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Original article

Trait-environment relationships over short taxonomic and abiotic gradients on *Sedum*/moss roofs

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ABSTRACT

One commonly constructed green roof type, the *Sedum*/moss roof, usually has a substrate depth less than 5 cm and thus can only support a limited plant community, typically dominated by drought-tolerant succulents. Despite this restricted plant community, variation in succulent community composition exists, likely influenced by roof characteristics such as age, slope, and shade. Since different plant species and traits are associated with different ecosystem services, there is a need to understand how even minor variation in green roof design or environmental setting can influence community composition and trait values. In this study, we examine a chronosequence of 31 *Sedum*/moss extensive green roofs, built in a similar manner, in Malmö, Sweden and Helsinki, Finland. The purpose of this research was to understand how slight changes in green roof environmental/abiotic features affect (1) plant community-level traits (means and diversity), as well as (2) intraspecific trait variation, that is, how traits of individual species (here *Sedum album*, *Phedimus spurius*, and *Phedimus hybridus*) vary along an environmental gradient. Based on our results, taller plant species are more likely to be observed on older roofs, with deeper substrate, less solar exposure, and on shorter buildings. Deeper substrates also promoted plants with higher specific leaf area (SLA). Furthermore, small changes in roof attributes led to intraspecific trait variation, with taller individuals of *P. hybridus* observed on roofs with a deeper substrate; taller individuals of *S. album* observed on younger roofs; and higher values of SLA for *P. hybridus* and *P. spurius* observed on roofs with higher solar exposure. Since both SLA and plant height have been associated with stormwater retention and thermal cooling, key green roof ecosystem services, our findings demonstrate the importance minor variation in environmental conditions can have on the benefits provided by vegetated rooftops.

1. Introduction

Vegetated, or green, roofs are constructed ecosystems built into the urban environment for the ecosystem services they provide. They can decrease stormwater runoff, increase thermal stability, reduce air pollution, and provide habitat for local fauna (Shafique, et al., 2018). These ecosystem services are influenced by roof vegetation, with different trait values promoting different ecosystem services. For example, taller individuals with larger leaves (i.e. specific leaf area (SLA)) tend to better promote stormwater retention and substrate cooling (Chu and Farrell, 2022; Lönnqvist et al., 2023). This trend occurs as these individuals tend to have greater water usage, leading to an increase in stormwater retention (Lundholm et al., 2015). Furthermore, the larger size of these individuals allows for increased evapotranspiration and shading, aspects that play an important role in the thermal regulation of green roof systems (Besir and Cuce, 2018; Tadeu et al., 2021). Previous studies have shown the importance of plant traits in providing ecosystem services. However, there is limited understanding of how minor variations in green roof design affect these traits, particularly in *Sedum*/moss roofs with shallow substrates.

Since different plant growth forms and species possess different traits that excel at different ecosystem services, biodiverse roofs have been associated with greater multifunctionality (Lundholm, 2015; Xie et al., 2018). These findings have led to an increased desire for green roofs

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planted with diverse growth forms and species. However, one common green roof type, the *Sedum*/moss roof, commonly has a substrate depth less then 5 cm (in recent decades) and can rarely support non-succulent vascular plant growth forms, thus presumably supporting exceptionally low diversity (Oberndorfer et al., 2007; Gabrych et al., 2016). Even so, trait variation exists among succulent species and individuals (Kuronuma and Watanabe, 2016; Pérez et al., 2020; Guo et al., 2021), which can influence the ecosystem services these *Sedum*/moss roofs provide. Research on how succulent communities vary among common rooftop environments is needed to provide accurate recommendations targeting the provision of specific ecosystem services.

The most common *Sedum*/moss roof vegetation are succulents from the family Crassulaceae, primarily from the genus *Sedum*, with species from the genera *Sempervivum*, *Phedimus* and *Hylotelephium* also commonly used on roofs in temperate climates (Durhman et al., 2007; Gabrych et al., 2016; Vanstockem al., 2018; Getter and Rowe, 2015). Members of this family are well adapted to drought-prone environments as they are some of the few species capable of crassulacean acid metabolism photosynthesis, which temporally decouples CO_2 absorption and fixation (Simpson, 2010). This type of photosynthesis reduces water loss, with stomata being closed during the hottest part of the day (Bloom, 1979). Additionally, the succulent leaves possessed by members of the Crassulaceae further enhance drought tolerance by storing water for later use (Von Willert et al., 1990). Although members of the Crassulaceae family share these key ecophysiological adaptations, trait differences exist among genera, species, and individuals. For instance, members of the genera *Phedimus* and *Hylotelephium* tend to have a more upright growth form than those in the genus *Sedum*. Further, genetic differences and plastic responses to the local environment can lead to intraspecific trait variation (Rosas et al., 2019). However, trait variation between rooftops has been largely ignored, with the majority of studies focused on individual rooftops or experimental systems (e.g. Lundholm et al., 2015; Du et al., 2018; Heim and Lundholm, 2022a).

