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Original article

Community assembly of mosses, lichens, and succulents across a green roof chronosequence in Malmö Sweden

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ABSTRACT

Research on the flora of green roofs has mainly focused on vascular plants. However, as green roofs age, they are spontaneously colonized by mosses and lichens, with mosses often becoming the dominant lifeform. There is thus a need to document and understand how moss and lichen communities assemble over time, and how these changes influence the provisioning of ecosystem services. To fill this knowledge gap, we analysed a chronosequence of 20 extensive green roofs, ranging from 0.4 to 28 years of age. For each roof, we measured environmental variables and collected percent cover data for all observed vascular plants, mosses, and lichens. Overall, all rooftops experienced spontaneous moss and lichen colonization over time. Increased shade, organic layer depth, and age appeared to favour perennial, pleurocarpous moss species over annual acrocarpous moss species. Based on the results of our study, the pleurocarpous mosses *Brachythecium albicans* and *Hypnum cupressiforme* are well adapted to rooftop conditions, making them suitable candidates for propagation onto *Sedum*/moss green roofs. Our findings suggest that careful selection of moss and lichen species, tailored to specific roof conditions at installation, could enhance colonization success (e.g. a stable community that can persist over multiple seasons). Future research should explore how these communities interact with other components of green roof ecosystems.

1. Introduction

Extensive green roofs are shallow (substrate $\leq$ 15 cm) vegetated rooftops built for the ecosystem services they provide. These man-made ecosystems have been found to aid in stormwater retention, thermal regulation, particulate matter capture, habitat provision, psychological well-being, and many other ecosystem services (Volder and Dvorak, 2014; Lee et al., 2015; Kyrö et al., 2018; Irga et al., 2022; Scolaro et al., 2024). These benefits are not provided equally by different plant species, largely due to interspecific trait variation (Heim et al., 2023). Characteristics such as stature, leaf water relations, rooting depth and nutrient use efficiency have a strong impact on ecosystem function, and therefore, service provisioning (Heim et al., 2021; Lönnqvist et al., 2023).

Research on green roof flora has mainly focused on vascular plants, particularly succulents, graminoids, and forbs (Leite and Antunes, 2023). Succulents, especially those in the family Crassulaceae, are one of the most common groups used on extensive green roofs (Oberndorfer et al., 2007). Species in this family are extremely drought tolerant and capable of CAM (crassulacean acid metabolism) photosynthesis. Rather than opening stomata during the day, as is done in C3 and C4 photosynthesis, CAM species can open their stomata at night, reducing water loss (Bloom, 1979). Furthermore, the succulent leaves of these species allow for water storage, making them well adapted to the drought prone green roof environment. Even so, not all Crassulaceae species are equal, with differences observed in drought tolerance and influence on ecosystem services (Heim et al., 2025).

Over time, the cover and distribution of initially established species, such as succulents, changes, with spontaneous colonization of ruderals, bryophytes and lichens common (Catalano et al., 2016; Gabrych et al. 2016; Vidaller et al., 2022). This increase in bryophytes and lichens is especially prevalent on one common green roof type, the *Sedum*/moss green roof. These roofs, common in Northern Europe, usually have a substrate depth less then 5 cm and an initial plant profile solely composed of species from the family Crassulaceae (Gabrych et al. 2016; Mitchell et al. 2021). There is thus a need to document and understand how moss and lichen communities assemble over time on these rooftops,

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and how these changes influence green roof ecosystem service provisioning.

Mosses are non-vascular plants with a poikilohydric hydration strategy, meaning they lack the ability to transport water from the soil to photosynthetic tissues, instead relying on direct atmospheric deposition. They play an important role in carbon cycling (Street et al., 2013) and many can host nitrogen fixing bacteria (DeLuca et al., 2002, 2008). They also capture atmospheric nutrients, transform soil microclimates, and provide habitat for a diversity of micro and mesofauna (Lindo and Gonzalez, 2010). Mosses occur from the Arctic to the Antarctic, as well as deserts and tropical rainforests (Budke et al., 2018). Many mosses can survive periods of desiccation (Budke et al., 2018), a trait that has encouraged researchers to explore their value in rooftop environments where they have been found to capture particulate matter (Seo et al., 2023), cool the substrate (Anderson et al., 2010; Jongsoo and Jeasun, 2026), and when wetted retain 8–10 times their dry weight in water (de Carvalho, 2020). Some mosses can inhibit germination of weed seeds (Drake et al., 2018) while others facilitate growth of neighboring vascular plants (Heim et al., 2014a; Schröder and Kiel, 2020). Although researchers have made great strides towards documenting the presence of mosses on green roofs in recent years, there remain many uncertainties surrounding their ecological role, assembly dynamics, and potential benefits as components of the built environment.

