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Effects of heterogeneity in solar exposure and soil moisture on the distribution of green roof plant functional groups

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ABSTRACT

Green roofs often have heterogeneous microclimates due to variation in surrounding conditions, for example shading from adjacent trees or buildings. However, little is known of the effects of fine-scale variation in microclimate on green roof plant community composition. This is important to understand because green roof ecosystem services are supported by the productivity, diversity, and functionality of the plants. We conducted a spatial survey of plant species distribution relative to solar exposure and soil moisture, on a 50 m^2 sloped extensive green roof originally established with nine *Sedum* species evenly distributed on the roof. After seven years in the presence of partial shading from adjacent trees, the number of plant species had increased to 28, with the new species mostly volunteer graminoids and forbs. Solar exposure strongly shaped plant species distribution on the roof along a gradient (high to low): succulents - graminoids - forbs. Plant species richness was highest in the transition zone between the sunny/dry and shady/moist parts of the roof. Our results demonstrate that spatial variation in microclimate can influence green roof plant communities over time. Thus, an awareness of microclimate variation should be incorporated into managing green roof plant communities to optimize ecosystem services.

Key words: *Microclimate; Species richness; Plant communities; Green roof management*

INTRODUCTION

Green roofs are constructed ecosystems that provide valuable ecosystem services for people living in cities. Most notably, they provide the benefits of stormwater retention and heat regulation, both of which increase with the rate of water capture and evapotranspiration by the roof ecosystem (Lundholm et al., 2010; Buckland-Nicks et al., 2016). Green roofs also provide air pollution abatement and energy-saving benefits (Currie and Bass, 2008; Francis and Jensen, 2017). By reducing building energy consumption, green roofs also indirectly reduce carbon emissions (Kotsiris et al., 2019; Rowe, 2011). Moreover, green roofs can also contribute to urban biodiversity and mitigate habitat fragmentation by serving as habitat for animals including pollinator species (Baumann, 2006; Williams et al., 2014). Through these different ecosystem services, well-designed and managed green roofs can help reduce many of the negative impacts of urbanization (Oberndorfer et al., 2007). Because of this, green roofs have become an increasingly attractive type of green infrastructure in urban planning (Chow and Bakar, 2019).

The effectiveness of green roofs in providing ecosystem services depends largely on the plant community. In general, ecosystems with higher diversity of species and/or functional groups (as plant growth form) have a greater potential for efficient use of limited resources, and for maintaining viable, productive ecosystems in the face of environmental change or disturbance (Cadotte et al., 2011; Cardinale et al., 2007; Hooper et al., 2005). Johnson et al. (2016) found that plant species richness was positively correlated with greater overall plant biomass and with inorganic nitrogen retention, the latter mitigating deleterious effects of nutrient leaching in runoff. The abundance of dominant plant species also plays an important role in driving ecosystem service delivery in natural ecosystems (Winfree et al., 2015). Moreover, the types of dominant plant species also play a role. Recent studies with green roofs generally reinforce these ecological paradigms, with for instance plant species choice influencing nutrient retention (Buffam and Mitchell, 2015). Vegetation type also impacts thermal properties of green roofs, with succulents outperforming herbaceous plants in the summer, and vice versa in the winter (Eksi et al., 2017). Recent studies have also indicated the importance of plant species richness, and/or functional group diversity, for the provision of ecosystem services on green roofs (Cook-Patton and Bauerle, 2012; Buckland-Nicks et al., 2016). In general, planting multiple species is expected to enhance water retention and roof surface cooling effects (Wolf and Lundholm, 2008). Mixtures of three or five different plant species outperformed green roof monocultures in terms of providing heat regulation and water retention; in addition, a mixture of different functional groups (tall forbs, grasses, and succulents) was found to be an optimal combination for providing multiple ecosystem services (Lundholm et al., 2010).

Due to the specific conditions of their surroundings, such as partial shade by buildings or tall trees, a single green roof (especially when atop a one or two-story building) often has spatial heterogeneity in its environmental conditions. Sloped roofs may also develop a spatial gradient of substrate depth and/or moisture over time, and dormer windows or other raised sections of roof create local microclimates (e.g., Buckland-Nicks et al., 2016). Some green roofs are even designed specifically with habitat heterogeneity in mind, for instance by intentional variation in substrate depth or characteristics (e.g., Brenneisen, 2006). All these factors can create different patches of microclimates of varying surface temperature, moisture content, substrate depth, and insolation (Buckland-Nicks et al., 2016; Xu et al., 2018).

Variation in microclimate can affect plant community distribution via differential response by specific plant species or functional groups (e.g., Chapin, 2003; Gehlhausen et al., 2000; Thuring and Dunnett, 2019). However, though the relationship between microclimates and plant communities is well-documented for natural ecosystems (e.g., Gehlhausen et al., 2000; Oliveras and Malhi, 2016), researchers have just recently begun to explore this topic for green roofs, with intriguing findings. In terms of plant growth for instance, seed germination on green roofs was found to be impacted by microclimates varying in solar radiation, surface temperature, and vapor pressure (Xu et al., 2018). Differences in substrate depth, solar exposure, and soil moisture all influenced growth rates of an evergreen dwarf shrub and an herbaceous perennial forb on an extensive green roof (Buckland-Nicks et al., 2016). Spatial variation of substrate temperatures in the degree of exposure to temperature fluctuations was also found to be important in determining the trajectory of plant community development over time in extensive green roofs (Brown and Lundholm, 2015). Another recent study found that installing substrate of different depths in adjacent patches could help maintain co-existing species patches and thus long-term species richness in green roofs (Heim and Lundholm, 2014).

In spite of this recent pioneering work, there remains an important knowledge gap regarding the degree to which spatial heterogeneity in microclimate influences the distribution of green roof plant species and plant communities. Because green roofs are constructed ecosystems with initial plant composition set by design, research regarding the relationship between plant composition (including species, forms, and sizes) and microclimatic environmental conditions could inform better green roof plant selections and lead to designs that are suitable in certain microclimates and climate zones. Better plant species selections can in turn enhance species diversity and ecosystem service delivery of green roofs, increasing energy savings, mitigating greenhouse gas emissions, and reducing urban heat island effects (Lundholm et al., 2010). Additionally, green roofs could be designed specifically with spatial heterogeneity in microclimate and microhabitat in mind, if this heterogeneity will lead to greater diversity and productivity of the plant communities, and thus enhanced ecosystem service provision.

Though plant community characteristics of different green roofs vary due to climate conditions, initial vegetation, surrounding environment, and maintenance, this study sought to shed light on how microclimate conditions affect green roof plant communities at a fine spatial scale, and to provide insight on how to better select initial plant species for best long-term performance. Our central research question was: To what degree is spatial variation in plant species and dominant plant functional groups on a green roof related to spatial variation in solar exposure and soil moisture?

