Increase in city area causes loss of habitats for species, an increase in spatial distance between remaining pockets of green, and a change in habitat quality (Seto et al., 2012). Moreover, the climate in urban areas is characterised by the so-called heat island effect, which also creates soil drought. On top of that, the increased amount of pollutants in cities can influence species directly or indirectly via food quality and quantity (Jones and Leather, 2013). Urbanization can also cause changes in soil structure as a result of conversion to different types of land use (Brazel et al., 2000; Byrne, 2007; Pickett and Cadenasso, 2009; Pickett et al., 2011). The result of all these changes combined is an overall decrease in species richness across many groups of organisms in urban areas (Beninde et al., 2015; Fenoglio et al., 2020; Piano et al., 2020). The severity of the impact on terrestrial ecosystems differs between situations, with stronger negative effects known to occur in more densely populated, larger, and/or older cities (Williams et al., 2009; Gagné et al., 2016).

To counter these negative environmental effects of urbanization on nature, the construction of green roofs is often promoted to increase the

---

* Corresponding author.
E-mail addresses: jeffrey.jacobs@uhasselt.be (J. Jacobs), m.p.berg@vu.nl (M. Berg), natalie.beenaerts@uhasselt.be (N. Beenaerts), tom.artois@uhasselt.be (T. Artois).

https://doi.org/10.1016/j.ecoleng.2022.106572
Received 5 August 2021; Received in revised form 4 February 2022; Accepted 6 February 2022

amount of green space in cities (Pataki et al., 2011). Green roofs could deliver several important ecosystem services otherwise provided by natural green spaces. They not only add an aesthetic value to an urban environment, but studies show benefits for water runoff and evapotranspiration (Mentens et al., 2006), reduction in heat flux due to insulation (Kumar and Kaushik, 2005; Jim and Tsang, 2011) and a beneficial role in carbon sequestration (Li et al., 2010). Previous studies have also shown that green roofs are an efficient solution to mitigate the heat island effect (Oberndorfer et al., 2007). In addition, green roofs in cities may increase habitat connectivity for mobile invertebrate species by acting as stepping stones between rural sites (Braaker et al., 2014). Moreover, during the last two decades studies have indicated that green roofs located in large cities have a high potential to support species that are negatively impacted by habitat loss (Brenneisen, 2006; Baumann, 2006; Kadas, 2006; Madre et al., 2013).

The most common type of green roofs are extensive roofs, consisting of a 5–20 cm deep layer of homogenous, shallow, rocky substrate. They are typically planted with allochthonous plants, such as species of *Sedum* or other drought-tolerant plants, as they require minimal maintenance and are adapted to summer drought (Li and Yeung, 2021). Arthropods and micro-organisms begin to colonize the green roof soils almost immediately, and are also often partly brought in with the planting material or substrate (Molineux et al., 2014; Macivor and Ksiazek, 2015). As natural systems go through successive transitions marked by increasing diversity (Turner et al., 1998), plant and associated animal communities on green roofs are expected to become more diverse over time. However, the processes of green roof soil fauna community assembly are currently not known (Francis and Lorimer, 2011).

According to island biogeography theory (MacArthur and Wilson, 1963; MacArthur and Wilson, 1967), species richness in isolated habitat fragments is predominantly determined by isolation and surface area. Green roofs can be seen as green islands in the sky surrounded by inhospitable surface areas (Blaustein et al., 2016), where both the size of the roof and the (vertical and horizontal) distance to other green areas have an impact on species richness, abundance and diversity (Ksiazek-Mikenas et al., 2018; Fabián et al., 2021). Generally isolated roofs seems harder to colonize for arthropod communities, because of lower rates of immigration from spatially distant habitat fragments or rural areas, although data to support this theory are inconsistent (Blank et al., 2017). Moreover, due to the high passive dispersal rate of Collembola, general source-sink dynamics do not apply for this group of organisms (Ingimarsdottir et al., 2012). Furthermore, the dispersal rate of Collembola is high enough for the mass effect (Aström and Bengtsson, 2011), where species can establish and maintain populations in sites that are suboptimal (Shmida and Wilson, 1985). Therefore, the effect of isolation from green areas might be negligible when collembolan communities are concerned. Nonetheless, the size of the roof might have an important impact on species richness as larger fragments will support larger populations making them less prone to extinction, and usually contain a greater diversity of microhabitats (MacArthur and Wilson, 1963; MacArthur and Wilson, 1967). Island biogeography theory has been used to explain species richness in nature fragments embedded in agricultural landscape (Ward and Blaustein, 1994; Goheen et al., 2003; Lepère et al., 2013), but might also be useful to explain the biodiversity of green roofs embedded in an urban landscape (Pickett and Cadenasso, 2008; Blank et al., 2017). Although data to support the applicability of island biogeography theory on arthropod communities exists (Ksiazek-Mikenas et al., 2018; Fabián et al., 2021), specific data on soil communities on green roofs are only present to a very limited extent (Blank et al., 2017).

On green roofs, most of the soil-dwelling arthropods belong to Collembola (springtails), accounting for up to 80% of the total community counts (Schrader and Böning, 2006; Davies et al., 2010; Rumble and Gange, 2013). Although Collembola are among the most abundant and widespread terrestrial arthropods, and although they have important functions in soil dynamics such as litter decomposition and nutrient cycling (Cortet et al., 1999; Cortet et al., 2003), the underlying mechanisms which determine their diversity and species composition in isolated, small habitat fragments are poorly resolved. Species traits in general can vary significantly within a group of soil fauna (Lindberg and Bengtsson, 2005; Ponge et al., 2006; Vandewalle et al., 2010). For instance, springtails can differ greatly in vertical distribution in soils, body size and moisture preference (Berg and Bengtsson, 2007). Especially traits related to vertical distribution in soil have been successfully used in understanding shifts in springtail community structures across environmental gradients or stresses (Parisi et al., 2005; Vandewalle et al., 2010; Makkonen et al., 2011; Bokhorst et al., 2015). In this sense, Collembola can be divided in three vertical stratification groups, i.e. epigeic or surface-living species, eu-edaphic or soil-dwelling species living deep in the soil, and hemiedaphic species that take a position between the two previous categories and live in the litter layer (Gisin, 1943; Bengtsson et al., 1994). Epigeous species are on average a little larger, are more tolerant to fluctuations in abiotic conditions, and are known to have a higher dispersal ability than deeper living species (Chust et al., 2003a; Ponge et al., 2006). Generally smaller, eu-edaphic and hemiedaphic species are more limited in movement, are more sensitive to environmental fluctuations and tend to have a lower dispersal ability (Bengtsson et al., 1994; Berg and Bengtsson, 2007). Previous studies have shown that habitat patches are perceived differently by species differing in body size and vertical distribution (Chust et al., 2003b; Bardgett et al., 2005). Therefore, linking these functional traits to green roof features allows us to assess the collembolan community assembly and composition. Few studies have shown that the diversity, community composition and abundance of organisms on green roofs are influenced by different characteristics of the roofs such as, age of the roof, substrate depth, substrate type and vegetation type (Schindler et al., 2011; Gabrych et al., 2015; Knapp et al., 2019). Furthermore, the input of compost to increase soil fertility (Al-Daikh et al., 2018) and even abiotic factors such as seasonality (Wiwatwitaya and Takeda, 2005) have been determined to influence the abundance of arthropods.

The aim of our study was to investigate whether roof characteristics influenced collembolan diversity, abundance (also referred to as density in this paper) and species trait composition of green roofs located in an urban environment. Therefore, we investigated 12 large green roofs in three urbanized areas of Flanders (cities of Antwerp, Ghent and Hasselt), Belgium. More specifically we expect that (i) the level of vertical isolation will decrease the species richness, abundance and diversity of Collembola on green roofs. We hypothesize (ii) that green roofs with a large surface area will have a higher species richness, abundance and diversity of springtails, because larger roofs can be more diverse in microhabitats. We expect to find (iii) more epigeic and hemiedaphic than eu-edaphic species of Collembola, due to the shallow substrate of green roofs. As species use traits to maximize their fitness in a changing environment, (iv) we also expect a change in species composition due to dissimilar roof features, such as vegetation type (Makkonen et al., 2011; Bokhorst et al., 2015; Widenfalk et al., 2016). Finally, we analysed if temporal differences, the three cities or other roof characteristics (age or vegetation type) of the roof influenced species richness, abundance or diversity of Collembola present on green roofs. Our data can be used to help future biological landscape planning on roofs to optimize soil fauna abundances, species composition and diversity in urban areas, which is important in view of their impact on ecosystem processes.

2. Material and methods

2.1. Study sites

Our study took place in three cities in Flanders, Belgium: Antwerp, Ghent and Hasselt. The city of Antwerp (51° 13′ N, 4° 24′ E) comprises a total area of 204.5km^2 with ±526.000 citizens (2413.1 inhabitants/km^2). The city of Ghent (51°3′ N, 3°42′ E) comprises a total area of 157km^2, with ±262.000 inhabitants (1584.2 inhabitants/km^2). The city of Hasselt (50° 56′ N, 5° 20′ E) comprises a total area of 102.24km^2 with

±78.000 inhabitants (721.9 inhabitants/km^2). We selected 12 green roofs in total, four roofs in each city (Table 1; for exact location of the different roofs see Appendix Figs. 1A–3A). We use mean annual air temperatures (11.5 °C ± 0.1) and precipitation average 798.6 mm for Flanders (KMI, 2020), because geographic and climatic conditions within the region are very similar (See Appendix Fig. 4A, for a graphical overview of the average temperatures and precipitation per month).

2.2. Green roof characteristics

On average the green roof surface was 310m^2 (range 25m^2–777m^2), the average age was 8.5y (range 5–16y), and their average height was 8.5 m (range 3–23 m) (Table 1). All roofs were surrounded by urban environments: 100% build-up area consisting of stones, concrete or other artificial materials. The roofs consist of a 5–20 cm deep layer of homogenous, shallow rocky substrate. They are typically planted with allochthonous plants, such as species of *Sedum* or other drought tolerant plants (e.g. species of mosses and grasses such as *Calamagrostis epigejos*). Extra nutrients are provided to all productive green roofs through annual or pluri-annual compost amendment, except to the 'Virga Jessa ziekenhuis' roof (Table 1). Roofs were separated into two groups according to the vegetation type *Sedum* roofs (ZWDO, UH, Dis, FPC and Onyx) and *Sedum*, herbs and grass roofs (Her, Apo, VJ, WZCP, WZC, Ell and Bra).

