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Bryophytes in black alder swamps in south Sweden: habitat classification, environmental factors and life-strategies

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A considerable part of black alder swamps in Europe are situated in south Sweden. These swamps are frequently rich in bryophytes, but the variation in species composition is often large between sites. In this study we focus on environmental variables that best predict biodiversity in terms of species number, cover and bryophyte composition. The bryophyte vegetation was analysed in 71 plots of size 10 × 10 m in 31 black alder swamps from south Sweden. A total number of 171 bryophyte species (including 52 liverwort species) were recorded. At plot level the species number ranged between 11 and 54 (0–19 for liverworts and 11–36 for mosses). The black alder swamps were classified into five groups, which turned out to be characterized by a combination of tree species composition and hydrological conditions. 22 environmental and geographic variables were recorded for each plot and used as predictor variables in a redundancy analysis (RDA). These variables explained about 50% of the distribution of bryophytes. The most influential variables along the first axis were slope (positive relationship), basal area of spruce (positive relationship) and basal area of black alder (negative relationship). Along the second axis slope, basal area of ash and water depth had the strongest impact. The variables were subdivided into four groups and analyzed by separate RDAs. The amount of dead wood was important for the species richness in black alder fens in combination with humidity. Epixylic bryophytes tended to occupy spruce dead wood as a primary substrate and alder dead wood as a secondary substrate if spruce is present. Black alder stools were important as substrate for various bryophytes during flooding periods, including *Plagiothecium latebricola* and some liverworts (*Calypogeia* spp. and *Riccardia* spp.). The life-strategy categories were represented by perennial stayers 11%, competitive perennials 28%, stress-tolerant perennials 9%, colonists *sensu stricto* 21%, pioneer colonists 13%, long-lived shuttles 15% and short-lived shuttles 3%. The composition of life-strategy types varied in the swamps. Stress-tolerant perennials were more common in flat swamps. Colonists were more frequent in swamps with dominance of spruce and in sloping swamps.

Species diversity of bryophytes is potentially high in boreal and nemoral forests, especially in swamp forest types, which permanently keep a high humidity. In Sweden, 300 bryophyte species regularly occur in forests (28% of all Swedish bryophytes) and a comparable number of species grow in wetlands (Hallingbäck 1996). Forest and wetland plant species meet in black alder *Alnus glutinosa* swamps. Plant communities in such swamps show a distinct differentiation along the land-water transect, forming characteristic distribution zones or mosaic patterns. Forested wetlands therefore have considerable structural diversity that creates many microhabitats for bryophytes (Vitt et al. 2003, Økland et al. 2008). In Scandinavian black alder swamps, vascular plant diversity has been analysed in de-

tail, whereas bryophytes have been treated more extensively (Fremstad 1983, Brunet 1990). Ingerpuu et al. (2001) have compared the diversity among both vascular plants and bryophytes in wet areas in Estonia.

Bryophytes are to a large extent dependent on free water in the environment for their growth and nutrition. The time spent in the hydrated state is important for their growth and is determined by availability of water and by microclimatic conditions. On the other hand, some bryophytes have a better capacity to persist dry periods than vascular plants. Black alder has a wide ecological range, but prefer to grow on wet soil. Different hydrological situations (Keddy 2002), including moving water in slopes or flooding in depressions, streams or shores could be ex-

pected to give rise to quite different conditions in terms of water stress for bryophytes in black alder swamps. The composition of tree species, affects the microclimate and therefore the vegetation pattern. Diekmann (1994, 1999) pointed out that microclimate parameters, such as light availability, temperature, and humidity, varies dependent on the species composition, age and density of the tree stand. Different tree species also affect the supply of nutrients in the rainwater by substances released from leaves and branches during through-fall (Weibull 2001).

Black alder is a pioneer and sometimes a secondary tree species that may occur in pure stands (usually in wet conditions) but equally often grows in mixed stands with birch *Betula pubescens*, ash *Fraxinus excelsior* or spruce *Picea abies*. If the position of the water-table is lowered, black alder is mostly successional replaced by spruce in boreal forest and by ash in nemoral forest. The composition of tree species in the swamps could be expected to influence the bryophyte flora stronger than the vascular plant flora, since the bryophytes are more sensitive concerning humidity and access to nutrients. Furthermore, bark and dead wood are important substrates for bryophytes, and different tree species have different qualities as substrates. Fallen logs are, for example, important for many desiccation intolerant bryophyte species and the quality of the log depends on the tree species, the dimension and structure of the log, and the position of the log in relation to water (Söderström 1988a, 1988b, 1997, McAlister 1997). Typi-

cal for black alder is its ability to give rise to huge stools, which often carry dead wood at a varying state of decay and water content.

The following questions are addressed in this paper:

1. How is bryophyte species composition in black alder swamps related to hydrological conditions, i.e. by flooding, standing or flushing water?
2. Does bryophyte species composition differ between black alder swamps with different mixtures of deciduous and/or spruce tree species? Is dead wood important as substrate and is it possible to demonstrate differences between different types of wood?
3. How many bryophytes are tied to the black alder and its stools and how are bryophyte habitats conditioned by the position of trees (in slopes or flat areas)?

Material and methods

Study area

The study area (Fig. 1, Appendix 1.) spans across five counties in south Sweden; Kronoberg (14 stands with 41 plots), Halland (6 stands with 13 plots), Östergötland (7 stands with 9 plots), Skåne (3 stands with 4 plots), and Jönköping (1 stand with 4 plots). The bedrock is acid and

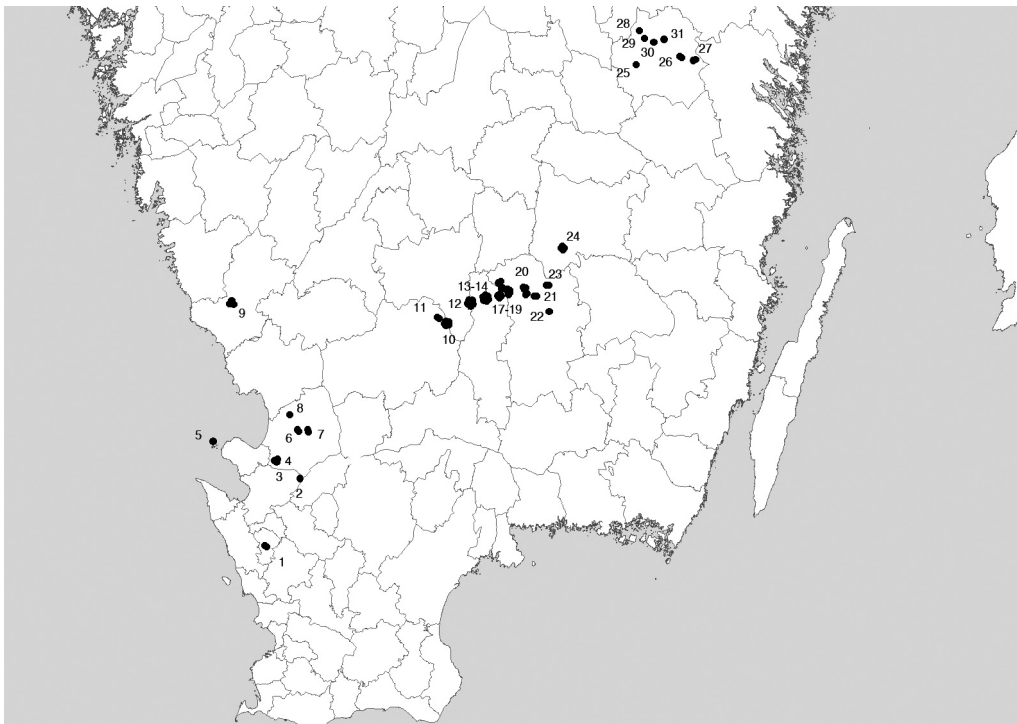


Figure 1. Map of south Sweden showing the location of sites included in this study.

dominated by granite or gneiss in this area, with exception for Skåne, where the forest stands grow on sedimentary bedrock with basic soils (Fredén 1994). The mean annual precipitation is up to 1000 mm in Halland, 800 mm in Kronoberg and 500 mm in Östergötland (averages for the last ten years; Raab and Vedin 1995). The altitude ranged from 10 m a.s.l. at Hallands Väderö to 250 m in Röshult (Jönköping). The climate is classified as suboceanic in Halland and continental in the other counties.

Since black alder swamps are highly productive, they were formerly open meadows and used for haymaking and grazing, and thus kept in an open or semi-open condition. When this management ceased around hundred years ago, a secondary succession started. This succession gradually changed the conditions and the microclimate for bryophytes and vascular plants towards more or less closed forests. Many wetlands have been drained in the agricultural districts of south Sweden, but some black alder swamps still remain relatively hydrologically unaffected. The stands included in this investigation have developed 'naturally', that is, they are reasonably untouched by hydrological manipulations and logging. Most of the selected stands are today rather closed forests older than 50 years. The size of black alder stools is probably the best measure of the age of the forest. The individual black alder trunks usually do not become older than about 100 years, but they regenerate from stools that are much older and expand with age.

Field work was carried out during 1998–2004. Each object was visited at least twice during summertime. The hydrology of selected stands was classified according to a modification of the categories described by Fremstad (1983): (1) waterlogged soils along streams and brooks; (2) wet or moist soils along flushed hillsides (3) black alder swamp in gentle slopes with moving soil water, that are rarely flooded (not mentioned in Fremstad 1983); (4) waterlogged soils at flat, seasonally flooded sites (black alder carr); (5) sheltered shores along fresh, brackish or saline waters. Stands with different composition of the tree layer were represented in the study: mixed black alder forest (with birch, spruce and/or ash) as well as pure black alder forest. The area of the stands ranged from 1 ha to 15 ha.

