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Bryophyte species and communities on various roofing materials, Estonia

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Abstract: Considering the recent growth of interest in using mosses in creating vegetated green roofs, we set the aim of our study to get an overview of the variety of moss and liverwort species and communities growing spontaneously on roofs. Data were collected from 67 roofs of five different types of materials: fibre cement, bitumen, stone, thatched and steel from Tallinn and rural areas on Hiiumaa Island and in South Estonia. Indicator species analysis, MRPP, cluster analysis and ordination methods (DCA, CCA) were used for data analysis. As a result of this research, generalist bryophytes occurring on all types of roofing materials were studied and bryophyte species characteristics for certain material types were identified. The thatched roofs differed most clearly from the other roof types in their species composition and had the highest species diversity. Stone and fibre cement roofs had similar species composition. The results revealed significant dependence of the composition of the bryophyte flora on roofs on the density of the bryophyte carpet formed over time on the roof and the presence of a tree canopy above the roof. Other important factors were roof relief, the height of the roof from the ground and the indicator of environmental pollution NOx. However, the studied roofs in Tallinn and rural areas did not show significant differences in the species composition of bryophytes. Five communities were delimited: (1) *Syntrichia ruralis – Schistidium apocarpum*; (2) *Orthotrichum speciosum – Bryum argenteum*; (3) *Brachythecium rutabulum – Hypnum cupressiforme*; (4) *Ceratodon purpureus – Rhytidiadelphus squarrosus*; and (5) *Pleurozium schreberi – Dicranum scoparium.* The mentioned communities inhabited locations that differed in environmental conditions. The findings of this research can help choose the roofing material and species suitable for a certain location in creating moss greenery on roofs.

Kokkuvõte: Samblaliigid ja -kooslused erinevatel katusematerjalidel
Katustel spontaanselt kasvavate samblaliikide ja -koosluste mitmekesisusest ja seda mõjutavatest teguritest ülevaate saamiseks koguti andmed 67-lt katuselt Tallinnas, Hiiumaal ja Lõuna-Eestis. Uuriti eterniit-, ruberoid-, kivi-, roo- ja plekk-katuseid. Uuringu tulemusena selgusid samblad-generalistid, keda leidus kõigil katusetüüpidel ning samblaliigid, mis olid iseloomulikud konkreetsele katusematerjalile. Kõige selgemalt eristusid liigilise koosseisu poolest rookatused, mis olid ühtlasi ka kõige liigirikkamad. Eterniit- ja kivikatustel kasvas suhteliselt sarnane samblafloora. Sammalde liigiline koosseis sõltus meie uuringu alusel eelkõige sellest, kui tihe samblavaip oli katusel aja jooksul kujunenud ning kas katuse kohal kõrgus puuvõra või oli tegemist täisvalguses oleva kasvukohaga. Olulisteks mõjuteguriteks osutusid ka katuse reljeefsus, kõrgus maapinnast ning keskkonnasaaste näitajana NOx keskmine kontsentratsioon õhus. Tallinna ja maapiirkondade katuste samblafloora liigilises koosseisus ei leitud märgatavaid erinevusi. Klasteranalüüsi käigus eristus viis samblakooslust: (1) *Syntrichia ruralis – Schistidium apocarpum*; (2) *Orthotrichum speciosum – Bryum argenteum*; (3) *Brachythecium rutabulum – Hypnum cupressiforme*; (4) *Ceratodon purpureus – Rhytidiadelphus squarrosus*; ja (5) *Pleurozium schreberi – Dicranum scoparium.* Nimetatud kooslused kasvasid erinevates keskkonnatingimustes. Uuringu tulemused on samblakatuste rajajatele toeks konkreetsele katusematerjalile ja asukohale sobivate liikide valimisel. Esimese valikuna võib soovitada meie uuringus erinevat tüüpi katustelt registreeritud ja maailmas laialt levinud liike – *B. rutabulum*, *C. purpureus*, *H. cupressiforme*, *Plagiomnium cuspidatum* ja *S. ruralis*. Avatud ja kuivades elupaikades on sobivaks valikuks liigid *B. argenteum*, *C. purpureus*, *Hedwigia ciliata*, *S. ruralis* ja *Racomitrium canescens*, varjulistes kasvukohtades *B. rutabulum* ja *P. cuspidatum*. Kõrgema õhusaastega alade jaoks sobivad liigid on *C. purpureus* ja *B. argenteum*, nagu on näidanud ka mitmed varasemad uuringud.

Keywords: mosses, liverworts, biodiversity, indicator species analysis, spontaneous green roofs, urban ecology, environment, pollution

INTRODUCTION

Bryophytes are pioneer species that are able to colonise habitats with no soil cover, and differently from vascular plants they assimilate nutrients from the air. Their small size and physiological peculiarities are characteristics enables to survive under extreme environmental conditions and, compared to vascular plants, to tolerate drought and high temperatures better (Sabovljevic & Grdovic, 2009; Perini et al., 2020). Therefore, bryophytes are more successful than vascular plants in colonising man-made surfaces constructed widely mostly in towns but also in rural settlements. Bryoflora forms an important part of urban vegetation; however, it has been less studied compared to vascular plants (Grant, 2006; Grdovic et al., 2009; Sabovljevic & Sabovljevic, 2009; Sukopp et al., 2011). Irrespective of systematic studies of bryophytes conducted during the last decades in Estonia (Ingerpuu et al., 1998, 2014, 2018; Ingerpuu & Vellak, 2000a,b; Vellak et al., 2015, 2017, 2019), also here the bryophyte flora in towns and rural settlements has mostly been neglected. Still, in Tallinn and the North-East Estonian industrial area, the moss *Pleurozium schreberi* has been studied as an accumulator of environmental toxins (Mäkinen & Liiv, 1996; Liiv et al., 1997). Yet a large part of bryophyte species is so sensitive to environmental pollution that they do not occur in polluted areas (Hill et al., 2007).

