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Moss species for bioreceptive concrete: A survey of epilithic urban moss communities and their dynamics

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ABSTRACT

Research into bioreceptive materials is gaining increased interest. However, while advances are being made on the material side of bioreceptivity, the underlying ecology of urban mosses is still underexposed. This research aimed to determine how the local environment affects the species composition of urban epilithic moss communities and assess which moss species are most suitable for the colonisation of pristine (bioreceptive) concrete surfaces, leading to recommendations for moss species selection to designers and engineers of bioreceptive structures. We conducted a field survey of 137 moss communities on concrete in the Dutch cities of Amsterdam, Rotterdam and The Hague. A total of 26 different species were found, of which the acrocarp species *Tortula muralis, Grimmia pulvinata, Ptychostomum capillare*, and *Orthotrichum diaphanum* and the pleurocarp species *Brachythecium rutabulum, Hypnum cupressiforme,* and *Rhynchostegium confertum* acted as most common pioneers and also formed a part of the climax community. We found some positive associations between acrocarp species but negative associations between acrocarp and pleurocarp species. Local environmental factors only played a small role in the community composition at a species level; however, when comparing acrocarp and pleurocarp species, the former preferred more exposed sites, whereas the latter preferred more shaded habitats. As such, we recommend that bioreceptive concrete structures use acrocarp pioneers for exposed locations and pleurocarp pioneers for more shaded locations.

1. Introduction

Nature-inclusive, green structures are receiving increased interest worldwide to offset the loss of green spaces through increased urbanisation. Green structures, as compared to traditional green areas such as parks, have the benefit of adding functionality to existing surfaces and infrastructure. Most modern green structures use vascular plants, which have proven positive environmental effects, such as increased thermal comfort, reduced stormwater run-off, and reduced air and noise pollution while providing ecological habitats (Berardi, 2016; Getter and Rowe, 2006; Kadas, 2006; Köhler and Ksiazek-Mikenas, 2018; Mentens et al., 2006; Rowe, 2018). Vertical green structures consist of direct green structures, where soil-bound plants can grow directly on the structure's surface, or indirect green structures, where plants are supported using an additional structure (Perini et al., 2011). The latter can either use soil-bound plants with a supporting structure or, as is the case with living wall systems (LWS) and green roofs, plants grown in a special growing substrate, often complemented with additional irrigation and nutrients. However, the widespread adoption of these nature-based solutions is still held back due to political reasons, uncertainty about their benefits and perceived high costs associated with them (Katia Perini and Rosasco, 2013; Sarabi et al., 2020).

In the last few years, several researchers (e.g. Cruz and Beckett, 2016; Manso et al., 2014; Morin et al., 2018; Veeger et al., 2021a; Veeger et al., 2021b) have attempted to create a new green concrete typology based on the principle of bioreceptivity. Bioreceptivity is defined by Guillitte (1995, p. 216) as: "the aptitude of a material to be colonised by one or several groups of living organisms without necessarily undergoing any biodeterioration". Instead of using vascular plants, bioreceptive structures could use mosses, a group of plants with very underdeveloped rootlike systems called rhizoids. Due to their high surface-to-volume ratio and limited surface resistance (due to a lack of a cuticle), they can take up water and nutrients directly through their outer surface (Glime, 2017a). Mosses, therefore, take up water and

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nutrients directly from the atmosphere through air humidity and rainfall and nutrients dissolved in rainfall and atmospheric dust. As such, mosses can colonise bare surfaces such as concrete structures without the need for the presence of soil and, in many cases, are, in fact, part of the pioneering species that start the soil formation process (Vanderpoorten and Goffinet, 2009). Additionally, mosses are poikilohydric, meaning that under periods of extended drought, instead of withering and dying, they will go into a dormant state and resume metabolic activity after rehydration (Vanderpoorten and Goffinet, 2009). This means that bioreceptive green structures, unlike other direct green structures, do not need to be soil-bound, and unlike indirect green structures, established moss communities on bioreceptive structures do not require additional irrigation or nutrients, nor do they need a supporting structure, significantly lowering construction and maintenance costs.

However, while some successes have been achieved in manipulating the material side of bioreceptive concrete (Veeger et al., 2023), the ecological side of biological growth on bioreceptive concrete in an urban setting is still underexplored. While several investigations of mosses in an urban setting exist (Isermann, 2007; Kirmaci and Agcagil, 2009; Pokorny et al., 2006; Sabovljevic and Grdovic, 2009; Sabovljević and Sabovljević, 2009; Skudnik et al., 2013), these are mainly focused on creating a general inventory of moss species that are present across all surfaces in the urban fabric without considering the effect of the local microclimate or moss community establishment dynamics, both of which are expected to be essential for the successful development of a moss layer on bioreceptive concrete.

Bare concrete surfaces in cityscapes typically represent a harsh environment for vegetation to establish and survive, mainly due to a lack of nutrients and water availability. Concrete surfaces also show a considerable variation in micro-environmental conditions, influenced by the location within the cityscape, concrete composition, surface smoothness and modifications caused by colonising pioneering moss species (Doulos et al., 2004; Wang et al., 2019). Under natural conditions, this environmental heterogeneity has been found to influence the species composition of epilithic moss communities (Spitale and Nascimbene, 2012). As such, it can be expected that the ideal moss species to be used for inoculating or seeding pristine bioreceptive structures will depend on the environment in which it will be placed.

Four main environmental factors are expected to govern moss community composition based on existing literature and previous field surveys. The first is the intensity of solar radiation. Whilst necessary for photosynthesis, mosses are adapted to shaded environments and have (very) low light compensation points (0.03–7.1 % of full sunlight) (Glime, 2017b). However, some species can apparently protect themselves from oxidative damage caused by high solar radiation, allowing them to occupy more exposed environments (Lüttge et al., 2008; Proctor and Smirnoff, 2011). The second is temperature. Partially related to exposure to solar radiation, for most moss species, optimal growth is achieved at a temperature of 15 to 25 degrees Celsius (Furness and Grime, 1982). The third is water availability. Despite their poikilohydric nature, mosses still need some water to grow, specifically during initial germination and establishment. Desiccation-sensitive species will hardly grow under dry conditions, whereas the opposite is not true, with desiccation-tolerant species also showing increased growth under humid conditions (Alpert, 2000; Glime, 2017a). As such, more humid sites will generally show higher biomass and moss community diversity (Tng et al., 2009). The final factor is air quality. Air quality directly affects mosses as they take up nutrients directly from the atmosphere. Therefore, the chemical composition in their tissues was found to change depending on the chemical composition of the surrounding atmosphere. Bignal et al. (2007) found that NOx pollution has both beneficial and deleterious effects on moss species, depending on the species' specific affinity for nitrogen. Mosses have also been found to readily absorb heavy metal ions from atmospheric pollution, showing species-specific tolerances and responses to these heavy metal ions (Mahapatra et al., 2019; Pescott et al., 2015; Stanković et al., 2018; Vats et al., 2010).