2.3. Sampling

Springtails were sampled in April, July and October 2019 and January, 2020 using a soil corer. Four soil cores (diameter 9 cm, height 6 cm, 381.7cm^3) were randomly sampled from all the roofs (>2 m from the edge of the roof and > 2 m apart), with the exception of April 2019 when only three cores were taken per roof while one roof was not yet accessible ("Ellerman") due to renovation of the building.

The cores were placed in plastic sealed cups and transported to the lab where they were stored at 4 °C until extraction, which was initiated within four days after sampling. Springtails were extracted using a high-gradient Tullgren extractor (Van Straalen and Rijninks, 1982) with a temperature gradient ranging from 30 °C at the top of the sample to 5 °C at the bottom over a period of three weeks. Identification of the species was done using a stereo (Leica EZ4) and an optical microscope (Olympus CX21). For species identification, we used the taxonomic keys of Fjellberg (1998 and 2007) and Hopkin (2007).

2.4. Collembolan traits

Traits related to their vertical distribution in soil have been successfully used in understanding shifts in collembolan community structures across environmental gradients or stress gradients. Therefore, species were divided into three groups based on life form (1: epigeous, species living on the surface or vegetation; 2: hemiedaphic, species living just below surface; 3: eu-edaphic, species living deep in the substrate) (Stierhof, 2003; Kuznetsova, 2003 & Fjellberg, 2007) (Table 2).

We also divided Collembola into five ecological groups based on moisture preference following Stierhof (2003), Kuznetsova (2003) and Fjellberg (2007) to determine whether there was any significant difference between them in total numbers of individuals as a function of roof characteristics (Table 2).

2.5. Statistical analysis

Measures of community diversity were quantified for each roof, including species richness, total abundance, Shannon-Wiener's index (H′), Simpson's diversity index (D), and Evenness (E). Species richness was defined as the number of species present in a sample (Levin et al., 2009). The Simpson index is a dominance index as it accounts for proportions of species in the sample; rare species have a small effect on this diversity index. The Shannon-Wiener index considers both species richness and equitability in distribution of individuals over species in a sample and it calculates the proportion of species relative to the total number of species. It assumes that all species are represented in a sample and that they are randomly sampled. We used the Pielou's evenness index (Pielou, 1966) to measure diversity along with species richness. Evenness is the relative abundance of the different species making up the richness of a given habitat, the calculated value ranging from 0 (no evenness) to 1 (complete evenness). When combined together with other diversity indices, a more detailed description of a community's structure can be given (Heip et al., 2001).

To determine whether the respective measures were significantly different between green roofs, Poisson generalized linear mixed models (GLMM) were applied, as Poisson distribution is typically used for count data. Green roofs characteristics (vegetation type (categorical), age (continuous), height (continuous), surface area (continuous), city (categorical)) and different months (categorical) were used as the fixed factors, roof and city as the random factors, and each diversity measure (richness, abundance, H′, D, E) as an independent variable. A lognormal distribution best fits all responses and therefore we used a penalized quasi-likelihood approach. A Tukey Honest Significant Difference (HSD) post-hoc test was run to compare all possible pairs of means when significant differences were identified in fixed categorical factors ($p < 0.05$).

Differences in species composition between roofs was tested by permutational analysis of similarities (ANOSIM) with Bray-Curtis as a dissimilarity measure (Faith et al., 1987; Clarke, 1993). ANOSIM tests were used to check for differences in roof's height, roof's surface area, roof's age, differences between cities and vegetation type. For this ANOSIM tests we divided roofs into three groups based on the green roof area (small: <150m^2, medium: 150–500 m^2, large >500m^2) and two groups were created for the age (young roofs: <10 years and old roofs: >10 years). Community weighted mean (CWM) trait values for each individual roof were calculated for body size, moisture preference and

Table 1
Overview of the roofs with their reference name, city, age, surface area, height above ground level, dominant vegetation and whether they received compost as organic amendment.

Name roof	Reference	City	Age (y)	Surface (m^2)	Height (m)	Dominant vegetation	Compost input
Onyx	Onyx	Antwerp	6	708	23	*Sedum*	Yes
District	Dis	Antwerp	12	280	9	*Sedum*	Yes
Brandweer	Bra	Antwerp	11	777	17	*Sedum*/Herbs/Grasses	Yes
Ellerman	Ell	Antwerp	5	312	9	*Sedum*/Herbs/Grasses	Yes
Uhasselt	UH	Hasselt	8	129	4	*Sedum*	Yes
Woonzorgcentrum Clarenhof	WZC	Hasselt	5	225	5	*Sedum*/Herbs/Grasses	Yes
Woonzorgcentrum Clarenhof P	WZCP	Hasselt	5	220	5	*Sedum*/Herbs/Grasses	Yes
Virga Jessa Ziekenhuis	VJ	Hasselt	16	175	3	*Sedum*/Herbs/Grasses	No
Zwarte Doos	ZWDO	Ghent	15	110	10	*Sedum*	Yes
Forensisch Psychiatrisch Centrum	FPC	Ghent	7	588	9	*Sedum*	Yes
Hermelien	Her	Ghent	6	25	3	*Sedum*/Herbs/Grasses	Yes
Apotheek	Apo	Ghent	5	76	4	*Sedum*/Herbs/Grasses	Yes

Table 2
List of the ten species of Collembola found on the green roofs, with their average body length (mm ±0.01), life-form group (1: epigeous, 2: hemiedaphic, 3: eu-edaphic) and their moisture preference group (1: xerophilous (not present in our data), 2: xero-mesophilic, 3: mesophilic, 4: meso-hygrophilous, 5: hygrophilous). With a list of the frequency and abundance of each of the ten species collected. (Abundance: percentage of individuals of a species relative to the total number of individuals caught; Frequency: percentage of times a species was caught relative to the total number of soil cores.) Species are arranged according to taxonomy.

Family	Genus	Species	Body length (mm)	Life form	Moisture preference	Abundance (%)	Frequency (%)
Isotomidae	*Cryptopygus*	*thermophilus* (Axelson, 1900)	1	2	4	33.8	83.0
	Proisotoma	*minuta* (Tullberg, 1871)	1.1	2	3	11.9	54.8
	Parisotoma	*notabilis* (Schäffer, 1896)	1	2	3	12.0	50.8
Entomobryidae	*Heteromurus*	*nitidus* (Moniez, 1889)	3	3	4	<0.1	1.1
	Entomobrya	*multifasciata* (Tullberg, 1871)	1.5	1	2	14.1	42.4
	Orchesella	*cincta* (Linnaeus, 1758)	6	1	2	0.4	1.7
Sminthurididae	*Sminthurides*	*malmgreni* (Tullberg, 1876)	0.45	2	5	<0.1	0.6
Katiannidae	*Sminthurinus*	*aureus* (Lubbock, 1862)	1	2	5	21.2	62.1
	Sminthurinus	*elegans* (Fitch, 1863)	0.7	2	5	1.3	14.7
Bourletiellidae	*Bourletiella*	*hortensis* (Fitch, 1863)	1.35	1	2	5.1	22.0

life form. Trait composition between green roof types (*Sedum* vs *Sedum*/grasses/herbs) were also tested by permutational analysis of similarities (ANOSIM). All values were gathered onto a single matrix (10 species × 12 roofs). Consequently, we performed a Principal Components Analysis (PCA) to investigate the differences in composition of collembolan communities between the 12 green roofs. All data were analysed using R version 3.6.3 (R Core Team, 2020), and the packages: "vegan" (Oksanen et al., 2014), "matrixStats" (Bengtsson, 2017), "lme4" (Bates et al., 2015), "MASS" (Venables and Ripley, 2002), "multcomp" (Hothorn et al., 2008) and "ggplot2" (Wickham, 2016).

3. Results

3.1. Collembolan diversity, abundance and species composition

In total we identified ten species of Collembola (Table 2) belonging to five different families. The most abundant species were *Cryptopygus thermophilus* with 34% of the individuals, *Sminthurinus aureus* with 21% and *Entomobrya multifasciata* with 14%. In 83% of the soil cores we found *C. thermophilus*, in 62% *S. aureus*, in 55% *Proisotoma minuta,* and in 51% *Parisotoma notabilis* (Table 2). Six species were found on all roofs (Appendix, Table 1A); *Sminthurinus elegans* was found on all roofs except two (roofs: Onyx and FPC); *Sminthurides malmgreni* was only found on one roof (roof: Bra). The average number of species per roof was seven ($\bar{x}$ = 7.3, sd = 0.7) and roofs housed between six to nine species.

We collected a total of 7006 individuals. Total density of Collembola ranged between 2554 and 8763 individuals/m^2 ($\bar{x}$ = 6257, sd = 1850). Despite the large density range, this range did not result in a large difference between the roofs in species diversity nor in evenness (average diversity in Shannon index: 1.582 (sd = 0.134), Simpson index: 0.755 (sd = 0.037) and Pielou's evenness of 0.381 (sd = 0.024)) (See Appendix Fig. 5A, for an overview of evenness and diversity indices per roof).

The collembolan density ranged from 2554 to 8266 ($\bar{x}$ = 6703, sd = 782) for the roofs of the city of Antwerp, from 4526 to 7553 ($\bar{x}$ = 6082, sd = 692) for Ghent and from 3789 to 8763 ($\bar{x}$ = 6367, sd = 687) for Hasselt. However, we did not find a significant difference between the three different cities in terms of collembolan densities (Table 3 and Fig. 1).

Fig. 3 shows the biplot of the PCA analysis for the composition of communities of Collembola on the different green roofs (sites). The Fig. 3 shows that species that co-occur differ in species traits to reduce the overlap in resource use (Table 2) (See appendix table 3A for loadings of PCA). Fig. 3 also shows that site 11 (roof Bra) is different in collembolan composition from most of the other sites, this is not surprising as it is the only green roof where we found *Sminthurides malmgreni* and one of the two roofs with *Sminthurinus elegans*.

Table 3
Fixed effects table for the generalized linear mixed model (GLMM) detected in the green roof samples for abundance and richness of Collembola. Table shows the estimate, standard error (std. Error), t-value and *p*-value (*Significant p-value ≤0.05).