METHODS

Site physical features and description

The study site is a 46 m^2 extensive green roof, sloped at 21˚, with the lower side about 2 m and the upper side about 4 m above the ground (Dvorak, 2015). It is located on the roof of the Cottage House at the Civic Garden Center of Greater Cincinnati (39.1298° N, 84.4989° W) (Figure 1). The site azimuth is 112˚, so the green roof faces mostly east and slightly south.

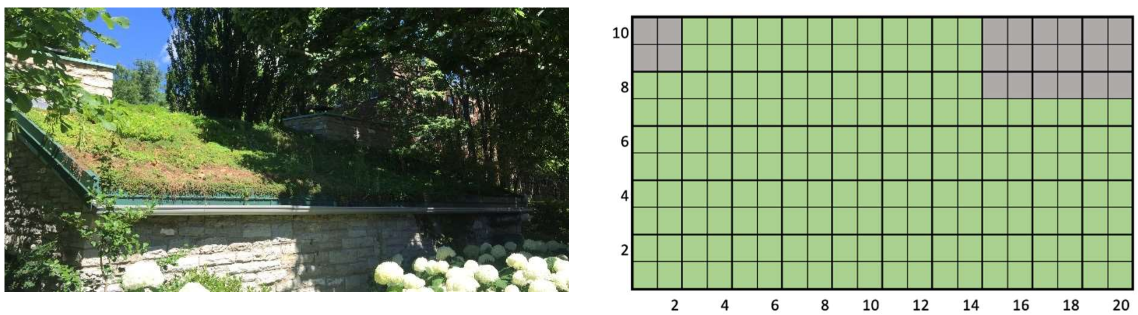

Figure 1. (a) Photo of the Civic Garden Center green roof during summer 2017 illustrating shading on the right side of the roof. (b) Site divisions for data collection, with 1 m x 1 m plots for solar exposure measurements, and 0.5 m x 0.5 m subplots for soil moisture and plant cover data collection. The top of the figure is the peak of the roof, with grey indicating chimney locations.

There are two chimneys on the two top corners, while the rest of the roof is covered in substrate and plants (Figure 1). This green roof was established in April 2010 by Tremco Inc. (Beachwood, OH, USA), with pre-planted Tremco Sedum Mats (Dvorak, 2015; Mitchell et al., 2017) overlain on 10 cm deep aggregated-based extensive green roof substrate. The dimensions of the sedum mats were 10 cm long (4 in), 15 cm wide (6 in), and 2.5 cm deep (1 in), with initial plant coverage of 85%. Initial plant distribution of the study site was all *Sedums*, with 50% *S. album*, *S. sexangulare*, and *S. acre*; and 50% *S. spurium* (several varieties), *S. rupestre* (several varieties), *S. floriferum*, *S.kamtschaticum*, *S. immergrunchen*, and *S. hispanicum* (Tremco Inc. 2010).

The study site is maintained by the Civic Garden Center staff. The roof undergoes only minimal maintenance, with weeding to remove woody species by hand at irregular intervals approximately 1-2 times per year, and it was also treated with an organic weed preventer, corn gluten meal, once in May 2012 (Buffam et al., 2016). The surrounding environment includes several deciduous trees that shade parts of the site – most notably, a tall cucumber magnolia tree (*Magnolia acuminata*) provides shade over the right third of the roof and extends slightly to the mid-third. After the first few years, the right third of the roof, which was most shaded, grew increasingly sparse in *Sedum* sp. cover and developed bare patches. In an attempt to maintain rooftop plant cover, prior to spring 2014 the bare patches were partly replanted with shade-tolerant live plants, including two non-native perennials *Polygonatum* *humile* (Dwarf Solomon's Seal) and *Galium odoratum* (sweet woodruff), along with *S. ternatum* 'Larinem Park' – a *Sedum* that is native to this region of Southwest Ohio.

All vegetation-related data was collected between July 1 and July 20, 2017. Summer 2017 experienced typical rainfall for the region, with 120 mm of rain in June and 116 mm in July, recorded at the Civic Garden Center, the location of the green roof (HOBO RX3000 weather station, Onset Computer Corporation). The green roof was divided into 1 m x 1 m (1.0 m^2) quadrants for solar exposure measurements, and further subdivided into 0.5 m x 0.5 m (0.25 m^2) quadrats for soil moisture and plant cover measurements (Figure 1b). Due to the presence of the two chimneys, there were only 178 viable 0.5 m x 0.5 m subplots and about 46 viable 1 m x 1 m plots. Plots along the right edge were shorter in width but are shown as full plots to simplify data visualization.

Plant identification and determining plant canopy percent coverage

The following resources were utilized to identify the existing plant species on the green roof: historical site information, "Green Roof Plants" (Snodgrass and Snodgrass 2006), the Emory Knoll Farms website's green roof planting section (Emory Knoll Farms, 2017), the photo section of the "Illustrated Handbook of Succulent Plants: Crassulaceae" (Eggli, 2003), "The Ohio Perennial and Biennial Weed Guide Photo Search" (Ohio State University, 2018), "A Guide to Woodland Plants in the Credit River Watershed" (Credit Valley, 2012), the "Edible 'Wild' Plants of Southeast Ohio" (Ballard, 2015), and consultation with a local green roof plant guru (Jill Bader).

To estimate the canopy percent coverage of plant species present in each subplot, a 0.5 m x 0.5 m (0.25 m^2 in area) PVC quadrat was used. The quadrat was divided into 25 mini-squares using string, so that each mini-square represented 4% of the entire subplot. The canopy percent coverage of each plant species within the quadrat was estimated to the nearest 2%, except for species with 5% or less cover which were estimated to the nearest 1%, or recorded as "trace" for <0.5% cover. In addition to the coverage of living plant species, the percent coverage of bare substrate, dead green roof plants, and fallen leaves from adjacent trees were also recorded. A photograph was taken of each subplot with the PVC quadrat above to record and later identify any unknown species. Samples of unknown plant species were also taken for further identification. This process was repeated for all 178 0.5 m x 0.5 m subplots.

The plant coverage data was grouped for analysis according to four different functional groups by growth form: succulents, graminoids (including all grasses and sedges), forbs, and woody (including tree and shrub seedlings). Plant species richness was also calculated for each plot, both at the 0.25 m^2 and 1 m^2 scales.