As of yet, little is known about how environmental factors in the built environment determine the community composition of epilithic mosses (growing on the surface of stony substrates) within an urban setting. In nature, local environmental factors significantly influence species richness and community composition (Pharo and Beattie, 2002). As such, it is expected that not all moss species can occur on all urban surfaces, and their presence or absence is dependent on both material characteristics and local environmental factors. This information is crucial when determining which mosses are most promising to be used on specifically produced and new bioreceptive structures, as this can help engineers and designers choose the suitable moss species for the conditions present on the surface of the bioreceptive structure.

Whilst a moss species may be found in a specific environment, this does not necessarily mean it is suitable for developing a moss layer on bioreceptive concrete. Kürschner and Frey (2012) describe seven different categories (annual shuttle species, short-lived shuttle species, perennial shuttle species, fugitives, geophytes, colonists, and perennial stayers) of life strategies that can occur within mosses and other bryophytes based on their life cycle, breeding system, sexual reproduction, asexual reproduction, spore size and dispersal. As such, some species can readily colonise fresh new habitats, where there are usually high levels of environmental stressors, whereas others can only establish themselves in already colonised habitats, where the environmental conditions have been ameliorated and are more suitable for their growth. For bioreceptive structures, it is essential to identify those moss species with a life strategy that allows them to establish a long-term colony on a fresh bioreceptive surface.

This research aims to determine which moss species have the greatest potential for colonising pristine (bioreceptive) concrete surfaces and how the local environment affects the species composition of urban epilithic moss communities. Based on this, designers and engineers will be given recommendations about which species are most suitable for bioreceptive concrete structures in specific urban settings.

2. Methodology

2.1. Study sites

A total of 137 moss communities growing on concrete were located in three major cities in the Netherlands. The climate in the Netherlands is temperate oceanic (Cfb in the Köppen-Geiger classification system), with a yearly mean temperature of 10 degrees Celsius and annual precipitation between 725 mm and 950 mm. All the sampling areas were towards the higher end of this precipitation range (KNMI, 2022).

The three cities, Amsterdam, The Hague, and Rotterdam, were chosen as they represent the highest building densities within the Netherlands and have less densely populated suburbs (Fig. 1a). Sampling took place along a representational gradient within these cities that included all its main functions (high and low-density residential, commercial, and green spaces) to ensure a wide range of different urban environments was included.

Within these areas, concrete structures containing moss growth were identified. We did not further distinguish between chemical composition as concrete structures in the Netherlands are made almost exclusively out of either Portland cement or blastfurnace slag cement, leading to similar chemical compositions. For a moss community to be included, it had to occupy at least 50 % of a 10x10cm surface area to ensure only well-established moss communities - presumably in balance with the local environment - were included. A random 10x10cm subsection was chosen to analyse communities larger than this. Only 1 sample was taken from each aspect of a concrete structure. If multiple aspects (i.e. horizontal and vertical or North and South) of a concrete structure had sufficient moss growth, one sample was taken from each aspect, ensuring that no moss communities were sampled that were continuous across the different aspects. A schematic overview is given inFigure 1b. Within the sampled moss communities, the mosses present were

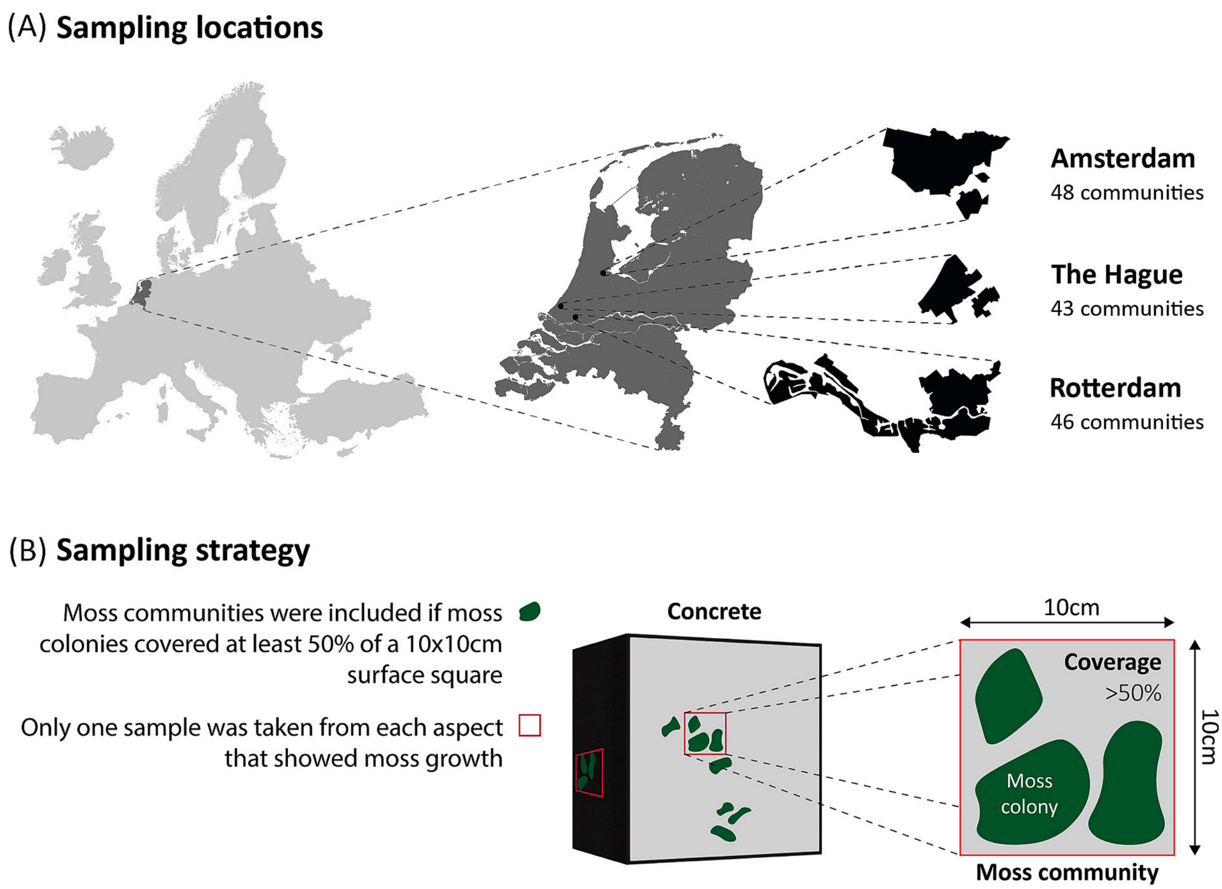


Fig. 1. (a) Geographical locations of sampling sites in three cities in the Netherlands. (b) Concrete structures with moss colonies (green shapes) were included if moss colonies covered at least 50 % of a 10 × 10 cm square surface. When moss colonies were present on several faces of a concrete structure, only one sample was taken from each face. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

determined using a bryophyte field key (Atherton et al., 2010).