	Estimate	Std. error	*t*-value	*P*-value
Richness				
Age	0.136	0.012	0.0847	0.320
Height	0.003	0.011	0.310	0.777
Vegetation	0.148	0.0817	1.815	0.119
Surface Area	−1.30E-05	2.40E-04	−0.054	0.958
Month January	−0.027	0.116	−0.236	0.825
Month July	−0.032	0.154	−0.245	0.784
Month October	−0.048	0.144	−0.314	0.817
City Hasselt	0.087	0.129	0.675	0.537
City Ghent	0.247	0.486	0.569	0.674
Abundance				
Age	0.047	0.024	2.101	0.033*
Height	0.011	0.042	0.268	0.802
Vegetation	0.049	0.284	0.176	0.869
Surface Area	4.60E-04	8.10E-04	0.571	0.598
Month January	−0.443	0.153	−2.907	0.027*
Month July	−0.140	0.139	−1.003	0.354
Month October	−0.486	0.155	−3.145	0.019*
City Hasselt	0.255	0.463	0.551	0.611
City Ghent	0.213	0.402	0.532	0.623

3.2. Temporal effects

We found a statistically significant difference in abundance of individuals between the different months (Table 3). Post hoc comparisons using the Tukey Honest Significant Difference (HSD) test indicated significant differences between months in numbers of individuals: April from January ($p = 0.002$), April from October ($p \leq 0.001$) and July from October ($p = 0.038$), with the highest number of individuals respectively found in the first month and the lower number in the latter (Fig. 2). GLMM results show no other statistically significant temporal effects on richness or diversity of Collembola (Table 3 and see appendix table 2A).

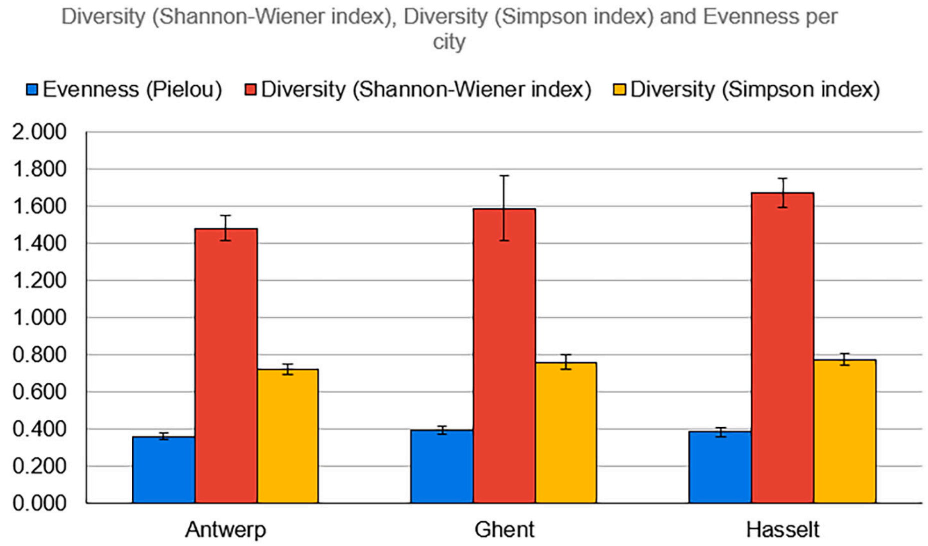

Fig. 1. Average of the Evenness (Pielou's number), diversity as Shannon-Wiener index and the diversity in Simpson index for each city. Error bars represent standard deviation.

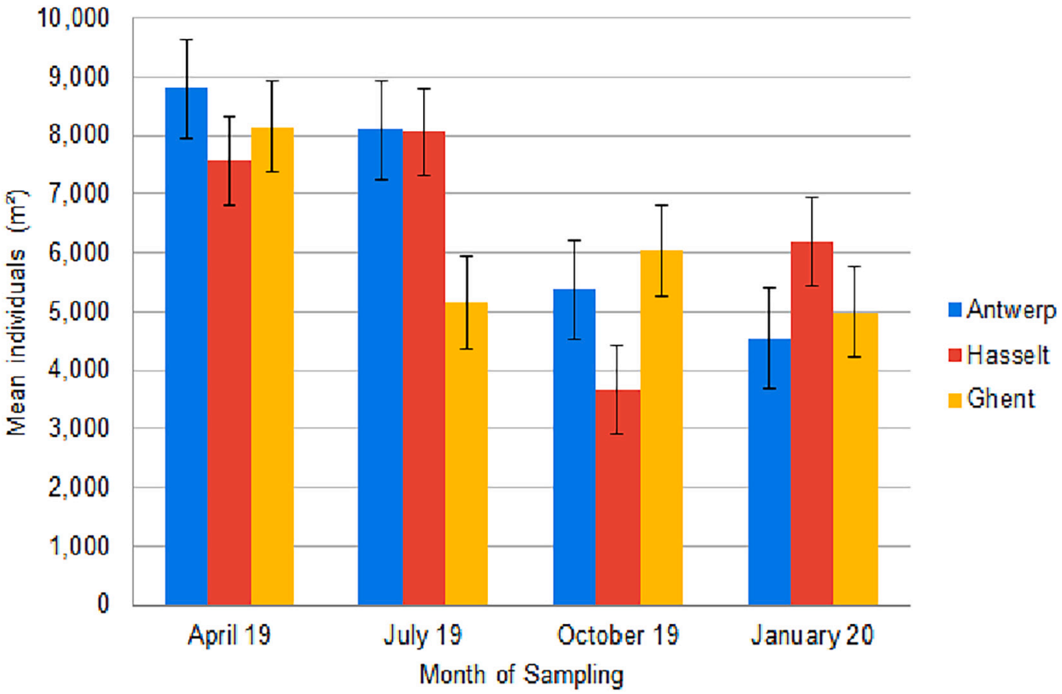

Fig. 2. Mean number of collembolan individuals per m2 between April 2019 and January 2020. Blue for the city of Antwerp, red for the city of Hasselt and yellow for the city of Ghent. Error bars represent standard deviation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. *Effect of roof characteristics on Collembola*

All ANOSIM tests with Bray-Curtis as a dissimilarity measure show no significant differences. We tested for differences between the height of the roofs ($p = 0.486$), the different cities ($p = 0.541$), green roof area ($p = 0.633$), age ($p = 0.741$) and vegetation type (group 1: *Sedum*, group 2: *Sedum*/herbs/grasses; $p = 0.976$).

Furthermore, no significant differences were found between species richness of Collembola and age, height, vegetation type (*Sedum* or *Sedum*/herbs/grasses) or surface area, nor between abundance and the height, vegetation type or surface area of roofs (Table 3). However, as shown in Table 3 the age of the roof has a positive significant impact on the abundance of Collembola present in our study. GLMM results for the fixed effects when looking at the diversity indices (H′, D and E) were all not significant (See appendix table 2A).

3.4. *Collembolan traits*

Community weighted mean (CWM) moisture preference ranged between 3.18 and 4.06 (see appendix, Fig. 6A), and the community can therefore be characterised as composed of mesophilic to meso-hygrophillic species. The CWM life-form in the group of *Sedum* monoculture roofs was 1.78 (sd = 0.075) and for the mixed *Sedum*, grass and herbs roofs 1.83 (sd = 0.058) (See appendix, Fig. 7A), showing a predominance of hemiedaphic species. CWM body length (1.14 mm with sd = 0.094), CWM moisture preference and CWM life form did not significantly differ between the two groups of vegetation type.

4. Discussion

We investigated collembolan species richness, abundance and community composition on twelve green roofs located in an urban environment in three different cities in Flanders. We found that overall collembolan diversity on the green roofs was low (Table 4) and we only found a significant difference in abundance, which appears to be higher on older roofs. No other significant differences in abundance, species richness or composition between roofs with different characteristics was found. Our results showed, there is a big chance of creating species-poor collembolan communities within a city and even across cities in case all the green roofs that are installed use more or less the same build-up within the Flanders regional landscape.

The amount of studies performed on collembolan communities on green roofs in Europe is very limited. More specifically, to the best of our knowledge, only three related studies exist: Schrader and Böning, 2006; Rumble and Gange, 2013 and Joimel et al., 2018 (Table 4). Given the fact that only a few studies have been performed on collembolan communities in Western Europe on green roofs, we will compare our results where possible with these studies (Schrader and Böning, 2006; Rumble and Gange, 2013; Joimel et al., 2018).

We found ten different species of Collembola from five different families (Table 2). Previous studies on collembolan communities on green roofs show varying results (Table 4). These differences in the number of species encountered are possibly related to the differences in substrate layers (Table 4). As species of Collembola differ in traits, we can assume that differences in substrate layers will have an effect on the number of species capable of thriving on these green roofs. However, further research, e.g. allowing for direct comparison within one study, on the effect of substrate type on green roof soil communities is needed. All of the collembolan species we encountered are common species in Western Europe or even cosmopolitan species that are introduced in several areas. Except for *H. nitidus* and *O. cincta*, all species encountered have been recorded from green roofs before (Schrader and Böning, 2006; Rumble and Gange, 2013; Joimel et al., 2018). Species abundance and frequencies in our study (Table 2) do not deviate much from what is known from literature, the same species are found to be most abundant. Furthermore, some of our most abundant species such as: *P. notabilis*, *P. minuta* and *C. thermophilus* are classified as frequently found cosmopolitan pioneers, while other frequently found species on our roofs *S. aureus, E. multifasciata,* and *Bourletiella hortensis* are classified as common pioneer species (Dunger et al., 2004). Combining our results with the results from these previous studies we can conclude that if a green roof is located in Western Europe, the majority of species of Collembola found are those that have a wide geographical distribution.

Table 4
overview of the studies by Schrader and Böning, 2006; Rumble and Gange, 2013; Joimel et al., 2018 and our study.

	Schrader and Böning, 2006	Rumble and Gange, 2013	Joimel et al., 2018	Our study
Location	Hannover (Germany)	London (United Kingdom)	Paris (France)	Gent, Antwerp, Hasselt (Belgium)
Number green roofs	10	2	15 (7 extensive)[a]	12
Substrate layer	expanded clay/shale pallets	crushed brick	coarse mineral aggregate	crushed brick
Time period sampling	June & July 2002	March 2010 until April 2011	April 2016	April 2019 until January 2020
Samples taken	Biweekly	Monthly	Once	Every 3 months
Average roof's height (m)	7.2	12	41	8.5
Average age green roofs	6.5	7	6.7	8.5
Average green roof surface area (m^2)	410	2100	370	310
Total number of species of Collembola	30	6	30	10
Average collembolan densities (individuals/m^2)	56,000	19,000	37,000	6300

[a] Only the 7 extensive green roofs were used to calculate the averages to compare with this study.