Vegetated roof characteristics and design influence the degree and type of stress that plants experience. This variation in stress can in turn influence plant community composition (i.e. roof level trait means and diversity) and phenotypic variation (i.e. individual plant trait values) (Getter and Rowe, 2009). One of the most influential environmental stressors on rooftops is desiccation, with several design features directly influencing water stress. Roofs with a steep slope, shallow substrate, and high solar exposure dry out faster, and thus reach higher temperatures (Getter et al., 2007; VanWoert et al., 2005; Bollman et al., 2021; Reyes et al., 2016). Plant adaptions to such conditions include shorter stature, thicker leaves, lower SLA, and higher leaf dry matter content (LDMC) (Niinemets 2001; Moles et al., 2009; Wright et al., 2004). Roof height is another design characteristic which can influence plant stress, with taller roofs associated with greater wind stress (Fang et al., 2022; Shu et al., 2024). This can lead to desiccation and increased tissue damage. To counteract this, plants under high wind stress tend to develop a shorter stature and possess thicker leaves (Nagashima and Hikosaka, 2011). Variation in substrate nutrients between rooftops can also influence community composition, with larger, more competitive individuals generally being more prevalent in nutrient rich environments (Wright et al., 2004). The above-mentioned trait/stress associations have been widely observed in natural ecosystems and can be used to infer how green roof succulents will respond to environmental stress. However, a large-scale study across multiple rooftops is needed to determine if previously observed trends are consistent across rooftops and geographic locations.

As vegetated roofs age, natural processes can lead to changes in several of these aforementioned abiotic features. For instance, over time the substrate nutrient content may decrease through runoff and uptake by organisms (Buffam and Mitchell, 2015). Some nutrients, specifically nitrogen, can increase with roof age (Köhler and Poll, 2010, Mitchell et al. 2021), with the presence of nitrogen fixing organisms likely playing an important role (Mitchell et al., 2018). For the thin substrate *Sedum*/moss roofs built in cold temperate climates, typical changes in the plant community over time include decreases in succulent cover, increases in moss and lichen cover, and colonization by weedy species from the surrounding environment (Gabrych et al. 2016, Mitchell et al. 2021, Lönnqvist et al., 2021). Data remains scarce, however, regarding how succulent trait values and diversity change over time. This is in part because very few studies have focused on long-term dynamics in green roofs (e.g., Andenaes et al., 2018). Furthermore, it is a particular challenge to isolate the effect of roof age when integrating multiple study roofs that have been built according to different design protocols (but see Mitchell et al., 2021).

By identifying how minor variations in roof design influence plant traits, this study aims to provide actionable insights for optimising green roof configurations to enhance their performance in urban environments. One of the strengths of this study is the use of a chronosequence, allowing for a robust analysis of temporal trends and environmental gradients. Specifically, this study utilizes a chronosequence of 31 *Sedum*/moss extensive green roofs in Malmö, Sweden, and Helsinki, Finland, examining temporal trends and environmental gradients. Here, the type of roof examined, the *Sedum*/moss roof, is the same across rooftops. However, building type and location varies. Although study roofs are located on a variety of structures, from bike shelters to office buildings, valuable insights can be gained, as this variety leads to variation in roof slope, building height, and solar exposure, all of which can influence plant traits.

This research had two objectives: 1) to understand how slight variation in roof attributes (e.g. substrate depth, roof slope, solar exposure, roof height, roof age, substrate nitrogen) affect community-level plant traits; and 2) how these environmental gradients influence intraspecific trait variation in three common green roof species, *Sedum album*, *Phedimus spurius*, and *Phedimus hybridus*. Understanding these relationships is crucial for optimising green roof designs to maximise ecosystem services such as stormwater management and thermal regulation, which are vital for urban sustainability. We hypothesis that variation in roof attributes will influence both community level and species-specific trait values. This variation will reflect the stress-trait gradients commonly observed in the natural environment. Additionally, due to the harsh nature of these rooftops, we hypothesis that even a relatively small change in environmental stress will impact plant traits.

2. Methods

This paper examines succulent plant traits on 12 vegetated roofs in and around Helsinki, Finland, and 19 vegetated roofs in and around Malmö, Sweden. These two cities were chosen as the green roofs in these cities were built in a comparable manner and share similar vegetation profiles. Furthermore, vegetation data from multiple years was available for both cities allowing us to increase the power of our temporal analysis. For Helsinki, all 12 roofs were examined once in 2011 and again in 2021; and for Malmö, 14 of the 19 roofs were examined in 2016, 18 in 2020, and all 19 in 2022 ($n = 75$ total datapoints). In this study, all the surveyed vegetated roofs are *Sedum*/moss roofs dominated by the family Crassulaceae. These roofs were established using pre-grown vegetated mats and have a substrate depth less then 5 cm (Fig. 1).

The city of Malmö (55.61° N, 13.00° E) is located on the southern coast of Sweden, in the nemoral (temperate) vegetation zone (Sjörs, 1999). It has a temperate oceanic climate with mild winters, warm summers, no dry season, and moderate seasonality (Köppen-Geiger classification: Cfb). During 1991–2020, the annual mean temperature was ca. 9 °C (mean 2 °C and 18 °C in January and July, respectively), while the annual average precipitation was 615 mm, spread fairly evenly throughout the year (SMHI, 2023). Snowfall is uncommon and snow cover rarely lasts more than a few days per winter, while the growing season lasts for ca. 220 days (Sjörs, 1999).

The city of Helsinki (60.17°N, 24.94°E), is located on the southern coast of Finland, is situated in the hemiboreal vegetation zone (Ahti

Fig. 1. Two *sedum*/moss Green roofs, the one on the left was built in Malmö in 2022 and the one on the right was built in Helsinki in 2005.

et al., 1968). Helsinki has a humid continental climate with severe winters, warm summers, and strong seasonality (Köppen-Geiger classification: Dfb). During 1981–2010, the annual mean temperature was 5 °C (mean −5 °C and 18 °C in January and July, respectively), while the annual average precipitation was 650–700 mm, spread unevenly across the year. The average number of days with snow cover is 115, and the growing season lasts for ca. 185 days (FMI, 2023).