In recent times possibilities of urban greening have been studied worldwide, one relevant area under this objective is to contribute to green roofs. Green roofs have been found useful for reducing harmful consequences of stormwater and urban heat island effects, they are reducing energy costs, improving the air quality, and increasing the fire safety of roofs. Even more, the benefits of green roof show that it plays an important role in making cities safe, sustainable, and resilient to climate change (Banting et al., 2005; Shafique, 2018). In addition to using vascular plants on roofs, the creation of moss roofs has also been studied. It has been observed that mosses may be beneficial to the survival of vascular plants on roofs, whereas under different conditions, or in the case of different combinations of species, mosses may hinder their survival (Emilsson, 2008; Heim et al., 2014; van Mechelen et al., 2015). Moreover, they may inhibit the germination of vascular plant seeds (Drake, 2018). Other authors have suggested for roof greening the use of native sandy dry grassland species together with local pleurocarpous and acrocarpous mosses and lichens (Schröder & Kiehl, 2020). Cryptogams requiring little or no soil may be valuable and more affordable alternatives to conventional green-roof plantings (Grant, 2006). Compared with roofs colonised by vascular plants, moss roofs need less care, they can undergo multiple cycles of dehydration/rehydration without losing photosynthetic performance, and they can be thinner, which makes their installation easier (Anderson et al., 2010; Burszta-Adamiak et al., 2019; de Carvalho et al., 2020; Perini et al., 2020). Bryophytes are suitable as substitutes for vascular plants in green facade and roof systems, taking advantage of some of their characteristics, such as their ability to colonize different construction materials (Garabito et al., 2017). Of particular interest to the green roof industry may be the cryptogamic crusts that form in a variety of horizontal and vertical barrens. In shallow-substrate green roof systems, it is possible that cryptogamic mats can contribute directly to the desired functions of green roofs by cooling the roof surface and retaining water (Lundholm, 2006). In Scandinavian countries vegetated green roofs were historically built with the aim to preserve a favourable indoor climate in the house as a moss-covered roof helps to avoid heat losses and hinders the penetration of water into the house (Emilsson, 2005). On the other hand, however, it is often suggested that a spontaneously formed moss cover on the roof should be removed (Burszta-Adamiak et al., 2019). A bryophyte cover may spare the roofing material as many bryophytes produce antibacterial and mould repellent compounds and hinder the spread of saprotrophic microorganisms (Asakawa, 1998; Hedderson et al., 2003). A moss carpet on the roof may be valued also for aesthetic reasons.

Shafique et al. (2018) has compiled a review article on the history of green roof, green roof components and environmental, social and economic benefits associated with green roof technology. Of the 155 literature sources used in this article, only some relate to mosses on roofs. Recently, mosses of green roofs have been studied in the Mediterranean region (de Carvalho et al., 2019, 2020; Perini et al., 2020).

However, bryoflora differs in the Nordic countries. In Finland, soil-based roof flora, including some species of mosses, has been studied by Gabrych et al. (2016).

The above-presented information indicates the importance of research into species composition of bryoflora and bryophyte communities on roofs, whereas more research needs to be done in different climatic as well as geographical areas. Data about roofs as spontaneous habitats of bryophytes are scarce in the literature (Hedderson et al., 2003; Studlar & Peck, 2009), where is presenting us the most suitable mosses growing on green roofs of certain geographical region and roof type. This work aimed to study the variety of bryophyte species and communities growing spontaneously on roofs in Estonia, and to find out factors affecting it.

MATERIAL & METHODS

During the fieldwork in 2015–2016, we took samples from 67 roofs (Fig. 1). Of these, 41 were taken in five quarters of Tallinn city: Nõmme, Mustamäe, Haabersti, Kesklinn and Pirita. The

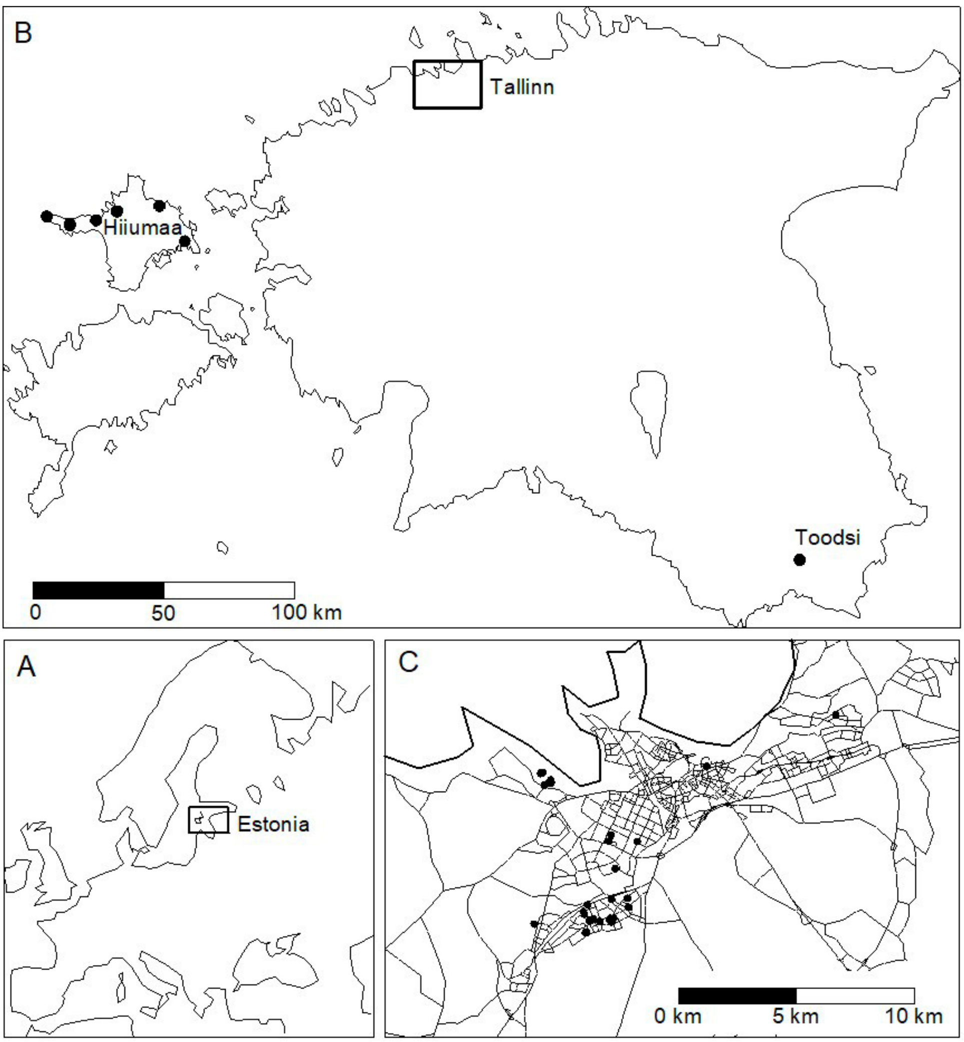

Fig. 1. (A) Location of Estonia in Europe. (B) Sampling sites (dots) on Hiiumaa Island and at Toodsi, South-East Estonia. (C) Sampling sites (dots) in the Tallinn city area. The clusters of sites close to each other are presented as a single dot.

remaining 26 studied roofs were in two rural areas: on Hiiumaa Island and in South-East Estonia (Toodsi).