We found collembolan densities varying between 2500 and 8700 individuals m^{-2}, with an average of 6257 individuals/m^2. In the few studies performed on collembolan communities on green roofs varying numbers are reported, from 0 to 152,000 individuals m^{-2} (Schrader and Böning, 2006; Rumble and Gange, 2013; Joimel et al., 2018). In these studies, the average number of individuals was higher than in ours (Table 4). As mentioned above the differences in substrate layer between the different studies (Schrader and Böning, 2006; Rumble and Gange, 2013; Joimel et al., 2018) could also have an impact on this average number of individuals present, because the abundance of Collembola can be positively correlated (e.g. organic material, nitrogen) or negatively correlated (e.g. Ph) to soil characteristics (Islam et al., 2018). However, differences in substrate layers are not fully explaining the higher mean average number between the results found in literature and ours. Other abiotic factors (e.g. sunlight, soil depth and humidity) not captured by our data could also play an important role. Furthermore, our results support the suggestion by Rumble And Gange (2013) that taking a single sample in the year can produce completely different results and conclusions compared to results from a complete annual cycle of sampling. That same study indeed covers a complete annual cycle of collembolan communities on green roofs, which makes it more comparable to our study. The average number of individuals was higher than in our study, but we are unable to explain these differences; the same sampling techniques were used and the roofs had more or less the same built up. Other factors beyond the scope of our study could have an impact on the average number of individuals and further research is needed.

We failed to demonstrate significant differences in species richness or total number of individuals between cities. Consequently, our assumption that green roofs in larger and more densely populated cities will have a lower richness and abundance is not supported. We even found a slightly higher number of individuals on the roofs in the largest and most urbanized city of the three, Antwerp. It seems that the level of urbanization measured as surface area and the population density of the city does not affect abundances of Collembola on green roofs. This contradicts our expectations which were based on previous studies on flora and birds in urban areas (Williams et al., 2009; Gagné et al., 2016). These studies suggest stronger negative effects on abundance of species in terrestrial ecosystems in more populated, larger and older cities. The most obvious explanation for these differences is that the above and belowground fauna and flora are influenced by urbanization in different ways. Additionally, one could argue that Flanders is a large continuous urbanized area with fragmented green areas. Therefore, the grade of urbanization does not differ enough between the three investigated cities. Further research is needed to check if our findings do apply for other cities worldwide.

In light of the island biogeography theory we anticipated that green roofs situated closer to the ground would have a higher collembolan diversity and abundance, but no statistically significant differences were found between species richness or abundance and the height of the roof. The collembolan community composition was also not influenced by the height of the roof. One possible explanation could be that the roofs' height did not differ enough in our study (3–23 m) to cause any differences in abundance or species richness within collembolan communities. Most buildings in Flanders are relatively low compared to other cities in other parts of the world and collembolan communities are known to be capable of colonizing new habitats over multiple kilometres due to their good dispersal abilities (Kaufmann et al., 2002; Ingimarsdottir et al., 2012). Not only do they appear to have good horizontal passive dispersal capabilities, specimens of Collembola have been sampled at altitudes of 2000 m and more (Freeman, 1952). Therefore, this relatively small distance of some building floors is possibly just a small bump in the road for the colonisation of new habitats for Collembola.

Considering the island biogeography theory, we also assumed that more species occur on roofs with a larger surface area, because larger roofs can be more diverse in microhabitats. However, no significant differences were found in species richness, abundance or species composition between roofs with different surface area. Due to intricate source-sink dynamics in Collembola (Ingimarsdottir et al., 2012), we did not check whether the horizontal distance to the nearest green space has any impact on the richness, species composition or even abundance of collembolan communities on the green roofs. Nonetheless, these results show that a relatively small roof possesses the same potential to harbour collembolan species biodiversity as a bigger roof. In accordance with the results of previous studies (Schrader and Böning, 2006), we did not find any difference between the youngest roof (5 years) and the oldest roof (16 years) in terms of collembolan species richness or collembolan community composition. However, we found that abundances of Collembola differ significantly when the age of the roof is considered. Older roofs tend to have higher collembolan abundances, presumably because of the species accumulation through immigration and species-specific very local optimal (environmental) growing conditions, for example due to a lack of predators. However, our results are in contrast to those of Schrader and Böning (2006), who found no significant differences in abundances between young and old roofs, nonetheless, collembolan densities were slightly higher on their old roofs compared with young roofs. As other factors may influence the abundances on green roofs, ideally an experimental set-up where all factors are controlled, with only the age of the roof as an explanatory variable would be recommended, however, practical difficulties in doing this will surely arise.

Only two categories of vegetation type were selected for the green roofs, representing the most common types of green roofs worldwide: roofs covered with only species of *Sedum* and roofs covered with *Sedum*, herbs and grasses. Previous studies have suggested that small differences in vegetation can have an impact on the fauna composition present (Castagneyrol and Jactel, 2012). However, we found no significant differences between green roofs covered with only species of *Sedum* and green roofs with a combined vegetation of *Sedum*, grasses and herbs. We suggest that future research should investigate whether larger differences in vegetation type (e.g. *Sedum* vs intensive roof) will have a significant impact on the biodiversity of soil communities present.

We expected that a change in species type due to dissimilar roof features, such as vegetation composition can be understood using species traits. Our results from the community weighted mean for moisture preference indicate that the composition of the collembolan community ranged from mesophilic to meso-hygrophilous independent of the roof characteristics. The species found on our green roofs in general prefer neutral to semi-moist conditions (Stierhof, 2003; Kuznetsova, 2003 & Fjellberg, 2007). These results are somewhat surprising because green roofs are known to be a dry and hot environment to survive in (Nektarios et al., 2015). Therefore, we expected more xero-mesophilic or even xerophilous species. However, collembolan species react differently to drought (Verhoef and Van Selm, 1983) and results can be influenced by different factors such as soil pore space, pH or CO_2 level in the soil. These factors are not included in our experimental set-up. Therefore, we assume that adaptation to the conditions on the roofs is a more complex process, not captured by our data. Moreover, we mostly found hemi-edaphic species, a result to be expected as an extensive green roof has a rather thin substrate offering adverse conditions for species living deep in the soil. These results are in accordance with the conclusions of previous studies that show that in drought induced plots the most tolerant collembolans were species living on the surface or just below the surface (Lindberg and Bengtsson, 2005).

Results from the principal component analysis (Fig. 3) show that some species are negatively correlated with each other (e.g. *P. minuta* and *S. elegans,* which have the same life-form and more or less the same body length (Table 2)), while others are positively correlated with each other. These findings are supported by previous studies (Makkonen et al., 2011; Bokhorst et al., 2015; Widenfalk et al., 2015; Widenfalk et al., 2016), which leads to the conclusion that the life-form and body length are useful traits to understand the community assemblage of collembolan communities. Furthermore, previous studies show that green roofs can harbour communities that are influenced by competition or local environmental factors (Ingimarsdottir et al., 2012). Our study illustrates this by the fact that species that co-occur differ in species traits to reduce the overlap in resource use (Fig. 3).

All together this study shows that as far as extensive green roofs are concerned, the collembolan fauna shows a significant difference in abundance with age of the roof, but no other significant differences on abundance, species richness or composition between roofs with different

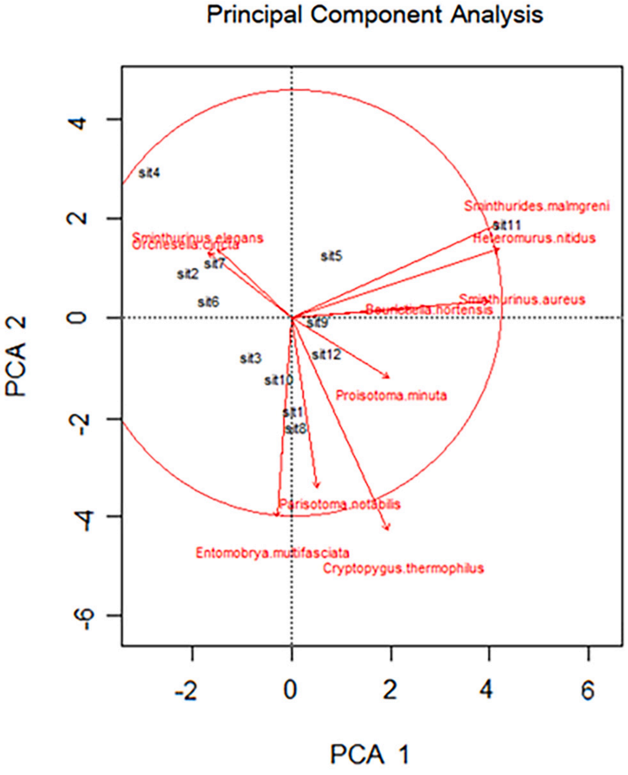

Fig. 3. Graphical display of the plot of the Principal Component Analysis (PCA) of the collembolan composition of the green roofs. (sit 1: VJ, sit 2: Her, sit 3: Apo, sit 4: Ell, sit 5: WZC, sit 6: WZCP, sit 7: UH, sit 8: Dis, sit 9: FPC, sit 10: ZWDO, sit 11: Bra, sit 12: Onyx) (axis 1: 29.6% and axis 2: 20.2%). Positively correlated variables are grouped together and negatively correlated variables are positioned on opposite sides of the plot's origins (quadrants). The closer a variable is to the circle of correlations, the more important it is to interpret these components. Both PC scores of samples (dots) and loadings of variables (vectors) are shown. The first two axes of the PCA respectively accounted for 29.6% and 20.2% of the total inertia.

characteristics. Furthermore, our results do not support the island biogeography regarding species richness of Collembola on green roofs. This is in accordance with previous studies that were unable to statistically support this theory for arthropod communities on green roofs (Schindler et al., 2011; Macivor and Lundholm, 2011), but in contrast to the study of Ksiazek-Mikenas et al. (2018) that proved that an increase in size of the vegetated area of the roof was associated with increased arthropod abundance, richness, and diversity. However, our results do show a significant difference in the number of individuals between the different seasons and it is, therefore, important to perform a complete annual cycle of sampling in further studies. In general, we can conclude that a green roof can be a suitable habitat for collembolan communities and for fulfilling the important functions they have in the soil, independent of the green roof characteristics or the location of the green roof.