Sampling of bryophytes and plants

In each stand, a square plot sized 10 × 10 m was positioned in a place subjectively regarded as representative of the object. This comparatively large plot size, was chosen in order to include all special habitat niches in black alder swamps, such as different tree species, stools of black alder, rotten wood, stone, peat and bark. At more complex sites, additional 1–5 plots were placed in the same manner. These additional plots were in general individually as different as plots from other sites. In total, 71 plots were analysed in 31 objects. Within plots, the coverage of all

bryophytes and plants was quantified according the following scheme: (1) single, (2) a few–1%, (3) 1–5%, (4) 5–25%, (5) 25–50%, (6) 50–75%, (7) 75–100%. For bryophytes were also recorded the substrate (dead wood, bark, soil, peat and stone) and whether sporophytes and/or vegetative propagules (gemmae) were encountered. The nomenclature for bryophytes follows Hallingbäck et al. (2006).

Sampling of environmental variables

Twenty-two environmental and geographic variables were recorded (cf. Table 1). Annual precipitation, mean temperature and annual sun radiation was also recorded but excluded from the analyses since these variables were strongly correlated with longitudinal and latitudinal coordinates. Tree leaf area and basal area have shown a strong correlation (Whittaker and Marks 1975, Parker et al. 1989) and the light penetration was therefore assumed to decrease in proportion to basal area in this investigation. The size of black alder stools was used as a measure of the age of the black alder trees. The average depth of soil was measured with a metal rod that was pressed down at ten positions in the square. The slope was measured in percent from the upper point to the lower point of the square.

Life-strategy types

We also compared the distribution of bryophyte life-strategies (sensu During 1979, 1992) among species in the black alder swamps. The species were assigned into different life-strategies according to Dierßen (2001; Table 3). It has to be noted that the assignment of species to a distinct strategy type is sometimes problematic due to lack of data of life-span, due to regional and annual variation in frequency of sporulation and due to the fact that the dispersal capacity is inferred solely from spore size. *Brachythecium rutabulum* is here treated as colonist but occurs also as a competitive perennial in the swamps. *Dicranum scoparium* is treated as a competitive perennial but occurs also as a stress-tolerant perennial as epiphyte.

Data analysis

To analyse differences in the bryophyte vegetation classification of the plots were made, based on bryophyte species data, using the computer program MOSAIC (Benjamin Smith, unpubl.; available at <www.nateko.lu.se/personal/benjamin.smith/software/frames.html>) with "dissimilarity measure: Euclidian distance" and "linkage method: average" (Jongman et al. 1987). Relationships between vegetational and environmental variables were visualized by constrained ordination. These analyses were conducted

Table 1. Environmental variables recorded for black alder swamps in southern Sweden. The bryophyte species composition and coverage was determined in 1–5 square plots of size 10 × 10 m from each swamp.

Hydrology	
Slope	Slope within each plot (%)
Depth-H ₂ O	Maximum depth of standing water in April/May (cm)
Stream	Width of streams (dm)
Tree species	
Basaraeal	Basal area of black alder at 1.3 m (m ² ha ⁻¹)
Basareaspr	Basal area of spruce at 1.3 m (m ² ha ⁻¹)
Basareabet	Basal area of birch at 1.3 m (m ² ha ⁻¹)
Basareafrax	Basal area of ash at 1.3 m (m ² ha ⁻¹)
Basareatot	Total basal area for all trees at 1.3 m (m ² ha ⁻¹)
Dead wood and size of tree	
Stool	Stool volume (m ³)
Alwood	Surface area of dead wood (log) of black alder in plot (m ²); largest diameter > 5 cm and minimum length = 0.5 m; calculated as length (m) × circumference (m)
Sprwood	Surface area of dead wood of spruce in plot (same dimension limits and calculation method as Alwood, above)
Betwood	Surface area of dead wood of birch in plot (same dimension limits and calculation method as Alwood, above).
Alsnag	Basal area of standing dead black alder tree (snag) at 1.3 m (m ² ha ⁻¹)
Sprsnag	Basal area of standing dead spruce tree (snag) at 1.3 m (m ² ha ⁻¹)
Betsnag	Basal area of standing dead birch tree (snag) at 1.3 m (m ² ha ⁻¹)
Alcirc	Circumference of the largest black alder tree in each plot (m)
Soil	
pH-soil	Soil pH, samples taken 1 cm beneath the surface and analysed in 0.2% KCl-solution
Depth-soil	Depth of soil, average in square (cm)
Stone	Total area covered by boulders (m ²)
Noveg	Percent of the plot without vegetation (%)
Spatial	
Long	Longitudinal coordinates estimated with a handheld GPS device
Lat	Latitudinal coordinates estimated with a handheld GPS device

using the computer program CANOCO (ter Braak and Smilauer 2002). A preliminary detrended correspondence analysis (DCA) revealed that gradient lengths were comparatively short (3.097), indicating that community–environmental relationships were predominately linear, rather than unimodal (Jongman et al. 1995). Redundancy analysis (RDA) was therefore preferred as the appropriate technique for a constrained ordination. All variables, with exception for soil depth, pH and circumference of the largest black alder tree, were square-root-transformed. RDA was initially carried out using the full set of parameters in Table 1. The environmental variables were then divided into four subgroups encompassing (1) hydrological variables, (2) tree species composition, (3) dead wood abundance and (4) soil variables (according to Table 1). A

partial RDA was then carried out for each of these subgroups. Spatial parameters were included because they may act as synthetic surrogates for certain environmental parameters which are difficult to measure directly. The spatial parameters were used as co-variables, to eliminate some of the variation between places, thereby emphasizing the relative significance of the four subgroups.

Results

Floristic results

Altogether, 171 taxa of bryophytes were found, which of 52 were liverworts. The number of bryophyte species in

the plots ranged between 11 and 54 (0–19 for liverworts and 11–36 for mosses). In sloping plots (more than 1% inclination) the mean species number of bryophytes was 34, as compared to 28 in flat plots.

Three of the observed species (*Calypogeia azurea*, *Hookeria lucens* and *Trichocolea tomentella*) are currently listed in the Swedish Red Data Book (Cronberg et al. 2005). Several species, such as *Bazzania trilobata*, *Dicranodontium denudatum*, *Herzogiella turfacea*, *Plagiotecium latebricola* and *Loeskobryum brevirostre* have been extensively used in Sweden as indicators for biologically valuable forests (Nitare and Hallingbäck 2000). *Riccardia latifrons*, *Riccardia palmata*, *Jungermannia leiantha*, *Jamesoniella autumnalis*, *Geocalyx graveolens*, *Conocephalum conicum*, *Pseudobryum cinclidioides* and *Plagiotecium ruthei* are other examples of species that are rare in southern Sweden, but not red-listed.

Classification

Five groups were obtained at the fourth level of division when the 71 plots were classified by the computer program MOSAIC. Among these groups there are rather distinct differences in the frequency of the tree species as well as differences in hydrological properties. Group A had ash as a dominant tree species (flat swamps and sloping swamps were grouped together); group B consisted of four plots with high abundance of birch which were joined together with somewhat lower support; group C was black alder swamps with an admixture of more than 10% spruce (flat swamps and sloping swamps were grouped together); group D had black alder as a dominant tree species in flat terrain; and group E consisted of black alder as dominant tree species in slopes. Main characteristics of the five groups are shown in Table 2. Group A, B, C, D and E

Table 2. The mean scores for the different environmental factors (Table 1) in the five groups of plots identified by the computer software MOSAIC. Factors that differed significantly between the groups according to an ANOVA are showed in bold. (* = 0.01 < p < 0.05, ** = p < 0.01 and *** = p < 0.001). Bryophytes = mean number of bryophyte species per plot; Vascplants = mean number of the vascular plant species per plot. The groups represent black alder swamps with a dominance of ash (group A), birch (group B), spruce (group C), or less mixed black alder forest on flat (group D) respectively sloping (group E) ground.

	Group A	Group B	Group C	Group D	Group E
No. of plots	4	4	13	38	12
Stone n.s.	2.5	1.9	1.2	3.3	2.2
Stream n.s.	13	6.75	5.8	12.8	3.9
Lat n.s.	629603	631374	634212	633710	630181
Long **	139161	140416	143200	142271	135966
pH-soil n.s.	5.47	5.21	5.31	5.08	5.09
Basareal ***	7.72	11.78	9.48	41.22	37.05
Basareabet ***	0	21.00	3.97	2.75	2.66
Basareaspr ***	0	1.88	21.07	3.18	2.85
Basareafrax ***	48.20	3.85	0	0.30	0.17
Basareatot n.s.	55.92	38.52	35.27	47.98	42.76
Alwood n.s.	0.9	1.1	1.9	3.95	2.5
Betwood n.s.	4.55	1.80	0.8	1.02	1.43
Sprwood *	0	1.56	2.97	0.49	0.9
Alsnag *	0	0.09	0.95	2.44	0.44
Betsnag n.s.	0	0.10	0.54	0.27	0
Stool n.s.	1.3	7.6	6.1	3.7	3.6
Alcirc ***	0.60	0.76	0.67	1.07	1.12
Slope ***	0.048	0.050	0.091	0.015	0.118
Depth-H ₂ O *	2.5	7.5	4.1	6.7	1.4
Depth-soil n.s.	46	101	83	65	68
Noveg n.s.	8	7	9	14	5
Bryophytes ***	24	35	42	28	33
Vascplants n.s.	15	23	23	20	20

were also separated in the RDA plot of sample scores (Fig. 2). However, the plots with birch (group B) as a dominant tree species did not form a distinct group along the two first canonical axes.