2.2. Data collection

Due to the large number of sampling sites, the dynamics of the four environmental drivers (water availability, light exposure, temperature and air quality) were measured mostly indirectly using structural characteristics as proxies (Table 1).

2.3. Light and temperature

As the field research will be conducted in The Netherlands, the southern surface will receive the highest solar radiation input, with the northern aspect receiving the lowest. Furthermore, more horizontal surfaces will receive higher solar radiation input than vertical ones. Finally, more exposed surfaces will also have higher solar radiation inputs than more shaded surfaces. By combining this data with the local solar irradiation throughout the year, it then becomes possible to estimate total light exposure. Furthermore, as solar radiation is the main driver of local surface temperature (Berry et al., 2013), the aforementioned structural characteristics are expected to also be good indicators of local temperature differences.

Table 1
Relationship between environmental variables and tested characteristics.

Environmental variable	Tested characteristic
Water	Orientation
	Inclination
	Shading
	Surface roughness
Light	Orientation
	Inclination
	Shading
Temperature	Orientation
	Inclination
	Shading
Air quality	NO2 concentration
	PM10 (Particulate Matter <10 μm) concentration

2.4. Water

In the Netherlands, Western and Southern winds carry air from the sea and, in general, correlate to more rainfall, both in terms of frequency and intensity (Manola et al., 2020). As such, surfaces facing this direction, in general, can be expected to receive more rain than the other directions. How long a surface stays wet also correlates with temperature, as a higher temperature incurs higher evaporation. Therefore, water availability is also related to those structural factors affecting temperature. Finally, the substrate itself will play a role in the availability of water. Whilst many of the characteristics (such as porosity and composition) cannot be readily tested in the field, surface roughness, which can be tested, has been previously shown to affect the water availability of concrete (Veeger et al., 2021a).

2.5. Air quality

As long-term measurements of both PM10 and NO2 are available for The Netherlands, these values can be assessed directly.

As such, for each location, the following factors were determined and recorded:

2.6. Orientation

Orientation was determined using a magnetic compass and double-checked with a map to avoid false readings due to magnetic interference. For the data analysis, the orientation was broken down into two fuzzy linear components using the fuzzy set theory as described by Roberts (1986). These two components are Northness (describing the low-high solar radiation gradient) and South-Westness (describing the wet-dry gradient in terms of precipitation in the Netherlands (Manola et al., 2020).

2.7. Inclination

Inclination was determined using an Inclinometer app for Android. The phone was placed on the surface on which the moss was growing, after which the inclination angle was recorded.

2.8. Light exposure

A light exposure analysis was performed on each site to determine the degree to which surrounding objects prevent direct light from reaching the surface. First, a Nikon D70s camera with a SIGMA 4.5 mm circular fisheye lens was used to take a hemispherical photo of the sky at the position of the moss community, with the top of the camera pointed North, to determine the degree of shaded sky at the surface. This photo was converted to a black-and-white bitmap in Adobe Photoshop, with the sky as white and any objects around the mosses as black. If necessary, any white or near-white objects were painted out manually. The photos were then analysed using the Gap Light Analyzer software (Simon Fraser University, 1999) to determine the degree of covered sky and subsequent average daily light exposure by both direct and indirect sunlight.

2.9. Air quality

As a measure of air quality, freely available maps of the average annual concentrations of PM10 and NO_2 at a spatial resolution of 25x25m were used. As such, the GPS coordinates of the moss communities were recorded and cross-referenced with these maps. The PM10 and NO_2 maps for 2019 were used for this purpose (Atlas Leefomgeving, 2019a, 2019b). Using an average yearly value was chosen over measuring the PM10 and NO2 at the time of collection, as average air pollution is more closely related to the intracellular chemical composition within mosses (Vanderpoorten and Goffinet, 2009).

2.10. Surface roughness

A profilometer was used for in-situ measurement of surface roughness. Using the profilometer, an impression was made of the surface on which the moss community was located, both vertically and horizontally. This impression was then photographed, made into a bitmap file, and converted to an Rp (roughness profile) rating using the MatLab script as provided by (Alameda-Hernández et al., 2014), with a higher Rp profile meaning a rougher profile. The exact procedure is described in detail in (Veeger et al., 2021b).

After the local environmental factors were recorded, the species in the moss community were identified using a field key, where possible. Otherwise, they were collected for microscopic analysis. Three specimens could not be reliably identified in this way and were not used in the data analysis. A total of 137 communities were sampled during the moss growth period (January to March 2021).

2.11. Data analysis

The relationship between environmental factors and urban epilithic moss community composition was analysed using a constrained Canonical Correspondence Analysis (CCA) conducted in Canoco5 (Šmilauer, 2012). The tested factors were included as environmental variables. The significance and effect of these factors were tested using a Monte Carlo permutation test with 500 permutations, and relevant factors were included using forward selection. *P* values were corrected using the false discovery rate algorithm in Canoco5, and adjusted P values were reported. These factors were checked for collinearity before analysis.

Species co-occurrence was analysed using the *cooccur* package (Griffith et al., 2016) in R version 4.2.3. Species pairs with an expected co-occurrence rate of less than one were removed from this analysis using the *thresh* function. Other options were left at their default values.

Differences between the distribution of pleurocarp and acrocarp growth forms along the tested environmental gradients were analysed using a Mann-Whitney *U* test performed in SPSS (version 29), with habitats grouped by those containing acrocarp or pleurocarp species. When habitats hosted both growth forms, they were included in both groups.