2.1. Percent cover

For all green roofs, percent cover data was collected for each individual vascular plant species, during July-August. For Helsinki (2011 and 2021) and Malmö (2020), percent cover data was collected using 0.5 m × 1.0 m quadrats with the number of quadrats used based on roof size (4 quadrats for the smallest roof, 32 quadrats for the largest). For data collected from Malmö in 2016 and 2022, percent cover data was collected using 0.5 m x 0.5 m quadrats, with twelve quadrats per roof. Once collected, quadrat-level data were averaged to determine species average cover per roof for each year. In this study, only species that represented at least 1 % of the total plant cover on at least one roof were included in the analysis. These species included: *Phedimus hybridus, Phedimus kamtschaticus var. Floriferum* (hereon *P. kamtschaticus*), *Phedimus spurius, Sedum acre, Hylotelephium ewersii, Sedum sexangulare, Hylotelephium telephium, Sedum rupestre, Sedum album, and Sedum annuum (*Table 1*).*

In this study, Helsinki cover data for *P. kamtschaticus* was counted as *P. hybridus*. This was done as these individuals were grouped as one species in 2011 and we wanted to be consistent in our analysis. For

Table 1

First half of table shows environmental variables: mean (± standard deviation), range, and maximum of roof variables across both cities and all years (n = 75). data for total nitrogen and organic matter are expressed as % of dry mass of the < 6 mm fraction of the substrate and only includes roofs from Malmö in 2022 (n = 19). second half of table shows overview of species percent cover and trait values from Helsinki (H) and Malmö (M). the cover data listed is the average from all roofs and dates for the specified country. The average trait data for Helsinki was collected in 2021 and the average trait data listed for Malmö was collected in 2022. For Helsinki, plant height (height) and specific leaf area (SLA) was gathered from every species present. For Malmö, plant height, SLA, leaf dry matter content (LDMC), and leaf thickness (thick) was only gathered for *s. album, p. hybridus,* and *p. spurius.* note: *s. rupestre* was only observed on three roofs in 2011 and *s. annuum* was only observed on one roof in 2011. *Indicates traits were collected from vegetated roofs not examined in this study; † indicates trait values were not available for this species; *na* indicates the specified data was not collected for that species.

Environmental Variables				
	All Years/Cities		**Malmö 2022**	
Roof Variables	**Range**	**Mean**	**Range**	**Mean**
Roof Age (Years)	0.4–29	11.5 ± 7.2	0.4–28	12.7 ± 7.9
Substrate Depth (cm)	1.3–5.9	3.0 ± 0.8	1.7–4.1	2.9 ± 0.7
Annual Solar Exposure (kWh m^{-2})	312–1030	742 ± 212	392–1030	785 ± 193
Roof Height (m)	1.3–5.5	3.2 ± 1.0	2.4–5.5	3.3 ± 1.0
Roof Slope (∘)	0–15	4.7 ± 4.8	0–15	4.7 ± 4.7
Total Nitrogen (%)	*NA*	*NA*	0.21–1.0	0.49 ± 0.24
Organic Matter (%)	*NA*	*NA*	8.9–32.3	16.6 ± 7.8

Species Traits	**# Roofs**		**Average % Cover**		**Height (cm)**		**SLA (cm2g−1)**		**Thick (mm)**	**LDMC (g g−1)**
Species	**H**	**M**	**H**	**M**	**H**	**M**	**H**	**M**	**M**	**M**
S. album	11	19	13.1	33.0	2.3	2.2	135.3	74.8	2.6	0.07
P. hybridus	6	16	17.3	16.1	10.6	7.4	140.6	91.9	1.3	0.11
P. spurius	4	19	0.8	8.8	5.4	3.3	184.2	114.2	1.3	0.08
*P. kamtschaticus**	7	17	0	9.6	11.0	*NA*	120.0	*NA*	*NA*	*NA*
S. acre	8	17	3.3	1.6	2.3	*NA*	179.6	*NA*	*NA*	*NA*
H. ewersii	4	12	1.7	2.1	5.9	*NA*	174.3	*NA*	*NA*	*NA*
S. sexangulare	3	17	0.6	1.2	3.2	*NA*	164.8	*NA*	*NA*	*NA*
H. telephium	1	0	0.1	0	20.6	*NA*	91.5	*NA*	*NA*	*NA*
*S. rupestre**	3	0	0.1	0	5.7	*NA*	84.5	*NA*	*NA*	*NA*
S. annuum†	1	0	0.1	0	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*

Malmö, *P. kamtschaticus* was differentiated from *P. hybridus* in 2016, 2020 and 2022 allowing us to incorporate both species in our Malmö cover data.

2.2. Plant traits

This study stands out for its comprehensive measurement of plant traits, including height, specific leaf area SLA, LDMC, and leaf thickness, providing a holistic view of how these traits respond to environmental variations. To our knowledge, this is the first time green roof plant traits have been collected at this scale, with data collected from 31 rooftops from multiple individuals of the same species per rooftop.

The four vascular plant traits examined in this study were chosen for their role in drought tolerance or their influence on two key ecosystem services, substrate cooling and stormwater retention. These traits are (1) plant height (drought tolerance/ecosystem services), (2) specific leaf area (SLA) (drought tolerance/ecosystem services), (3) leaf dry matter content (LDMC) (drought tolerance), and (4) leaf thickness (drought tolerance) (Chu and Farrell, 2022; Tardy et al., 2015; Vile et al., 2005). Traits were collected following Pérez-Harguindeguy et al. (2016). Briefly, SLA was calculated as the leaf area to dry mass ratio; LDMC represents the dry mass to fresh mass ratio; leaf thickness was measured using a Wukong stainless steel digital caliper (ISO9001:2000); and plant height represents the distance between the substrate and the highest vegetative part of each measured individual. Traits were collected from ten randomly selected mature, non-flowering individuals, per species per roof (except in rare cases when 10 individuals could not be found on the roof) (Table 1).