The variation in soil pH was small. Highest pH had plots with *Fraxinus*. Peat production was considerable in many of the swamps but least in swamps classified in group A. In this group some of the plots were situated on mineral soil close to comparatively large streams. Table 2 shows that stools were found in all groups (but few in group A). This is explained by the fact that both black alder and spruce (and even birch in some cases) give rise to huge stools in swamps. Boulders were unevenly distributed among the swamps, with the highest frequency in group A and D. The bryophyte distribution and life-strategies in the five groups A, B, C, D and E are shown in Table 3. It is notable that the mean number of bryophyte species per plot in all five vegetation groups was consistently much higher than the corresponding number for vascular plants.

Influence of the environmental variables

A first RDA with all parameters included is shown in Fig. 3. The positions of the 56 bryophytes best explained by the first and the second axes are plotted in the diagram. The most influential variables along the first axis were slope, basal area of spruce and basal area of black alder. Along the second axis slope, basal area of ash and water

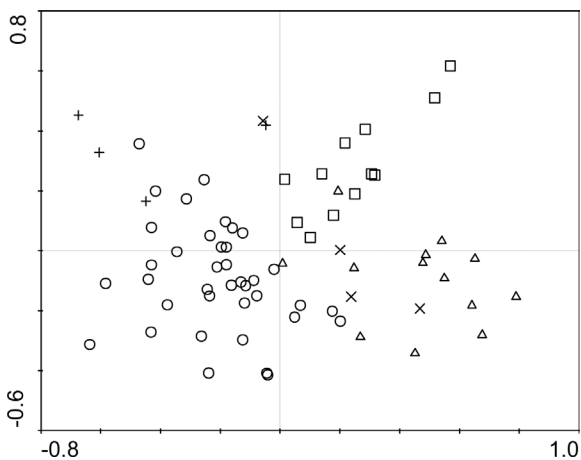


Figure 2. Results from a RDA analysis of bryophyte vegetation in black alder swamps. The plot illustrates sample scores along the two first canonical axes for 71 squares representing 31 black alder swamps. The analysis classified the vegetation plots into five groups (groups A–E) with different composition of tree species and topology (see Table 2 and the text). Different symbols are used for four different tree layer group. Group A +, group B x, group C Δ, group D O and group E □. Eigenvalues for axis 1 = 0.123 and axis 2 = 0.055. Explained variation was 0.45; $p < 0.002$.

depth had the strongest impact. RDAs based on each of the four groups of environmental variables according to Table 1 are summarized in Table 4. These results show that dead wood and size of tree and tree species parameters had the highest explanatory power, but also hydrology and soil parameters contributed significantly.

Ordination of bryophytes species according to the four groups of environmental variables

Hydrology

The hydrological group of variables (Fig. 4) reveal that a species rich bryophyte ground flora is associated with moving water near the surface (typically in slopes). Bryophyte species number increases with increasing slope ($r = 0.51$ and $p < 0.0001$). There were many competitive perennials and long-lived shuttle species in 'sloping swamps', among others *Brachythecium rivulare*, *Dicranodontium denudatum*, *Plagiomnium undulatum*, *Rhytidiadelphus* spp., *Thuidium tamariscinum*, *Trichocolea tomentella*, *Rhizomnium punctatum* and *Sphagnum palustre*. In the sloping swamps the species diversity of liverworts that colonize small brooks, stone, dead wood and stools was also high, exemplified by *Aneura pinguis*, *Calypogeia integristipula*, *Cephalozia bicuspidata*, *Jamesoniella autumnalis*, *Riccardia latifrons* and *R. multifida*. This trend in the slopes with high species richness and predominantly perennial competitive, long-lived shuttles and colonist species, is similar in black alder swamps with less than 10% spruce trees. In 'gentle slopes', under waterlogged conditions, *Brachythecium rutabulum*, *Calliergon cordifolium*, *Cirriphyllum piliferum* and *Plagiomnium ellipticum* were common. The conditions in 'flat swamps' with inundation during winter and varying depth of stagnant water during summer are quite different from the swamps in slopes. Only relatively large and erect mosses, such as *Calliergon cordifolium*, *Plagiomnium ellipticum* and *Sphagnum squarrosum* occurred on the ground. There were often no bryophytes in the pools except on roots, pegs, sticks and stones where *Brachythecium rutabulum*, *Sanonia uncinata*, *Dicranum scoparium*, *Aulacomnium androgynum* and *Lophocolea heterophylla* were widespread. The most common species on bark, wood and stone in this environment showed to be stress-tolerant perennials such as *Herzogiella seligeri*, *Hypnum cupressiforme*, *Plagiothecium laetum*, *P. latebricola*, *Plagiothecium cavifolium*, *Platygrium repens* and *Sanionia uncinata*. Only closer to the ground, on stools and stones, where conditions were more humid and shaded, *Mnium hornum* and *Scapania nemorea* could occur. The hydrology group of variables revealed relatively few species associated with 'streams'. In the inundated zone we found *Chiloscyphus polyanthos*, *Conocephalum conicum* and *Pellia epiphylla*, whereas *Brachythecium plumosum*, *Fontinalis antipyretica* and *Warnstorfia fluitans* grew in the stream. In

Table 3. Distribution of bryophytes in black alder swamps. The swamps have been classified into five vegetation types (groups A–E; see text, Table 2 and Fig. 2). For each species the number of observations (n) from a total number of 71 analysed 10 × 10 m plots is given and the median value (M) of the estimated coverage (see text for details) for these plots. Bryophyte life strategies are indicated after the species names: c = colonist s. s.; cp = pioneer colonist; p = perennial stayer; pc = perennial stayer, competitive; ps = stress-tolerant perennial; l = long-lived shuttle; and s = short-lived shuttle. Note that the species are sorted according to their main abundance in the different vegetation groups, starting with group A.

	Group A		Group D		Group B		Group E		Group C	
	n	M	n	M	n	M	n	M	n	M
Number of plots	4		38		4		12		13	
<i>Cirriphyllum piliferum</i> (pc)	4	3	7		2	1,5	3		1	
<i>Antitrichia curtispindula</i> (l)	3	2,5	1		1					
<i>Climacium dendroides</i> (pc)	3	2,5	26	2	2	1	3		1	
<i>Isothecium alopecuroides</i> (ps)	3	2,5	8		1	1	5		1	
<i>Eurhynchium striatum</i> (p)	2	1	4							
<i>Frullania dilatata</i> (l)	2	1	2		1					
<i>Plagiomnium cuspidatum</i> (pc)	2	1	3		4	3,5				
<i>Loeskeobryum brevirostre</i> (ps)	2	1	4		1		1			
<i>Oxyrrhynchium hians</i> (cp)	1								1	
<i>Homalia trichomanoides</i> (ps)	1		2		1					
<i>Orthotrichum affine</i> (c)	1				1					
<i>Orthotrichum lyellii</i> (s)	1									
<i>Radula complanata</i> (l)	1		2		1				1	
<i>Hypnum cupressiforme</i> (ps)	3	2,5	38	3	4	3	12	3	11	2
<i>Lophocolea heterophylla</i> (cp)	1	0	35	2	3	2	10	2	10	2
<i>Dicranum scoparium</i> (cp)	2	1	34	3	4	3	12	4	12	3
<i>Mnium hornum</i> (l)	3	2,5	33	3	4	4	12	4	12	3
<i>Plagiothecium laetum</i> (ps)	2	1	30	2	3	1,5	10	2	5	
<i>Brachythecium rutabulum</i> (cp)	3	4	28	3	3	2,5	5		7	1
<i>Dicranum montanum</i> (pc)	2	1	28	2	4	2	11	2,5	9	2
<i>Tetraphis pellucida</i> (cp)	2	0,5	27	2	3	2	12	2	11	2
<i>Ptilidium pulcherrimum</i> (s)			26	2	3	1,5	1		10	2
<i>Calliergon cordifolium</i> (pc)			23	2	1		2		6	
<i>Aulacomnium androgynum</i> (c)	1	0	21	1			2		6	
<i>Plagiomnium ellipticum</i> (pc)	2	0,5	18				2		2	
<i>Plagiothecium latebricola</i> (ps)	1		16				3			
<i>Sciuro-hypnum reflexum</i> (ps)	1	0	16		1		2		3	
<i>Plagiothecium curvifolium</i> (pc)			15		1		1		7	1
<i>Plagiothecium denticulatum</i> (ps)	2	1	15		1		3		4	
<i>Sphagnum squarrosum</i> (l)			15		1		5	1	9	2
<i>Sciuro-hypnum plumosum</i> (pc)			14							
<i>Plagiothecium succulentum</i> (pc)	1		14				5		3	
<i>Sanonia uncinata</i> (ps)	1	0,5	15		3	2,5			4	

Table 3. Continued.