Lichens are formed by a symbiotic relationship between a heterotrophic mycobiont (fungus) and one or more autotrophic photobiont(s), typically a green alga and/or a cyanobacteria (Asplund and Wardle, 2017). Lichens are stress tolerant, long lived, slow growing organisms and are found in most terrestrial ecosystems (Nash, 2008; Mallen-Cooper et al., 2023). Owing to their capability for stress tolerance and their poikilohydric nature, lichens may comprise a large percentage of biomass in some ecosystems (Kranner et al., 2008) such as nutrient poor, drought prone, and/or cold environments (Nash, 2008). Lichens can capture nutrients from dry and wet atmospheric deposition and about 10 % of lichen species are able to fix nitrogen via their cyanobacterial photobiont. Lichens also provide habitat and/or food for a variety of organisms (Asplund and Wardle, 2017). In green roof ecosystems, some lichen species have been found to reduce substrate temperature and to facilitate the growth of neighboring species (Heim and Lundholm, 2014a; Schröder and Kiel, 2020).

Mosses and lichens commonly colonize green roof ecosystems (e.g. Gabrych et al. 2016; Mitchell et al., 2021, Lönnqvist et al., 2021) and thus influence ecosystem services. A review by Gärtner (2025) identified only 37 research articles that discuss the mosses of green roofs. Of these, two thirds were experimental, while the rest were observational (Gärtner, 2025). Recent studies have intentionally established particular mosses on green roofs (Tani et al., 2012; Perini et al., 2020; Nagase 2023) and evaluated their influence on ecosystem services (Anderson et al., 2010; Heim et al., 2014a). These studies, however, largely neglect the process of spontaneous colonization of green roof by mosses as part of natural community succession. The few studies that have looked at long-term development of plant communities on roofs have tended to consider all moss species together as one group or unit (e.g., Mitchell et al. 2021). This overlooks the taxonomic, and potentially functional, diversity in this group of plants (Bates, 2013; Vidaller, 2023). In comparison to mosses, *"green roof lichen"* research is even less common with only three articles identified by the Web of Science (Web of Science, 2025). Researchers have examined intentionally established lichens (Heim and Lundholm, 2014a; Schröder and Kiel, 2020) and one study looked at spontaneously colonizing lichen species in relation to roof age (Gabrych et al. 2016). There is thus a clear need to understand the factors influencing moss and lichen community assembly and change over time on green roofs.

Since moss and lichen have been found to influence green roof ecosystem services, it is important to understand which species commonly colonize green roofs and how these bryophyte and lichen communities change over time and across environmental gradients. Using a chronosequence of 20 *Sedum*/moss green roofs in Southern Sweden, we begin to fill the above-mentioned knowledge gaps. Our objectives for this study were to 1) determine how age influences total lichen, moss, and succulent cover, as well as the composition and taxonomic diversity of the moss and lichen species on the roof; and 2) determine which environmental variables have the greatest influence on the dominant lichen, moss, and succulent vascular plants. The results from this study can be used to select moss and lichen species for establishment on new green roofs that will likely survive, thrive, and provide ecosystem services long-term.

2. Methods

2.1. Study site

In June and July 2022, data was collected across 20 *Sedum*/moss green roofs in Southern Sweden (Fig. 1). The Majority (16) were located in the city of Malmö (55.61° N, 13.00° E), with four roofs located just outside the city in Alnarp (55.39° N, 13.05° E) ($n = 2$), and Lund (55.42 N°, 13.11° E) ($n = 2$). The farthest distance between two study roofs was 23 km while the closest distance was a few meters. Meaning, these roofs are largely exposed to similar moss and lichen colonizers. These roofs were built between 1994 and 2022 by Vegtech (Vislanda, Sweden), in a similar manner, using pre-grown vegetated mats planted with Crassulaceae, mainly species of *Sedum* and *Phedimus* (Mitchell et al., 2021). These roofs had a substrate depth ranging between 1.7 and 4.1 cm, areas between 403 and 19 m^2, building heights between 2.4 and 5.5 m, and ages that ranged from 4 months to 28 years (see supplementary of Heim et al., 2025 for individual roof details).

Malmö has a temperate oceanic climate with mild winters, warm summers, no dry season, and moderate seasonality (Köppen-Geiger classification: Cfb). The annual mean temperature is 9 °C, with mean January temperatures of 2 °C and mean July temperatures 18 °C. The annual precipitation is distributed fairly evenly throughout the year and on average is 615 mm per year (SMHI, 2023).

2.2. Community abundance

Cover data were collected for each roof using twelve 0.5 × 0.5 m quadrats to calculate the percent cover of each species of bryophyte, lichen, succulent and colonizing vascular plants (all non-succulents), as well as the bare substrate, and any humified moss. The quadrats were distributed in a stratified random pattern, by dividing the roof into 12 evenly sized segments, with one quadrat sampled at a random location within each segment. When a species was observed on a roof, but not in any of the twelve quadrats, the percent cover of that species was recorded as "trace", and for purposes of statistical analyses, a cover value of 0.001 % was used.

Succulents and colonizing vascular plants were identified to species in the field. Bryophytes and lichens could not be identified to species in the field, so each different morphotype was given an ID upon sampling, the percentage cover of that morphology in each quadrat was estimated, and samples were brought back to the lab for identification. Where one bryophyte or lichen morphotype was identified as more than one species in the lab, the percentage cover data was evenly split between each of these species (See supplementary).