The sample included roofs of various buildings in Tallinn and rural areas: dwelling houses, saunas, cattle sheds, auxiliary buildings, but also a schoolhouse, a station building and a cellar. In most cases, samples were taken from roofs of lower buildings. Bryophytes on the following types of roofing materials were sampled: fibre cement (21), bitumen (24), stone (baked clay, 7), zinc-coated steel (6) and thatched (reed, 9). One wood shingle roof from Toodsi was added as a sixth type.

One side of roofs in Tallinn was divided into imaginary segments: 1 – in the upper left or right corner, 2 – in the middle of the left or right side of the roof, 3 – in the lower left or right corner, 4 – in the middle of the upper edge of the roof, 5 – in the middle of the roof and 6 – in the middle of the lower edge of the roof. From each segment one 20 × 20 cm plot was described, a total until six plots from one side of the roof. However, not every segment had bryophytes. Part of the roofs different sides were studied. For the 26 roofs from Hiiumaa and Toodsi, one 20 × 20 cm plot was described from each roof from the area with the highest bryophyte coverage. In the comparative analyses of Tallinn and rural areas, one plot with the highest bryophyte coverage per roof was also used from Tallinn. The total number of the analysed plots was 291.

Per each 20 × 20 cm plot, the following data were recorded: bryophyte coverage, tree litter coverage, presence/absence of conifer litter, presence/absence of deciduous tree litter, crown coverage above the plot, height of the plot from the ground. Additionally, the following data were recorded per whole roof side: bryophyte coverage, tree litter coverage, roof pitch (slope), roof orientation (facing north, south, east or west), height difference on the roofing material, and the habitat air pollution index, calculated based on NOx and PM10.

The long-term average concentrations of the air pollutants fine particulate matter (PM10) and nitrogen oxides (NOx) in Tallinn were modelled with AEROPOL 5.3 model (Kaasik et al., 2017). The meteorological data set was based on observations (2015–2018) from the Tallinn-Harku Meteorological Station of the Estonian Weather Service. The street emissions were based on the traffic flow modelling made by AS Stratum for urban planning purposes, the reference year 2017. The domestic heating emissions were included (based on expected energy consumption in locally heated urban areas), but these were found to be of minor importance, according to modelling results. Although wood and coal heating emissions are often a reason for high concentrations of particulate matter in certain urban areas, this appears not the case of this study, as most of the samples were taken near major traffic streets in areas of district heating and some of them, in contrary, originate from relatively clean sites.

In the urban domain of Tallinn, the concentrations of PM10 and NOx in the air were modelled with 50 m grid resolution. The concentration in a certain sampling point was calculated as distance-weighted of four nearest grid points. In the central part of the city (3 km by 3 km) the concentrations were modelled in a grid with 10 m resolution and the concentration in the nearest grid point was taken as the proxy for the sampling point. Before the application to certain sampling points, the concentrations in the entire grid were validated against three monitoring stations in the urban domain (one of these in the central part), and regression against measured values was applied to correct systematic discrepancies.

The concentrations of NOx and PM10 outside of Tallinn were estimated as the annual average rural background concentration measured in the nearest air pollution monitoring station (these concentrations vary within a narrow range on the territory of Estonia: 1.8–2.1 $\mu g/m^3$ of NOx and 3.9–4.5 $\mu g/m^3$ of PM10) plus the dispersion of emissions from major roads nearby. In the Hiiumaa domain the dispersion from roads was modelled (grid resolution 50 m) with emissions based on traffic data by the Estonian Transport Administration (2021), which counted 300–1500 vehicles per day on the island's major roads near the sampling points. In the vicinity of two sampling sites of Toodsi, South-East Estonia, the daily traffic flow was less than 100 vehicles, which was considered too small to contribute beyond the regional background concentration.

Nomenclature of bryophytes is according to Vellak et al. (2015).

Data processing

Species difference between the roofs of different materials was estimated using the Multi-Response Permutation Procedure (MRPP; McCune & Mefford, 2011). First, all roofing material types were compared (except wood shingle), and then pairs of roofing material types were compared – all with all, except wood shingle. To identify species characteristic for each roofing material, the method by Dufrene and Legrendre (1997), according to which the relative abundance of a species is multiplied by its relative presence, was applied. The statistical significance of the obtained indicator values was evaluated by the Monte Carlo permutation test (N = 499). For MRPP and indicator species analysis, data obtained from all plots were used. Bryophyte communities were identified using the data collected in Tallinn by applying cluster analysis, for which Ward's linkage method and relative Euclidean distance measure were used (McCune & Mefford, 2011). The average per cent coverage of bryophyte species determined in six plots from one roof side per roof was used as the data matrix. The species indicator values for each community were calculated by the Dufrene and Legrendre (1997) method. Ecological indicator values for each community habitat lightness, moisture, acidity, nitrogen, and heavy metal content were calculated by means of calibration (Jongman et al., 1995), using the weighted averaging algorithm and indicator values of bryophyte species (Hill et al., 2007).

For indicator species analysis, cluster analysis and MRPP the program PC-Ord 5.0 was used. For ordination of the sample plots and species variables, the Detrended Correspondence Analysis (DCA) was applied. As the data matrix, data of the plot with the highest coverage of bryophytes from the roofs both of Tallinn and rural areas was used. For ordination of plant communities and environmental factors, Canonical Correspondence Analysis (CCA) was used. To detect environmental parameters that best describe the species variation on roofs, the forward selection procedure was applied. In the CCA the following environmental parameters were used: bryophyte coverage per plot and on the entire roof side, tree litter coverage per plot and on the entire roof side, presence/absence of conifer litter, presence/absence of deciduous tree litter, crown coverage above the plot, height of the plot from the ground, roofing material, roof pitch (slope), roof orientation (facing north, south, east or west), height difference on the roofing material, roof segment (as a nominal variable) and the habitat air pollution index, calculated based on NOx and PM10. The statistical significance of the relationship between the response variables (species data) and explanatory variables (environmental data) was evaluated by using Monte Carlo permutation tests; a total of 499 permutations were made. One of the CCA analyses was conducted with averaged data of six roof segments from Tallinn and for another data of the plots with the highest bryophyte coverage in Tallinn and the rural area were used. In conducting the DCA and CCA log-transformation and down-weighting of rare species were applied. The program CANOCO 5 was used (ter Braak & Šmilauer, 2012).