Soil moisture

Soil water content was measured for each 0.5 m x 0.5 m subplot using HydroSense II soil-water sensor (Campbell Scientific, Inc., Logan, UT, USA). The soil-water sensor was used at the center of each 0.5 m x 0.5 m subplot, and inserted at an angle so it be as parallel to the substrate surface level as possible; in practice this led to the measurement integrating the top (approximately 3 cm) of substrate. The soil moisture data for the right half of the roof (columns 13-20) was collected from 14:00-15:00 on July 19, 2017, and data from the remainder of the roof was collected from 9:30-10:00 on the following day, July 20, 2017. At the point we began taking soil moisture readings it had been 5 days since the last rain, which consisted of a few heavy downpours (thunderstorms) on July 13 and light rainfall at mid-day of July 14, totalling 35 mm of precipitation. In the intervening 5-day period, the average air temperature was 26 °C (range 18-35 °C), relative humidity averaged 67% (range 45-95%), and wind speed averaged 0.15 m s^{-1} (range 0-2 m s^{-1}) (HOBO weather station RX3000).

The soil moisture data were corrected for the fact that the measurements were taken on two consecutive days. We used longer-term data from four soil moisture probes in place to calculate the change in soil moisture due to evapotranspiration, and the change across the roof between the aforementioned two measurement periods was minor, averaging a drop of 0.225% in volumetric water content (VWC). To correct for the sampling condition difference between the two days, we added 0.225% to the soil moisture values from the second day. Compared to the longer-term data collection for soil moisture at four locations on the green roof, the soil conditions during our sampling on July 19 and 20 were somewhat drier than average: 26th and 24th percentile, respectively, relative to the annual mean.

Solar exposure

Solar exposure was measured on July 17 and 18, 2017 for each 1 m x 1 m plot using Solar Pathfinder (Solar Pathfinder™, Linden, TN, USA) that acts as a fish-eye lens taking images of canopy cover (Xu et al., 2018). The Solar Pathfinder was placed directly at the substrate surface and at the center of each 1m x 1m plot, and a photo was taken directly above. We later analyzed the photos using the Solar Pathfinder Assistant PV Software, and we chose the actual unshaded solar radiation (kWh m^{-2} per day) with azimuth = 101.1, tilt = 21.0 as a quantitative measurement for mean annual solar exposure at a given plot.

Slope position

Slope position was calculated as the distance in meters from the center of a given sample plot to the peak of the roof, along a direct line upwards.

Statistical methods and data analysis

We used R (v. 3.3.3) to visualize the distribution of plant species, plant species richness, plant functional groups, solar exposure, and soil moisture. A multivariate analysis was also carried out using the program CANOCO (v.5), to relate the variation in environmental conditions (solar exposure, soil moisture, and slope position) to the variation in plant communities. Two separate analyses were carried out: One using the cover of the most common individual plant species or ground cover types (n = 20) as response variables, and a second analysis using different plant functional groups or ground cover types as response variables (n = 8). We focus on the results of the plant functional group analysis in this paper, while the individual species results can be found in the supplementary material. The analysis was carried out with data aggregated to 1 m^2 plots (n = 46 samples). Based on the gradient length of the response data, redundancy analysis (RDA) was selected (ter Braak and Smilauer, 2012). Log-transformation of selected variables was applied as suggested by the CANOCO program to improve normality, and each variable was centered and standardized before analysis. Note, the RDA analysis did not include spatial autocorrection, but instead treated each subplot separately, thus not accounting for possible species interactions between the subplots.

RESULTS

Spatial heterogeneity in environmental conditions

The solar exposure varied greatly due to the adjacent trees, with mean annual solar exposure ranging from 0.146 to 0.583 kWh m^{-2} d^{-1} for different locations on the roof. The shading was greater at the right (north) end of the roof and decreased gradually to the left (south) end (Figure 2a). The soil moisture was generally greater on the lower right corner of the roof and low on the upper part of the roof, which was quite dry (<2% VWC, volumetric water content) (Figure 2b). The soil moisture also correlated with the vertical roof position, as the roof slope contributed to water gathering on the lower end (roof bottom).

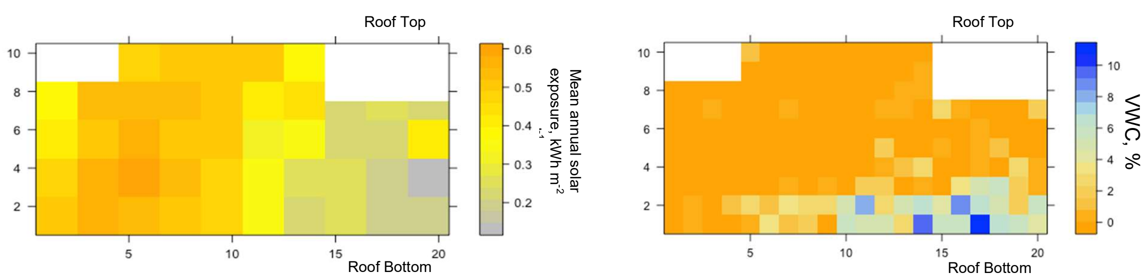

Figure 2. (a) Mean annual solar exposure in 1 m^2 plots across the green roof, demonstrating a gradient from high solar exposure (left side), transition (middle), to shady (right side). (b) Spatial distribution of soil volumetric water content (VWC) (min = 0.1%, max = 10.7%) measured on 0.25 m^2 subplots in mid-July 2017.

Plant communities and individual species distributions

We identified 28 different plant species on the roof, with individual species varying in overall cover from <0.1% to 13% (Table A1, Appendix). Seven of the nine *Sedum* species that were originally planted during installation were found, the exceptions being *S. sexangulare* and *S. hispanicum*. The *Sedum* which had been identified as 'Floriferum' at the time of installation was subsequently identified as *Phedimus takesimensis* 'Golden Carpet' and we found this concentrated at the upper part of the roof. *S. ternatum* 'Laurinum Park' was also found in a few subplots on the right (shady) side. In addition to these succulents, several volunteer plants were present, including wood sorrels (*Oxalis* sp.), clover (*Trifolium* sp.), dandelion

(*Taraxacum officinale*), onion (*Allium canadense*), wild ginger (*Asarum canadense)*, *Hosta* sp., asparagus (*Asparagus officinalis*), and horseweed (*Conyza canadensis*). There was a substantial coverage of graminoids including nutsedge (*Cyperus esculentus*) and crabgrass (*Digitaria sanguinalis*). Finally, we found coverage of the species planted in bare spots on the shady side of the roof, namely dwarf Solomon's seal (*Polygonatum humile*) and sweet woodruff (*Galium odoratum*).