All samples were dried at 40 °C for 48 h, then stored at room temperature. Lichens and bryophytes were identified to species using Brodo (2016), Smith (2004), and Paton (2014) respectively. Voucher samples for each species observed in this study were donated to the herbarium at the Nova Scotia Museum of Natural History (Accession N024.007).

2.3. Abiotic environmental variables

Nine environmental variables were collected for each green roof: age, slope, height, area, solar exposure, substrate depth, substrate

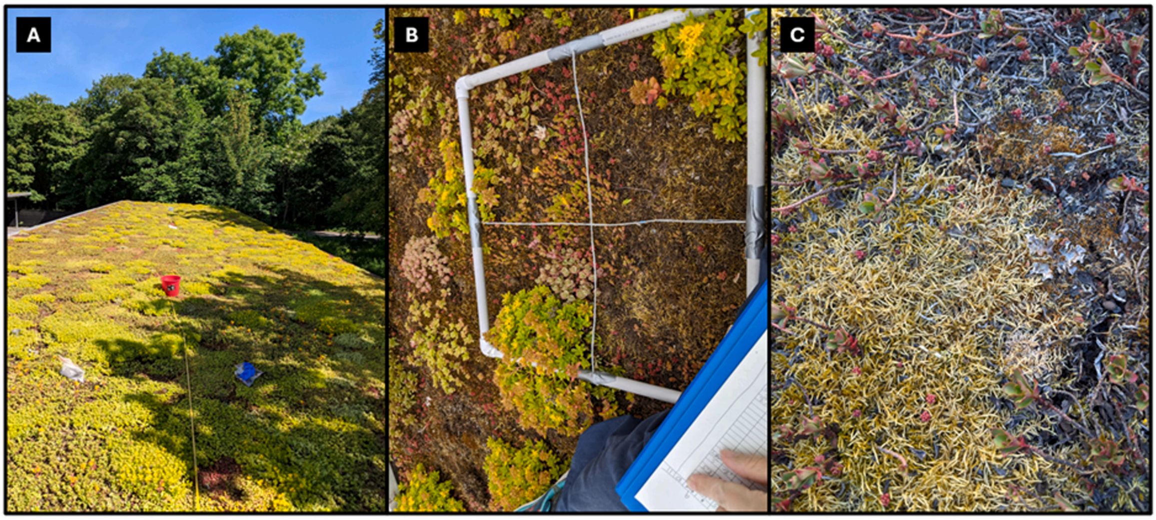

Fig. 1. A) One of the study green roofs, located above a carport and bicycle shelter. B) 0.5 × 0.5 m quadrat showing the variation in growth forms. C) Close-up of an acrocarpous moss, a pleurocarpous moss, a lichen *Peltigera sp., Sedum album*, and *Phedimus spurius*.

nitrogen content, $\delta^{15}N$ (15 N) signature, and substrate organic matter content. Solar exposure was measured using a Solar Pathfinder and the Solar Pathfinder Assistant software (Solar Pathfinder Company, Linden, TN, USA). Substrate for nutrient analysis was gathered using a stratified random pattern. The roof was divided into 8 evenly sized segments, with even numbers annotated as subsample *A* and odd samples annotated as subsample *B*. Each subsample was collected using a 7 cm diameter core collected at a random location within each segment. For each core, subsamples encompassing the full substrate depth was taken. Subsamples were then pooled based on their designated letter, creating two composite samples per roof. Substrate samples were refrigerated for no more than 48 h, then sieved to < 6 mm and dried for 48 h at 70°C. Once dried, substrate organic matter content was determined by loss-on-ignition at 550 °C (Dean, 1974). The remaining portions of each sample were then milled for 4 min at a frequency of 30 Hz (Retsch MM400) to achieve a fine (<1 mm) texture before analysing total substrate nitrogen and 15 N using a Flash EA 2000 Elemental analyzer (Thermo Fisher Scientific, Bremen, Germany).

2.4. Statistical analysis

In order to analyze the associations between environmental variables and roof flora, we used ordination, and linear mixed-models. We conducted four ordinations (non-metric multidimensional scaling, NMDS with default $k = 2$) using the taxonomic data for bryophytes, lichens, succulents, and the combination of all three (all-species). For this data we fitted environmental and abundance data vectors onto each ordination.

Multiple linear regressions, using a gaussian distribution, were used to further understand the environmental variables associated with species abundance. This analysis was conducted for all species that occurred on at least five rooftops (response variable), with the environmental variables identified as significant ($p \leq 0.05$) through the all-species NMDS used as the explanatory variables. These explanatory variables were then further examined for suitability in the final model using Akaike information criterion. In this step every combination of environmental variables was tested and models with a delta score below seven were selected (Burnham and Anderson, 2002). If a model had multiple delta scores below seven, model averaging was used. In this case all models with a delta score below seven were averaged, weighted by the delta score. Meaning, 95 % confidence intervals of beta-coefficients are averaged from these chosen models, weighted by the sum of the AIC scores for those models (Burnham and Anderson, 2002). The number of models averaged for each response variable is listed in the supplementary. If the confidence interval for an environmental variable did not cross zero it was considered to be associated with the abundance of the specified species. All data used in this analysis were tested for normality using the Shapiro-Wilks test and when necessary, transformed as close as possible to normality using Tukey's ladder of transformations (Tukey, 1977). For each regression, model diagnostics were checked.