Differences in NOx and PM10 values between Tallinn and rural areas and differences in environmental characteristics between clusters were evaluated by Welch's ANOVA because of the heteroscedasticity of this data. Welch's ANOVA was also used to compare species richness on different roofing materials at 20 × 20 cm sample plot level because of heteroscedasticity. The difference between the clusters was found by pairwise comparisons using Games-Howell test. Differences in species numbers between clusters and between roofing materials (on one roof side in Tallinn) were evaluated by one-way ANOVA (McDonald, 2014).

RESULTS

The total number of bryophyte species growing on the studied roofs was 40 of which 37 occurred on roofs in Tallinn (Table 1). The total number of species found on five different types of roofing materials was from 15 to 20 (Table 2). Bryophyte species richness at 20 × 20 cm sample plot level was quite similar in the case of different roofing material (Welch's ANOVA, $F(4,113) = 1.8$, $p = 0.142$). A maximum number of species per sample plot (8) was found from thatched roofs. The number of unique species was also highest on thatched roofs – 8 species were found only on this roofing material.

Table 1. List of moss species found in Tallinn (Tn), Hiiumaa (Hi) and Toodsi (To), growing on different roofing materials: Fc – fibre cement, Bi – bitumen, So – stone, Th – thatched, Se – steel, Sh – wood shingle. Species characteristics for different roofing material types (based on the analysis of indicator species, $p < 0.05$) are indicated in bold and marked with the letter 'i' for the corresponding roofing material. Heavy-metal tolerance (HM): 0 – species that are absent from substrates with moderate or high concentrations of heavy metals; 1 – species that are recorded on substrates with moderate or high concentrations of heavy metals but only rarely; 2 – species that are occasional or frequent on substrates with moderate or high concentrations of heavy metals; 3 – species that are frequent and often abundant on substrates with moderate or high concentrations of heavy metals but are also frequent in other habitats (Hill et al., 2007). Abb – abbreviation of the species names.

No	Abb.	Species	Tn	Hi	To	Fc	Bi	So	Th	Se	Sh	HM
1	***Abi abi***	***Abietinella abietina***	x	x		x	x	x		i		0
2	*Amb ser*	*Amblystegium serpens*	x	x	x	x	x	x	x	x	x	0
3	*Bar bar*	*Barbilophozia barbata*	x						x			2
4	*Bra vel*	*Brachytheciastrum velutinum*	x					x				1
5	***Bra rut***	***Brachythecium rutabulum***	x	x	x	x	x	x	x	i	x	0
6	*Bra sal*	*Brachythecium salebrosum*		x			x					0
7	***Bry arg***	***Bryum argenteum***	x				i	x				1
8	***Cal cus***	***Calliergonella cuspidata***	x					i				1
9	*Cam som*	*Campylidium sommerfeltii*	x							x		
10	*Cer pur*	*Ceratodon purpureus*	x	x	x	x	x	x	x	x	x	3
11	*Cli den*	*Climacium dendroides*	x			x						2
12	***Dic pol***	***Dicranum polysetum***	x						i			0
13	***Dic sco***	***Dicranum scoparium***	x	x			x		i			2
14	*Hed cil*	*Hedwigia ciliata*	x	x		x		x				0
15	*Hom ser*	*Homalothecium sericeum*	x						x			0
16	*Hyl spl*	*Hylocomium splendens*	x	x			x		x			2
17	***Hyp cup***	***Hypnum cupressiforme***	x	x	x	x	x	x	x	i		1
18	*Lop het*	*Lophocolea heterophylla*	x						x			0
19	***Ort ano***	***Orthotrichum anomalum***	x	x		x		i				0
20	Ort pum	Orthotrichum pumilum		x		x						0
21	***Ort spe***	***Orthotrichum speciosum***	x	x	x	i	x	x		x	x	0
22	*Oxy hia*	*Oxyrrhynchium hians*	x					x				0
23	*Pla aff*	*Plagiomnium affine*		x			x					1
24	*Pla cus*	*Plagiomnium cuspidatum*	x	x	x	x	x	x		x	x	1
25	*Pla und*	*Plagiomnium undulatum*	x	x			x	x		x		1
26	*Pla rep*	*Platygyrium repens*	x						x			0
27	***Ple sch***	***Pleurozium schreberi***	x				x	x	i			1
28	*Poh nut*	*Pohlia nutans*	x					x				3
29	*Pol jun*	*Polytrichum juniperinum*	x							x		2
30	***Pti pul***	***Ptilidium pulcherrimum***	x						i			0
31	***Pti cri***	***Ptilium crista-castrensis***	x						i			0
32	*Pty mor*	*Ptychostomum moravicum*	x	x			x			x		0
33	*Rac can*	*Racomitrium canescens*	x	x		x	x	x				0
34	***Rhy squ***	***Rhytidiadelphus squarrosus***	x			x	x		x	i		2
35	*Rhy tri*	*Rhytidiadelphus triquetrus*	x						x	x		1
36	*San unc*	*Sanionia uncinata*	x					x	x			1
37	***Sch apo***	***Schistidium apocarpum***	x	x		x	x	i				0

No	Abb.	Species	Tn	Hi	To	Fc	Bi	So	Th	Se	Sh	HM
38	*Sci cur*	*Sciuro-hypnum curtum*	x							x		
39	***Syn rur***	***Syntrichia ruralis***	x	x	x	i	x	x		x	x	0
40	***Syz aut***	***Syzygiella autumnalis***	x						i			0

Table 2. Bryophyte species richness by roof types at 20 × 20 cm sample plot level. The number of species per plot – mean with standard deviation, minimum and maximum. Unique species – species found only on particular roofing material. Roofing materials: Fc – fibre cement, Bi – bitumen, So – stone, Th – thatched, Se – steel, Sh – wood shingle.