Plant communities varied substantially in different parts of the roof, as illustrated by the distributions of eight of the most common species (Figure 3), whose total cover ranged from 1.5 to 13%. Multivariate analysis confirmed that distribution of individual plant species was correlated with the environmental conditions – with the degree of solar exposure, soil moisture and slope location explaining 30% of the overall variance in species cover data (Figure A2, Appendix). Of the common species, the two succulents *P. takesimensis* and *S. hybridium* were both concentrated in an area with high solar exposure on the left-third of the roof, but in largely distinct patches (Figure 3). *S. spurium* and *S. kamtschaticum* were each found distributed across much of the roof spanning a wide gradient in solar and moisture conditions, but were largely absent from the right third of the roof which had the lowest solar exposure. *P. takesimensis* was particularly common on the upper part of the slope, and *S. spurium* on the lower part of the slope. *C. esculentus* and *D. sanguinales* were both found in the middle-third (solar transition zone) with *D. sanguinales* particularly prevalent near the bottom of the roof where moister conditions were found. The introduced forbs *P. humile* and *G. odoratum* maintained a presence in the shady, moister right-third of the roof, where they had been introduced intentionally 3 to 4 years earlier to re-cover bare patches which had developed (Figure 3).

Plant species richness

The total number of plant species increased over time from nine *Sedum* species, to 28 species at the time of our July 2017 survey. Most of the increased species richness is due to volunteers presumably established by wind or animal transport. Of the 28 species identified, seven are *Sedums* (six of the original species plus one introduced later, intentionally), four are graminoids (volunteers), four are woody seedlings (volunteers), and twelve are forbs (all volunteers except two which were introduced intentionally on bare patches). Most of the volunteer species were found only in trace amounts (<1% overall cover), except for two volunteer graminoids and the two introduced forbs (which each had overall coverage of 1-6%).

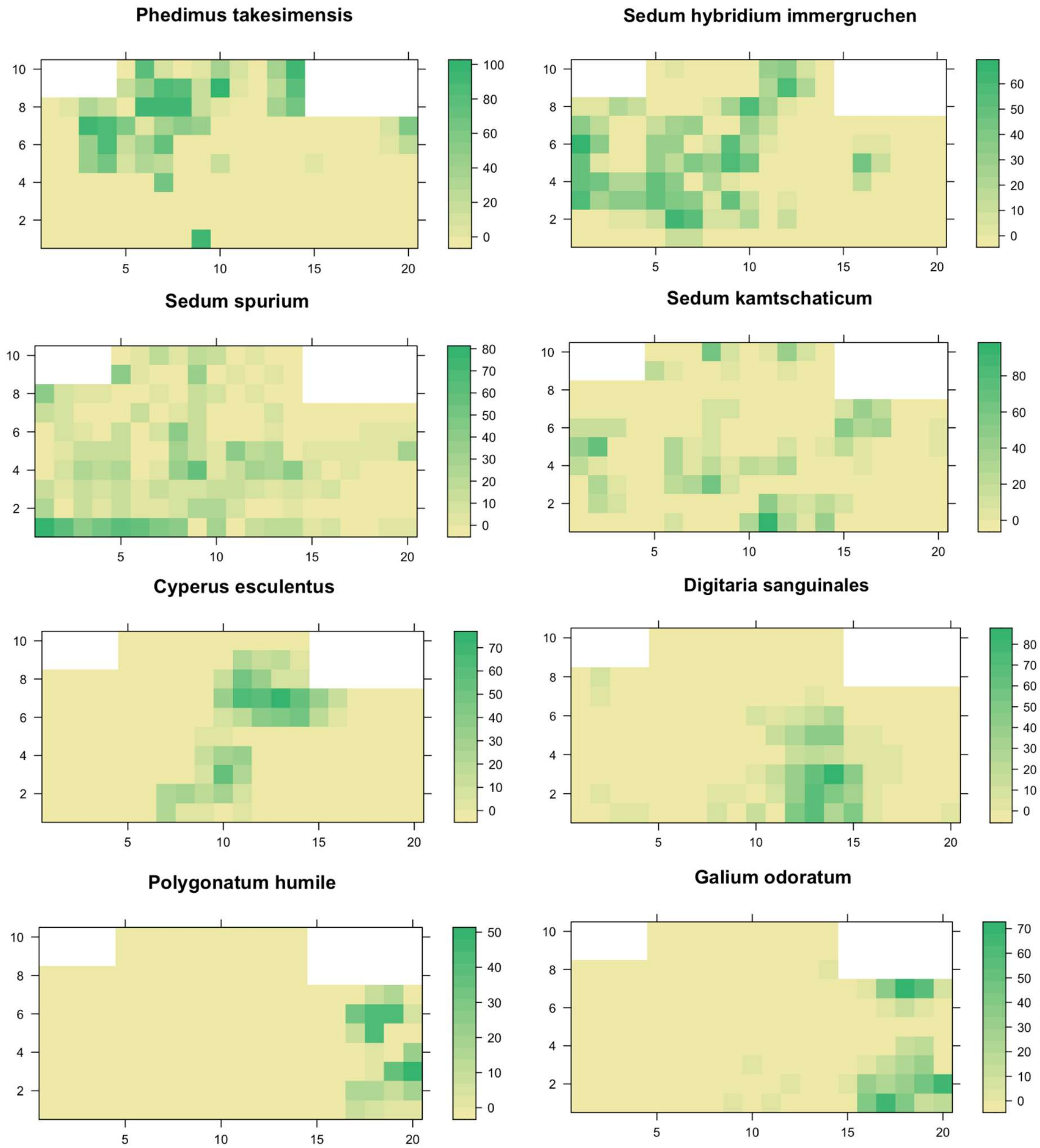

Figure 3. Spatial distribution of % cover for 8 common plant species on the green roof, measured on 0.25 m^2 subplots: *P. takesimensis, S. hybridium immergruchen*, *S. spurium*, *S.kamtschaticum*, *C. esculentus*, *D. sanguinalis*, *P. humile*, and *G. odoratum*.

Plant species richness varied across the roof (Figure 4). The range of values for species richness was 0 to 9 for the 0.25 m^2 subplots, and from 3 to 13 when aggregated to 1 m^2 plots. Areas with low species richness were concentrated on the left-third of the roof (sunny, dry), which was dominated by succulents. The areas with highest species richness were concentrated in the lower part of the middle-third of the roof (solar transition zone with moister conditions), where a mixture of succulents, graminoids, and forbs could be found. This was an area with high graminoid coverage. The right third of the roof (shady) with a high proportion of bare ground and forbs had intermediate species richness with several dominant species.

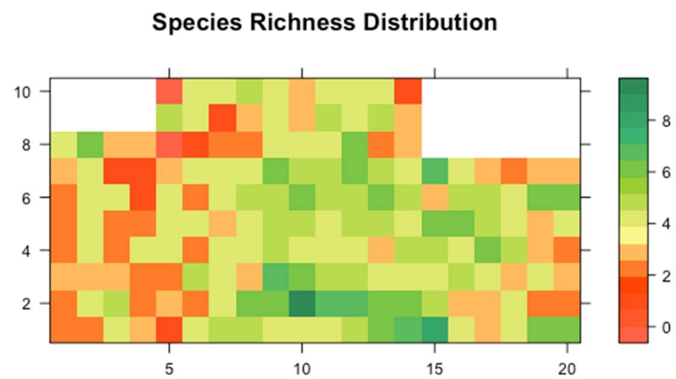

Figure 4. Spatial distribution of plant richness (from min 0 to max 9 species), measured on 0.25 m^2 subplots.