All statistical analysis were conducted in R v4.4.1 (R Core Team, 2024). The following R libraries were used in this paper: lme4 was used to calculate regression models, MuMIn was used to calculate delta scores and conduct model averaging; vegan was used to calculate NMDS; Tukey's ladder of transformations was calculated using rcompanion; and graphs were created using ggplot2, dotwhisker, and ggfortify. Details for all statistical tests, including the R code used, is provided in the supplementary material.

3. Results

On the 20 sampled green roofs, 9 lichen species, 30 moss species, 1 liverwort species, 8 succulent species and 11 colonizing vascular species were recorded. Of these, 22 species were observed on at least five rooftops (Table 1). None of the observed species were on Sweden's red list (SLU Artdatabanken, 2020). Species richness varied between study sites, with 0–5 lichen species and 2–11 moss species observed. Lichen cover remained scarce for roofs upon which lichens were found, with an average cover of 1.5 ± 0.4 % (±standard error). The most common species of lichen was *Peltigera canina* (mean cover when present: 1.1 ± 0.2 %), a cyanolichen observed on 12 of the 20 green roofs. Mosses, in comparison, achieved higher percent cover (37 ± 7 %) with individual roofs containing 3–11 species. The most prevalent species was *Ceratodon purpureus* (cover: 5.1 ± 1.9 %), a small acrocarpous species found on 16 rooftops. However, the moss species with the greatest average percent cover was the pleurocarpous moss *Brachythecium albicans* (cover: 22.1 ± 7 %) found on 13 rooftops.

Succulents were found to have the highest percent cover, at 64 ± 4 %, with 3–8 species observed per roof. Of these, only *Sedum album* (cover: 25 ± 6.1 %) was found on all 20 rooftops. When colonizing vascular species were assessed, although all rooftops had spontaneous vascular colonizers, no individual species occurred on more than two rooftops. Additionally, colonizing vascular plants represented less than 1 % of total cover for all roofs except for one, roof labeled M3, for which the total cover was 14 % (Mostly *Vicia cracca*). For this reason,

Table 1
List of all species that were found on at least five of the 20 green roofs. Data include the number of rooftops on which a given species was found (Roofs), the mean percent cover of a species on the roofs where it is found (Cover), and the standard error of percent cover (SE). The only group containing intentionally planted species is the succulent group.

Mosses	**Roofs**	**Cover**	**SE**
Ceratodon purpureus	16	5.1	1.9
Brachythecium albicans	13	22.1	7.0
Syntrichia intermedia	10	11.0	9.3
Abietinella abietina	8	1.7	0.9
Hypnum cupressiforme	8	20.6	11.3
Gymnostomum aeruginosum	8	1.3	0.4
Bryum argenteum	6	0.6	0.2
Flexitrichum flexicaule	6	0.4	0.04
Tortella tortuosa	6	0.7	0.1
Pseudocrossidium hornschuchianum	5	2.2	1.1
Total Moss	20	37	7.0
Lichens	**Roofs**	**Cover**	**SE**
Peltigera canina	12	1.1	0.2
Xanthoria parietina	10	0.4	0.1
Physcia adscendens	7	0.5	0.1
Cladonia fimbriata	7	0.7	0.1
Peltigera didactyla	5	1.1	0.4
Total Lichen	16	1.5	0.4
Succulent	**Roofs**	**Cover**	**SE**
Sedum album	20	25.0	6.1
Phedimus spurius	18	8.2	2.9
Phedimus kamschaticum	18	10.7	2.4
Phedimus hybridus	16	14.7	3.4
Sedum acre	15	1.6	0.8
Sedum sexangulare	11	1.3	0.2
Hylotelephium ewersii	11	1.2	0.3
Total Succulents	20	64.2	4.1

colonizing vascular species were excluded from further statistical analysis. Finally, a single liverwort in the genus *Cephaloziella* was observed growing on one moss specimen (*Hypnum cupressiforme*) that had been collected for identification; this anecdotal observation was thus excluded from further statistical analysis.

All NMDS ordinations had a small stress value, indicating good two-dimensional fit with the data: all-species (stress: 0.103), succulent (stress: 0.096), moss (0.145), and lichen (0.94). When a NMDS was conducted on all species found on at least five rooftops, the species *Phedimus spurius, Hypnum cupressiforme,* and *Peltigera didactyla* were associated with older roofs with deeper substrate and more organic matter, while *Brachythecium albicans* was associated with roofs on the opposite end of this environmental spectrum. The species *Phedimus hybridus* and *Phedimus kamschaticum* were associated with less solar exposure while *Sedum album* was associated with more solar exposure. For the NMDS conducted on only the succulent species, *Sedum album* was associated with more solar exposure and *Phedimus hybridus* was associated with less solar exposure. *Phedimus spurius* was positively associated with steeper slopes, higher substrate nitrogen content, and taller buildings, while the reverse was true for *Phedimus kamschaticum*. For the NMDS conducted on moss abundance data, *Brachythecium albicans* was associated with roofs that were younger roofs, with mild slopes, shallower substrates, and on shorter buildings; and *Syntrichia intermedia* was associated with roofs that were older and with a steeper slope. Finally, for the NMDS conducted on the lichen abundance data no associations were observed between species and the tested environmental variables (Fig. 2), which may be explained at least partly by the very short gradient in species abundances (with average percent covers ~ 1 %).