Nonetheless, it remains difficult to compare different studies on green roofs, because of the large heterogeneity in urban areas (Rosenzweig, 2016). Therefore, comparing our data and the data of previous or future studies should be done with caution.

Considering our results and findings we suggest that future studies on collembolan communities on green roofs try to investigate: (i) the underlying mechanisms and patterns of collembolan community changes in response to the environmental gradients of urbanization, (ii) whether larger differences in height can have a significant impact on collembolan abundance, composition or species richness, (iii) how colonisation is progressing on a newly installed roof, and at what age the collembolan colonisation is completed and (iv) whether our findings do apply to other groups of soil-living invertebrates on green roofs.

CRediT authorship contribution statement

Jeffrey Jacobs: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Resources. **Matty Berg:** Conceptualization, Writing – review & editing. **Natalie Beenaerts:** Writing – review & editing, Supervision. **Tom Artois:** Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Special thanks to Thomas Van Dijck for his help during the sampling period and thanks to Armando Cruz for his help with the statistical part. We would also like to thank all the owners from the green roofs for allowing us to collect data on their properties.

The author J.J. and the research was funded by the SBO project ‘Ecocities: Green roofs and walls as a source for ecosystem services in future cities’, S002818N.

Appendix

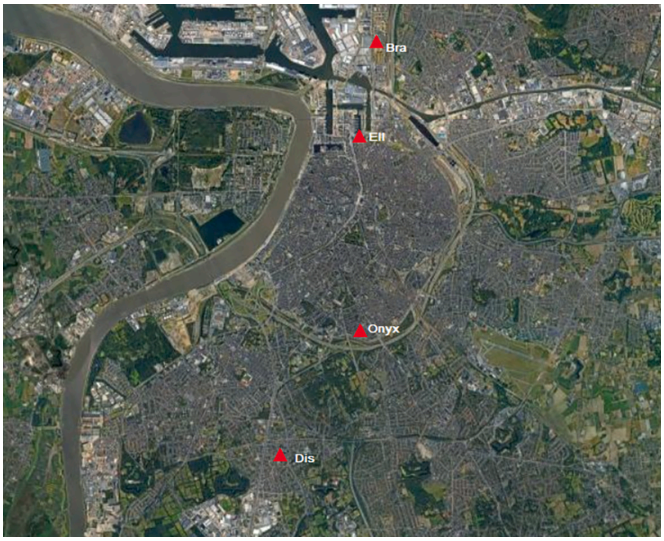

Fig. 1A. Map of the city of Antwerp and location of the roofs we investigated.

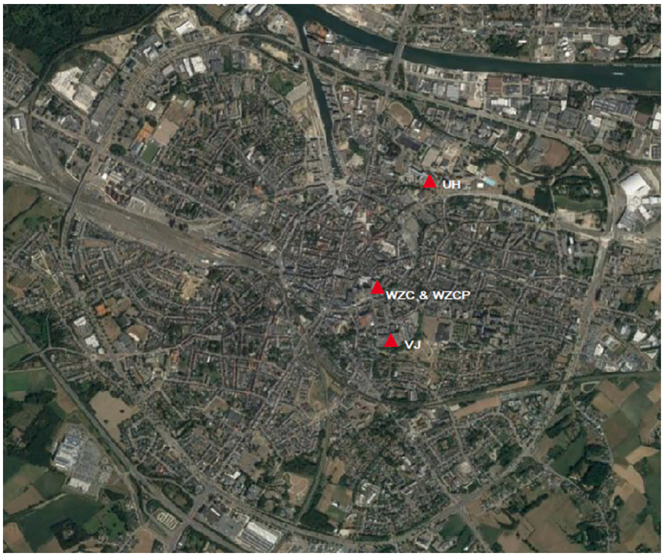

Fig. 2A. Map of the city of Hasselt and the location of the roofs we investigated.

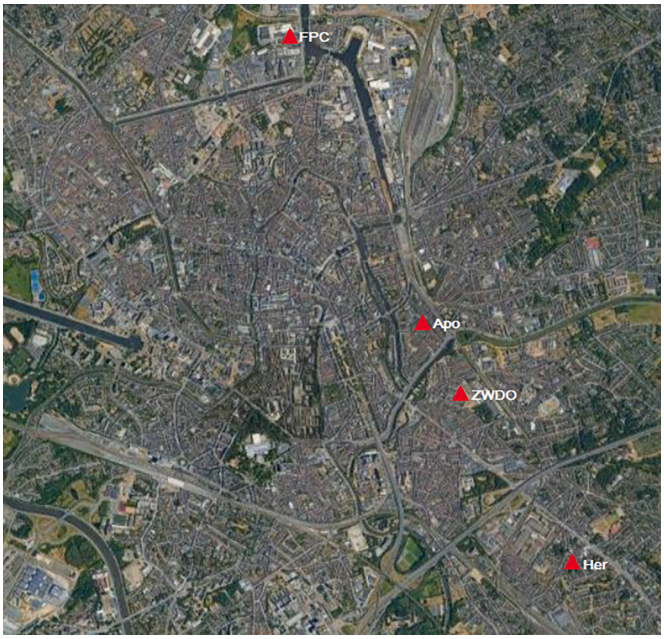

Fig. 3A. Map of the city of Ghent and location of the roofs we investigated.

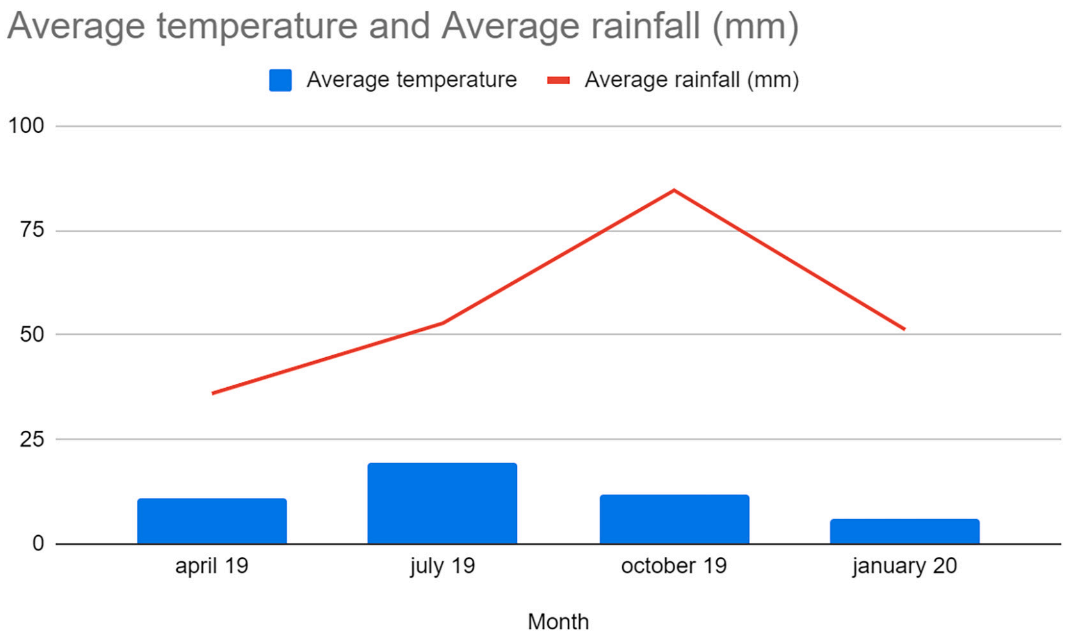

Fig. 4A. Average temperature (°C, blue bars) and average rainfall (mm, red line) for each of the months that were sampled. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1A
Species found on each roof, (number of individuals per roof).

Species	VJ	ZWDO	Bra	Onyx	Her	Apo	Ell	WZC	WZCP	UH	Dis	FPC
Entomobrya multifasciata	108	121	22	193	53	78	37	62	92	48	145	52
Cryptopygus thermophilus	266	221	234	180	148	240	16	158	219	158	347	199
Sminthurinus aureus	139	49	249	143	19	124	86	168	89	86	122	200
Sminthurinus elegans	17	2	4	0	4	4	17	13	20	6	3	0
Sminthurides malmgreni	0	0	1	0	0	0	0	0	0	0	0	0
Bourletiella hortensis	3	67	65	2	34	4	2	79	8	12	42	15
Heteromurus nitidus	0	0	2	1	0	0	0	0	0	0	0	0
Proisotoma minuta	154	87	99	126	74	1	3	117	84	29	27	55
Orchesella cincta	0	0	0	0	25	0	0	1	0	4	0	0
Parisotoma notabilis	150	117	68	3	70	140	13	40	27	25	94	75

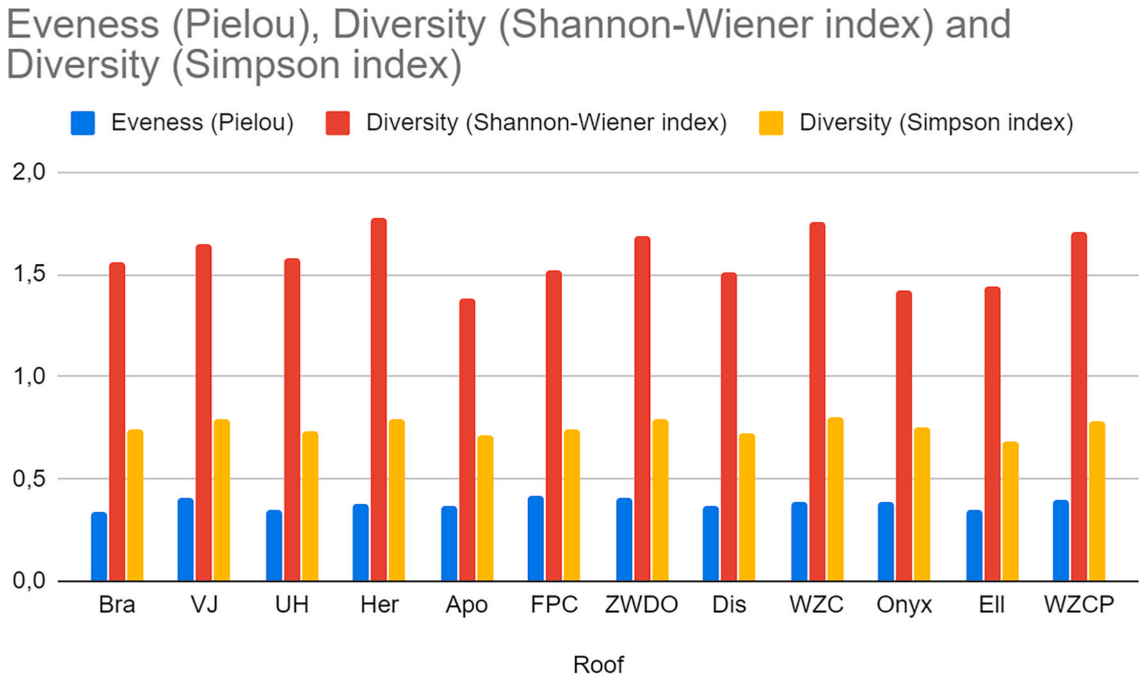

Fig. 5A. Overview of the evenness (Pielou's number (blue)), diversity as Shannon-Wiener index (red) and the diversity in Simpson index (yellow) for each individual roof. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2A

GLMM results of the fixed factor for the diversity indices (Shannon Wiener: H′, Simpson: S and Pielou's Evenness: E). No significant results were found. Table shows the estimate, standard error (std. Error), *t*-value and *p*-value.