3. Results

3.1. Community composition

Across all 137 sampling locations, 26 different moss species were found (Table 2). The most commonly found species (Fig. 2b) were *Tortula muralis* (64 times) and *Grimmia pulvinata* (61 times). On the other hand, *Zygodon viridissimus*, *Bryoerythrophyllum recurvirostrum, Orthotrichum cupulatum, Didymodon vinealis, Synthrichia virescens, Didymodon luridus, Bryum caespiticium, Leptodictyum riparium, Didymodon sinuosus, Synthrichia montana, Bryum radiculosum, Rhynchostegium murale*, and *Leskea polycarpa* were very rare, having been found fewer than four times. Most species occurred primarily in multispecies colonies, especially the rarer species. The only species that were found as a monoculture somewhat frequently were the acrocarp species *Tortula muralis,*

Table 2
Overview of all moss species found during field survey.

Botanical name	Common name
Tortula muralis Hedw.	Wall Screw-moss
Grimmia pulvinata (Hedw.) Sm.	Grey-Cushioned Grimmia
Ptychostomum capillare (Hedw.)	Holyoak & N.Pedersen
(formerly *Bryum capillare* Hedw.)	Capillary Thread-Moss
Orthotrichum diaphanum Schrad. ex Brid.	White-tipped Bristle-moss
Bryum argenteum Hedw.	Silver-moss
Schistidium crassipilum H.H. Blom	Thickpoint Grimmia
Didymodon rigidulus Hedw.	Rigid Beard-moss
Rhynchostegium confertum (Dicks.) Schimp.	Clustered Feathermoss
Orthotrichum anomalum Hedw.	Anomalous Bristle-moss
Hypnum cupressiforme Hedw.	Cypress-leaved Plait-moss
Brachythecium rutabulum (Hedw.) Schimp	Rough-stalked Feather-moss
Amblystegium varium (Hedw.) Lindb.	Willow Feather-moss
Syntrichia ruralis (Hedw.) F.Weber & D.Mohr	Great Hairy Screw-moss
Zygodon viridissimus (Dicks.) Brid.	Green Yoke-moss
Bryoerythrophyllum recurvirostrum (Hedw.) P.C.Chen	Red Beard-moss
Orthotrichum cupulatum Brid.	Hooded Bristle-moss
Didymodon vinealis (Brid.) R.H.Zander	Soft-tufted Beard-moss
Synthrichia virescens (De Not.) Ochyra	Lesser Screw-moss
Didymodon luridus Hornsch. ex Spreng.	Dusky Beard-moss
Bryum caespiticium Hedw.	Tufted Thread-moss
Leptodictyum riparium (Hedw.) Warnst.	Kneiff's Feather-moss
Didymodon sinuosus (Mitt.) Delogne	Wavy Beard-moss
Synthrichia montana Nees.	Intermediate Screw-moss
Bryum radiculosum Brid.	Wall Thread-moss
Rhynchostegium murale (Hedw.) Schimp.	Wall Feather-moss
Leskea polycarpa Hedw.	Many-fruited Leskea

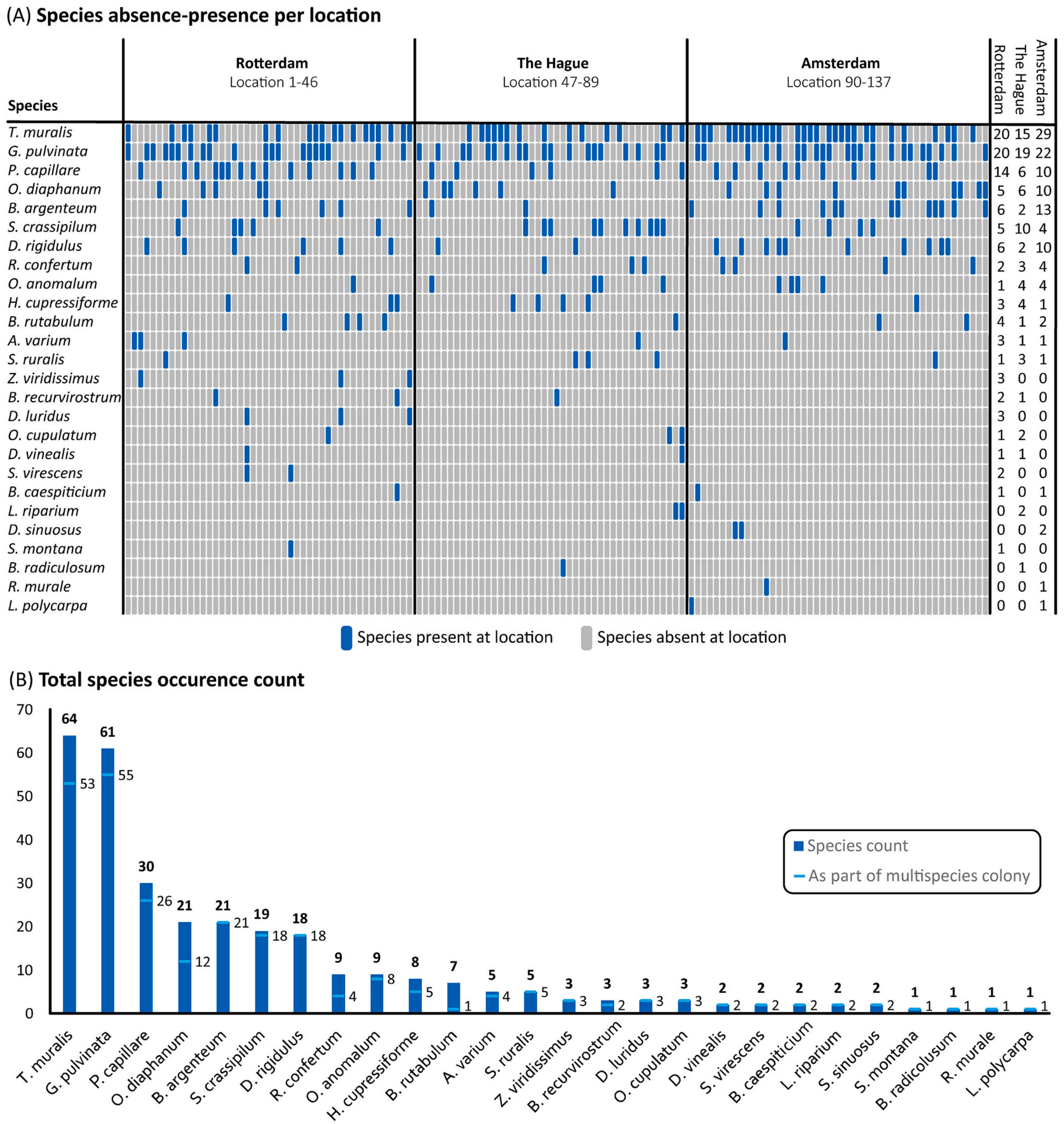


Fig. 2. (a) Absence-presence matrix of all the species found in the field survey per sampling location and (b) Occurrence count of all species found, both in total and as a part of a multispecies colony.