For the mosses observed on at least five rooftops, three species were associated with our tested environmental variables. *Brachythecium albicans* and *Abietinella abietina* were more common on rooftops with shallower slopes; and *Bryum argenteum* was more common on roofs that were younger, on shorter buildings, and those with more shade. For the lichens, only total lichen abundance was associated with any environmental variable, with more lichen observed on older roofs. Finally, four species of succulents were associated with the tested environmental variables. *Sedum acre* was more common on roofs that were younger, had more shade, and on taller buildings; *Sedum album* was more common on roofs with less organic matter and more solar exposure; *Phedimus hybridus* was more common on roofs with more shade; and *Phedimus spurius* was more common on rooftops with higher organic matter content in the substrate (Fig. 3).

4. Discussion

Moss and lichen communities have potential to impact ecosystem services of green roofs, particularly as those roofs age and become dominated by these organisms (Lindo and Gonzalez, 2010; Asplund and Wardle, 2017; Leite and Antunes, 2023). In our study, mosses and/or lichens spontaneously colonized all rooftops over time, with source populations presumably being the neighbouring green spaces, or propagules colonizing the green roof mats during their production. Overall, the most common mosses observed in this study were *Ceratodon purpureus* and *Brachythecium albicans,* while the most common lichen was

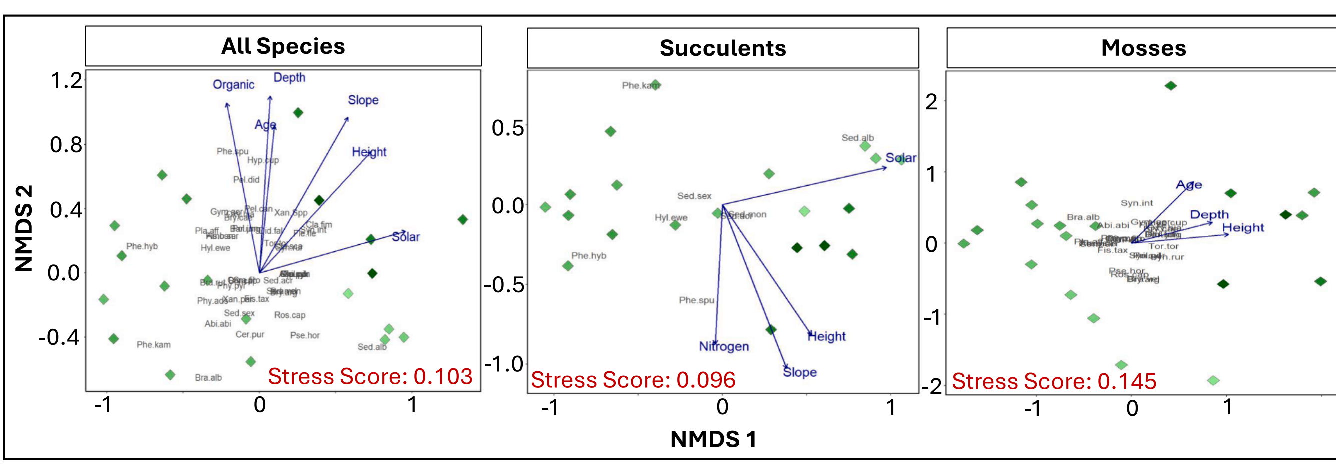

Fig. 2. NMDS organized by the abundance of all species (left panel), succulents (middle panel) and mosses (right panel). Environmental corelates with a p-value ≤ 0.05 are displayed as blue arrows, species are shown in black, and stress scores for the NMDS are displayed in red. The green diamonds represent study roofs and are scaled to roof age, with darker green indicating older roofs and lighter green indicating younger roofs. Species scores were calculated as weighted averages of site scores and were displayed as black labels in the NMDS ordinations. An NMDS was conducted for lichen (Stress 0.094), however the environmental variables did not meet the above-mentioned criteria. For this reason, no lichen graph is shown.

