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Diversity of *Alnus glutinosa* dominated swamp forests in Estonia

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Abstract

The *Alnus glutinosa* swamps are the most species-rich forest communities in the Fennoscandian hemiboreal zone. Considering the species abundance in different layers and their indicator values, in Estonia these stands can be classified into ten community types: 1) *Calliergonella cuspidata–Carex acutiformis–Thelypteris palustris–Alnus glutinosa*; 2) *Brachythecium rutabulum–Scutellaria galericulata–Rubus caesius–Alnus glutinosa*; 3) *Brachythecium rutabulum–Urtica dioica–Aegopodium podagraria–Alnus glutinosa*; 4) *Plagiomnium elatum–Galeobdolon luteum–Oxalis acetosella–Alnus glutinosa*; 5) *Sphagnum fallax–Filipendula ulmaria–Phragmites australis–Alnus glutinosa*; 6) *Sphagnum riparium–Vaccinium myrtillus–Impatiens noli-tangere–Alnus glutinosa*; 7) *Calliergon cordifolium–Lysimachia thyrsiflora–Carex elongata–Alnus glutinosa*; 8) *Calliergonella cuspidata–Deschampsia cespitosa–Filipendula ulmaria–Alnus glutinosa*; 9) *Climacium dendroides–Calamagrostis canescens–Athyrium filix-femina–Alnus glutinosa*; 10) *Calypogeia integristipula–Filipendula ulmaria–Ulmus laevis–Alnus glutinosa.* The species composition of the communities is determined mainly by the soil reaction and nitrogen content in the soil of their habitats.

Keywords: community types; indicator species; Ellenberg's indicator values; habitats' reaction gradient; nitrogen content gradient

Introduction

Alnus glutinosa dominated swamp forests (alder carrs) occur in Europe usually at strongly waterlogged sites on the banks of ponds, lakes and seacoast, floodplain depressions and mire margins (Dierβen 1996, Douda et al. 2016). In Estonia, they are also represented at the coast of the Baltic Sea behind or between the coastal dunes in areas flooded by seawater (Paal and Rooma 2001). Moreover, they are found on non-waterlogged sites of scree at the foot of the North-Estonian Klint and on the coastal plains adjacent to these sites (Paal 2007, 2009).

According to the data from 1984 the swamp forests area constituted 2.5% of the total area of state forests but by the data from 2003 only 1.2% (Lõhmus 2004). Due to the sites of various hydrological regimes and soil properties, as well as due to varying microtopography these stands present the most species-rich forests communities in the Fennoscandian hemiboreal zone (Prieditis 1997, Paal et al. 2008). At the same time, alder carrs are highly vulnerable to man-made impact, alien plant species invasion and natural disturbances in some localities (Richardson et al. 2007, Douda et al. 2016, Slezák et al. 2022), therefore they are qualified as threatened forest communities of all-European importance: types 9080 Fennoscandian deciduous swamp woods and 91E0 Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (*Alno-Padion*, *Alnion incanae*, *Salicion albae*) (EC 1992).

The purposes of this study were the following: (i) to establish the classification structure of these forests in Estonia, (ii) to establish the indicator species of all community types, and (iii) to characterize the environmental conditions of communities of different types.

Material and methods

Field study

With the aim to obtain a representative sample, field data were collected in different regions and landscape facies all over Estonia. The total number of analysed forest stands was 252. In each stand one circular sample plot with a radius of 17.8 m (0.1 ha) was established, considering that (i) the size of analysed stand is at least 0.5 ha, and (ii) it has trees of all age classes and lacks obvious human impacts.

In every sample plot the tree layer was characterized on the basis of their species average basal area at breast height (m^2 ha^{-1}) estimated by means of basal area gauge. Recordings were carried out in three randomly selected

points in the central part of the sample plot. All stems of shrub layer species were counted in five randomly located circular subplots with 2 m radius; young trees (saplings) with a height less than 4 m and/or with a diameter less than 5 cm at breast height (1.3 m) were also interpreted as belonging to the shrub layer. For further analysis, again, the average data was used. Shrub species outside the circular subplots were noted with a value of one. The projective cover of all herb and moss layer species was estimated on 5–10 randomly located sample quadrats of 1 × 1 m. If some additional species were recorded outside the sample quadrats, they were introduced into species list and in data processing considered conditionally with coverage of 0.1%. Bryophytes growing on tree stems, decaying windthrown trees or rocks on screes were registered separately and not involved in statistical analysis.

The names of vascular plants are given by Krall et al. (2010) and the nomenclature of bryophytes by Ingerpuu and Vellak (1998).