Grimmia pulvinata, *Ptychostomum capillare*, and *Orthotrichum diaphanum*, and the pleurocarp species *Rhynchostegium confertum*, *Hypnum cupressiforme* and *Brachythecium rutabulum* (Fig. 2a).

3.2. Species associations

In total, five negative species associations were found (Fig. 3), most between acrocarp and pleurocarp species: *Brachythecium rutabulum* – *Tortula muralis*, *Hypnum cupressiforme* – *Tortula muralis*, *Brachythecium rutabulum* – *Grimmia pulvinata*, and *Rhynchostegium confertum* – *Grimmia pulvinata*, but one negative association was also found between two acrocarp species: *Schistidium crassipilum* – *Orthotrichum diaphanum*. All three positive associations were between acrocarp species: *Orthotrichum anomalum* – *Schistidium crassipilum*, *Schistidium crassipilum* – *Grimmia pulvinata*, and *Grimmia pulvinata* – *Tortula muralis*. All other associations were found to be random, although, in the case of the rarer species, this may be caused by their low occurrence count.

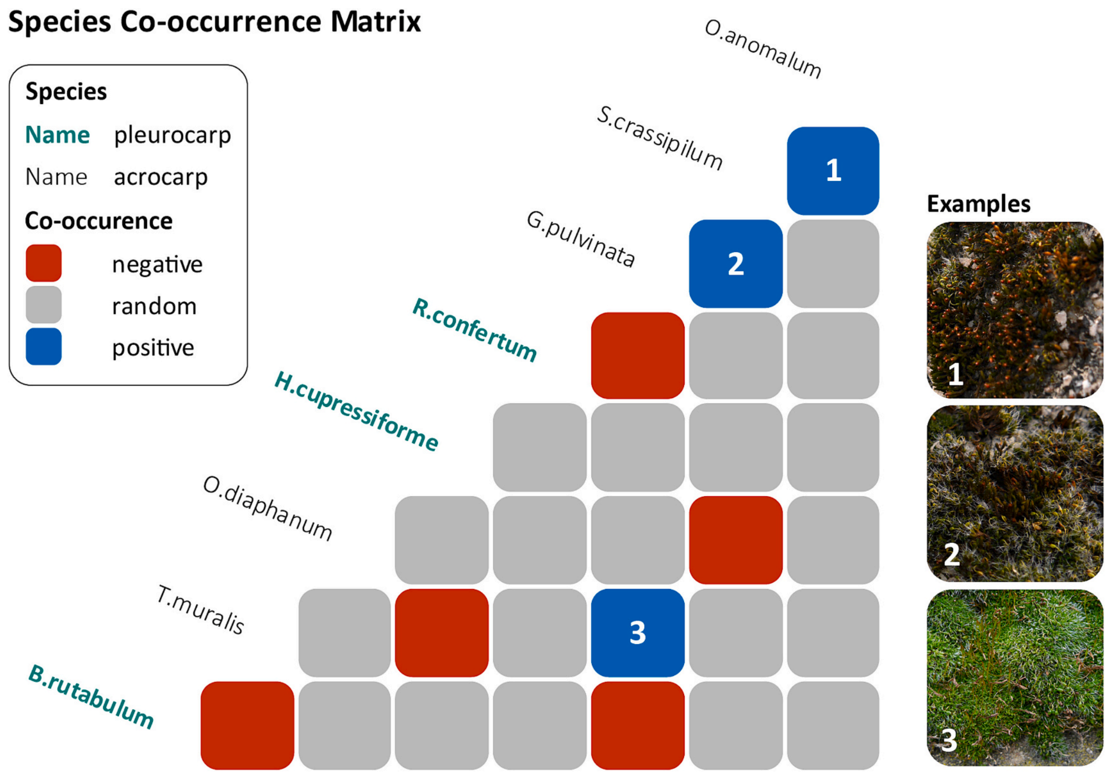


Fig. 3. Species co-occurrence matrix showing positive, negative or random changes in occurrence count between species pairings. Species with only random relations are excluded. On the right are examples of communities where those species with positive co-occurrence rates grew together.

3.3. Influence of environmental factors

Two of the tested environmental factors were found to constrain species distribution significantly. These two factors were the surface roughness (2.4 %, $p = 0.048$) and direct sunlight (1.9 %, $p = 0.032$). In the CCA plot (Fig. 4), it can be observed that the pleurocarp species primarily drive this ordination. *Leskea polycarpa* and *Leptodictyum riparium* prefer surfaces with a higher surface roughness than the other species found. It should be noted, however, that these species were found only once and twice, respectively. Direct sunlight, however, appears to inhibit most pleurocarp species, including more common ones such as *Brachythecium rutabulum* and *Rhynchostegium confertum.* Nevertheless, while these two environmental factors were found to have a statistically significant influence, the total variance explained by these factors amounts to only 4.33 % of the total variance.