In order to create a green roof trait database and assign an average height/SLA value to each species, height and SLA were collected from green roof species from the Helsinki roofs between July 12 – August 15, 2021. All 12 study roofs were examined and if a roof contained at least 10 individuals of a species plant height and SLA were collected from that roof for that species. In total, trait values were collected from individuals of *P. hybridus* ($n = 60$), *P. kamtschaticus* ($n = 70$), *P. spurius* ($n = 40$), *S. acre* ($n = 80$), *H. ewersii* ($n = 40$), *S. sexangulare* ($n = 30$), *H.telephium* ($n = 10$), and *S. album* ($n = 110$). For two species, *S. rupestre* and *S. annuum*, individuals were not observed on Helsinki roofs during the 2021 trait collection period but were present on roofs in 2011. Therefore, alternative methods were needed to assign a trait average to these species. For *S. rupestre*, the traits used in this study were gathered from 30 individuals from neighboring meadow green roofs (deeper substrate, graminoid/forb dominate) in 2021. Unfortunately, no *S. annuum* individuals were observed on these additional meadow rooftops or found in trait databases. One of the solutions for addressing missing data in trait-based analyses is to use the average trait values of functionally similar species as a surrogate for missing data points (Taugourdeau et al., 2014). We thus used trait values averaged from the four *Sedum* species observed in this study as surrogates for *S. annuum* traits. Since both *S. annuum* and *S. rupestre* occurred rarely, and when present, had low percent covers, we expect these adjustments to have very minor (if any) impact on our results.

We also wanted to take a closer look at how traits can vary within a species. Using the methods described above, we collected plant height, SLA, LDMC, and leaf thickness for three abundant species: *S. album*, *P. spurius*, and *P. hybridus*. This more in-depth trait collection was conducted on the 19 Malmö *Sedum*/moss green roofs between July 4–13, 2022. In total, 190 individuals of *S. album*, 178 individuals of *P. spurius*, and 126 individuals of *P. hybridus* were measured.

2.3. Environmental variables

The environmental variables available for each roof and year as potential predictors, include age, slope, roof height, solar exposure, and substrate depth. In 2022, we also measured substrate organic matter and total nitrogen content for all 19 Malmö roofs (Table 1). For each roof, an annual estimate of solar exposure was calculated using a Solar Pathfinder and the Solar Pathfinder Assistant software (Solar Pathfinder Company, Linden, TN, USA). Based on roof slope, aspect, and the location of nearby deciduous trees (counted as inducing 50 % shading from October–April and 100 % shading from May-September), buildings and evergreen trees (counted as inducing 100 % shading year-round), solar exposure (kWh m^{-2}) was estimated as the annual amount of solar radiation reaching the roof surface.

Substrate depth was measured by inserting a 4 mm diameter metal rod vertically into the substrate until resistance was met, with depth measurements taken at the location of each vegetation sampling quadrat (8 or more locations per roof) and averaged to give a roof mean value. Substrate depth was re-measured on each occasion except for 2022 for the Malmö roofs; as the substrate depth did not vary significantly from 2016 to 2020, we used the 2020 substrate depth measurements for 2022. Substrate for nutrient analysis was gathered by collecting substrate from eight locations on each roof. More specifically, cores measuring 7 cm in diameter, and encompassing the entire depth of the substrate, were collected in a stratified random sampling design at eight locations spaced relative to roof area. The cores were then pooled to create two composite substrate samples per roof, which were subsequently homogenized, sieved to < 6 mm, then milled for four minutes at a frequency of 30 Hz (Retsch MM400) to achieve a fine (<1 mm) texture. Substrate samples were then analyzed for organic matter content by loss-on-ignition at 550 °C (Dean, 1974) and for total nitrogen content using a Flash EA 2000 Elemental Analyzer (Thermo Fisher Scientific, Bremen, Germany), at the Department of Forest Ecology and Management, Swedish University of Agricultural Sciences.

2.4. Trait mean and diversity calculations

In order to see how community-level SLA and height change as a function of roof properties, we calculated community weighted means (CWM). This approach estimates mean trait values for the whole plant community by weighing species average traits with their relative abundances (Lavorel et al., 2008), here values were estimated using percent cover. This provided us with a CWM for each roof, year, and country ($n = 75$). The Helsinki green roof height/SLA trait database was used to assign each species an average height and SLA value.

To evaluate height and SLA variability within roofs, we calculated community functional dispersion following Laliberté and Legendre (2010). This approach estimates the mean functional trait distance between community members and the community centroid. The functional dispersion was calculated for both height and SLA, for each roof, year, and country ($n = 75$). The Helsinki green roof height/SLA trait database was used to assign each species an average height and SLA value. This analysis allowed us to examine how similar or different a roof community was in terms of height and SLA. For instance, a value of 0 for the functional dispersion of height would indicate all species in the rooftop community are the same height, whereas a higher value would indicate shorter and taller species are present.

2.5. Statistical analyses

The study employs rigorous statistical analyses, including linear mixed effect models, to account for nested data structures and ensure the reliability of the results.

All statistical analyses were conducted in R version 4.0.5 (R core team, 2022). All raw data 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, as implemented in the *rcompanion* R package (Mangiafico, 2024). Before multiple linear regressions were conducted, simple pairwise regressions were used to identify potential highly collinear roof environmental variables. For pairs of variables having a coefficient of determination for the model (R^2) of 0.70 or higher, the variable least correlated with the response variables was excluded from downstream regression models.