Plant functional groups

The overall cover of the roof by plant functional group was 44% succulents, 11% graminoids, 9% forbs, and 0.2% woody, with each of these groups showing a clear spatial arrangement on the roof (Figure 5). The remaining 36% cover consisted of bare ground, dead and dormant green roof plants (mostly graminoids), or dead leaves from adjacent trees (Figure A1, Appendix).

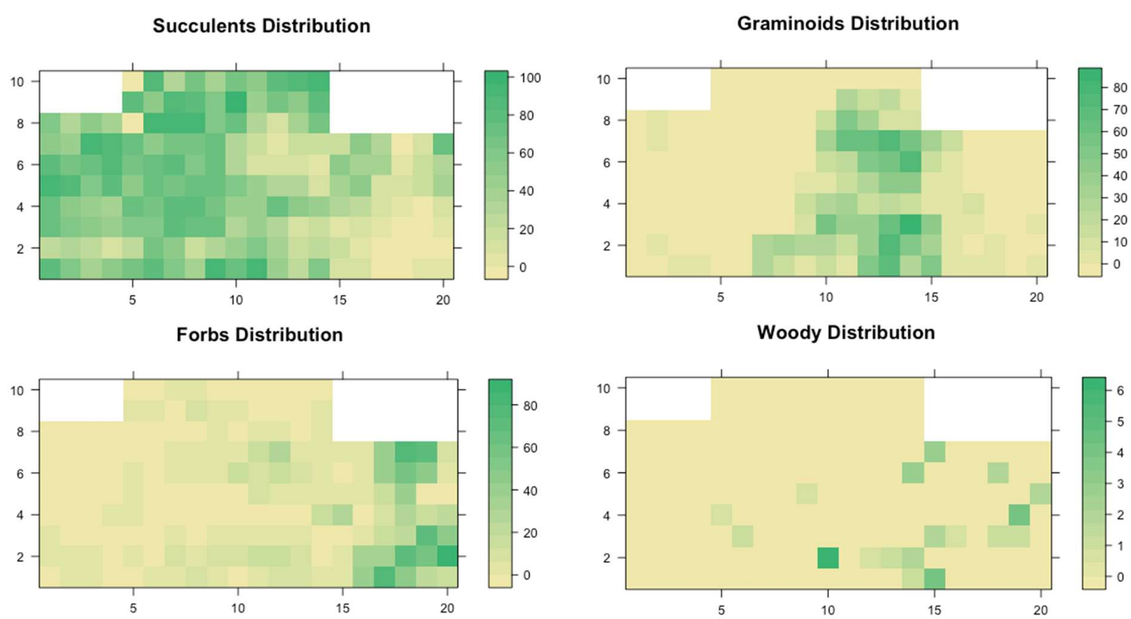

Figure 5. Spatial distribution of % cover by plant growth form on the green roof, measured on 0.25 m^2 subplots for Succulents, Graminoids, Forbs, and Woody seedlings.

Multivariate analysis relating plant functional groups to environmental conditions

Multivariate analysis (Redundancy Analysis or RDA) confirmed that the spatial distribution of the different plant functional groups was correlated with the measured environmental conditions, The RDA analysis explained 32% of the variance in the plant functional group coverage data (Figure 6). The only gradient with appreciable power in explaining the functional group distributions is the first ordination axis (Axis 1). This can be interpreted as the gradient on the roof from sunny and dry (upper left of roof) to shady and moist (lower right), and explained 31% of the variance in plant coverage data. Solar exposure was the environmental variable most clearly and strongly associated with this axis, but soil moisture and to a lesser degree, slope position, were also important. Succulent species were associated with the sunny/dry parts of the roof, while forbs, graminoids, woody plants, and high species richness were all associated with the more shady/moist parts of the roof – with forbs showing the strongest association. This gradient can be qualitatively observed in the spatial map figures which show a shift from succulent to graminoid to forb/bare ground dominance as one moves from left (sunny) to center (transition) to right (shady) on the roof (Figure 5). Woody plants, though sparse overall (only 0.2%), were very rare on the sunny side, but more common on the shady side of the roof (Figure 5, Figure 6).

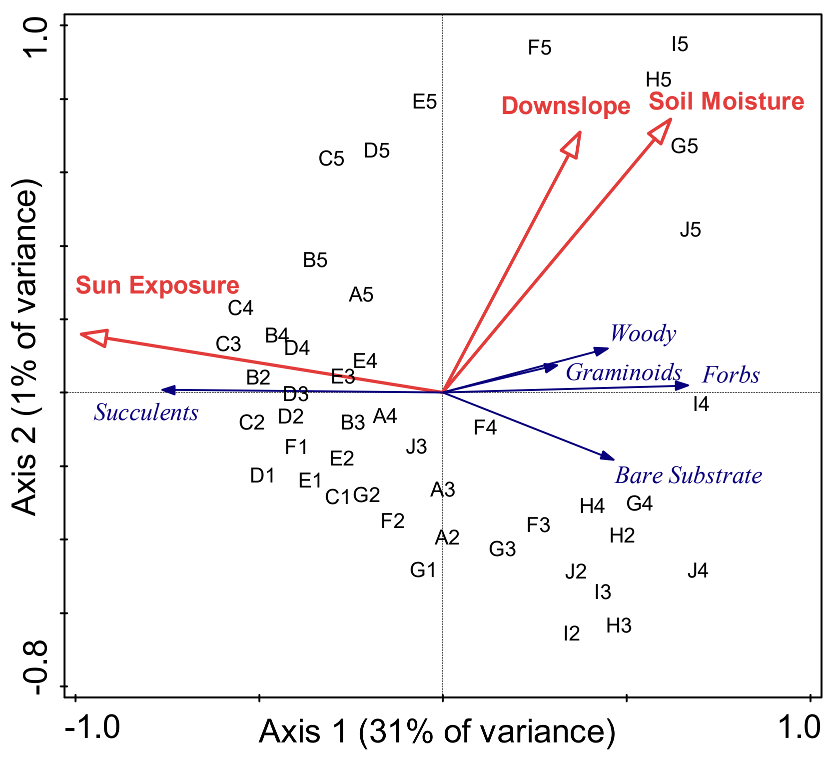

Figure 6. Results of redundancy analysis (RDA) relating environmental conditions to the relative cover of different plant functional types, plus bare substrate. Red arrows and text are the environmental variables, dark blue are the plant cover variables, and the black digits indicate the location of the individual sample plots.