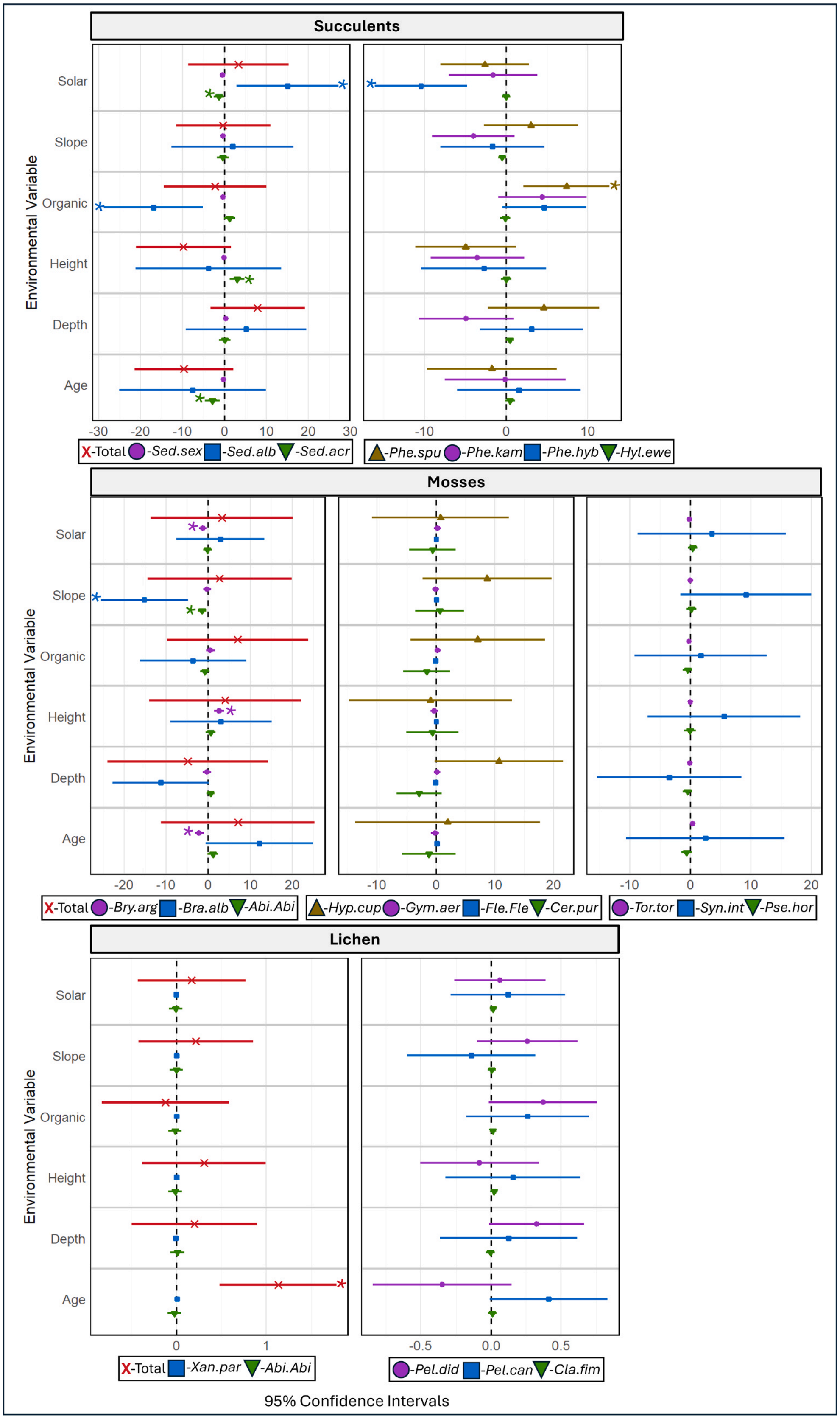

Fig. 3. Multiple linear regressions conducted for succulent, moss and lichen species found on at least 5 rooftops and for total succulent, lichen and moss cover. Here, environmental variables are the explanatory variables. Those with 95 % confidence intervals that don't cross 0 have an "*" and are considered to be significantly associated with the specified response variable. Data is separated into multiple graphs to improve clarity. Code: Total indicates the total percent cover for all succulents, mosses, or lichens.

Peltigera canina and *Xanthoria parietina.*

4.1. Mosses

Across this green roof chronosequence, two distinct moss morphologies were commonly observed, short (~1 cm) acrocarpous mosses, and pleurocarpous mosses, with the former frequently observed growing beneath succulent vegetation. The most common acrocarpous moss, *Ceratodon purpureus*, is a cosmopolitan species found from arctic to tropical ecosystems. In urban centers it is frequently observed in exposed and disturbed environments such as sidewalks and rooftops. The species is highly tolerant to drought and pollution, making it well suited to the urban green roof environment (Biersma et al., 2020). It was also commonly found on the most sun exposed *Sedum*-dominated green roofs in Helsinki, Finland (Gabrych et al., 2016). The six other commonly observed acrocarpous mosses (present on at least 5 rooftops) also favor open disturbed habitats, such as stone walls or rocky outcrops (BBS, 2025). Most of the acrocarpous mosses we observed were associated with young to middle-aged roofs (Fig. 2). By During's (1979) classification, most of these mosses are colonists or short-lived shuttle species, typically exhibiting monoecy (male and female organs on the same individual), rapid growth to reproductive maturity, and high spore production. Such life-history traits are in line with expected successional patterns and may suggest stature-related and reproductive traits are useful proxies for successional stage in green roof moss communities.