	Estimate	Std. error	*t*-value	*P*-value
Diversity (H′)				
Age	0.013	0.011	1.277	0.270
Height	0.002	0.010	0.179	0.866
Vegetation	0.076	0.068	1.129	0.322
Surface Area	−1.50E-05	1.90E-04	−0.081	0.939
MonthJanuary	0.087	0.091	0.952	0.395
MonthJuly	0.072	0.087	0.871	0.424
MonthOctober	0.215	0.164	0.789	0.478
CityHas	0.160	0.100	1.595	0.185
CityGhe	0.223	0.421	0.547	0.645
Diversity (S)				
Age	0.005	0.006	0.939	0.401
Height	0.007	0.005	1.232	0.285
Vegetation	0.038	0.037	1.037	0.358
Surface Area	−2.60E-05	1.10E-04	−0.251	0.814
MonthJanuary	0.098	0.050	1.966	0.121
MonthJuly	0.077	0.064	0.873	0.478
MonthOctober	0.135	0.174	0.597	0.531
CityHas	0.127	0.055	2.296	0.183
CityGhe	0.241	0.356	0.647	0.684
Evenness (P)				
Age	−0.002	0.008	−0.281	0.792
Height	0.003	0.008	0.397	0.711
Vegetation	−0.036	0.053	−0.686	0.530
Surface Area	2.30E-05	1.40E-04	0.156	0.884
MonthJanuary	0.115	0.071	1.611	0.182
MonthJuly	0.138	0.094	0.554	0.437
MonthOctober	0.182	0.072	1.235	0.221
CityHas	0.087	0.080	1.094	0.335
CityGhe	0.097	0.092	1.237	0.412

Table 3A
Principal component analysis (PCA) loadings.

	PC1	PC2
Entomobrya multifasciata	−0.036	−0.532
Cryptopygus thermophilus	0.023	−0.566
Sminthurinus aereus	0.476	0.044
Sminthurinus elegans	−0.179	0.184
Sminthurides malmgreni	0.505	0.252
Bourletiella hortensis	0.284	0.022
Heteromurus nitidus	0.501	0.183
Proisotoma minuta	0.235	−0.161
Orchesella cincta	−0.200	0.173
Parisotoma notabilis	0.062	−0.454

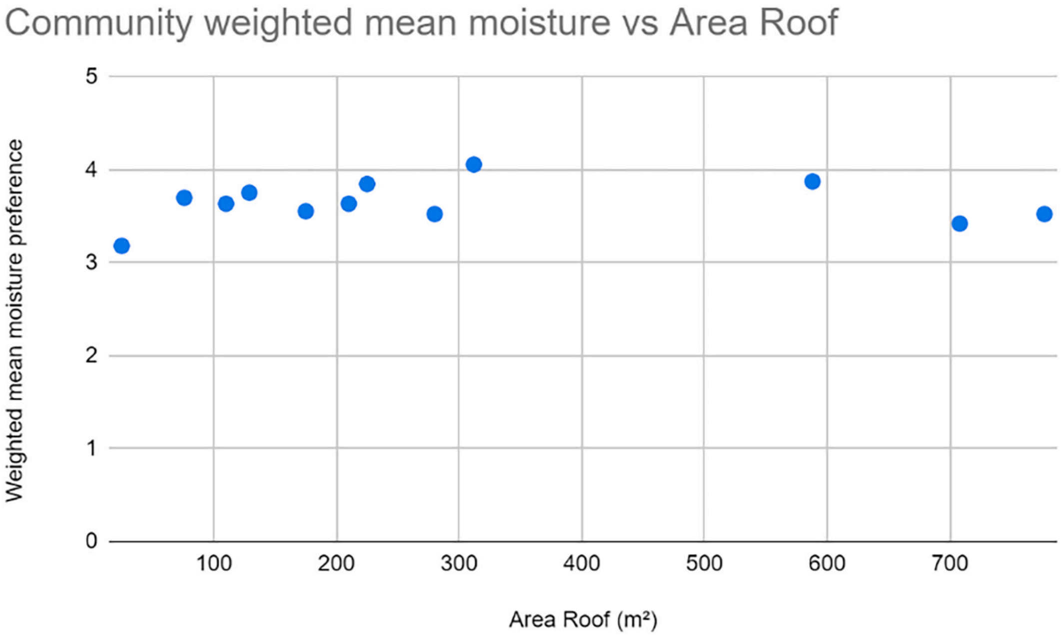

Fig. 6A. Community weighted mean (CWM) moisture preference (1: xerophilous, 2: xero-mesophile, 3: mesophile, 4: meso-hygrophilous and 5: hygrophilous) vs area roof (m^2).

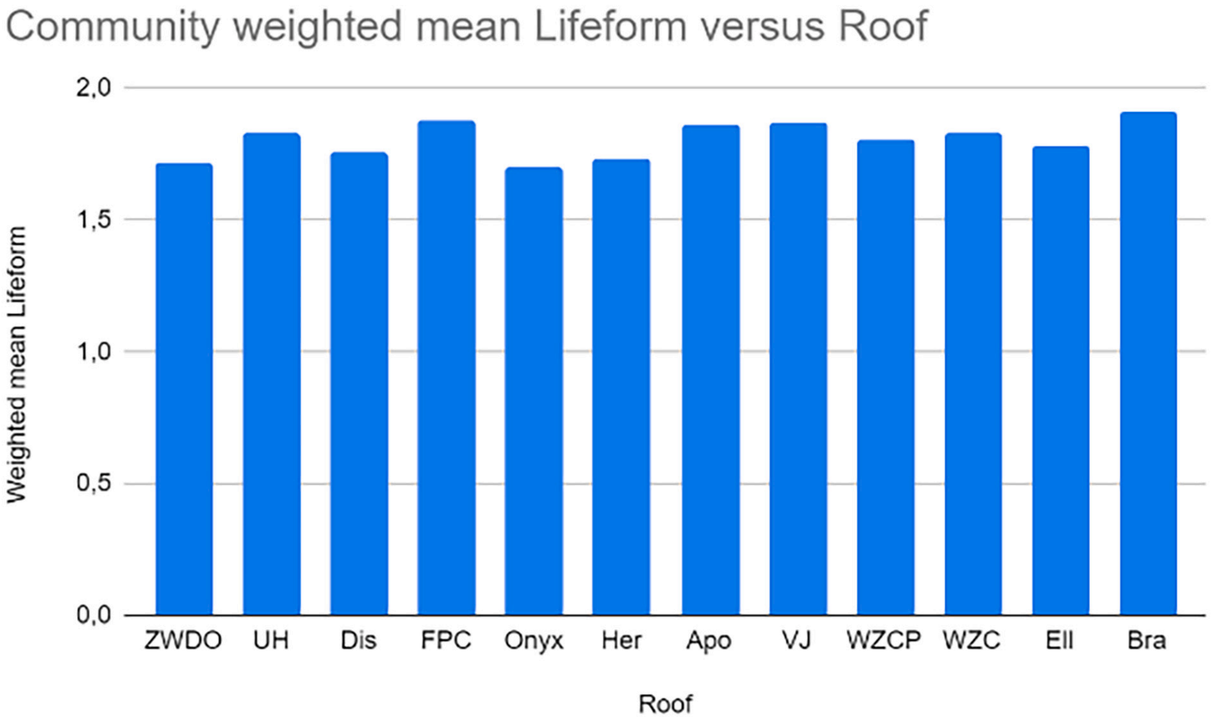

Fig. 7A. Community weighted mean life-form vs roof (1: species live on the surface or vegetation, 2 species live just below vegetation, 3 species live deep in the substrate). Roofs ZWDO, UH, Dis, FPC and Onyx are *Sedum* roofs, Her, Apo, VJ, WZCP, WZC, Ell and Bra are *Sedum*/grass/herbs roofs.

References

Al-Daikh, O.B.H., Hussein, S., Mabrouk, A.H., 2018. Efficiency of bio fertilizers and compost on soil arthropod diversity and species abundance in organic tomato field. Integr. Pest Manag. Crops 21, 56–62.

Aström, J., Bengtsson, J., 2011. Patch size matters more than dispersal distance in a mainland-island metacommunity. Oecologia 167, 747–757. https://doi.org/10.1007/s00442-011-2024-y.

Bardgett, R.D., Bowman, W.D., Kaufmann, R., Schmidt, S.K., 2005. A temporal approach to linking aboveground and below-ground ecology. Trends Ecol. Evol. 20, 634–641. https://doi.org/10.1016/j.tree.2005.08.005.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67 (1), 1–48. https://doi.org/10.18637/jss.v067.i01.

Baumann, N., 2006. Ground-nesting birds on green roofs in Switzerland: preliminary observations. Urban Habit. 4, 37–50.

Bengtsson, H., 2017. matrixStats: Functions that Apply to Rows and Columns of Matrices (and to Vectors). R Package Version 0.52.2.

Bengtsson, G., Hedlund, K., Rundgren, S., 1994. Food-and density-dependent dispersal: evidence from a soil collembolan. J. Anim. Ecol. 63, 513–520. https://doi.org/10.2307/5218.

Beninde, J., Veith, M., Hochkirch, A., 2015. Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. Ecol. Lett. 18, 581–590.

Berg, M.P., Bengtsson, J., 2007. Temporal and spatial variability in soil food web structure. Oikos 116, 1789–1804. https://doi.org/10.1111/j.2007.0030-1299.15748.x.