Axis 2 of the RDA analysis additionally described a gradient in moisture that was not related to shade, i.e. the gradient observed from top to bottom of the sloped roof, with the bottom ("Downslope") having higher moisture (Figure 6). This axis only explained 1% of the overall variance in the plant functional group cover data and describes a slightly greater occurrence of graminoid-containing plant communities on the lower, moister sections of the roof, and a slightly greater occurrence of bare substrate on the upper, drier sections of the roof.

DISCUSSION

Effects of spatial variation in microclimate on plant communities

There was a strong interrelationship observed between the vegetation patterns and the spatial variation in green roof microclimate. For this green roof, shading from adjacent trees resulted in a distinct spatial gradient in solar exposure. That gradient, together with the variation in soil moisture arising from roof slope and variability in solar exposure, gave rise to a clear spatial pattern in microclimate, which allowed us to explore the resulting impact on green roof communities. When measured seven years after being planted with a homogenous community of nine different *Sedum* species across the roof, the vegetation had changed considerably and showed clear evidence of the impact of the microclimatic gradient. *Sedums* remained dominant on the sunny, drier parts of the roof ecosystem, but other plant functional groups have established on other parts of the roof, though in some places interspersed with remaining *Sedums*. These include various forbs and a few woody seedlings which have established primarily on the shadiest part of the roof, as well as thick patches of graminoids dominated by two species in the climate transition zone between the sunny and shady sides of the roof.

These vegetation community patterns are sensible based on what we know of the physiology of the plant functional groups. Succulents, including most of the originally planted *Sedum* species, were well concentrated on the sunny dry side, and they were the functional group with the most coverage overall (44%). Generally, *Sedum* or *Phedimus* species are particularly successful in terms of long-term survival and plant coverage on extensive green roofs in the American northeast and Midwest (Butler and Orians, 2011). This success is often attributed to *Sedum* species' crassulacean acid metabolism (CAM) which endows this genus with efficient water use and strong drought-tolerance (Starry et al., 2014; Van Mechelen et al., 2014). Within the *Sedum* genus, different species also have varying degrees of CAM and water use efficiency (WUE) (Starry et al., 2014). This may explain why certain *Sedum* species, such as *S. spurium*, were concentrated in patches with higher soil moisture on this green roof. Water availability is one of the factors most limiting to plant growth on extensive green roofs, which resemble cliff or rock barren habitats (Benvenuti and Bacci, 2010; Lundholm and Marlin, 2006). In our study, both environmental variables (solar exposure and soil moisture) are related to overall water availability.

Both graminoids and forbs were typically concentrated in areas of higher moisture than the *Sedums*, as expected based on differences in the physiology of these functional groups relative to the succulent drought-tolerant sun-loving *Sedums*. Further, the graminoids were found in relatively higher-sun areas of the roof compared to the forbs. The distribution of woody volunteer species showed a positive association with soil moisture, which is sensible based on their need for water and nutrients for survival and growth in the green roof environment (e.g., Snodgrass and McIntyre, 2010). Note that the seedlings undergo periodic weeding (on the order of 1-2 times per year) so would likely be more prevalent if not for this maintenance intervention.

Although this study primarily focused on the spatial variation in functional groups as defined by plant growth form, spatial patterns are determined by the spatial distribution of the individual plant species. The spatial distributions of individual species were also related to variation in microclimate (Appendix A2), but there remained considerable unexplained variance, and the observed distributions of some of the dominant species could not have easily been predicted a priori even given knowledge about the typical habitat preferences or the plant's physiology. For instance, of the two graminoids which dominated coverage of the center part of the roof (solar transition zone), the C4 grass *D. sanguinales* (crabgrass) which is known to prefer sunny conditions, was found in the shadier, moister section of the transition zone relative to the nut sedge (*C. esculentus*). *C. esculentus* is moderately drought tolerant and has low moisture use, which may have helped it to thrive on the upper middle part of the green roof in the drier part of the solar transition zone.

We observed several species which had formed distinct non-overlapping spatial distributions on the roof that appear to be correlated with the shade and moisture gradient (Figure 3, Figure A2). This is evidence that spatial variation in microclimate can enhance plant species heterogeneity, as plant species occupy distinct ecological niche on the same roof. Thus, environmental heterogeneity at the roof scale could lead to enhanced species coexistence and higher plant diversity as suggested by Buckland-Nicks et al. (2016).

Implications for ecosystem service provision on green roofs

In this study, a green roof that was established with a single growth form (a homogenous mat of nine succulent *Sedums*) has developed over time, in the presence of varied microclimates, into an ecosystem with a number of different functional groups spatially distributed throughout the roof. Different plant functional groups will have varying impacts on the ecosystem services provided. While no one plant species or functional group could provide all desired services, synergies may occur in ecosystem service provision from biodiverse roofs. For instance, while many succulents (including a number of *Sedums*) are drought-resistant and thus can survive in the challenging conditions on a roof, they are not particularly effective for retaining water runoff relative to other plant functional groups (Farrell et al., 2013). However, succulents are effective in thermal regulation (Heim et al., 2017) and can facilitate growth and performance of neighboring plants in droughts by decreasing peak soil temperature (Butler and Orians, 2011). This facilitation in turn would lead to overall higher vegetation coverage that could improve stormwater management of the entire roof (Nagase and Dunnett, 2012). As a result, a coverage of succulents, especially in the presence of other types of plants can enhance green roof ecosystem services such as heat regulation and stormwater retention (Van Mechelen et al., 2014).

Graminoids contribute differently to ecosystem services, including by sequestering soil organic carbon with their high root and rhizome biomass (De Deyn et al., 2008). They are also the most effective functional group in terms of stormwater retention, more so than the herbaceous forbs (Nagase and Dunnett, 2012). And in terms of ecosystem dis-services, the persistence of woody volunteer species could damage the roof membrane and block drains and gutters, outcompeting other desired green roof species and causing water damage (Archibold and Wagner, 2007). Thus, in part due to the spatial variation in microclimate caused by shading, the ecosystem services provided by the Civic Garden Center green roof have almost certainly changed over time. Though direct measurements were not made, we expect that the increasing graminoid distribution increases carbon sequestration and stormwater retention.

Role of plant diversity

Species richness in green roofs can influence ecosystem services provision (Cook-Patton and Bauerle, 2012), and extensive green roofs with a mixture of different species increase diversity and habitat value (MacIvor et al., 2011). In our study, the alpha (local fine-scale) diversity varied considerably across the roof, and a sizable proportion of variation was correlated with the environmental conditions. The most species-rich area of the roof was in the transition zone in the center of the roof with intermediate sun exposure, especially the area towards the bottom of the roof where moisture tended to be higher. This is an area that forms an ecotone of sorts, with overlap between several different plant communities and representatives of all four plant functional groups. High biodiversity in a microclimate transition zone has also been observed in other ecosystems like the tropical forest-savannah transition, which is strongly shaped by water availability (Oliveras and Malhi, 2016).