	Fc	Bi	So	Th	Se	Sh
Number of plots	75	69	58	61	27	1
Mean	3.2	2.7	3.2	3.2	2.9	6
Standard Deviation	1.0	1.4	1.1	1.7	1.3	-
Minimum	1	1	1	1	1	6
Maximum	7	7	6	8	6	6
Unique species	2	2	4	8	3	0
All species	15	19	20	18	15	6

In the case of the other four types of roofing materials on each two, three or four species were not registered elsewhere. The number of bryophyte species determined on one roof side (from six plots) in Tallinn was between 2 and 11, being on average the highest on thatched roofs (M = 6.1, SD = 2.7) and the lowest on steel roofs (M = 4.5, SD = 1.0), but did not differ statistically between five roof types (ANOVA, $F(4,41) = 0.705$, $p = 0.593$) or in pairs. Four species, *Amblystegium serpens*, *Brachythecium rutabulum*, *Ceratodon purpureus* and *Hypnum cupressiforme*, occurred on all five types of roofing materials; the first three were present also on the shingle roof. Three species, *Orthotrichum speciosum*, *Plagiomnium cuspidatum*, and *Syntrichia ruralis* were detected on all types of roofing materials except for thatched roofs. Results of the MRPP test of the species composition revealed a statistically significant difference ($p < 0.05$) between the roofing material types. The within-type variation was the highest in the case of bitumen roofing and the lowest in the case of fibre cement roofs of Tallinn. Pairwise comparison of roofing types showed differences between all of them in species composition, except for stone and fibre cement roofs between which no difference was observed (Table 3).

Table 3. Pairwise comparison of species composition growing on different roofing material using the Multi-Response Permutation Procedure (MRPP). Abbreviations: Fc – fibre cement, Bi – bitumen, So – stone, Th – thatched, Se – steel.

	Fc	Bi	So	Th
Bi	< 0.0001	x		
So	0.0702	0.0001	x	
Th	< 0.0001	< 0.0001	< 0.0001	x
Se	< 0.0001	< 0.0001	< 0.0001	< 0.0001

Based on the analysis of indicator species for roofing materials, species characteristic for different roof types ($p < 0.05$) were differentiated. These were *S. ruralis* and *O. speciosum* for fibre cement roofs; *Bryum argenteum* for bitumen roofs; *Orthotrichum anomalum*, *Schistidium apocarpum* and *Calliergonella cuspidata* for stone roofs; *Dicranum scoparium*, *Syzygiella autumnalis*, *P. schreberi*, *Dicranum polysetum*, *Ptilium crista-castrensis* and *Ptilidium pulcherrimum* for thatched roofs; and *B. rutabulum*, *Abietinella abietina*, *Rhytidiadelphus squarrosus* and *H. cupressiforme* for steel roofs (Table 1).

Cluster analysis differentiated five clusters and the following bryophyte communities were labelled based on the indicator and dominant species: (1) *S. ruralis – S. apocarpum*; (2) *O. speciosum – B. argenteum*; (3) *B. rutabulum – H. cupressiforme*; (4) *C. purpureus – R. squarrosus*; and (5) *P. schreberi – D. scoparium*. The *S. ruralis – S. apocarpum* community occurred mainly on fibre cement, but also on some stone and bitumen roofs. This community was distributed on more embossed roofs and more polluted areas (Table 4). According to habitat indicator values, this community grew in full lit and dry places, on basic substrata (Table 4). The *O. speciosum – B. argenteum* community inhabited mainly bitumen roofs but occurred also on two stone roofs and one fibre cement roof. This community occurred on higher roofs (average height 7 m) with a slight slope and low moss coverage, and according to ecological indicator values on a quite dry habitat. The *B. rutabulum* – *H. cupressiforme* community was registered on steel, bitumen, stone and thatched roofs. This community stood out for the high coverage of moss and tree canopy, as well for the high litter amount, especially from conifers.

Table 4. Environmental characteristics of bryophyte communities (clusters) on roofs in Tallinn. Number – number of roofs in a cluster. Average parameters per cluster: NOx – modelled NOx value (µg/m^3); PM10 – modelled PM10 value (µg/m^3), Height – the height of the plot from the ground (m); Relief – height difference on the roofing material (cm); Incline – roof slope (angle angular, degree); CovBr – bryophyte coverage in the sampled plot and on the whole roof side, latter in brackets (%); CovTree – tree canopy coverage above the plot (%); Litter – tree litter coverage in the plot and on the whole roof side, latter in brackets (%); ConLit – the occurrence of conifer litter and its proportion on roofs in a cluster in brackets (%); DecLit – the occurrence of deciduous tree litter and their proportion on roofs in a cluster in brackets (%). Habitats' ecological indicator values (Ellenberg values) for light: 5 – semi-shade plant, rarely in full light, but generally with more than 10% relative illumination when trees are in leaf, 7 – plant generally in well-lit places, but also occurring in partial shade; Ellenberg values for moisture: 3 – dry-site indicator, more often found on dry substrata than on moist places, 4 – on substrata with some shelter, 5 – on moderately moist substrata in moderately humid places; Ellenberg values for reaction: 3 – on acid substrata, 5 – on moderately acid substrata, 6 – on basic substrata, 7 – on strongly basic substrata; Ellenberg values for nitrogen: 2 – an indicator of infertile sites, 3 – indicator of moderately infertile sites, 5 – an indicator of moderately fertile sites (Hill et al., 2007). Indicator values for heavy-metal tolerance see in Table 1. A statistically significant difference (Welch's ANOVA, $p < 0.05$) in mean environmental characteristics between all five groups is marked with an asterisk. Different letters in the same row indicate significant statistical differences ($p < 0.05$, Games-Howell test)

Characteristic	Clusters					Average
	1	2	3	4	5	
Number	15	8	7	4	6	8
NOx*	14.1^{a}	13.8^{a}	12.4^{ab}	12.8^{ab}	9.0^{b}	12.8
PM10*	10.8^{a}	10.7^{ab}	10.5^{ab}	10.8^{ab}	9.9^{b}	10.6
Height*	2.5^{abc}	7.0^{a}	2.1^{ac}	2.1^{abc}	2.6^{ab}	3.3
Relief	2.9^{a}	1.4^{a}	1.1^{a}	0	0	1.6
Incline*	27^{bc}	4^{bd}	26^{abcd}	35^{ab}	46^{a}	26
CovBr*	60^{a} (64^{a})	31^{b} (16^{b})	60^{ab} (60^{ab})	41^{ab} (41^{ab})	38^{ab} (33^{b})	50 (47)
CovTree*	16^{ab}	11^{ab}	46^{a}	8^{ab}	4^{b}	18
Litter	14^{a} (19^{a})	14^{a} (11^{a})	34^{a} (34^{a})	12^{a} (13^{a})	12^{a} (13^{a})	17 (18)
ConLit	10 (67)	4 (50)	6 (86)	2 (50)	3 (50)	5 (60)
DecLit	7 (50)	3 (22)	2 (16)	0 (0)	5 (56)	3 (39)
Habitats' ecological indicator values						
Light*	7.4^{a}	6.8^{ab}	6.3^{bc}	6.4^{abc}	5.8^{c}	6.7
Moisture*	3.5^{b}	3.8^{b}	5.1^{a}	4.8^{ab}	5.1^{a}	4.2
Reaction*	6.4^{a}	6.0^{ab}	5.4^{b}	5.4^{ab}	2.9^{c}	5.5
Nitrogen*	4.0^{abc}	4.3^{a}	4.6^{a}	4.2^{ab}	2.5^{b}	4.0
Heavy metal*	0.3^{ad}	0.4^{acd}	0.7^{abc}	1.6^{a}	1.0^{ab}	0.6