Blank, L., Vasl, A., Schindler, B.Y., Kadas, G.Y., Blaustein, L., 2017. Horizontal and vertical island biogeography of arthropods on green roofs: a review. Urban Ecosyst. 20, 911–917. https://doi.org/10.1007/s11252-016-0639-9.

Blaustein, L., Kadas, G.J., Gurevitch, J., 2016. Integrating ecology into green roof research. Israel J. Ecol. Evol. 62, 1–6. https://doi.org/10.1080/15659801.2016.1208943.

Bokhorst, S., Phoenix, G.K., Berg, M.P., Callaghan, T.V., Kirby-Lambert, C., Bjerke, J.W., 2015. Climatic and biotic extreme events moderate long-term responses of above- and belowground sub-Arctic heathland communities to climate change. Glob. Chang. Biol. 21, 4063–4075. https://doi.org/10.1111/gcb.13007.

Braaker, S., Ghazoul, J., Obrist, M.K., Moretti, M., 2014. Habitat connectivity shapes urban arthropod communities: the key role of green roofs. Ecology 95, 1010–1021. https://doi.org/10.1890/13-0705.1.

Brazel, A., Selover, N., Vose, R., Heiser, G., 2000. The tale of two climates-Baltimore and phoenix urban LTER sites. Clim. Res. 15, 123–135. https://doi.org/10.3354/cr015123.

Brenneisen, S., 2006. Space for urban wildlife: designing green roofs as habitats in Switzerland. Urban Habit. 4, 27–36.

Byrne, L., 2007. Habitat structure: a fundamental concept and framework for urban soil ecology. Urban Ecosyst. 10, 255–274. https://doi.org/10.1007/s11252-007-0027-6.

Castagneyrol, B., Jactel, H., 2012. Unravelling plant- animal diversity relationships: a meta-regression analysis. Ecology 93 (9), 2115–2124.

Chust, G., Pretus, J.L., Ducrot, D., Bedos, A., Deharveng, L., 2003a. Identification of landscape units from an insect perspective. Ecography 26, 257–268. https://doi.org/10.1034/j.1600-0587.2003.03325.x.

Chust, G., Pretus, J.L., Ducrot, D., Bedos, A., Deharveng, L., 2003b. Response of soil fauna to landscape heterogeneity: determining optimal scales for biodiversity modelling. Conserv. Biol. 17, 1712–1723. https://doi.org/10.1111/j.1523-1739.2003.00564.x.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x.

Cortet, J., Vauflery, A.G.D., Poinsot-Balaguer, N., Gomot, L., Texier, C., Cluzeau, D., 1999. The use of invertebrate soil fauna in monitoring pollutant effects. Eur. J. Soil Biol. 35, 115–134. https://doi.org/10.1016/S1164-5563(00)00116-3.

Cortet, J., Joffre, R., Elmholt, S., Krogh, P.H., 2003. Increasing species and trophic diversity of mesofauna affects fungal biomass, mesofauna community structure and organic matter decomposition processes. Biol. Fertil. Soils 37, 302–312. https://doi.org/10.1007/s00374-003-0597-2.

Davies, R., Simcock, R., Toft, R., 2010. Islands in the sky: urban biodiversity enhancement in NZ on indigenous living roof landscapes. In: 44th Annual Conference of the Architectural Science Association, ANZAScA 2010. United Institute of Technology.

Dunger, W., Schulz, H.J., Zimdars, B., Hohberg, K., 2004. Changes in collembolan species composition in eastern German mine sites over fifty years of primary succession. Pedobiologia 48, 503–517.

Elmqvist, T., Zipperer, W., Güneralp, B., 2016. Urbanisation, habitat loss, biodiversity decline: solution pathways to break the cycle. In: Seta, K., Solecki, W.D., Griffith, C. A. (Eds.), Routledge Handbook of Urbanisation and Global Environmental Change. Routledge, London, UK and New York, NY, pp. 139–151.

Fabián, D., González, E., Domínguez, M.V.S., Salvo, A., Fenoglio, M.S., 2021. Towards the design of biodiverse green roofs in Argentina: assessing key elements for different functional groups of arthropods. Urban For. Urban Green. 61, 127107.

Faeth, S.H., Bang, C., Saari, S., 2011. Urban biodiversity: patterns and mechanisms. Ann. N. Y. Acad. Sci. 1223, 69–81. https://doi.org/10.1111/j.1749-6632.2010.05925.x.

Faith, D.P., Minchin, P.R., Belbin, L., 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69, 57–68.

Fenoglio, M.S., Rossetti, M.R., Videla, M., 2020. Negative effects of urbanization on terrestrial arthropod communities: a meta-analysis. Glob. Ecol. Biogeogr. 29, 1412–1429.

Fenoglio, M.S., Calviño, A., González, E., Salvo, A., Videla, M., 2021. Urbanisation drivers and underlying mechanisms of terrestrial insect diversity loss in cities. Ecol. Entomol. 46, 757–771. https://doi.org/10.1111/een.13041.

Fjellberg, A., 1998. Collembola of Fennoscandia and Denmark: Part I. Poduromorpha, Brill, Leiden.

Fjellberg, A., 2007. Collembola of Fennoscandia and Denmark: Part II. Entomobryomorpha and Symphypleona, Brill, Leiden.

Francis, R.A., Lorimer, J., 2011. Urban reconciliation ecology: the potential of living roofs and walls. J. Environ. Manag. 92, 1429–1437. https://doi.org/10.1016/j.jenvman.2011.01.012.

Freeman, J.A., 1952. Occurrence of Collembola in air. In: Proceeding of the Royal Entomological Society of London, Series A. General Entomology, pp. 27–28.

Gabrych, M., Lehvävirta, S., Kotze, J., 2015. Substrate depth and roof age strongly affect plant abundances on sedum-moss and meadow green roofs in Helsinki, Finland. Ecol. Eng. 86, 95–105. https://doi.org/10.1016/j.ecoleng.2015.10.022.

Gagné, S.A., Sherman, P.J., Singh, K.K., Meentemeyer, R.K., 2016. The effect of human population size on the breeding bird diversity of urban regions. Biodivers. Conserv. 25, 653–671. https://doi.org/10.1007/s10531-016-1080-3.

Gisin, H., 1943. Ökologie und Lebensgemeinschaften der Collembolen im schweizerischen Exkursionsgebiet Basels. Rev. Suisse Zool. 50, 131–224.

Goheen, J.R., Swihart, R.K., Gehring, T.M., Miller, M.S., 2003. Forces structuring tree squirrel communities in landscapes fragmented by agriculture: species differences in perceptions of forest connectivity and carrying capacity. Oikos 102, 95–103. https://doi.org/10.1034/j.1600-0706.2003.12336.xˆ.

Heip, C.H.R., Herman, P.M.J., Soetaert, K., 2001. Indices of diversity and evenness. Oceanis 24 (4), 61–87.

Hopkin, S.P., 2007. A Key to the Collembola (Springtails) of Britain and Ireland. Field Studies Council, Strewberry.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biom. J. 50 (3), 346–363.

Ingimarsdottir, M., Caruso, T., Ripa, J., Magnusdottir, O.B., Migliorini, M., Hedlund, K., 2012. Primary assembly of soil communities: disentangling the effect of dispersal and local environment. Oecologia 170 (3), 745–754. https://doi.org/10.1007/s00442-012-2334-8.

Islam, M.D.S., Hossain, M., Yasmin, M., 2018. Impact of climatic factors and soil quality on the abundance and population density of Collembola in the Rajshahi University Campus, Bangladesh. J. Entomol. Zool. Stud. 6, 1119–1125.

Jim, C.Y., Tsang, S.W., 2011. Biophysical properties and thermal performance of an intensive green roof. Build. Environ. 46, 1263–1274. https://doi.org/10.1016/j.buildenv.2010.12.013.

Joimel, S., Grarda, B., Auclerc, A., Heddea, M., Le Doaréa, N., Salmone, S., Chenua, C., 2018. Are Collembola "flying" onto green roofs? Ecol. Eng. 111, 117–124.

Jones, E.L., Leather, S.R., 2013. Invertebrates in urban areas: a review. Europ. J. Entomol. 109, 463–478. https://doi.org/10.14411/eje.2012.060.

Kadas, G., 2006. Rare invertebrates colonizing green roofs in London. Urban Habit. 4, 66–86.

Kaufmann, R., Fuchs, M., Gosterxeier, N., 2002. The soil fauna of an Alpine glacier foreland: colonization and succession. Arct. Antarct. Alp. Res. 34, 242–250. https://doi.org/10.1080/15230430.2002.12003491.

Kmi, Koninklijk Meteorologisch Instituut, 2020. Analyse Van Het Jaar 2019. Available from. https://www.meteobelgie.be/klimatologie/waarnemingen-en-analyses/jaar-2019/2254-analyse-van-het-jaar-2019 [accessed on 9/12/2020].

Knapp, S., Schmauck, S., Zehnsdorf, A., 2019. Biodiversity impact of green roofs and constructed wetlands as progressive eco-technologies in urban areas. Sustainability 11, 5846. https://doi.org/10.3390/su11205846.

Ksiazek-Mikenas, K., Herrmann, J., Menke, S.B., Kohler, M., 2018. If you build it, will they come? Plant and arthropod diversity on urban green roofs over time. Urban Nat. 1, 52–72.

Kumar, R., Kaushik, S.C., 2005. Performance evaluation of green roof and shading for thermal protection of buildings. Build. Environ. 35, 1505–1511. https://doi.org/10.1016/j.egypro.2011.12.1047.

Kuznetsova, N., 2003. Habitat humidity and distribution of springtails. Entomol. Rev. 83, 230–238.

Lepère, C., Domaizon, I., Taïb, N., Mangot, J.F., Bronner, G., Boucher, D., Debroaz, D., 2013. Geographic distance and ecosystem size determine the distribution of smallest protists in lacustrine ecosystems. FEMS Microbiol. Ecol. 85, 85–94. https://doi.org/10.1111/1574-6941.12100.

Levin, S.A., Carpenter, S.R., Godfray, H., Charles, J., Kinzig, A.P., Loreau, M., Losos, J.B., Walker, B., Wilcove, D.S., 2009. The Princeton Guide to Ecology III.1 Biodiversity: Concepts, Patterns, and Measurement, pp. 257–263. https://doi.org/10.1515/9781400833023.257.