This part of the green roof was also an area of high overall plant coverage. Visual observations would suggest that this species-rich area is also a zone of high annual productivity, since the dominant species were quick-growing graminoids which had a sizeable apparent biomass by the middle of the growing season when our measurements were taken. Other studies have noted better provision of ecosystem services such as substrate cooling in the summer and maintaining substrate temperature in the winter in areas of high canopy density on green roofs (Lundholm et al., 2015). This suggests that the middle-third of the Civic Garden Center green roof (solar transition zone) may provide the highest "quality" in terms of providing ecosystem services such as temperature control by tempering rooftop heating and cooling. The specific relationships between these patterns and other ecosystem services (such as supporting pollinators and sequestering carbon) would require further study for this green roof.

Role of maintenance and management actions

Although the intent of this study was to examine the role of "naturally" occurring spatial heterogeneity in microclimate caused by shading from roof-adjacent trees, human intervention also played a role in directing the green roof plant community over time. This is a common factor since green roof ecosystems are often designed and engineered to provide specific ecosystem services in the first place – and commonly some level of maintenance is required or intended during the lifespan of the roof to maintain the plant community. Maintenance may include irrigation, fertilization, weeding, leaf removal, clipping of herbaceous species prior to spring, and/or introduction of additional plant species. For this particular roof, three species of plants were introduced intentionally to bare spots which had developed on the shady section of the roof after the first few years following installation. These plants remained in the shady (cooler, moister) microclimate to which they had been introduced, and two of the three species maintained a substantial foothold on that section of the roof even after 3-4 more years. The role of maintenance and management regimes, difficult as they are to account for within the scope of a traditional ecological study, are critical to consider in order to understand the development of engineered ecosystems like green roofs over time. Thus, we encourage the integration of this aspect of study into ecological inquiries of green roof development.

Limitations of this study, and future directions

The short timeframe within which data were collected in this study presents several limitations. First, data were collected in the summer as a single snapshot, so this study did not capture seasonal environmental changes which may impact plant communities. Though the solar exposure analysis calculates the total sunlight exposure at a given location for the entire year, the soil moisture can vary considerably over time depending on the frequency and amount of precipitation and subsequent temperature and evapotranspiration rate (Wadzuk et al., 2013). However, the soil moisture for this study was collected just 5-6 days after a precipitation event, and spatial variation in soil moisture was observed, so it is reasonable to assume that the data recorded was representative of the relative pattern between different locations of the roof over time, at least during the summer months. This highlights the importance of roof slope and drainage layers, both of which affect soil moisture levels on a given green roof. Plant communities can also shift in the long-term due to other factors that are outside the scope of this study, such as succession, interspecific interactions, soil development and soil microbes, nutrient and pollution limitations, pollinator interactions, and macro climatic changes (Chapin et al., 2011). Thus, the snapshot that we collected for this study may be representative of the environment-plant spatial relationships for only a period in the development of the green roof ecosystem. Finally, we only considered two variables for the spatial variation related to specific environmental conditions, namely solar exposure and soil moisture. There are other variables that impact plant growth on green roofs such as substrate depth and soil pH (Getter and Rowe, 2008; Zheng and Clark, 2013). To further examine the relationship between plant communities and heterogeneous environmental conditions within green roofs, controlled experiments could be carried out (Lundholm and Marlin, 2006), and long-term data on plant communities in relation to spatial variation in environmental conditions should be collected. Further studies could explore interspecific relationships as a response to varying microclimates in order to refine suggestions for an informed green roof plant selection.

SUMMARY

Overall, the roof is considerably more species-rich than when initially planted (28 vs. 9 species), having gone from being a completely homogenous community with a mixture of *Sedums*, to a spatially organized ecosystem with distinct patches dominated by different plant communities and functional groups. This was mostly due to successful colonization by volunteer plants, though human management (planting new species and weeding some unwanted volunteers) also played a role. The spatial patterns in plant species and functional groups correlated with spatial patterns in environmental conditions (solar exposure and soil moisture) on this green roof. The ecophysiological characteristics of the different plant functional groups are well reflected in their distribution on the microsite mosaic, despite the fact that the roof was originally planted in a uniform manner. Succulents thrived in areas with high sunlight and low moisture. Graminoids were concentrated in the transition zone with medium sunlight and moisture. Forbs were found in the area with low sunlight and relatively high moisture. Woody plants appeared sporadically on the roof primarily in or near bare patches in the shady part of the roof. There was also a detectable gradient from top to bottom of the roof, both in soil moisture and in plant communities. These results are consistent with the idea that certain plant functional groups are more fit for certain green roof microclimates, i.e. spatial variation in environmental conditions affects plant communities on this green roof. The abundance and diversity of different plant species on green roofs will influence ecosystem service provision – thus, an awareness of microclimate variation should be incorporated into planning and managing green roof plant communities to optimize ecosystem services.

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APPENDIX

Table A1. List of plant species found on the green roof. Plant Functional Group (Growth Form): S=succulent, G=graminoid, F=forb, W=woody seedling; Origin: O=original *Sedum* mat, P=planted later, V=volunteer. Shorthand refers to shorthand names used for species in RDA ordination analysis (only the more common plants were used, see methods section for details).

Plant species/taxon	Shorthand	Plant Functional Group	Origin	Cover (%)
P. takesimensis 'Golden Carpet'	PheTak	S	V	13.0
S. hybridium 'Immergruchen'	SedHyb	S	O	10.6
S. spurium	SedSpu	S	O	9.6
S. katschaticum	SedKat	S	O	7.4
C. esculentus (nutsedge)	CypEsc	G	V	5.6
D. sanguinales (crabgrass)	Digit	G	V	5.4
G. odoratum (sweet woodruff)	GalOdo	F	P	3.8
S. rupestre	SedRup	S	O	3.4
P. humile (dwarf Solomon's seal)	PolHum	S	P	2.2
Oxalis sp.	Oxalis	F	V	1.3
T. officinale (dandelion)	TarOff	F	V	0.63
S. ternatum 'Larinem Park'	SedTer	S	P	0.33
Asarum canadense (wild ginger)		F	V	0.20
Trifolium sp.	Trifol	F	V	0.17
Allium canadense (onion)	AllCan	F	V	0.14
C. canadensis (horseweed)	ConCan	G	V	0.14
Ailanthus altissima (tree of heaven)	AilAlt	W	V	0.13
Hosta sp.		F	V	0.12
Bryophyta (moss)	Moss	Moss	V	0.11
S. album		S	O	0.10
Brunnera sp.		F	V	0.09
Celtis occidentalis (hackberry)		W	V	0.03
Cercis canadensis		W	V	0.03
Ageratina altissima (white snakeroot)		F	V	0.02
Asparagus officinalis		F	V	0.01
Robinia pseudoacacia (black locust)		W	V	0.01
Vitis vinifera (grape)		F	V	0.01
Unidentified Grass		G	V	<0.01
Other cover				
Bare Substrate/Soil	Bare			14.6
Dead Grass/Roots				11.9
Dead Leaf				7.8