According to habitat indicator values this community grew on moderately moist and moderately fertile sites. The *C. purpureus* – *R. squarrosus* community occurred on fibre cement, bitumen, stone, and thatched roof, of all types from only one roof. This community was located in open areas and the surface of the roofs was smooth. The *P. schreberi* – *P. scoparium* community occurred on six thatched roofs, which were located in places with lower-than-average NOx values and had the sharpest roof angle. According to habitat indicator values, this community grew on infertile moderately moist acid substrata. The acidity value is significantly lower (Games-Howell test, $p < 0.05$) in this habitat than in all others. The species *S. autumnalis*, *P. pulcherrimum* and *D. polysetum* were beside the title species characteristic for this community ($p < 0.05$). Welch ANOVA revealed that there was a statistically significant difference in the case of most of the environmental characteristics between all five communities ($p < 0.05$) besides the characteristics as roof relief and tree litter coverage (Table 4). Communities did not differ in species richness (ANOVA, $F(4,35) = 0.257$, $p = 0.903$) – an average of 4.8 – 5.9 species occurred on one roof side per 6 plots.

Results of the DCA of bryophytes growing on roofs in Tallinn and two rural areas are depicted in Fig. 2a. The first axis explained 16.4 % of the total variance and the second axis – 8.8 %. In the figure plots from Tallinn and rural areas are mixed. All plots in the right third of the figure

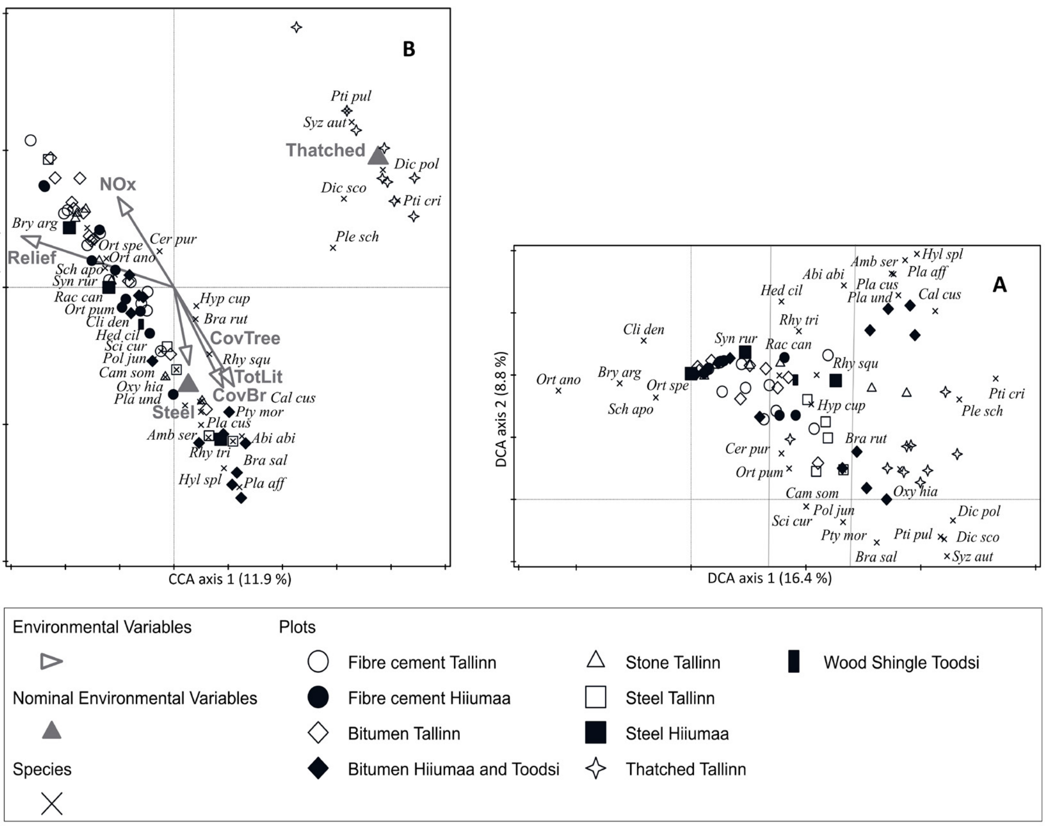

Fig. 2. Ordination of plots with the highest bryophyte coverage according to data from Tallinn city and rural areas. (A): DCA, (B): CCA of species data and their association with environmental parameters that best describe the species variation on roofs. Abbreviations: CovBr – bryophyte coverage in the plot; CovTree – tree canopy coverage above the plot, TotLit – coverage of tree litter on the roof side; Relief – roof relief; NOx – modelled NOx indicator. Species full names are given in Table 1.

were described either from the Tallinn Open-Air Museum (eight thatched and two stone roofs) or from a wooded area on Hiiumaa (seven bitumen roofs). In addition to the Hiiumaa and Open-Air Museum samples, the right side of the figure contains samples collected from different roofs at Nõmme, which is a quarter of Tallinn located in a forest stand, and from the shingle roof at Toodsi. The results clearly differentiate habitats with organic and inorganic substrate: when a thick tree litter layer had accumulated on a bitumen roofing, at ordination the habitat fell in the same area as thatched roofs (Fig. 2a).