<i>Scapania undulata</i> (pc)			14					3		1	
<i>Atrichum undulatum</i> (s)			13		1			5		3	
<i>Herzogiella seligeri</i> (ps)	1		12		1			2		2	
<i>Pellia epiphylla</i> (c)	1		12		1			2		4	
<i>Plagiothecium cavifolium</i> (ps)			11		1			1			
<i>Amblystegium serpens</i> (p)	1		10		2	0,5		1		1	
<i>Pseudobryum cinclidioides</i> (l)			9								
<i>Dicranum fuscescens</i> (pc)			9					4		3	
<i>Warnstorfia fluitans</i> (l)			9							3	
<i>Fontinalis antipyretica</i> (p)			9								
<i>Platygyrium repens</i> (ps)	1		7		1			4		1	
<i>Plagiomnium affine</i> (pc)			7		1			4		3	
<i>Racomitrium aciculare</i> (cp)			6								
<i>Sciuro-hypnum populeum</i> (p)			5					1			
<i>Dicranella heteromalla</i> (c)			5							1	
<i>Plagiothecium ruthei</i> (pc)			4		1			2		1	
<i>Plagiomnium medium</i> (pc)			4							1	
<i>Sphagnum fallax</i> (l)			4					2			
<i>Sphagnum fimbriatum</i> (l)			4								
<i>Dicranum bonjeanni</i> (pc)			3		2	1		1			
<i>Kindbergia praelonga</i> (p)	1		3							1	
<i>Conocephalum conicum</i> (l)			2								
<i>Calypogeia azurea</i> (c)			1								
<i>Calypogeia fissa</i> (c)			1					1			
<i>Geocalyx graveolens</i> (cp)					1						
<i>Herzogiella turfacea</i> (c)					1						
<i>Sphagnum palustre</i> (l)			4		3	3		11	3	10	3
<i>Thuidium tamariscinum</i> (p)	1		10		2	1,5		10	5	12	3
<i>Polytrichum formosum</i> (pc)	2	1	24	2	3	2,5		10	2	12	2
<i>Lophocolea bidentata</i> (pc)			11		2	1		8	2	6	
<i>Trichocolea tomentella</i> (p)	1		1		1			9	2,5	5	
<i>Plagiomnium undulatum</i> (pc)	2	0,5	13		1			9	1,5	4	
<i>Thuidium delicatulum</i> (p)	3	3	15		2	1		8	2	8	2
<i>Dicranodontium denudatum</i> (pc)								7	1,5	5	
<i>Brachytheciastrum velutinum</i> (p)	1		6		1			7	1,5	2	
<i>Brachythecium rivulare</i> (pc)	3	2,5	18		3	2		7	2,5	5	
<i>Rhytidiadelphus loreus</i> (pc)	1		4					6	1	3	
<i>Frullania tamarisci</i> (l)	1							5			
<i>Plagiochila asplenioides</i> subsp. <i>porelloides</i> (ps)	1		6		1			5			
<i>Jamesoniella autumnalis</i> (c)								5		3	

Table 3. Continued.

<i>Chiloscyphus pallescens</i> (pc)		6		1		4		3	
<i>Leucobryum glaucum</i> (p)		4		1		3		2	
<i>Barbilophozia attenuata</i> (cp)						2		5	
<i>Blindia acuta</i> (cp)						1			
<i>Odontoschisma denudatum</i> (c)						1			
<i>Lophozia longidens</i> (c)						1			
<i>Lepidozia reptans</i> (cp)	1	15		4	2,5	8	2	13	3
<i>Calypogeia integristipula</i> (c)		4		3	2	8	2	12	2
<i>Calliergon cuspidata</i> (pc)		22	2	4	3,5	7	1,5	11	3
<i>Pleurozium schreberi</i> (pc)		15		2	1	5		11	3
<i>Rhizomnium punctatum</i> (l)	2	19	0,5	3	2	6	1	11	3
<i>Rhytidiadelphus triquetrus</i> (pc)	1	5		2	1	4		11	3
<i>Scapania nemorea</i> (p)		13				8	2	11	2
<i>Hylocomnium splendens</i> (pc)	2	22	2	3	2	6	0,5	10	2
<i>Cephalozia bicuspidata</i> (cp)	1	15		2	1	9	2	10	2
<i>Aneura pinguis</i> (s)						3		8	2
<i>Nowellia curvifolia</i> (c)		2		2	1	5		8	1
<i>Blepharostoma trichophyllum</i> (c)		7		2	0,5	4		8	2
<i>Aulacomnium palustre</i> (pc)		2		2	1,5	2		7	2
<i>Chiloscyphus polyanthos</i> (pc)		16		2	1	6	1	7	2
<i>Dicranum majus</i> (pc)		1		1		3		7	1
<i>Riccardia multifida</i> (c)				2	1	7	1	7	1
<i>Fissidens adianthoides</i> (c)		4				1		7	1
<i>Plagiochila asplenioides</i> (p)		1				1		6	
<i>Sphagnum fallax</i> (l)		4				2		6	
<i>Plagiomnium elatum</i> (pc)	1	18		1		2		6	
<i>Campylium stellatum</i> (pc)		2		1				6	
<i>Plagiothecium undulatum</i> (pc)		1				1		6	
<i>Riccardia latifrons</i> (cp)		1				4		6	
<i>Polytrichum commune</i> (pc)	1	5		1		1		5	
<i>Jungermannia subulata</i> var. <i>leiantha</i> (c)								5	
<i>Lophozia silvicola</i> (cp)		1				2		5	
<i>Cephalozia lunulifolia</i> (c)						1		5	
<i>Calypogeia muelleriana</i> (c)				1		1		4	
<i>Sphagnum subnitens</i> (l)				2	1,5	1		4	
<i>Rhytidiadelphus subpinnatus</i> (pc)		3		1		4		4	
<i>Sphagnum flexuosum</i> (l)						1		3	
<i>Bryum pseudotriquetrum</i> (pc)		3						4	
<i>Sphagnum capillifolium</i> (l)		1						4	
<i>Sphagnum warnstorffii</i> (l)								3	

Table 3. Continued.

<i>Rhizomnium pseudopunctatum</i> (l)				3
<i>Eurhynchium angustirete</i> (p)	1			3
<i>Rhodobryum roseum</i> (c)			1	3
<i>Calypogeia sphagnicola</i> (c)			1	3
<i>Bazzania trilobata</i> (pc)			1	2
<i>Sphagnum girgensohnii</i> (l)	4	1	3	2
<i>Sphagnum russowii</i> (l)				2
<i>Riccardia palmata</i> (cp)				2
<i>Lophozia incisa</i> (c)				2
<i>Scorpidium revolvens</i> (pc)				2
<i>Pohlia nutans</i> (cp)				2
<i>Sphagnum quinquefarium</i> (l)				1
<i>Hookeria lucens</i> (p)				1
<i>Philonotis fontana</i> (pc)				1
<i>Palustriella commutata</i> (pc)				1

In addition, the following species were found in a single plot: *Anastrophyllum hellerianum*, *Anastrophyllum minutum*, *Brachythecium salebrosum*, *Bryum capillare*, *Bryum moravicum*, *Cephalozia connivens*, *Ceratodon purpureus*, *Dicranella cerviculata*, *Dicranum polysetum*, *Fissidens osmundoides*, *Frullania fragilifolia*, *Hylocomniastrum umbratum*, *Lophozia ascendens*, *Metgeria furcata*, *Mylia anomala*, *Paraleucobryum longifolium*, *Polytrichum strictum*, *Pseudoscleropodium purum*, *Ptilium crista-castrensis*, *Rhytidiadelphus squarrosus*, *Scapania umbrosa*, *Sphagnum angustifolium*, *Sphagnum auriculatum*, *Straminergon stramineum*, *Syntrichia ruralis* and *Tritomaria quinqueidentata*.

the zone beside the stream where a short period of inundation during spring is followed by waterlogged conditions *Brachythecium rivulare*, *Pseudobryum cinclidioides*, *Plagiomnium elatum* and *Sphagnum squarrosus* were the most typical mosses.

Tree layer

Among tree species, black alder, spruce and ash influenced significantly the distribution of bryophytes (Fig. 5). Swamps where black alder is mixed with 'spruce' had a rich bryophyte flora and species number increased with increased abundance of spruce ($r = 0.60$ and $p < 0.0001$). We found spruce to be associated with forest floor bryophytes such as *Blepharostoma trichophyllum*, *Calypogeia integristipula*, *Dicranum majus*, *Jungermannia subulata* var. *leiantha*, *Leucobryum glaucum*, *Plagiochila asplenioides*, *Pleurozium schreberi*, *Rhytidiadelphus triquetrus*, *Scapania nemorea*, *Sphagnum palustre*, *S. subnitens*, *Thuidium tamariscinum* and on dead wood, *Cephalozia bicuspidata*, *Lepidozia reptans* and *Nowellia curvifolia*. 'Birch' was common as a subdominant in black alder swamps, but seemed to have a limited influence on the species composition. 'Ash' was associated with epiphytes such as *Antitrichia curtipendula*, *Frullania dilatata*, *Metzgeria furcata*, *Orthotrichum*

lyellii O. *affine* and *Radula complanata*. These epiphytes (except for *O. affine*) were not found on the bark of black alder trees in this investigation. They usually occur on trees with subneutral-basic bark and therefore avoid the bark of black alder. Where the subsoil water level position was relatively low ash replaced black alder and bryophytes associated with subneutral-basic soils were more common. Species we found in this environment included: *Brachythecium salebrosum*, *Cirriphyllum piliferum*, *Climacium dendroides*, *Eurhynchium striatum*, *Homalia trichomanoides*, *Isoetecium alopecuroides*, *Loeskobryum brevirostre* and *Plagiomnium cuspidatum*. Closer associated with 'black alder' were *Calliergon cordifolium*, *Climacium dendroides*, *Plagiothecium cavifolium*, *Pseudobryum cinclidioides*, *Scapania undulata*, *S. palustre* (common only in slopes) and *S. squarrosus*. In Småland we found *Loeskobryum brevirostre* in swamps with ash trees, while it occurred in pure stands of black alder further to the west, on the ridge Hallandsåsen. The epiphytic bryophyte flora on black alder trees is usually species poor. *Dicranum montanum*, *Hypnum cupressiforme*, *Lophocolea heterophylla*, *Plagiothecium laetum*, *P. latebricola* and *Ptilidium pulcherrimum* were common epiphytes in Kronoberg on black alder, while *Dicranodontium denudatum*, *Frullania tamarisci* and *Platygyrium repens* were rare as epiphytes in Kronoberg but rather com-