Linear mixed effect models (LMMs) were used to determine associations between traits and roof properties. For the CWM and functional dispersion analysis (community-level analysis), which incorporated 75 datapoints, city ($n = 2$), year ($n = 5$), and roof ID ($n = 31$) were included as random effects. For the species-level analysis, which examined the variation in the traits of three species across Malmö roofs in 2022, only roof ID was included as a random effect. Model selection was based on Akaike information criterion 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 (Bartoń, 2020). From these models, 95 % confidence intervals were calculated. When the confidence interval of a roof property did not cross zero it was considered to be associated with the dependent variable (trait variable). Additionally, one-way ANOVAs were calculated to determine if species-level trait values varied significantly between rooftops, with traits (plant height, leaf thickness, SLA, LDMC) as dependent variables and roof ID as the independent variable. 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; and graphs were created using *ggplot2*, *dot-whisker*, and *ggfortify*. Details for all statistical tests, including the R code used, can be found in the supplementary material.

3. Results

3.1. Community-level: trait filtering by roof properties

At the community-level, community-weighted mean (CWM) (i.e. mean trait values for the whole roof community), and functional dispersion (i.e. degree of roof level trait similarity/dissimilarity) varied among roofs. Across all rooftops and years ($n = 75$), community-level mean height varied between 2.3 cm and 10.6 cm (mean ± standard error, 5.4 ± 0.3 cm), and the community-level SLA varied between 128.9 g and 177.2 g (146.3 ± 1.0 g). Overall, four roof attributes correlated with the community-level trait variables: substrate depth roof height, roof age, and solar exposure. CWM of plant height was higher on older roofs, those with more solar exposure, and on shorter buildings. Additionally, the confidence variables for the CWM of plant height and substrate depth barely crossed zero ((2.5 %: −0.026) to (97.5 %: 0.971)) and is worth highlighting. In general plant height tended to be higher on roofs with deeper substrate. The CWM of SLA was higher on roofs with deeper substrate. Higher values of functional dispersion for specific leaf area (SLA) were observed on roofs with deeper substrate, and on taller and older buildings. Functional dispersion in plant community height was not correlated to any of the tested roof properties. (Fig. 2).

3.2. Species-level: intraspecific trait variation

All four traits (height, leaf thickness, SLA, LDMC), for all three species (*P. spurius*, *P. hybridus*, *S. album*), varied significantly ($p < 0.05$) among rooftops. On average, the tallest species was *P. hybridus* (5.7 cm); the species with the thickest leaves was *S. album* (2.6 mm); the species with the highest SLA values was *P. spurius* (113.4 g); and the species with the highest LDMC value was *P. hybridus* (0.12 g g^{-1}).The greatest range in plant height was observed for *P. hybridus* (3.9–9 cm); the greatest range in leaf thickness was observed for *S. album* (2.2–3.5 mm); the greatest range for SLA was observed for *P. spurius* (74.9–179.1 cm^2g^{-1}); and the greatest range in LDMC was observed for *S. album* (0.05–0.09 g g^{-1}) (Table 2).

Trait-environment relationships differed across the three species, with at least one trait per species associated with at least one roof attribute. Although the results varied somewhat across species, taller individuals were usually found on roofs that were younger, with deeper substrate, and more substrate nitrogen. Individuals with higher SLA values were usually found on roofs having higher solar exposure. Thicker leaves were associated with individuals on roofs that were older, those with more substrate, and those with more solar exposure. Finally, LDMC was largest on roofs with shallower slopes. Interestingly, species response to substrate depth different for LDMC. With the LDMC of *S. album* usually lower on roofs with deeper substrate and the LDMC of *P. hybridus* usually higher on roofs with a deeper substrate (Fig. 3).

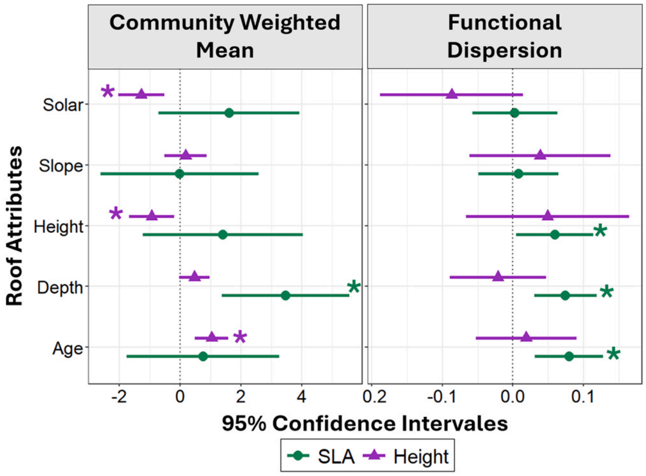

Fig. 2. Data depicted here is from all dates for both Malmö and Helsinki ($N = 75$, from altogether 31 different roofs). linear mixed models between community-level traits and roof attributes (age (years), substrate depth (cm), annual solar exposure (kWh m^{-2}), roof slope (°), roof height (m)) were used to calculate 95 % confidence intervals for the functional dispersion of plant height (height) and specific leaf area (SLA); and the community weighted mean of plant height and SLA. Roof attributes with confidence intervals that did not cross zero were considered associated with the specified community-level trait and are highlighted with an "*".