3.4. Differences between acrocarp and pleurocarp distribution

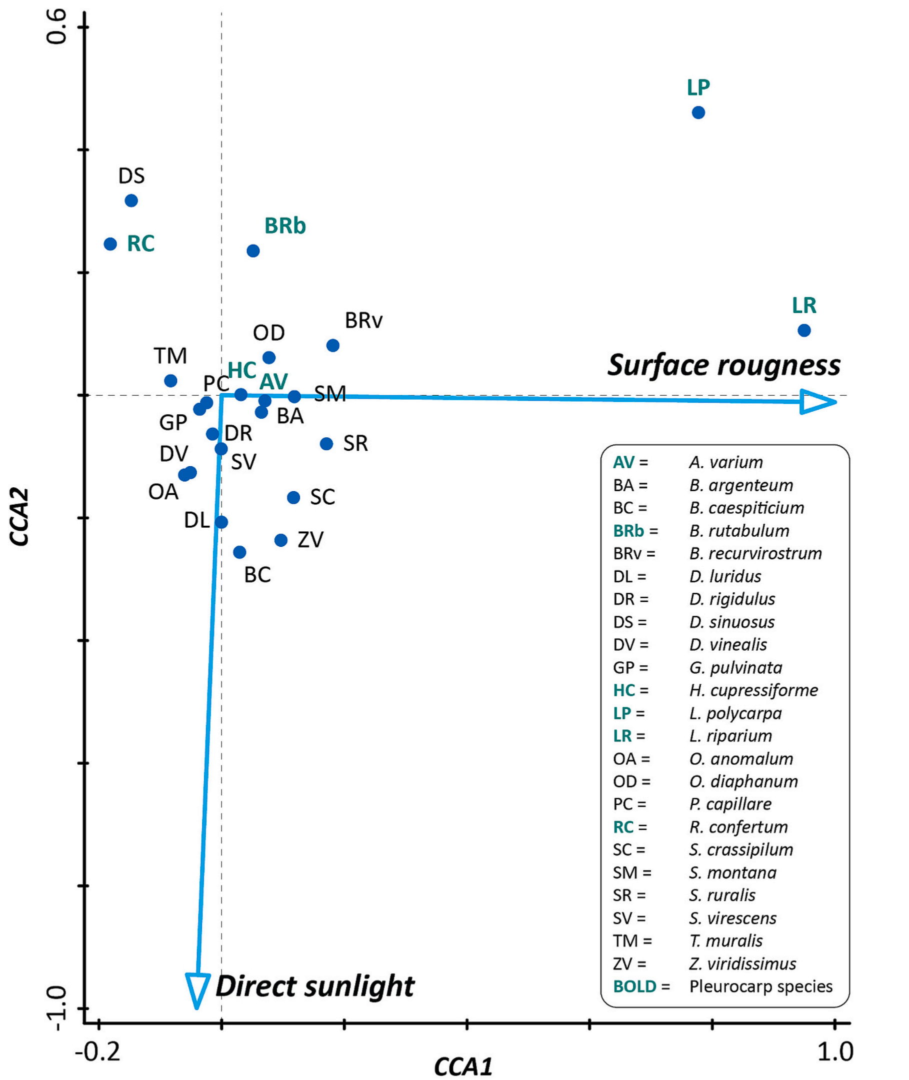
Pleurocarp and acrocarp mosses showed slight differences in their occurrence across environmental gradients.Particularly when considering orientation, pleurocarp species seem to be showing a stronger Northern preference (Fig. 5f), although this difference initially falls just short of statistical significance (U = 612.5, $p = 0.057$). However, as can be seen in Fig. 5f, there are two outliers in the pleurocarp group, and if one (U = 543.5, $p = 0.027$) or both (U = 481.5, $p = 0.013$) outliers are removed, the differences between acrocarp and pleurocarp species in terms of their preference for a northern orientation is found to be statistically significant. On the other hand, the distribution of acrocarps and pleurocarps along a south-west to north-east gradient (Fig. 5e) showed no significant difference (U = 944.5, $p = 0.382$). For both direct (Fig. 5d) and diffuse sunlight (Fig. 5c), the distribution of acrocarp species trends towards higher levels of light exposure. In contrast, pleurocarp species seem to prefer habitats with slightly lower light exposure levels, however the differences are not statistically significant for either direct (U = 2260.5, $p = 0.078$) or diffuse (U = 2207.5, $p = 0.129$) sunlight. Finally, when it comes to sensitivity to air quality, there is no difference between acrocarps and pleurocarps when considering NO_2 (U = 2046.5, $p = 0.782$; Fig. 5g). However, acrocarp species were found in locations with somewhat higher levels of PM_{10} exposure (Fig. 5h) than those of their pleurocarp counterparts, although the differences fell short of statistical significance (U = 2237.5, $p = 0.098$). Finally, for inclination (U = 1814.5, $p = 0.778$; Fig. 5b) and surface roughness (U = 1920.5, $p = 0.837$; Fig. 5a), acrocarp and pleurocarp species were found to have similar distributions along the respective gradients.

4. Discussion

4.1. Moss community composition

Based on the obtained results, most moss species (19 out of 26) growing on concrete in urban areas only occurred in multispecies colonies. This suggests that for most of these species, the often harsh initial (environmental) conditions in this kind of habitat are not suitable for their growth until these conditions are ameliorated by the presence of other, more tolerant pioneering species or that they do generally not reach the minimum patch size used in this field survey. The other pioneering species can withstand the initial conditions on the concrete surface and develop larger moss patches. As they do, they may increase the moisture levels on the concrete surface and provide the shading necessary for the less tolerant species to develop.

Based on our findings, only seven species of moss can be considered common pioneering species of concrete in an urban environment, as they commonly occur as a monospecies colony. These are the four acrocarp species *Tortula muralis, Grimmia pulvinata, Ptychostomum capillare*, and *Orthotrichum diaphanum*, as well as the pleurocarp species *Brachythecium rutabulum, Hypnum cupressiforme,* and *Rhynchostegium confertum.* Furthermore, at least one of these species is present in all but



CCA statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.2132	0.1656	0.9763	0.7719
Explained var. (cumulative)	2.44	4.33	15.51	24.34
Pseudo canonical correlation	0.6216	0.5539	0.0000	0.0000
Explained fitted var. (cumulative)	56.28%	100.00%		

Fig. 4. CCA (canonical correspondence analysis) plot of all found moss species showing their distribution with surface roughness and direct sunlight as constrained axes.

seven of the sampled locations, further suggesting these species are the main pioneers of epilithic urban moss communities. Of these seven species, *Tortula muralis* and *Grimmia pulvinata* were by far the most prevalent, similar to findings by Rishbeth (1948). It also appears that these pioneering species stay present or even dominant throughout the lifecycle of the moss colonies, which is similar to natural epilithic communities, which are dominated by cushion- and shot turf-forming species with a paucennial colonists life strategy (colonisers which usually live for a few years), with "moderate" perennial stayers dominating more mesic to subhumid, shaded sites (Kürschner and Frey, 2012). Furthermore, this also mirrors the findings of Floyed and Gibson (2012), who found that urban bryophyte communities are often characterised by colonists as their climax species due to the continuous disturbance of urban surfaces. Of the seven other locations not colonised by these common pioneering species, four were inhabited by a monoculture of either *Schistidium crassipilum, Orthotrichum anomalum, Amblystegium varium*, or *Bryoerythrophyllum recurvirostrum,* suggesting these might occasionally act as a pioneering species, with the final three consisting of two multispecies colonies of *Bryum argenteum* and *Leskea polycarpa* and one multispecies colony of *Didymodon rigidulus* and *Syntrichia ruralis*.