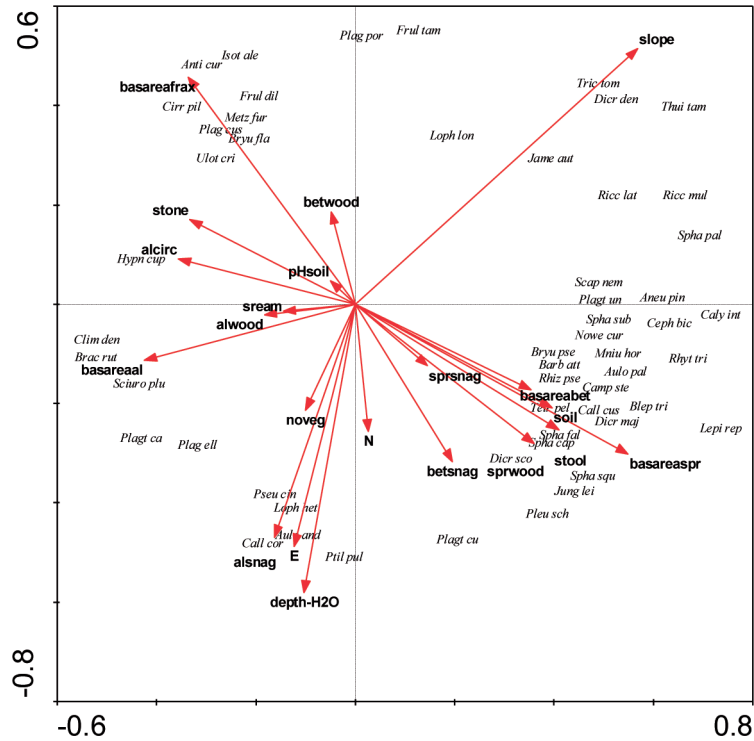


Figure 3. RDA for all squares and bryophytes. Bi-plot of the first two canonical axes of species and environmental variables (eigenvalues for axis 1 = 0.123, and axis 2 = 0.055). Species–environment correlations for the first two axes were 0.922 and 0.923. Explained variation was 0.45, $p < 0.002$. Bryophyte species are indicated by the first four letters of the first part of the binomial and first three of the second part of the binomial). Indifferent species (near zero) are not shown in the plot.

mon in the swamps to the west where the climate is more humid.

Substrate

Substrates such as stone, soil (Fig. 6) and dead wood (Fig. 7) had together the greatest explaining value for bryophyte distribution in black alder swamps. Boulders and soil are important substrates for bryophytes. Among the species on ‘boulders’ were *Barbilophozia barbata*, *Climacium dendroides*, *Isothecium alopecuroides*, *Plagiothecium cavifolium*, *Rhizomnium punctatum*, *Sciuro-hypnum reflexum* and *Thuidium delicatulum*. ‘Soil-pH’ had little association with the distribution of bryophytes in the investigated black alder swamps. Deeper ‘soil’ (peat) was associated with *Aulacomnium palustre*, *Calliergonella cuspidatum*, *Calypogeia integristipula*, *Campyllum stellatum*, *Sphagnum palustre* and *S. subnitens*. Dead wood was important as substrate in the black alder swamps, but there were great differences between different tree species. The amount of dead ash wood was always low. Rather few epixylic bryophytes were found on black alder and birch logs, but on ‘spruce logs’ we found among others *Anastrophyllum hellerianum*, *Blepharostoma trichophyllum*, *Cephalozia bicuspadata*, *Dicranodontium denudatum*, *Lepidozia reptans*, *Lophocolea*

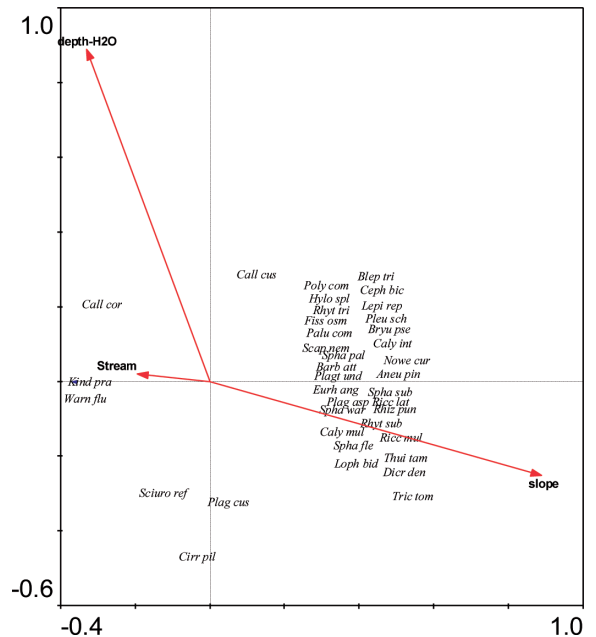


Figure 4. RDA for hydrology group of variables (cf. Table 1 and 4). Indifferent species (near zero) are not shown in the plot.

Table 4. RDA for four groups of environmental variables (Table 1). Longitudinal and latitudinal coordinates were covariables.

	Trace (% expl. Var.)	F-ratio	p	Eigenvalue Axis 1	Eigenvalue Axis 2	Eigenvalue Axis 3
Hydrology (n = 3)	9.7	2.491	0.0001	0.057	0.023	0.017
Tree layer (n = 4)	14.7	2.950	0.0001	0.085	0.032	0.019
Soil (n = 3)	8.3	2.088	0.0001	0.051	0.017	0.015
Wood (n = 7)	17.0	1.649	0.0001	0.059	0.032	0.022

heterophylla, *Lophozia incisa*, *Nowellia curvifolia* and *Tetraphis pellucida*. All but the two first were also found on 'black alder logs' but less frequently than on spruce logs and mostly in plots with strong slope or in presence with spruce. The bryophytes on 'stools' varied a lot dependent on the 'type' of stool. When the plots with more than 10% spruce were excluded in a renewed analysis of the wood and bark group of variables (in total 56 swamps; eigenvalues axis 1 = 0.043, axis 2 = 0.034; explained variation = 0.16 and $p < 0.002$; figure not shown), it was evident that the black alder stool provided habitats for bryophytes demanding humid conditions, especially liverworts and colonists. Accordingly, high old stools in humid climate hosted a lot of liverworts, among others *Calypogeia integristipula*, *C. azurea*, *Cephalozia bicuspidata*, *Jamesoniella autumnalis*, *Jungermannia subulata* var. *leiantha*, *Lepidozia reptans*, *Odontoschisma denudatum* and *Riccardia latifrons*. *Plagiothecium latebricola* was mostly found in flat black alder swamps on dead black alder wood on stools and stumps but also on black alder bark. It was rather common in Kronoberg but rare in Halland and Skåne. *P. latebricola* was rarely found on birch stools in alder swamps and only once on a spruce root. In this investigation, *P. latebricola* was rare in habitats where the black alder swamps had a high abundance of spruce.

Species richness and distribution of species according to life strategy classification

The bryophyte species richness in terms of species number was significantly positively correlated with the parameters slope, basal area of spruce and surface area of spruce logs (Table 5). Liverworts species richness was significantly positively correlated with spruce, slope, spruce wood and stool. Both bryophytes and liverworts were significantly negatively correlated with black alder basal area. The life strategy categories were represented as follows: perennial stayers 11%, competitive perennials 28%, stress-tolerant perennials 9%, colonists *sensu stricto* 21%, pioneer colonists 13%, long-lived shuttles 15% and short-lived shuttles 3%. The life strategy categories were unevenly distributed among the various swamp types (Fig. 8, Table 5). Colonists *sensu stricto*, pioneer colonists and perennial stayers were significantly positively correlated with basal area of spruce,

spruce log, slope and stool and negatively correlated with basal area of black alder and alder circumference. Stress-tolerant perennials were significantly positively correlated with basal area of black alder and circumference of black alder. Ash trees were associated with competitive perennials on the ground and long-lived shuttle bryophytes as epiphytes; black alder was mainly associated with competitive perennials on the ground and stress-tolerant perennials as epiphytes. Spruce was associated with long-lived shuttle and competitive perennials on the ground and colonists and pioneer colonist on wood and no epiphytes.

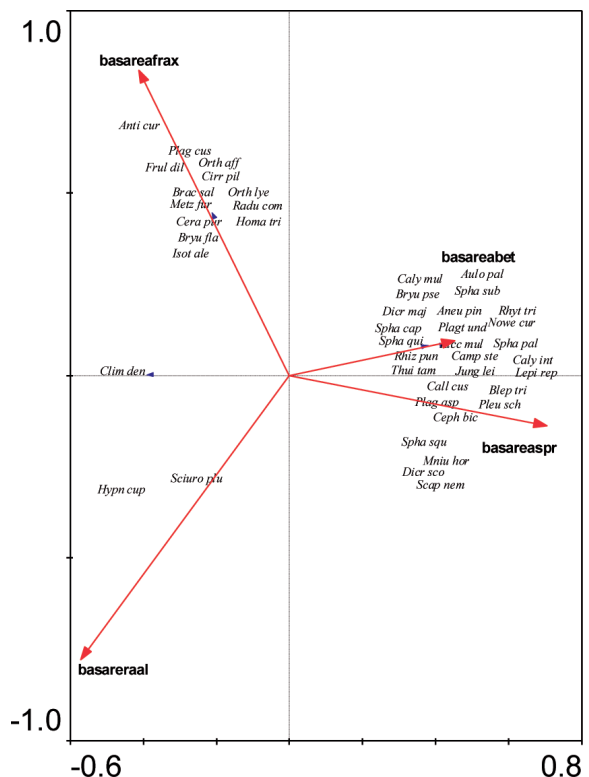


Figure 5. RDA for tree layer group of variables (cf. Table 1 and 4). Indifferent species (near zero) are not shown in the plot.