4. Discussion

In this study, all rooftops represented the high end of the plant stress gradient, leading to a vegetation profile dominated by mosses and succulents. Even so, minor variations in roof attributes influenced trait variables at both the community and species level. For the most part, roofs with less stressful conditions tended to select for taller plant species with thinner leaves, lower LDMC and higher SLA. At the community-level, substrate depth, solar exposure, roof height, and roof age all influenced at least one trait variable. Of these, substrate depth, roof age, and solar exposure also influenced trait variation at the species-level. Thus, supporting our hypothesis and providing ecologically meaningful results that can inform vegetated roof design.

4.1. Community-level: community weighted mean of height and SLA

Plant communities tended to be taller overall on shorter, older roofs with less solar exposure and deeper substrate. This result is largely in line with *a priori* expectations as to how these roof properties should influence plant stress. Higher stress levels are expected to filter out taller species, encouraging convergent trait values. Conversely, low stress roofs are expected to support taller, more competitive species (Heim and Lundholm, 2022b). Specifically, lower solar exposure should result in lower rates of substrate evaporation, thus lowering water stress and allowing taller plant species and individuals to persist in the community (van der Kolk et al., 2020). This is in line with our observation that high solar exposure acts as a convergent filter promoting shorter species (Fig. 2). Likewise, shallow substrates tended to be associated with a selection for low-SLA plants, another trait assumed to be associated with higher water use efficiency (Wright et al., 2004). As for roof height, plant stress associated with high wind usually increases with roof height

Table 2
Results of one-way ANOVAs examining whether plant height (cm), leaf thickness (mm), specific leaf area (SLA (cm^{2}g^{-1})), and leaf dry matter content (LDMC (g g^{-1})) of *p. spurius*, *p. hybridus*, and *s. album* varied among Malmö rooftops in 2022. Range and mean ± standard error are based on roof averages and so depict variation among roof tops (n = 19). *p. hybridus* was only observed on 14 of the 19 roofs. See supplementary material for within-roof variation (Appendix H).

S. album	**Range**	**Mean ± SE**	**DF**	**Sum Sq**	**Mean Sq**	**F-Value**	**Pr(>F)**
Plant Height	1.5–3	2.2 ± 0.1	18	0.034	0.002	9.385	< 2e−16
Leaf Thickness	2.2–3.5	2.6 ± 0.1	18	0.508	0.028	14.17	< 2e−16
SLA	56.0–108.9	72.6 ± 3.4	18	0.01	0.001	2.306	0.003
LDMC	0.05–0.09	0.07 ± 0.002	18	0.016	0.001	2.48	0.001
P. hybridus	**Range**	**Mean ± SE**	**DF**	**Sum Sq**	**Mean Sq**	**F-Value**	**Pr(>F)**
Plant Height	3.9–9	5.7 ± 0.3	13	0.163	0.013	20.23	< 2e−16
Leaf Thickness	0.8–1.6	1.2 ± 0.05	13	11.06	0.851	15.22	< 2e−16
SLA	51.9–121.3	81.8 ± 4.7	13	0.036	0.003	12.67	< 2e−16
LDMC	0.1–0.13	0.12 ± 0.002	13	0.006	0.0005	3.306	0.0003
P. spurius	**Range**	**Mean ± SE**	**DF**	**Sum Sq**	**Mean Sq**	**F-Value**	**Pr(>F)**
Plant Height	2.4–4.8	3.3 ± 0.13	18	0.295	0.016	8.238	3.59e−15
Leaf Thickness	1.1–1.4	1.3 ± 0.02	18	0.385	0.021	2.212	0.005
SLA	74.9–179.1	113.4 ± 6.5	18	69.33	3.851	12.78	< 2e−16
LDMC	0.07–0.09	0.08 ± 0.002	18	4762	264.58	2.789	0.0003

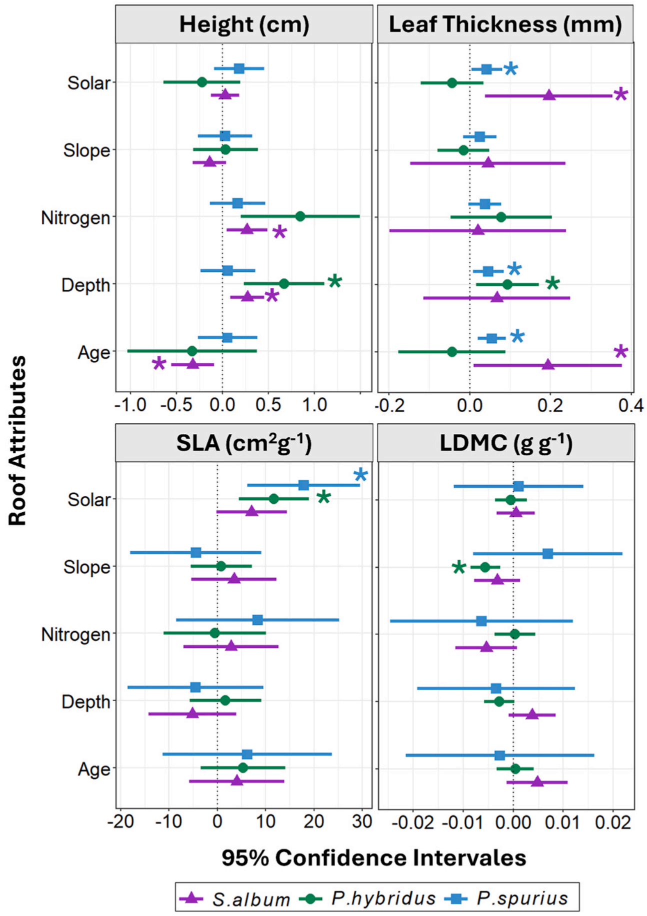

Fig. 3. Species-level plant trait responses on Malmö Green roofs in 2022 (n = 19). linear mixed models were used to examine the response of species-level traits (plant height (cm), specific leaf area (SLA (cm^{2}g^{-1})), leaf dry matter content (LDMC (g g^{-1})), leaf thickness (mm)) to roof attributes (age (years), substrate depth (cm), annual solar exposure (kWh m^{-2}), roof slope (°), substrate nitrogen (%)). These models were run to calculate 95 % confidence intervals for *p. spurius*, *p. hybridus*, and *s. album*. Roof attributes with confidence intervals that did not cross zero were considered associated with the specified species-level trait and are highlighted with an "*".