Regarding the associations between species, most were found to be random, which could suggest that the less common species do not have a specific preference for a pioneering species. However, this lack of positive or negative associations found for the less common species can likely also be attributed to their low occurrence count, leading to insufficient data to reliably determine associations. The positive relations.

found were all between pioneering acrocarp species, suggesting that co-occurrence may benefit this type of moss. On the other hand, pleurocarps had random associations with one another, whereas all the

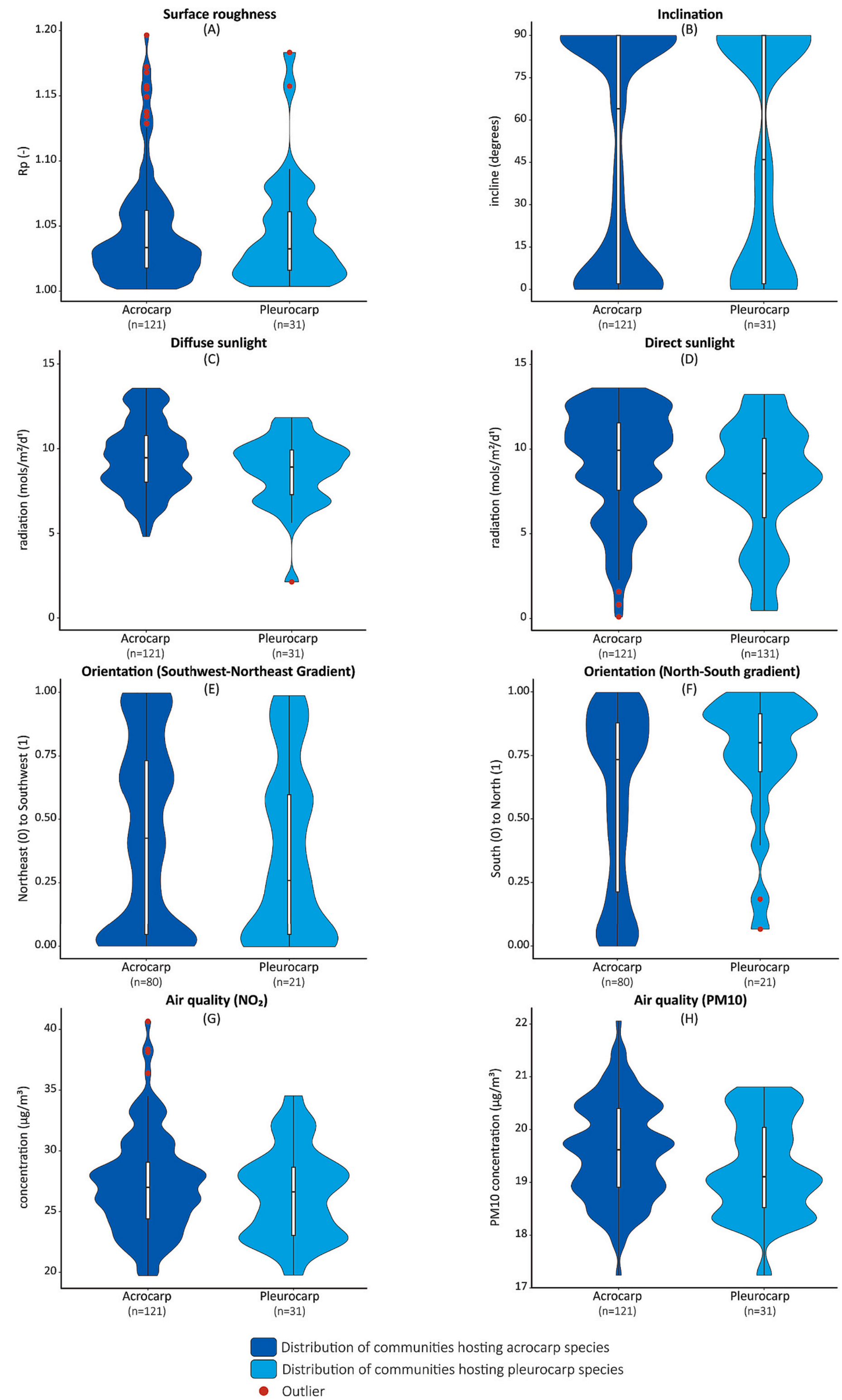


Fig. 5. Violin plots showing the mean, median and outliers (red dots) of the distributions of acrocarp (dark blue) and pleurocarp (light blue) moss species in relation to (a) roughness profile (Rp), (b) slope, (c,d) radiation, (e,f) orientation and (g,h) air quality. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

negative associations were found to be between acrocarp and pleurocarp species. This may be caused by one of two reasons. The first is due to the fast growth rate of pleurocarp mosses. Due to this fast growth rate, pleurocarp species can overgrow acrocarp species, thereby out-competing them (competitive exclusion) (Lloret, 1991; McAlister, 1995), although this effect may be species-dependent (Zamfir and Goldberg, 2000). The second explanation is that this negative association is caused not by direct competition between the two moss types but by habitat differences (niche differentiation). The data collected in this research does indeed suggest that pleurocarp species prefer less exposed sites than acrocarp species, which could then cause a lower-than-expected co-occurrence driven by differences in the local environment.

4.2. The effect of the local environment on species composition

Based on our findings, two local environmental factors play a statistically significant role in the distribution patterns of moss species: direct sunlight and the roughness of the substrate surface. However, the variance that is explained by these factors is limited (4.33 %). While distribution patterns of natural epilithic moss communities have been found to be influenced by the local environment by some researchers (Spitale and Nascimbene, 2012), in urban epilithic moss communities, other factors may influence their distribution, such as human disturbance, which was found by (Hernández-Hernández et al., 2019) to affect (epilithic) moss species diversity and induce a change in life strategies, leading to more cosmopolitan species becoming dominant in more disturbed sites. Another option has been suggested by (Silva et al., 2014), who postulated that stochastic events rather than environmental factors may determine the community composition of rock outcrops in Brazil.