In contrast, the three pleurocarpous mosses, *Brachythecium albicans, Hypnum cupressiforme,* and *Abietinella abietinum*, were associated with shorter buildings, deeper substrates, and for *Hypnum cupressiforme* and *Abietinella abietinum,* older roofs. These associations suggest that these species are more generalists, capable of occupying mesic habitats with features such as partial shade or greater humidity, but they were also occasionally found in open areas such as lawns and meadows (BBS, 2025). By During's (1979) classification, these pleurocarps would be mostly considered perennial stayers, with slower growth to reproductive maturity and lower reproductive output. The shift towards increasing dominance by *Hypnum cupressiforme* and *Abietinella abietinum* in older roofs likely represents a natural succession of the bryophyte community from short-lived colonists to longer-lived perennials. Similar shifts in bryophyte composition over periods of a decade or more have been demonstrated in Pyrenean oak woodlands (Monteiro et al. 2024) and Alaskan boreal forests (Jean et al. 2017). This shift could likely be accelerated if pleurocarpous mosses were intentionally inoculated alongside sedum plants during roof installation, as several studies have shown good growth responses of pleurocarpous mosses in early post-installation years (Nagase et al. 2023, Haughian & Lundholm, 2024).

4.2. Lichens

In this study, the cyanolichen *Peltigera canina* was most common on older rooftops. Species in the genus *Peltigera* are capable of fixing nitrogen and can be found on every continent (Knowles et al., 2006; Wijayawardene et al., 2020). *Peltigera* has previously been observed growing on extensive green roofs (Gabrych et al. 2016; Anwar et al., 2017) and may even be an important contributor to the increase in substrate nitrogen observed in some green roof systems over time. For instance, a study by Mitchell et al. (2021), conducted on the same green roofs examined here, observed an increase in substrate nitrogen over time. This increase was found to not be due to natural atmospheric deposition or due to human intervention (e.g. fertilizer additions) (Mitchell et al., 2021). Since *Peltigera* lichen can lead to an increase in substrate nitrogen levels within 1.5 m of the thallus (Knowles et al., 2006), this lichen may have contributed to the observed increase in substrate nitrogen over time. However, research explicitly testing this theory is needed.

The genus *Cladonia* was also observed on many of the green roofs, with *C. fimbriata* being the most abundant. Although green roof lichen research is limited, two *Cladonia*-specific studies have been employed in experimental studies by Heim and Lundholm (2014 a, b). They found that *C. terranova* and *C. boryi* reduced substrate temperature, retained more moisture, and reflected more solar radiation than lichen-free controls. However, *Cladonia* species found in Sweden (*C. fimbriata, C. pyxidata, C. scabriuscula*) seem to differ from Heim and Lundholm (2014 a, b), in that those in the current study had very small stature (~1 cm vs 5 cm). Their small stature may limit the degree to which they influence ecosystem services.

Two other commonly observed species, *Xanthoria parietina* and *Physcia adscendens*, were observed growing together on the stems of *Phedimus spurius* or on the black plastic mesh structural component in the substrate of the green roof mat. These species typically grow upon relatively impermeable substrata like rock, wood, bark, or asphalt, and are common in urban environments around the world (Brodo, 2001; Hinds and Hinds, 2007). These lichens are likely too small and infrequent to contribute meaningfully to the ecological services that green roofs provide. However, their presence is a clear illustration that such bare-substrate colonists can occur on green roofs post roof installation.

4.3. Succulents

The succulent species observed on these rooftops possess two distinct growth forms, short creeping succulents from the genus *Sedum* and upright relatively taller succulents largely from the genus *Phedimus*. *Sedum album* was the most common succulent, found on all 20 rooftops with an average cover of 25 %. This species was most abundant on rooftops with high solar exposure and low organic matter, conditions less favorable to the upright succulents. The two other *Sedums* commonly observed, *S. acre* and *S. sexangulare*, occurred in much lower abundance (>2 %), an indication that these species may be less competitive and/or stress tolerant than the more abundant *S. album*.

The three most common upright succulents where *Phedimus spurius*, *Phedimus kamschaticum,* and *Phedimus hybridus*. These species were observed on 16–18 green roofs and had an average percent cover between 8 % and 15 %. All three appeared to occupy slightly different niches, with *P. spurius* more common on roofs with more organic matter, *P. kamschaticum* more common on rooftops with a deeper substrate layer, and *P. hybridus* more common on rooftops with low solar exposure. Other studies have also observed that upright succulents, in comparison to the short creeping *Sedums*, are less adapted to the harshest rooftop conditions particularly in relation to substrate depth (Durhman et al., 2007; Gabrych et al., 2016).

4.4. Implications for green roof design

Mosses and lichens have the potential to assist neighboring vascular species by reducing substrate evaporation and temperatures (Heim and Lundholm, 2014a). Drought-tolerant moss species can inhabit microsites inhospitable to many vascular species, reducing the amount of exposed substrate (Budke et al., 2018). Finally, cyanolichens, which are capable of nitrogen fixation, may reduce the quantity of mineral nitrogen fertilizers added to green roof systems. In this study, we identified which species of moss and lichen are dominant in extensive green roofs in this climate, this information could be used to select species for propagation or dispersal on newly established green roofs.