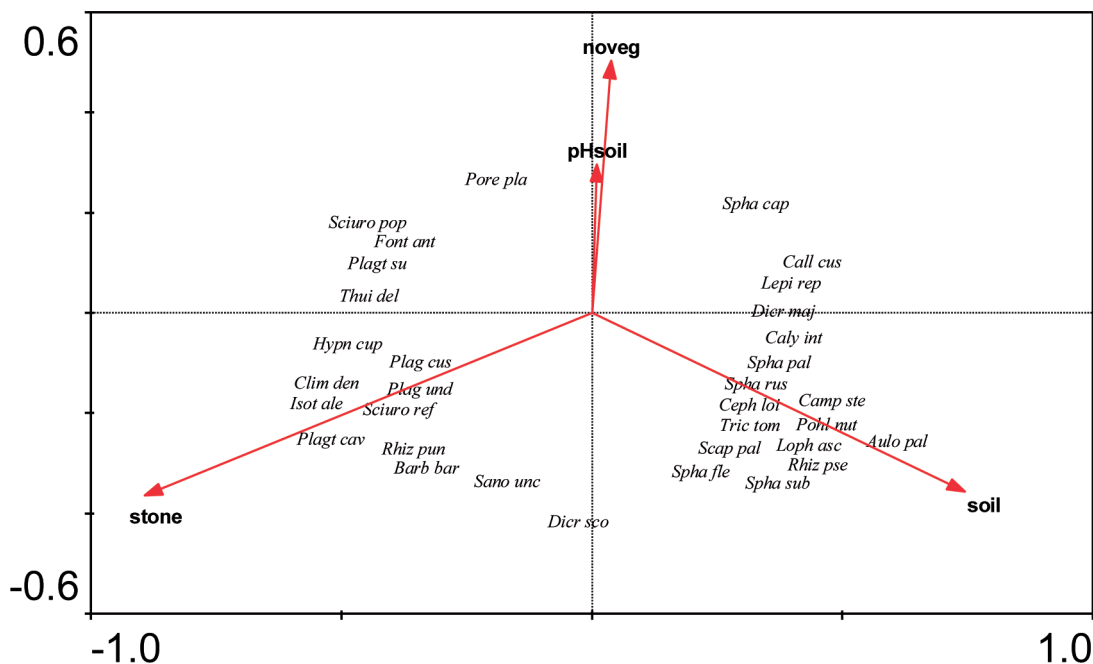


Figure 6. RDA for soil group of variables (cf. Table 1 and 4). Indifferent species (near zero) are not shown in the plot.

Discussion

The diversity of bryophytes in black alder swamps is related to local environmental variables, ecological processes – such as disturbance, succession, substrate-turnover – and landscape factors. The environmental variables chosen in this investigation, focussing on substrate and microclimatic variation together with hydrological factors, explained nearly 50% of the distribution of bryophytes. Environmental variables not examined here, such as topography, surrounding landscape structure and historical land use are factors potentially responsible for the unexplained part of the variation. For example, it is known that topography and the surrounding landscape affect the moisture and humidity conditions (Pharo and Baettie 2002). Most of the studied black alder swamps occur as small fragments in the landscape, which means that they are affected by microclimatic edge effects (Gignac and Dale 2005, Hylander 2004). It is also likely that the distance to other black alder swamps or to other types of forests is important for the dispersal of bryophytes among the black alder swamps (Söderström and Jonsson 1992, Zobel 1997). Many black alder swamps occur as isolated islands in a cultivated landscape. Historically they have been used for hay harvest, grazing and selective logging. Fallen logs have certainly been rare during for centuries in south Sweden because of the need for fire wood and it is probable that species specialized to this substrate have locally gone extinct without possibility for re-colonization due to poor dispersal capacity.

Hydrology and disturbance

Slope was used as a variable to compare the contrasting hydrological conditions in different types of black alder swamps. One condition for the development of black alder swamps in slopes is moving water during most of the year, often with several springs and small brooks. For bryophytes of forest floor this is important and the species diversity was high in this type of black alder swamps. Fremstad (1983) described similar black alder swamps in flushed hillsides in Norway where the precipitation is high. Another factor that showed to be important was disturbance by flooding. Black alder swamps in depressions, in lower part of drumlins, and along lakes, streams and brooks are flat and seasonally flooded. In this investigation we used depth of water, soil depth and width of streams to study the hydrological conditions. From investigations of vascular plants it is known that flooding is one of the major abiotic factors determining the distribution of plant species in river areas (Keddy 1984, Crawford 1989, Silvertown et al. 1999, Vervuren et al. 2003). The flooding regime, mainly duration, depth, and frequency (Vervuren et al. 2003) are important also for bryophytes. The differences can be large between north- and south-facing slopes as well as if the swamp is situated in a narrow valley or in more open places.

The 'flat swamps' are usually flooded at least once during the winter/spring season but can also be flooded during heavy rain during summer or autumn. Flooding can physically or physiologically damage the bryophytes.

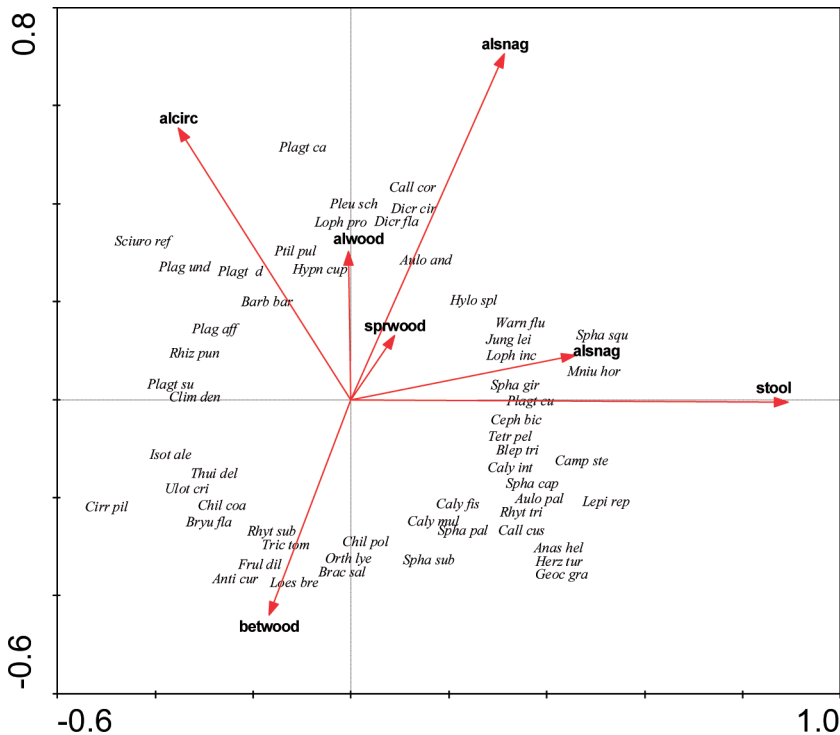


Figure 7. RDA for wood and bark group of variables (cf. Table 1 and 4). Indifferent species (near zero) are not shown in the plot.

Long time of submersion especially in stagnant and eutrophic waters can lead to too slow diffusion of CO_2 and low assimilation (Proctor 1982), to oxygen deficiency, but also deposition of litter and sediment. In the part of the swamps where water is stagnant it seems that mere survival is the most prominent explanation for species occurrence. In drier years, with lower water level, bryophytes can establish in the open patches. In 1998 *C. cordifolium* was quite frequent at one locality but during the following six years there were only few individuals located at the edge of the swamp. The most important constraint that vascular plants have to deal with during flooding is oxygen deficiency (Crawford and Brändle 1996). Some of the black alder swamps lacked vascular plants and also the bryophytes had difficulties to establish at these sites. Probably, the dry period is too short for annuals/ephemerals to establish. Bryophytes typically occupy open patches only if long periods of dry weather with low water level occur. For bryophytes adapted to drier conditions the physiological stress can be considerable but on the other hand bryophytes adapted to wetter conditions will be stressed as well. Few bryophytes can live several months under water and the rest of the year under dry conditions. Differential tolerance of flooding frequency and magnitude (Kimmerer and Allen 1982) is decisive for the distribution of those bryophytes. The bryophytes are zoned in the swamps as follows: usually no species in the stagnant water, a few at the edge

of the stagnant water (for example erect mosses, mostly *Calliergon cordifolium*, *Sphagnum squarrosum* and *Plagiomnium ellipticum*), more species at the banks of the streams and sometimes rather many at the flooded part of the stools of black alder (some hepatics including *Pellia epiphylla*, *Scapania nemorea* and *Chiloscyphus polyanthos*). Higher up on the black alder stools and on the bark there are again few species.

In 'gentle slopes', under only temporarily waterlogged conditions (with peat production), more vascular plants and bryophytes can establish. In this zone inundation is shorter and bryophytes can survive and grow during spring and autumn. During summer the irradiance is low, due to shading by tall vascular plant vegetation, so growth will be slow. The dominating vascular plants at such sites were *Urtica dioica*, *Filipendula ulmaria* and *Athyrium filix-femina*. Bryophytes with a high growth rate can rapidly colonize during spring and autumn. *Brachythecium rutabulum*, common in those swamps, is known to have one of the largest differences among bryophytes in relative growth between low and high irradiance and, furthermore, to exploit stem litter of *U. dioica* (Rincon 1993).