Forward selection procedure of CCA performed based on the same set of species data (Fig. 2b) selected thatched roofs, all located in the Open-Air Museum (explained 10.3% of the total variance), bryophyte coverage in a plot (4.7%), tree litter coverage (4.2%), roof relief (4.1%) and modelled NOx (3.7%) as statistically significant ($p < 0.05$) environmental parameters determining bryophyte species variance in a plot. These variables describe all together 27% of the variance. Figure 2b shows that the mutually correlated parameters tree litter coverage, bryophyte coverage and tree canopy coverage contrast with the indicator of environmental pollution (NOx) and roof relief. Roofs with a more grooved relief are associated with the species *O. speciosum*, *O. anomalum* and *S. apocarpum* while *C. purpureus* and *B. argenteum* are associated with roofs located in areas with higher NOx pollution (Fig. 2b). As PM10 was strongly correlated with the NOx level (inflation factor greater than 20), this parameter was left out of the final analysis. For both NOx and PM10 average modelled indicators were much higher in the studied areas in Tallinn than in rural areas: NOx in Tallinn was 7.9 – 19.5 $\mu g/m^3$ and in rural areas 1.8 – 4.6 $\mu g/m^3$ (Welch's ANOVA $F(1,42) = 436$, $p < 0.001$); PM10 in Tallinn was 9.9 – 12.7 $\mu g/m^3$ and in rural areas 4.0 – 4.5 $\mu g/m^3$ ($F(1,44) = 3461$, $p < 0.001$).

The results of CCA carried out with data from Tallinn were similar to the results of CCA with data from both Tallinn and rural areas. In both cases, thatched roofs stood most clearly out in the description of species variance (19.3% in the case of Tallinn), but roof relief and bryophyte coverage were also important, explaining in Tallinn respectively 3.2 % and 3.1% of the species variance. In this analysis, the height of the plot from the ground came second after thatched roofs explaining 7.6% of the species variance. It was associated with the occurrence of *B. argenteum.* Somewhat higher *O. anomalum* and *O. speciosum* were registered. In Tallinn, the species variance was significantly described also by the density of the canopy above the plot (5%). The modelled indicators of environmental pollution NOx and fine particles (PM10) were statistically not significant in Tallinn.

DISCUSSION

According to Vellak et al. (2015), all species found in our study occur frequently in Estonia. Most of the identified species grow naturally on stones both in nature and on man-made structures (e.g., *B. argenteum*, *O. anomalum*, *S. apocarpum*); in addition, species growing on the ground (e.g., *Hylocomium splendens*), tree trunks (e.g., *O. speciosum*) and decaying wood (e.g., *S. autumnalis*) were represented (Ingerpuu et al., 1998). The bryoflora of the studied different roofing materials included also ecological generalists: *A. serpens*, *B. rutabulum*, *C. purpureus*, *H. cupressiforme*, *S. ruralis, P. cuspidatum* and *O. anomalum*, which occurred on most types of roofing materials. Although *S. ruralis* tolerates a wide range of soils and moisture conditions, it needs much light. The nitrogen requirement of most of the registered species is low except for *B. argenteum* and *B. rutabulum* (Hill et al., 2007).

Several identified species have also been found previously among spontaneous roof vegetation in different parts of the world, e.g., *C. purpureus*, *H. cupressiforme*, and *B. rutabulum* on south-facing sandy and dry roofs and *R. sqaurrosus*, *B. rutabulum*, and *C. cuspidata* on north-facing wetter roofs in London (Grant, 2006). Species *Hedwigia ciliata*, *P. cuspidatum*, *Platygyrium repens*, *P. pulcherrimum*, and *S. apocarpum* have been found spontaneously growing on four partly shaded roofs (two asphalt shingles, one bare cement, and one tar paper roof) near Terra Alta, West Virginia (Studlar & Peck, 2009). Among the list of species that prefer sunny and dry habitats suitable for Mediterranean green roofs (de Carvalho et al., 2019) were some species identified in our study: *A. abietina*, *B. argenteum*, *C. purpureus*, *H. ciliata*, and *S. ruralis*.

Among the 12 species registered by Gilbert (1970) from asbestos roofs in 11 sites of urban areas in northeast England, eight species were found in our study. Of these species, *S. ruralis* was in our study characteristic for fibre cement roofs (in terms of characteristics similar to asbestos roofing) and *O. anomalum* and *S. apocarpum*, for stone roofs, where *O. anomalum* was found only from stone and fibre cement roofs. MRPP analysis showed in our study that fibre cement and rock roofs did not differ in the species composition of mosses. According to Gilbert (1970), several indicator species grown on our stone roofs grew on the asbestos, which confirms that the two roofing materials are similar growth substrates for mosses.

According to cluster analysis, some bryophyte communities linked to concrete roofing materials and others did not. This suggests that the species composition on roofs depends on environmental conditions that on certain substrates either foster or hinder bryophyte growth rather than on roofing material. Moreover, the species composition of bryophyte communities on roofs may depend on the occurrence and abundance of bryophyte species as sources of propagules in the neighbourhood.