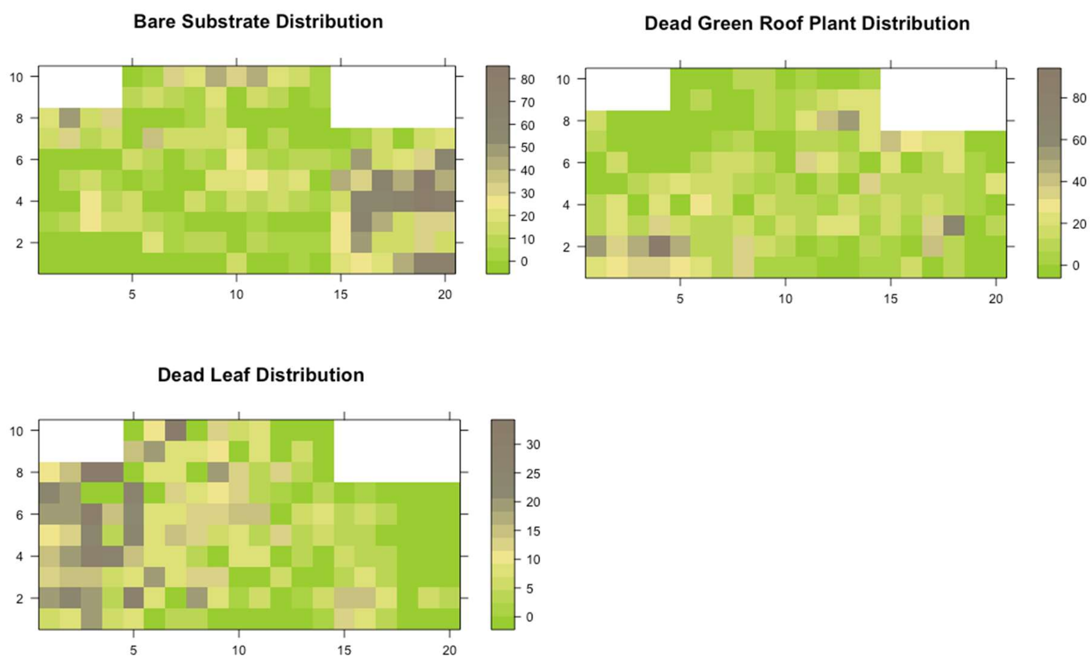

Figure A1. Spatial distribution of % cover for the and non-vegetated patches on the green roof, measured on 0.25 m^2 subplots: Bare substrate, Dead plants, and Fallen leaves from nearby deciduous trees.

Appendix A2. Multivariate Analysis: Correlation between plant species spatial distribution and environmental variables (microclimate)

The spatial variation in environmental factors was able to explain a total of 30% of the overall variance in coverage of individual plant species or taxa. The relationship could be explained largely by two ordination axes, with the first axis explaining 20% and the second 9% of the overall variance (Figure A2). This first axis describes an environmental gradient from high solar exposure and low moisture (on the left in the figure), to low solar exposure and high moisture (on the right); and this gradient is associated with a shift in species with *P. takesimensis*, *S. hybridium* and *S. spurium* most prevalent at the dry, sunny end of the spectrum, and *G. odoratum*, *C. canadensis*, *P. humile* and *D. sanguinalis* most prevalent at the moist, shady end, with the other species falling in between. This gradient largely corresponds to a physical gradient from upper left to lower right on the roof itself (Figure 2). The second axis describes a gradient from the top to bottom of the roof which is not as clearly related to soil moisture – with for example *P. takesimensis* more prevalent towards the upper part of the roof, and *S. spurium* and *Trifolium* sp. more prevalent towards the lower part of the roof (Figure A2).

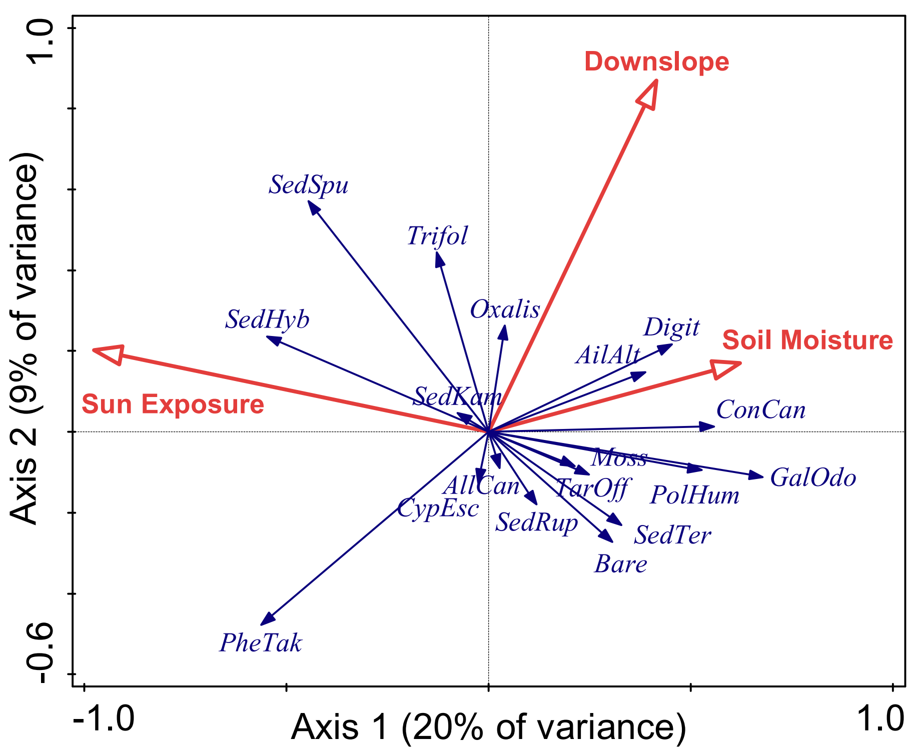

Figure A1. Results of redundancy analysis (RDA) relating environmental conditions to the relative cover of different green roof plant species. Red arrows and text are the environmental variables, dark blue are the plant species cover variables. See Table A1 for key to shorthand species names.