In 'slopes', such as flushed hillsides, the conditions are quite different as compared to the flooded swamps. The difference in microclimate between winter and summer seasons is less pronounced and the humidity, emanating from continuously moving water, can be high in such

Table 5. Pearson correlation coefficients between environmental variables and number of bryophyte species per plot, number of liverwort species per plot and number of species belonging to separate life strategies per plot. Significance levels: $p < 0.05$ *, $p < 0.01$ **, $p < 0.001$ ***.

	Species richness bryophytes	hep	p	ps	pc	l	cp	c
Basareal	-0.35**	-0.34**	-0.24*	0.26*	-0.29*	-0.34**	-0.27*	-0.41***
Basareaspr	0.45***	0.43***	0.36**	ns	0.30**	0.46***	0.34**	0.56***
Basareabet	ns	ns	ns	ns	ns	ns	ns	ns
Basareafrax	ns	ns	ns	ns	ns	ns	ns	ns
Alcirc	ns	ns	ns	-0.35**	ns	-0.30*	ns	ns
Slope	0.48***	0.60***	0.57***	ns	0.28*	0.40***	0.27*	0.55***
Alwood	ns	ns	ns	ns	ns	ns	ns	ns
Sprwood	0.35**	0.39**	ns	ns	ns	ns	0.46***	0.49***
Stool	ns	0.27*	ns	ns	ns	0.43***	0.27*	0.33**
Longitude	ns	ns	ns	ns	ns	ns	ns	ns
pH-soil	ns	ns	ns	ns	ns	0.24*	ns	ns

swamps without deficiency of carbon dioxide or oxygen. Permanently flowing water from springs accumulates minerals in the peat, resulting in a rich fen bryophyte flora (Sjörs and Gunnarsson 2002). Black alder swamps in slopes therefore have a rich bryophyte ground flora,

with many competitive perennials and long-lived shuttle species. Liverworts of small stature, vulnerable to drought, are best represented in this habitat due to the high and even humidity which enables them to colonize small brooks, stones, dead wood and stools. The most

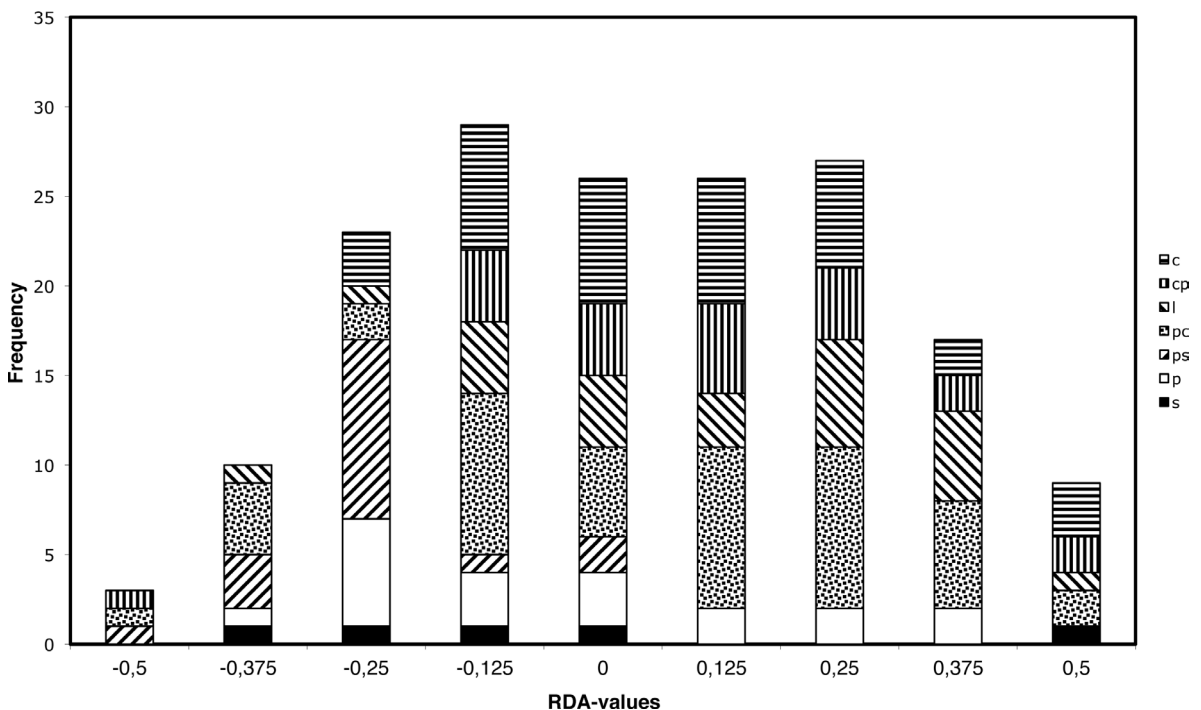


Figure 8. Frequency diagram displaying the number of species belonging to different life strategy categories along the first axis in a RDA with all variables included (cf. Fig. 3). Figures under the x-axis are mid-values of intervals. Abbreviations for life strategy categories are given in Table 3.

important environmental challenge in this habitat is assumedly competition among large perennial mosses.

Tree species

The tree mixture had pronounced effects on the composition of bryophytes. The impact of spruce is important in the swamps with respect to shading, humidity, chemical composition and the physical structure of litter. We found a significantly positive relationship between the proportion of spruce and the species richness of bryophytes. Swamps with spruce contained more forest floor species but also more epiphytes and epixylics. The correlation between the proportion of spruce and the number of liverworts was also positive and significant. In an investigation of epiphytes on aspen Hazel et al. (1998) found that a higher density of spruce, had positive effect on the cover of *Pylaisia polyantha* and *Radula complanata* due to more efficient shade. Simmons and Buckley (1992) found that cover and species numbers of ground-dwelling mosses were positively correlated with the proportion of spruce trees in mixed stands of spruce and broad-leaved trees. Soil and air moisture was crucial for bryophyte survival and reproduction and they suggested that shade-tolerant bryophytes might have a competitive advantage over vascular plants in low light. The low light intensities below spruce could decrease the risk of desiccation, and thus enhance the growth of the bryophytes. Similarly, Sætre et al. (1997) found a higher cover and heterogeneity of mosses and liverworts in the pure spruce stands than in the mixed spruce–birch stands. They proposed differences in chemical composition and physical structure between spruce needles and birch leaves as likely factors causing the observed differences in ground vegetation. To summarize, it is possible that spruce, as an evergreen tree species, buffers the differences in humidity between seasons. Pure stands of black alder have less species than the mixed stands. Black alder have more epiphytes than spruce, but fewer forest floor species and epixylics.

The litter layer in black alder forest is thin as compared to forests of other deciduous tree species (Oechel and van der Cleve 1986, Ódor and van Hees 2004). The leaves of black alder are rich in nitrogen and decompose fast in a moist environment, which means that the shading effect of leaves after defoliation is temporary, often allowing the development of a rich moss carpet as long as the water level is not too high. Weibull (2000) found that boulders and plots below the base-rich deciduous trees, ash, elm and maple, roughly held twice as many species as those below Norway spruce. Through-fall and litter quality were the main factors for the species composition and richness. Our results agree better with the result of Simmons and Buckley (1992) probably because birch and black alder are not base-rich trees in combination with the fact that our study was not restricted to

bryophytes on stones. We used pH as indicator of nutrient availability. pH is not a nutrient factor per se but reflects the general nutrient status of the soil, and is, for example, strongly affecting the nitrification rate (Falkengren-Grerup et al. 1998). Gradient analyses of data from 661 Swedish deciduous forests have shown that the site scores along the first ordination axes (reflecting the floristic variation) are highly correlated to pH (Diekmann and Falkengren-Grerup 1998). In this investigation there were no plots situated in calcareous districts and the pH varied between 4–7. Admixture of ash in the black alder swamps markedly changed the bryophyte flora on stems, stones and somewhat on the ground due to a higher pH. The bryophyte flora on the ground in ash forests, if not overgrown by vascular plants, can be species rich due to a rather thin litter layer.

Dead wood

Epixylic bryophytes are frequent in mixed black alder and spruce swamps. The relationship between frequency of spruce logs and the number of liverwort species was significantly positive. On logs of black alder, we found few epixylic bryophytes in flat swamps as compared to swamps in slopes or in ravine-like, north-facing swamps. We can see two explanations for this difference. First, there are differences in the surface structure and the decomposition time of the logs. Many decorticated black alder logs have a relatively smooth surface for many years so propagules have difficulties to establish until the logs are well rotted and pitted (McAlister 1997). It seems to be easier for liverworts to establish on spruce logs. Second, the logs are exposed to more open and dry conditions in flat black alder swamps as compared to evergreen spruce, or mixed spruce swamps, particularly during the winter months. In comparison, Ódor and van Hees (2004) found that climatic factors determine the composition of bryophytes on beech logs. They found that more species and especially more epixylic species such as liverworts were found in ravine-like near-natural beech stands than in zonal beech forest situated on plateaux. The species richness of individual logs was also higher in the ravine-like forest and the proportion of logs colonized by bryophytes was higher. To sum up, we believe that surface structure, humidity and isolation explain why dead wood of black alder has less bryophyte species than dead wood of spruce. Where the humidity is high, logs of black alder can be colonized by many of the epixylics that are otherwise confined to spruce logs (Fig. 7), e.g. *Nowellia curvifolia*, *Jamesoniella autumnalis*, *Lepidozia reptans*, *Riccardia latifrons* and *Plagiothecium laetum*. In contrast, *Plagiothecium latebricola* is almost exclusively found in flat black alder swamp, where it grows on black alder dead wood, on stools and snags, but also on black alder bark. It was rarely found on birch stools in alder swamps and

only once on a spruce root. Thus *P. latebricola* is rare in biotopes dominated by spruce trees in contrast to many other epixylic bryophytes.