Based on the results of our study, the pleurocarpous mosses *Brachythecium albicans* and *Hypnum cupressiforme* are well suited to rooftop conditions in northern Europe. Although species- and location-specific experiments are needed to expand upon these results, the dense mats these mosses produce likely enhance green roof function through reduced substrate temperature and could facilitate the growth of neighboring species through moisture retention. Such results have been observed previously when growing the large dense moss species *Polytrichum commune, Polytrichum piliferum, and Atrichum undulatum,* alongside forbs and graminoids (Heim et al., 2014; Heim and Lundholm 2014a). In this study, the acrocarpous mosses *C. purpureus* and *S. intermedia* had some of the highest abundances on young roofs and are capable of surviving in arid microsites inhospitable to other species. Although these species are likely less efficient at the abovementioned ecosystem services, their presence still shelters the substrate from erosion while hosting diverse microorganisms and enhancing the substrate for colonizing flora. Of the lichen species observed, the cyanolichens *Peltigera canina* and *Peltigera didactyla* have the capacity for nitrogen fixation, thus could enhance green roof function by increasing the availability of reactive nitrogen. However, research examining the degree to which these species influence substrate nitrogen is first needed to determine the impact this lichen could have on green roof ecosystems.

Overall, both moss and lichen communities were found to change over time, with older green roofs possessing a more ecologically diverse community than younger green roofs. Increased shade, organic layer depth, and age appeared to favour perennial, pleurocarpous species over annual acrocarpous species. The changes are likely due to natural successional changes, as well as the difference in environmental conditions between field sites (where vegetation mats are grown) and roof tops. A Finnish green roof study by Gabrych et al. (2016), also found distinct differences between younger (>4 years) and older (<4 years) green roofs, with younger roofs dominated by *Sedums* and older roofs having a moss-dominated community. Based on abundance data and species characteristics, introducing moss and lichen species onto newly established green roofs could enhance moss and lichen colonization, to the benefit of ecosystem function. However, species-specific research and knowledge of rooftop environmental conditions should be considered to determine the best conditions for growth of lichens and mosses on extensive green roofs; failure to do this could result in green roof failure or suboptimal coverage (Haughian and Lundholm, 2024).

Do to the harsh growing conditions, a limited number of species can persist on *Sedum*/moss green roofs. This constrained plant palette is further limited by individual rooftop conditions which can favor one species over another, as was observed in this study where *S. album* dominated rooftops with high solar exposure. Expanding beyond succulents and incorporating bryophytes and lichens into green roof construction can increase initial roof diversity. However, species will still be limited by individual rooftop conditions. Therefore, intentionally adding heterogeneity to *Sedum*/moss roofs is recommended to encourage coexistence between species adapted to slightly different growing conditions. For example, if a rooftop has high solar exposure, adding shade features could encourage coexistence between flora that prefer more sunlight and flora that prefer less sunlight. Based on the results of this study, heterogeneity in substrate depth, roof slope, and organic matter can also be used to create niches favorable to different flora. This reasoning is not new, with previous green roof research already demonstrating how heterogeneity can encourage coexistence between different vascular plants (Buffam and Starry, 2020; van der Kolk et al., 2020; Ganthaler et al., 2025). However, the influence of green roof heterogeneity on bryophytes and lichen in conjunction with vascular plants is lacking, with research needed to fill this knowledge gap.

This research provides a baseline for green roof moss and lichen dynamics. However, there are several limitations that should be addressed in future research. First, this study only examines one growing season. To better understand how green roof features influence moss and lichen community assembly, examining the same rooftop across multiple growing seasons is needed. Second, although we believe based on previous research that the moss and lichen examined here play an important role in the provision of ecosystem services, empirical research experimentally testing how these species influence key ecosystem services, such as stormwater retention and thermal regulation, is needed. This is especially true for our most abundantly observed species of moss and lichen: *Ceratodon purpureus*, *Brachythecium albicans, Syntrichia intermedia, Hypnum cupressiforme* and *Peltigera canina.*

5. Conclusion

In conclusion, this study highlights the importance of moss and lichen communities in the functioning of green roofs, revealing how these communities are influenced by key environmental variables such as roof age and slope. The presence of drought-tolerant mosses and nitrogen-fixing lichens underscores their potential to contribute to ecosystem services such as moisture retention, substrate stabilization, and nutrient cycling. As green roofs age and develop, the transition from colonist species to perennial, mesic generalists points to the dynamic nature of these ecosystems. Our findings suggest that careful selection of moss and lichen species, tailored to specific roof conditions at installation, could enhance colonization success or the likelihood of long-term establishment. Future research should continue to explore how these communities interact with other components of green roof ecosystems.

CRediT authorship contribution statement

David Richardson: Writing – review & editing, Supervision, Resources, Investigation, Data curation. **Ishi Buffam:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Amy Heim:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Pierre-Luc Chagnon:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Sean Haughian:** Writing – review & editing, Supervision, Resources, Investigation, Data curation.

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ufug.2026.129303.

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