When comparing pleurocarp and acrocarp species, our observed *p*-values for the differences between the two groups narrowly exceed the conventional threshold for statistical significance, potentially due to the overlap in sites inhabited by both pleurocarp and acrocarp species and the existence of two outliers. However, the trend that emerges is that acrocarp species occurred under higher irradiation levels (both direct and indirect) than pleurocarp species, with no strong preference for orientation. Pleurocarp species, on the other hand, appeared to have a preference for somewhat lower amounts of direct and indirect sunlight and are almost absent from more southern-oriented surfaces, even though southern- and eastern-facing surfaces receive higher amounts of rain in The Netherlands (Manola et al., 2020). They also may be somewhat less tolerant of high levels of air pollution. This discrepancy can be explained by their difference in structure. Most acrocarpous mosses have structures such as cushions, which minimise evaporative water loss. In contrast, most pleurocarps have structures, such as wefts, optimised to maximise photosynthetic light gain (Kürschner and Frey, 2012). The acrocarpous mosses are, therefore, better suited for very xeric habitats with higher light intensities, whereas the pleurocarpous species are most suited for more humid and shaded habitats. This is also in line with the findings of other researchers, who found that pleurocarpous species prefer sites with less light exposure and higher humidity (Gimingham and Birse, 1957; Grace, 1995; Tarja and Paul, 2009). This also holds when looking specifically at the pioneering species found, with the acrocarp species (*Tortula muralis, Grimmia pulvinata, Ptychostomum capillare*, and *Orthotrichum diaphanum*) being species which in general prefer moderately wet to very dry habitats with moderate to high light intensities, whereas the pleurocarp species (*Brachythecium rutabulum, Hypnum cupressiforme,* and *Rhynchostegium confertum*) generally prefer wet to moderately dry habitats with moderate light intensities or shade (Dierßen, 2017). Based on our findings, however, it does appear that - for the species found in our study- light intensity plays a larger role in their preferred habitat choice, at least in terms of orientation, than precipitation frequency and intensity.

4.3. Implications for bioreceptivity research and design

When choosing moss species for successful inoculation of bioreceptive structures, many considerations (e.g. aesthetic, economic, secondary functions) are involved, many of which are beyond the scope of this research. However, a few implications can be inferred based on the obtained results.

When choosing moss species for use on a bioreceptive concrete surface, the seven common pioneering species found in this research (*Tortula muralis, Grimmia pulvinata, Ptychostomum capillare, Orthotrichum diaphanum, Brachythecium rutabulum, Hypnum cupressiforme,* and *Rhynchostegium confertum*) are the most promising candidates, as these will be most suited to provide initial moss cover. After this initial moss cover has been established, the modified environmental conditions caused by this cover can then host other moss species through natural colonisation or human intervention.

The choice of which pioneering species to use will depend on the local environmental conditions of the site, specifically the aspect and/or shading of the bioreceptive surface. Based on this research, combined with previous literature on the topic, the pleurocarp pioneers (*Brachythecium rutabulum, Hypnum cupressiforme,* and *Rhynchostegium confertum*) will likely work best on structures facing north and/or those shaded by other objects. These species are fast-growing, which can lead to quick coverage of the bioreceptive structure. However, they are generally not well-suited to sites exposed to higher levels of sunlight and possibly air pollution. In this case, one of the acrocarp pioneers (*Tortula muralis, Grimmia pulvinata, Ptychostomum capillare,* and *Orthotrichum diaphanum*) would be a better choice. The combination of *Tortula muralis* and *Grimmia pulvinata* is particularly promising as these two species have shown a positive co-occurrence rate. Finally, a combination of acrocarp and pleurocarp species is unlikely to succeed due to either the pleurocarp species overgrowing the acrocarp species if the conditions are right for the pleurocarps species or the pleurocarp species dying off if they are not.

Finally, as this inventory was done in the Netherlands, one must consider how well this could translate to other countries and climates. Except for *Orthotrichum diaphanum*, all these species have a cosmopolitan distribution, which means they are found in a wide range of climate zones across most continents (Dierßen, 2017). Furthermore, all of these seven pioneering species that have been identified have also been found in other urban inventories of bryophyte communities, e.g. in Cologne (Germany) (Sabovljević and Sabovljević, 2009), Belgrade (Serbia) (Sabovljevic and Grdovic, 2009), and Trento (Italy) (Pokorny et al., 2006), whereas inventories of Bremen (Germany) (Isermann, 2007), and Ljubljana (Slovenia) (Skudnik et al., 2013) found all species but *Rhynchostegium confertum*. An inventory done in Enna (Italy) found all species but *Brachythecium rutabulum* (Guidice et al., 1997) and one done in Valencia (Spain) found all but *Grimmia pulvinata, Hypnum cupressiforme*, and *Rhynchostegium confertum* (Segarra Moragues et al., 2021). Finally, an inventory from Aydin (Turkey) (Kirmaci and Agcagil, 2009) located all acrocarp pioneers and *Hypnum cupressiforme*; however, *Rhynchostegium confertum* and *Brachythecium rutabulum* were absent in this city. This suggests that our results should translate well to other locations, although carefully selecting which pleurocarp pioneers to use may be necessary.

5. Conclusion

This research aimed to determine which moss species have the greatest potential for colonising pristine (bioreceptive) concrete surfaces and what effect the local environment has on the success of different moss species, in order to aid engineers of these structures in their moss species selection. Based on this research, the following conclusions can be drawn:

- Seven species commonly occur as colonisers on concrete surfaces in Dutch cities: *Tortula muralis, Grimmia pulvinata, Ptychostomum capillare, Orthotrichum diaphanum, Brachythecium rutabulum, Hypnum cupressiforme, and Rhynchostegium confertum.*
- Local environmental variables have only a minor effect on the composition of moss communities on urban concrete structures on a species level;
- When considering the distribution of acrocarp and pleurocarp species, acrocarp species show a tendency to prefer more exposed sites with higher light intensities, with pleurocarp species preferring less exposed sites with lower light intensities;

As such, if a bioreceptive structure is to be placed in a shaded location or one facing north, the use of the pleurocarp pioneers *Brachythecium rutabulum, Hypnum cupressiforme, and Rhynchostegium confertum* shows the most promise, mainly because of their fast growth rate. When a bioreceptive structure is to be placed in a more exposed location, however, the use of the acrocarp pioneers of *Ptychostomum capillare* or *Orthotrichum diaphanum* and especially *Tortula muralis* and *Grimmia pulvinata* appears to be the right choice. Nevertheless, other considerations may also influence species selection, such as the ability to cultivate these species, which would be necessary for larger-scale commercial applications or the potential benefits they may provide in ecosystem services, requiring further research.

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CRediT authorship contribution statement

M. Veeger: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **E.M. Veenendaal:** Writing – review & editing, Supervision, Methodology. **J. Limpens:** Writing – review & editing, Supervision, Methodology. **M. Ottelé:** Writing – review & editing. **H.M. Jonkers:** Writing – review & editing, Supervision.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

M. Veeger reports a relationship with ReSpyre B.V. that includes: consulting or advisory.

M. Ottele reports a relationship with ReSpyre B.V. that includes: equity or stocks.

H.M. Jonkers reports a relationship with ReSpyre B.V. that includes: equity or stocks.

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

Data availability

Data is available on Mendeley Data under the following DOI: 10.17632/5wv7b48bhs.1

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