Our study revealed no difference in the bryophyte flora on roofs between Tallinn and rural areas although the indicator of environmental pollution NOx was found to be a significant descriptor of species variance in the analysis of plots with the highest bryophyte coverage. Both experimental works and national-scale correlative studies along nitrogen deposition gradients have found significant effects of nitrogen pollution on bryophyte species composition, bryophyte cover and species richness (Mitchell et al., 2005; Pescott et al., 2015). Bryophyte species number and composition varied in Gilbert´s (1970) study on asbestos roofs (11 sites) in 17.6 km transect upwind from the centre of pollution in north-east England, where 8 species coincide with those found in our study: *C. purpureus* (1.6 km), *B. argenteum* (1.6 km), *S. ruralis* (11.2 km), *O. anomalum* (12.8 km), *H. cupressiforme* (14.4 km), *S. apocarpum* (14.4 km), *H. sericeum* (14.4 km), and *B. rutabulum* (16 km) – the nearest distance from the source of pollution is given in brackets (Leblanc & Rao, 1974). Species richness was near the source of the pollution (1.6 km away) two and grew gradually, moving away from the source, up to 12 species (distance 17.6 km from the source; Gilbert, 1970). According to indicator values by Hill et al. (2007), 51% of the bryophyte species registered on roofs in Tallinn do not tolerate heavy metal pollution. This suggests that environmental pollution in the studied areas in Tallinn is not high enough to have a significant effect on bryophytes as a group of organisms sensitive to environmental pollution. The sites in Tallinn that our research covered were mostly in the south-western part of the city, which according to the study by Sander and Lensment (1996) based on lichens is the cleanest area of Tallinn. The moss species *S. ruralis* is according to Hill et al. (2007) sensitive to heavy metals but this species is widely spread all over Tallinn, registered also in the neighbourhood of roads with heavy traffic. Contrary to the Hill et al. (2007) work, Naszradi et al. (2007) found *S. ruralis* (*Tortula ruralis*) to be a suitable moss for indication of heavy metal pollution due to its resistant nature against stress factors, including heavy metals. At the same time in the Gilbert (1970) study *S. ruralis* was found much further (11.2 km) from the source of the pollution than *C. purpureus* and *B. argenteum* (1.6 km). The mosses *C. purpureus* and *B. argenteum*, which in our analysis were related to higher levels of environmental pollution, were also found on the roofs in areas with polluted air by other researchers (Gilbert 1970, 1971; Köhler, 2006). The moss *C. purpureus* is a species that is frequent and often abundant on substrates with moderate or high concentrations of heavy metals, sometimes occurring as dominants over large areas, but is also frequent in other habitats (Hill et al., 2007). Stevenson and Hill (2008) registered *C. purpureus* also among species that were significantly more common in the urban area than would be predicted from their regional frequency. In Köhler (2006) study in Berlin and Burszta-Adamiak et. al. (2019) experiment in Wrocław, *C. purpureus* was a species that spontaneously spread well on roofs and was the only dominant moss species. In Köhler (2006) study *C. purpureus* was able to colonize spontaneously on a grassy green roof in the second year of its functioning and had coverage of 60% − 88% during the study period over 15 years. According to Burszta-Adamiak et al. (2019), *C. purpureus* on green roofs might be the optimal solution for the improvement of the urban hydrology and ecology through forming long-lasting green cover able to survive in harsh urban environment and function during the whole year. According to Hill et al. (2007), *B. argenteum* is recorded on substrates with moderate or high concentrations of heavy metals but only rarely, they are much more frequent elsewhere. In the studies mentioned above (Köhler, 2006; Burszta-Adamiak et al., 2019), *B. argenteum* was the other species next to *C. purpureus* in urban environments, but the coverages were much lower – up to 5%.

According to the CCA, thatched roofs differed clearly from other roofs (Fig. 2). This is most probably due to the higher acidity of thatched roofs as the growth substrate compared to other sampled types of roofing materials. Thatched roofs were associated with species needing an acidic and moist environment (e.g., *S. autumnalis*, *P. crista-castrensis*, *D. polysetum*); on other roofing materials species that prefer alkaline and dry habitats were more common (Hill et al., 2007). The moss *D. scoparium*, which is very frequent in Estonia, was found only on thatched roofs. Hedderson et al. (2003) also found *D. scoparium* to be a highly characteristic species of thatched roofs: it occurred on over half of the roofs of their study and dominated in several bryophyte communities on thatched roofs. Other species that were the same on thatched roofs in our study, as in Hedderson et al. (2003) study, were: *B. rutabulum, C. purpureus, Homalothecium sericeum, H. cupressiforme* and *Lophocolea heterophylla*. Among our studied roof types, thatched roofs were the richest in species. Thatched roofs characteristically support an extensive bryophyte cover and appear to be a favourable habitat for a considerable number of bryophyte species (Hedderson et al., 2003). Thatched roofs were on the DCA ordination scatterplots closest to the bitumen roofing located in a shaded woody area on Hiiumaa and covered with a thick layer of tree litter, which makes the substrate acidic. Like on thatched roofs, on these bitumen roofs, bryophytes had evidently been growing for a long time undisturbed, without having been mechanically removed or controlled by any other means, and the thick tree litter layer together with semi-decomposed bryophytes had made the growth environment on the bitumen surface similar to that on thatched roofs. The bryophyte species that were associated with thatched roofs and other roofs located on the right-hand third of the DCA scatterplot (Fig. 2a) are all associated with woods, and an overwhelming majority of them grow on the ground, some also on decaying wood (Ingerpuu et al., 1998).

The importance of roof height in describing the variation of bryophyte species growing on roofs in Tallinn was most probably related to better light conditions and drier habitat on higher roofs; this is corroborated by the characteristic of high roofs species *B. argenteum* and *O. anomalum*, which preferably grow in well illuminated and rather dry sites. *B. argenteum* belongs among the bryophyte species with the highest tolerance to desiccation (Gao et al., 2015). Desiccation tolerance of *O. anomalum* is also high: it occurs for example in arctic regions and at higher altitudes in the Himalayas (Kolodziejczyk & Summerer, 2016). Ellenberg's indicator value of light of *B. argenteum* and *O. anomalum* is 8, which means that these species rarely grow in sites where the relative illumination in summer is below 40% (Hill et al., 2007). The reason why *O. speciosum* grows on higher roofs may be its dissemination from trees as its favoured habitat is tree trunks and branches.

The results of the present study indicate that although the bryophyte flora on roofs of different materials was different and it was possible to distinguish characteristic species of different types of roofing materials, for the development of bryophyte communities on roofs two factors are most important: firstly, presence or absence of a tree canopy above the roof and, secondly, the thickness of the bryophyte cover that has developed on the roof over time. Other important factors are roof relief and height; the latter affected the species composition of bryophyte communities primarily in the city. Our results agree well with the findings by Hohenwallner and Zechmeister (2001), according to which in Vienna the habitat and substrate diversity are the most influential parameters of species richness and population vitality of bryophytes, therewith environmental pollutants are of minor importance.

Results of the present research might be of assistance in selecting suitable bryophyte species for a vegetated green roof on certain roofing materials and in certain locations. As the first choice, species registered on several types of roofs and widespread in the world – *B. rutabulum*, *C. purpureus*, *H. cupressiforme*, *P. cuspidatum*, and *S.*

ruralis – can be recommended. At the same time, it is important to consider in selecting suitable species the location of the roof, i.e., whether it is in an open or a shaded area. For open and dry roofs suggested taxa in the Mediterranean Basin – *B. argenteum*, *C. purpureus*, *H. ciliata*, and *S. ruralis* (de Carvalho et al., 2019), in North America – *H. ciliata* (Studlar & Peck, 2009) and in Japan – *Racomitrium canescens* (Aisar et al., 2018), are according to our study also good choices for dry habitats in the Baltic area. Based on our work and previous research (Grant, 2006; Studlar & Peck, 2009), species *B. rutabulum* and *P. cuspidatum* are suitable for more shady places. If the level of air pollution in the area is at the same level as in the areas we sampled, pollution is expected not to be hazardous to the mentioned bryophyte species. For more polluted areas, species *C. purpureus* and *B. argenteum* are suitable, as shown by several previous studies.

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