(Fang et al., 2022), a pattern also observed in this study. Since taller individuals are more vulnerable to wind damage, shorter statures are more enduring in wind prone environments (Nagashima and Hikosaka, 2011). However, roof height remains a somewhat indirect proxy for wind stress, and research is needed to further understand the relationships between roof height, wind speed, and plant stress.

The positive association between plant community height and roof age may be due to the trait/stress gradient associated with changes in the green roof substrate over time. Previous green roof research has found that substrate nitrogen and organic matter can build up over time (Mitchell et al., 2021; Getter et al., 2007). As in natural ecosystems, this increase in nutrient availability may encourage the prevalence of larger more competitive individuals.

4.2. Community-level: trait dispersion

Sedum/moss roofs that were older, with a deeper substrate, and on taller buildings tended to have plant communities with greater trait divergence in SLA. For substrate depth, roofs with a deeper substrate tended to have a diversity of high and low SLA species whereas roofs with a shallower substrate were dominated by species with a lower SLA. For our study roofs, this meant that one species, usually *S. album,* tended to be largely dominant on roofs with a substrate less than 2.5 cm. Roofs with a deeper substrate, on the other hand, tended to be more diverse, usually co-dominated by *S. album*, *P. hybridus,* and *P. spurius* (Malmö) or *S. album*, *P. hybridus, S. acer, and H. ewersii* (Helsinki). This pattern likely reflects a filtering effect, with species possessing higher SLA values unable to persist in the shallowest substrate observed in this study. This finding is particularly interesting as the range of substrate depth between roofs in our study was only 1.3–5.9 cm (average: 3.0 ± 0.8), indicating that even minor adjustments to roof attributes can greatly influence community composition. Our finding is in agreement with previous studies (e.g. Gabrych et al. 2016 and Jauni et al., 2020) showing that even a few centimeters change in substrate depth can affect vegetation structure.

The association observed here between roof age and intraspecific variation in SLA may be due to substrate changes occurring in a heterogenous manner. Specifically, variation in roof microclimates (e.g., shade, substrate depth, leaf litter, moisture) can influence the rate at which organic matter, nitrogen, and microorganisms change over time (Lagrue et al., 2011; Rousk et al., 2018), promoting niche partitioning. However, more research is necessary to further support this association between roof age and environmental heterogeneity. Specifically, trait-environment correlations should be evaluated at finer scales within sites, and spatial heterogeneity in roof properties characterized in more detail.

In our study, functional dispersion in plant height was not correlated with any roof attribute. This finding may be due to the limited species pool on our roofs, allowing only nine species to be analysed. However, this pattern could also indicate a filtering effect at each end of our stress gradient. For example, if low stress leads to a greater prevalence of taller species and high stress leads to a greater prevalence of shorter species both ends of the stress gradient would have low functional diversity in plant height. This reasoning is supported by the raw data, with the functional dispersion of height and the CWM of height forming a humped distribution (Appendix E).

4.3. *Species-level trait variation*

In natural ecosystems, variation in environmental features can lead to intraspecific trait variation, either via individuals adjusting traits through phenotypic plasticity, or via selection for particular genotypes bearing specific traits (Sandel and Low, 2019; Kichenin et al., 2013; Stotz et al., 2021). These changes occur because different trait values may confer a higher competitive ability in different environments (Violle and Jiang, 2009). Here we show that even minor changes in rooftop conditions can significantly influence the traits of three common green roof species, *P. spurius*, *P. hybridus*, and *S. album*. However, the specific traits influenced by roof features varied among species.

In our study system, environmental stress was likely lowest on roofs with deeper substrate, more substrate nitrogen, less solar exposure, and shallower slopes. Based on natural ecosystems, we predicted that lower stress levels should favor taller, high-SLA, low-LDMC individuals, with thinner leaves. (Cornwell and Ackerly, 2009). Here, the relationships that reflect predicted trait patterns include taller individuals on roofs with deeper substrate (*P. hybridus, S. album*) and more substrate nitrogen (*P. hybridus, S. album*); lower LDMC values on roofs with shallower slopes (*P. hybridus*); and thinner leaves on roofs with less solar exposure (*S. album; P. spurius*). In this study, the patterns divergent from the expected include higher SLA values on roofs with more solar exposure (*P. spurius, P. hybridus*); and thicker leaves on roofs with deeper substrate (*P. hybridus*). Here, increased substrate depth may have led to an increase in resource availability, allowing individuals of *P. hybridus* to construct larger leaves. As for SLA and solar exposure, the pattern observed here is not as easy to explain. Usually, plants will have lower SLA in stressful environments, a strategy that prioritizes resistance to environmental stress over resource acquisition (Freschet et al., 2010; Griffith et al., 2016). Since increased solar exposure can lead to increased drought stress, we hypothesised a negative correlation between solar exposure and SLA. In order to fully understand this unexpected pattern, further research is needed. Since many of the trait/stress gradients observed in natural ecosystems focus on non-succulents, studies examining how the traits of succulent species change along common stress gradients is needed. Previous research has also observed that succulent species do not always fit expected trait covariation patterns and/or trait-environment relationships. For example, research on 77 Argentinian species found that the quantity of water stored in succulent leaves resulted in a higher SLA than expected from stress-tolerant individuals (Vendramini et al., 2002); and a study from southern Spain comparing succulent rich and succulent poor plant communities found that trait correlations observed in non-succulent communities didn’t occur in succulent rich communities (Grubb et al., 2015).