Life-strategy categories

Bryophyte life categories are correlated with habitats factors and in particular with the degree of environmental fluctuations (During 1979). In flat black alder swamps the seasonal differences with respect to hydrology and light conditions are much more pronounced than in sloping swamps. We found that the stress-tolerant perennials were overrepresented in flat swamps, especially in swamps that are more open, due to flooding and a patchy canopy (a lot of black alder stems continuously die rather young). The irradiance can here be high. If the water between the stools disappears during the summer, it can be rather dry on tree trunks, stools, stones, and dead wood. On the other hand, competitive perennials and long-lived shuttle species tend to dominate in the sloping swamps and in ravine-like places. Here the forest is less disturbed and the microclimate more constant. The long-lived shuttle category occurs mostly on the forest floor (*Plagiomnium* and *Sphagnum* species) and as epiphytes. The epiphytes on black alder were few and mostly stress-tolerant in the continental climate in Småland, while epiphytes were relatively common on the black alder trees in the suboceanic and more humid climate in Halland. The long-lived shuttle species have been shown to correlate with epiphytic habitats in the tropics and in cloud forests (During 1979, Kürschner et al. 2007, Hernandez-Garcia 1996). In Gomera (Canary Islands) long-lived shuttle bryophytes were more frequent in the ericaceous forest with the highest mist precipitation and throughfall (González-Mancebo et al. 2004). In central Norway long-lived shuttle bryophytes grows on the forest floor, but much more frequently in old-growth spruce forest than in managed spruce forest. Many of these are dependent on both stable microclimatic and soil conditions (high humidity and moisture) and such qualities disappear when forests are clear-cut (Frisvoll 1997). In this investigation the colonists were more common in the humid swamps, in particularly growing on dead wood, stools, tree trunks and occasionally in brooklets (e.g. *Fissidens* spp., *Calypogeia* spp.). Bare soil after flooding, in pools, was seldom colonized, but when it occurred, by competitive perennials and long-lived shuttle species. In comparison, the colonists in central Norway (Frisvoll 1997) constitutes an important fraction of the spruce forest, nearly half of the number of species (47% colonists, 31% perennials and 15 long-lived shuttles). In the young planted and thinned forests there were few colonist species in contrast to older forest where decaying wood is an abundant substrate. Frisvoll (1997) also pointed out the importance of the site – the most species rich vegeta-

tion type tall fern/tall herb occupies the bottom of slopes where the humidity and soil moisture is high.

Conclusions

The environment is complex in black alder swamps and the major factor determining the distribution of bryophytes is the hydrological conditions, in particular since hydrology also influences the tree species composition. Different degrees of water availability and drought stress give the mosaic character to the swamps.

We found comparatively much dead wood in black alder swamps, both as snags and logs. The amount of dead wood is important for the species richness in black alder swamps in combination with humidity. If the humidity is low there are few epixylics but the species diversity increases with higher humidity (in flushed hillsides, and to the west due to more precipitation) and with higher spruce content. Spruce has an important role in the swamps because it changes the microclimate to become more humid and creates a lot of dead wood. Most epixylic bryophytes tend to occupy spruce dead wood as a primary substrate and black alder dead wood as a secondary substrate, provided that spruce is present.

Black alder stools are important as substrate for the survival of various bryophytes during flooding periods. The most exclusive bryophyte on the black alder stools is *Plagiothecium latebricola*. Large stools in flushed hillsides are potentially especially rich of liverworts.

The predictor variables used in this study, mostly habitat variables, explained about 50% of the distribution of bryophytes. Variables not studied in here for practical reasons, but probably important for species composition and diversity, includes the amount and timing of flooding, management history, and the degree of historical isolation in the landscape. Humidity, which is also affected by landscape topography, was here only indirectly measured by longitudinal position (which is known to be highly correlated with annual precipitation).

Black alder swamps are relatively species rich in Sweden and since most of the investigated swamps are secondary forests of age about 70 years after abandoned management, the species composition and diversity will certainly change in the future. The amount of snags and logs will probably increase. The most important factor in a conservation perspective is the hydrology. Small changes in hydrology can radically change the conditions for drought sensitive species, particularly since most swamp fragments are small in size. Spruce is currently the dominant commercial tree species in Sweden. There is a risk that spruce by spontaneous spreading shortens black alder swamps life-length. Some spruce is good – too much is bad.

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Appendix 1

Appendix 1. Locality, plot number, coordinates, hydrological classification, size and number of vegetation plots.

Locality	Plot	North	East	hydrological classification	area (ha)
1. Bjuv	1	62°17'54"	13°25'02"	waterlogged soil along stream	2
	2	62°17'46"	13°25'02"	waterlogged soil along stream	
2. Snäckebotorp	1	62°45'32"	13°37'76"	flushed hillside and stream	1
3. Algustorp	1	62°55'50"	13°26'20"	black alder carr	4.8
	2	62°55'52"	13°26'22"	black alder carr	
4. Tjuvhult	1	62°56'30"	13°25'39"	black alder carr	12.9
	2	62°56'34"	13°25'67"	black alder carr	
	3	62°56'03"	13°25'12"	flushed hillside and stream	
5. Tånga	1	62°62'25"	12°99'01"	black alder carr	2
6. Hjörnered	1	62°68'71"	13°41'34"	flushed hillside	2
	2	62°68'77"	13°41'35"	flushed hillside and stream	
7. Västralt	1	62°68'22"	13°45'80"	flushed hillside	3
	2	62°68'24"	13°45'88"	flushed hillside	
8. Göstorp	1	62°78'89"	13°39'28"	flushed hillside	3
9. Överås	1	63°24'27"	13°12'40"	flushed hillside	2
	2	63°23'80"	13°12'42"	flushed hillside	
	3	63°24'21"	13°12'39"	flushed hillside	
10. Fylleskog	1	63°15'28"	14°02'81"	black alder carr	4
	2	63°15'29"	14°02'74"	black alder carr	
	3	63°15'32"	14°02'72"	black alder carr	
	4	63°15'31"	14°02'67"	black alder carr	
	5	63°15'38"	14°02'52"	ash swamp	
11. Tykatorp	1	63°16'71"	13°98'72"	black alder carr	1
	2	63°16'71"	13°98'76"	black alder carr	
12. Brotorpabäck	1	63°23'48"	14°11'32"	black alder carr	15
	2	63°22'88"	14°11'54"	black alder carr	
	3	63°22'74"	14°11'49"	flushed hillside	
	4	63°22'78"	14°11'58"	black alder carr	
	5	63°26'45"	14°12'65"	mixed swamp	
13-14. Bästerna	1	63°26'61"	14°17'16"	flushed hillside	6
	2	63°26'59"	14°17'17"	flushed hillside	
	3	63°26'51"	14°17'18"	flushed hillside	
	4	63°26'53"	14°17'26"	flushed hillside	
	5	63°26'69"	14°17'17"	flushed hillside	
	6	63°26'66"	14°17'20"	flushed hillside	
15. Eske	1	63°26'94"	14°24'67"	black alder carr	16
	2	63°26'97"	14°24'76"	black alder carr	
	3	63°27'43"	14°24'67"	black alder carr	
	4	63°27'13"	14°24'71"	black alder carr	

16. Lidsjö	1	63°28'66"	14°27'43"	flushed hillside	19
	2	63°28'30"	14°27'72"	flushed hillside	
	3	63°28'46"	14°27'44"	flushed hillside	
	4	63°28'41"	14°27'44"	flushed hillside	
	5	63°28'46"	14°27'41"	ash swamp	
17. Sandvik	1	63°29'54"	14°27'60"	black alder carr	4
	2	63°29'61"	14°27'65"	black alder carr	
18. Vråen	1	63°31'05"	14°27'91"	black alder carr	5
	2	63°31'09"	14°27'73"	black alder carr	
19. Gynkelstorp	1	63°30'33"	14°35'73"	waterlogged soil along stream	6
	2	63°30'32"	14°35'69"	waterlogged soil along stream	
	3	63°30'57"	14°35'73"	waterlogged soil along stream	
20. Näset	1	63°28'67"	14°36'83"	waterlogged shore	4
	2	63°28'78"	14°36'84"	waterlogged soil along stream	
21. Nykulla	1	63°26'87"	14°41'06"	waterlogged soil along stream	5
	2	63°26'86"	14°41'12"	waterlogged soil along stream	
22. Kråkenäs	1	63°17'27"	14°47'58"	waterlogged shore along lake	3
23. Bråna	1	63°31'30"	14°45'93"	black alder carr	6
	2	63°31'23"	14°45'94"	black alder carr	
24. Röshult	1	63°47'30"	14°52'45"	mixed swamp	2
	2	63°47'29"	14°52'47"	mixed swamp	
	3	63°47'42"	14°52'30"	mixed swamp	
	4	63°47'48"	14°52'23"	mixed swamp	
25. Misterfall	1	64°27'85"	14°84'84"	waterlogged soil along stream	0.8
26. Gunhem	1	64°29'68"	15°03'81"	flushed hillside	0.8
	2	64°29'78"	15°03'81"	waterlogged soil along stream	
27. Dymle	1	64°30'39"	15°10'94"	waterlogged soil along stream	1.3
	2	64°30'39"	15°11'03"	waterlogged soil along stream	
28. Trehörna	1	64°42'62"	14°86'47"	black alder carr	0.9
29. Mörtgölen	1	64°41'00"	14°89'81"	waterlogged shore along lake	0.5
30. Slätmon	1	64°38'24"	14°91'86"	mixed black alder carr	0.9
31. Hägerstad	1	64°40'50"	14°97'70"	waterlogged shore along lake	4