Li, W.C., Yeung, K.K.A., 2021. A Comprehensive study of green roof performance from environmental perspective. Int. J. Sustain. Built Environ. 3, 127–134.

Li, J.F., Wai, O.W.H., Li, Y.S., Zhan, J.M., Ho, Y.A., Li, J., Lam, E., 2010. Effect of green roof on ambient CO2 concentration. Build. Environ. 45, 2644–2651. https://doi.org/10.1016/j.buildenv.2010.05.025.

Lindberg, N., Bengtsson, J., 2005. Population responses of oribatid mites and collembolans after drought. Appl. Soil Ecol. 28, 163–174.

MacArthur, R.H., Wilson, E.O., 1963. An equilibrium theory of insular zoogeography. Evolution 17, 373–387. https://doi.org/10.2307/2407089.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.

Macivor, S., Ksiazek, K., 2015. Invertebrates on green roofs. Ecol. Stud. Analys. Synthes. 223, 333–355. https://doi.org/10.1007/978-3-319-14983-7_14.

Macivor, S., Lundholm, J., 2011. Insect species composition and diversity on intensive green roofs and adjacent level-ground habitats. Urban Ecosyst. 14, 225–241.

Madre, F., Vergnes, A., Machon, N., Clergeau, P., 2013. A comparison of 3 types of green roofs as habitats for arthropods. Ecol. Eng. 57, 109–117. https://doi.org/10.1016/j.ecoleng.2013.04.029.

Makkonen, M., Berg, M.P., Van Hal, J.R., Callaghan, T.V., Press, M., Aerts, R., 2011. Traits explain the responses of a sub-arctic collembola community to climate manipulation. Soil Biol. Biochem. 43, 377–384. https://doi.org/10.1016/j.soilbio.2010.11.004.

Mentens, J., Raes, D., Hermy, M., 2006. Green roofs as a tool for solving rainwater runoff problems in the urbanized 21st century? Landsc. Urban Plan. 77, 217–226. https://doi.org/10.1016/j.landurbplan.2005.02.010.

Molineux, C.J., Connop, S.P., Gange, A.C., 2014. Manipulating soil microbial communities in extensive green roof substrates. Sci. Total Environ. 493, 632–638. https://doi.org/10.1016/j.scitotenv.2014.06.045.

Nektarios, P., Ntoulas, N., Nydrioti, E., Kokkinou, I., Bali, E.M., Amountzias, I., 2015. Drought stress response of Sedum sediforme grown in extensive green roof systems with different substrate types and depths. Sci. Hortic. 181, 52–61.

Oberndorfer, E., Lundholm, J., Bass, B., Coffman, R.R., Doshi, H., Dunnett, N., Gaffin, S., Köhler, M., Liu, K.K.Y., Rowe, B., 2007. Green roofs as urban ecosystems: ecological structures, functions and services. Bioscience 57, 823–834. https://doi.org/10.1641/B571005.

Oksanen, J., Blanchet, G., Roeland, K., Legendre, P., Minchin, P.R., O'hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2014. Vegan: community ecology package. R Package 280.

Parisi, V., Menta, C., Gardi, C., Jacomini, C., Mozzanica, E., 2005. Microarthropod communities as a tool to assess soil quality and biodiversity: a new approach in Italy. Agric. Ecosyst. Environ. 105, 323–333. https://doi.org/10.1016/j.agee.2004.02.002.

Pataki, D.E., Carreiro, M.M., Cherrier, J., Grulke, N.E., Jennings, V., Pincetl, S., Pouyat, R.V., Whitlow, T.H., Zipperer, W.C., 2011. Coupling biogeochemical cycles in urban environments: ecosystem services, green solutions, and misconceptions. Front. Ecol. Environ. 9, 27–36. https://doi.org/10.1890/090220.

Piano, E., Souffreau, C., Merckx, T., Baardsen, L.F., Backeljau, T., Bonte, D., Brans, K.I., Cours, M., Dahirel, M., Debortoli, N., Decaestecker, E., De Wolf, K., Engelen, J.M.T., Fontaneto, D., Gianuca, A.T., Govaert, L., Hanashiro, F.T.T., Higuti, J., Lens, L., Martens, K., Matthysen, E., Pinseel, E., Sablon, R., Schon, I., Stoks, R., Van Doninck, K., Van Dyck, H., Vanormelingen, P., Van Wichelen, J., Vijverman, W., De Meester, L., Hendrickx, F., 2020. Urbanization drives cross-taxon declines in abundance and diversity at multiple spatial scales. Glob. Chang. Biol. 26, 1196–1211. https://doi.org/10.1111/gcb.14934.

Pickett, S.T.A., Cadenasso, M.L., 2008. Linking ecological and built components of urban mosaics: an open cycle of ecological design. J. Ecol. 96, 8–12.

Pickett, S.T.A., Cadenasso, M.L., 2009. Altered resources, disturbance, and heterogeneity: a framework for comparing urban and non-urban soils. Urban Ecosyst. 12, 23–44. https://doi.org/10.1007/s11252-008-0047-x.

Pickett, S.T.A., Cadenasso, M.L., Grove, J.M., Boone, C.G., Groffman, P.M., Irwin, E., Kaushal, S.S., Marshall, V., Mcgrath, B.P., Nilon, C.H., Pouyat, R.V., Szlavecz, K., Troy, A., Warren, P., 2011. Urban ecological systems: scientific foundations and a decade of progress. J. Environ. Manag. 92, 331–362. https://doi.org/10.1016/j.jenvman.2010.08.022.

Pielou, E.C., 1966. The measurement of diversity in different types of biological collections. J. Theor. Biol. 13, 131–144. https://doi.org/10.1016/0022-5193(66)90013-0.

Ponge, J.F., Dubs, F., Gillet, S., Sousa, J.P., Lavelle, P., 2006. Decreased biodiversity in soil springtail communities: the importance of dispersal and land use history in heterogeneous landscapes. Soil Biol. Biochem. 38, 1158–1161. https://doi.org/10.1016/j.soilbio.2005.09.004.

R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rosenzweig, M.L., 2016. Green roofs: new ecosystems to defend species diversity. Israel J. Ecol. Evol. 62, 7–14. https://doi.org/10.1080/15659801.2015.1121600.

Rumble, H., Gange, A.C., 2013. Soil microarthropod community dynamics in extensive green roofs. Ecol. Eng. 57, 197–204. https://doi.org/10.1016/j.ecoleng.2013.04.012.

Schindler, B.Y., Griffith, A.B., Jones, K.N., 2011. Factors influencing arthropod diversity on green roofs. Cities Environ. CATE 4, 5–20. https://doi.org/10.15365/cate.4152011.

Schrader, S., Böning, M., 2006. Soil formation on green roofs and its contribution to urban biodiversity with emphasis on Collembolans. Pedobiologia 50, 347–356. https://doi.org/10.1016/j.pedobi.2006.06.003.

Seto, K.C., Güneralp, B., Hutyra, L.R., 2012. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. Proc. Nat. Acad. Sci. USA 109, 16083–16088. https://doi.org/10.1073/pnas.1211658109.

Shmida, A., Wilson, M.V., 1985. Biological determinants of species diversity. J. Biogeogr. 12 (1), 1–20.

Stierhof, T., 2003. Collembolagemeinschaften in Baden-Wurttenbergischen Waldboden. Thesis Giessen: Institut für Allgemeine und Spezielle Zoologie, Bereich Tierökologie. Justus-Liebig-Universität Gießen, 375 p.

Turner, M., Baker, W.L., Peterson, C.J., Peet, R.K., 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems 1, 511–523. https://doi.org/10.1007/s100219900047.

United Nations Development Programme, 2014. Human Development Report 2014. Communications Development Incorporated, New York. Available from. http://hdr.undp.org/sites/default/files/2015_human_development_report.pdf [accessed on 10/12/2020].

Van Straalen, N.M., Rijninks, P.C., 1982. The efficiency of Tullgren apparatus with respect to interpreting seasonal changes in age structure of soil arthropod populations. Pedobiologia 24, 197–209.

Vandewalle, M., De Bello, F., Berg, M.P., Bolger, T., Dole, S., Dubs, F., Feld, C.K., Harrington, R., Harrison, P.A., Lavorel, S., Da Silva, P., Moretti, M., Niemela, J., Santos, P., Sattler, T., Sousa, J.P., Sykes, M.T., Vanbergen, A.J., Woodcock, B.A., 2010. Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. Biodivers. Conserv. 19, 2921–2947. https://doi.org/10.1007/s10531-010-9798-9.

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, 4th ed. Springer, New York. ISBN 0-387-95457-0. https://www.stats.ox.ac.uk/pub/MASS4/.

Verhoef, H.A., Van Selm, A.J., 1983. Distribution and population dynamics of Collembola in relation to soil moisture. Holarct. Ecol. 6, 387–394. https://doi.org/10.1111/j.1600-0587.1983.tb01234.x.

Ward, D., Blaustein, L., 1994. The overriding influence of flash floods on species-area curves in ephemeral Negev Desert pools: a consideration of the value of island biogeography theory. J. Biogeogr. 21, 595–603. https://doi.org/10.2307/2846034.

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York. ISBN 978-3-319-24277-4.

Widenfalk, L.A., Bengtsson, J., Berggren, A., Zwiggelaar, K., Spijkman, E., Brugman, F., Berg, M.P., 2015. Spatially structured environmental filtering of collembolan traits in late successional salt march vegetation. Oecologia 179 (2), 537–549.

Widenfalk, L.A., Malmström, A., Berg, M.P., Bengtsonn, J., 2016. Small-scale Collembola community composition in a pine forest soil – Overdispersion in functional traits indicates the importance of species interactions. Soil Biol. Biochem. 103, 52–62. https://doi.org/10.1016/j.soilbio.2016.08.006.

Williams, N.S.G., Schwartz, M.W., Vesk, P.A., Mccarthy, M.A., Hahs, A.K., Clemants, S.E., Corlett, R.T., Duncan, R.P., Norton, B.A., Thompson, K., Mcdonnell, M.J., 2009. A conceptual framework for predicting the effects of urban environments on floras. J. Ecol. 97, 4–9. https://doi.org/10.1111/j.1365-2745.2008.01460.x.

Wiwatwitaya, D., Takeda, H., 2005. Seasonal changes in soil arthropod abundance in the dry evergreen forest of north-East Thailand, with special reference to collembolan communities. Ecol. Res. 20, 59–70. https://doi.org/10.1007/s11284-004-0013-x.