In this study, roof age influenced both the height and leaf thickness of individuals. As described above, age can influence multiple aspects of a vegetated rooftop, including species composition and substrate nutrients (Mitchell et al., 2021; Getter et al., 2007; Gabrych et al., 2016). Although further exploration is needed, the pattern observed here for *S. album* (shorter with thicker leaves on older roofs) may be a stress response leading to die back increasing associated with increased competition from neighboring species. Indeed, three of the youngest roofs in this study, which were 4–5 years old contained 81–96 percent cover of *S. album* with the next most dominant species only covering 2–12 percent of the rooftop. In contrast, the oldest roofs in this study, which were 28 years old, contained 35–37 % cover of *S. album* with the next most dominant vascular species at 35–50 % cover.

4.4. *Implications for green roof design*

Previous research has found that tall and leafy plant communities (e.g. those with high SLA and plant height) tend to be more proficient at reducing stormwater runoff and substrate temperatures, two key green roof ecosystem services (Nagase, and Dunnett, 2012; Lundholm et al., 2015; Chu and Farrell, 2022). Based on our results, taller plant communities will likely be observed on *Sedum*/moss roofs with more shade (less solar exposure), deeper substrate, and on those closer to ground-level; and roofs possessing deeper substrate will likely form plant communities with higher values of SLA. Since our study system has relatively little variation in attributes among roofs, our findings demonstrate the importance minor adjustments can have on the provision of ecosystem services. For example, the substrate depth between our roofs only ranged from 1.3 to 5.9 cm, but this variation had a major implication for community plant traits - indicating that adding even a small amount of additional substrate can greatly influence the community composition of succulents.

In our study, small changes in roof attributes resulted in variation in the physical characteristics of individuals of the same species, with taller individuals observed on roofs with deeper substrate and more substrate nitrogen; and individuals with larger leaves (i.e. higher SLA values) observed on roofs with greater solar exposure. Using plant species that have a higher capacity to adapt to local conditions could better guarantee the provision of ecosystem services during varying conditions (e.g. weather). For example, in this study *P. hybridus* had the greatest range in plant height. An adaptation that may have allowed it to persist on rooftops with less substrate and thrive on rooftops with deeper substrate.

In addition to optimising mean trait values (community and species-level), the provision of ecosystem services can also be enhanced by offering trait diversity (Ksiazek-Mikenas et al., 2023; Lundholm, 2015; Chu and Farrell, 2022). For example, Ksiazek-Mikenas et al. (2023) found that green roofs with a high diversity 10 species prairie mixture had 10–16 % greater stormwater retention than a low diversity six species *Sedum* mixed treatment (Ksiazek-Mikenas et al., 2023). Along similar lines, Johnson et al. (2016) found that a 6 species-rich roof plant community retained nitrogen more effectively than the average monoculture. Furthermore, when examined across multiple seasons, trait diversity can improve green roof function (Lundholm, 2015). For instance, during dry seasons, drought-sensitive species tend to either die back or enter dormancy, while drought resistant species remain physiologically active. Since, drought-sensitive species tend to provide more ecosystem services (in mesic conditions), the combination of drought-sensitive and drought-tolerant species in temporally variable climates may enhance resilience and ensure ecosystem provisioning across wet and dry seasons.

Although the results presented here can be used to inform green roof design, we acknowledge the presence of several limitations that could be addressed in future research. First, measuring the microclimate surrounding all measured individuals would allow us to better understand how specific environmental conditions influence plant traits. Second, tracking the same individuals across years and throughout a season would provide us with a broader understanding of how climatic conditions influence phenotypical plasticity. Future research should conduct these long-term seasonal studies in conjunction with a common garden experiment to ensure the variations observed between roofs are not due to genetic differences. Finally, our findings are limited to temperate climates with research in warmer climates, such as the Mediterranean, needed to determine how universal the trends observed here are.

5. Conclusion

This study contributes to the existing body of knowledge by providing new insights into how minor variations in green roof design affect plant trait diversity and ecosystem service provision, addressing a key gap in the literature. Our findings have significant practical implications for green roof design, providing actionable insights on how to optimise substrate depth and other roof features to enhance ecosystem services such as stormwater retention and thermal regulation. Based on our results, minor variations in roof physical/environmental attributes can influence plant traits in terms of community-level plant means, community-level diversity, and species-level trait values. At both the community and species-level, trait associations largely reflect the predicted gradient between environmental stress and plant traits (trait/stress gradient). However, noticeable differences between anticipated and actual trait values were observed at the species-level. This deviation is likely due to the unique nature of succulent leaves, highlighting a need for a succulent focused trait/stress gradient. Even so, recommendations can be made for green roof architects. Taller plants with greater values of SLA (i.e. values associated with stormwater retention and temperature reduction), can be encouraged by the addition of a few centimetres of substrate and by reducing solar exposure (through shade) by a few kWh m^{-2}.

CRediT authorship contribution statement

Pierre-Luc Chagnon: Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Maria Kunle:** Writing – review & editing, Investigation, Data curation. **Susanna Lehvävirta:** Writing – review & editing, Supervision, Project administration, Data curation. **Ishi Buffam:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **Amy Heim:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence 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.2025.128915.

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