Data processing

Cluster analysis was performed on data from the field and moss layers, using the β-flexible algorithm (McCune and Mefford 2011) and the relative Sørensen distance as the measure of dissimilarity (McCune and Grace 2002). The clusters (i.e. community types) were established based on a dendrogram on the level of 75% remaining information. Objectivity of the established clusters was tested by the multi-response permutation procedures (MRPP, *see* McCune and Mefford 2011), considering correction for multiple comparisons.

For every stand, the mean Ellenberg indicator values of habitats were calculated on the ground of field layer species cover values and revised indicator values (Chytrý et al. 2018) by weighed averaging (Schaffers and Sýkora 2000). Differences between mean values of environmental variables were checked by the χ^2 test (StatSoft 2005, 2011).

The species indicator values in community types were calculated by the Dufrêne and Legrendre (1997) method included in PC-ORD software package (McCune and Mefford 2011). The statistical significance of the obtained indicator values was evaluated by the Monte Carlo permutation test ($N = 499$).

For ordination of the sample plots and environmental variables, the detrended correspondence analysis (DCA, McCune and Mefford 2011) with detrending-by-segments and down-weighting of rare species was used. Species occurring in the data set less than three times were filtered out prior to the analysis.

Results

In total, 54 species were recorded in the tree and shrub layers, 383 species in the field layer and 199 species in the moss layer. According to the cluster analysis dendrogram, on the level of remaining information 75% all forests were divided into ten community types (Table 1). Testing by the multi-response permutation procedures confirmed that the species content of all community types was significantly different at $p < 0.001$.

In the tree layer of the communities of the first type, besides the dominant *Alnus glutinosa*, birches are also rather frequent; in the field layer, besides of *Carex acutiformis* and *Thelypteris palustris*, the most abundant species are there *Filipendula ulmaria*, *Ranunculus repens*, *Caltha palustris*, *Carex vesicaria*, *Carex elongata* and *Solanum dulcamara*. Significant ($p < 0.001$) indicator species are *Caltha palustris*, *Carex acutiformis*, *C. vesicaria*, *Lysimachia nummularia*, *Ranunculus repens*, *R. lingua*, *Thelypteris palustris*, *Veronica longifolia*, etc., in the moss layer *Calliergonella cuspidata*, *Plagiomnium ellipticum* and *Callitriche cophocarpa* (Table 2). According to the Ellenberg indicator values, the habitats of these communities are comparatively moist (Table 3). The communities of this type occur mostly on floodplains (Table 4).

The communities of the second type have a comparatively dense shrub layer prevailed by *Padus avium*, but including *Frangula alnus*, *Corylus avellana*, *Lonicera xylosteum*, *Sorbus aucuparia*, *Ribes nigrum*, *Viburnum opulus*, etc. In the field layer *Geum rivale*, *Filipendula ulmaria*, *Lysimachia vulgaris*, *Galium palustre*, *Rubus idaeus*, *Iris pseudacorus* are observed, and in the moss layer *Calliergonella cuspidata* is the outstanding species (Table 1). As significant indicator species, the shrubs such as *Grossularia reclinata*, *Lonicera xylosteum*, *Swida sanguinea*, *Ribes nigrum* and *Rhamnus catharticus* are in the foreground, herbaceous plants, such as *Filipendula vulgaris*, *Fragaria vesca*, *Geranium sylvaticum*, *Rubus caesius*, *Scutellaria galericulata*, *Veronica officinalis*, *Galium palustre*, *Lysimachia vulgaris*, *Polygonatum odoratum* were found in the field layer; *Brachythecium rutabulum*, *B. populeum*, *Eurynchium pulchellum* and *Amblystegium varium* in the moss layer should be mentioned (Table 2). The habitat indicator value of soil reaction is rather high (Table 3). These communities were described mostly in Karula National Park, southern Estonia, but also between the coastal dunes (Table 4).

Fraxinus excelsior occurs quite often in the tree layer of the third type communities, but some *Acer platanoides*, *Fraxinus excelsior*, *Ulmus laevis* or *U. glabra* are characteristic as well. The dominant species in the field layer is *Filipendula ulmaria*, while *Impatiens noli-tangere*, *Lunaria rediviva*, *Stellaria nemorum* and *Mercurialis perennis* occur pretty frequently too (Table 1). Several nemoral species, such as *Aegopodium podagraria*, *Stellaria nemorum*, *Allium ursinum*, *Mercurialis perennis* are indicators of this community type in the field layer, and *Mnium hornum* and *Fissidens gracilifolius* in the moss layer (Table 2). These communities are found in various habitats and regions (Table 4); by ecological indicator values their habitats have the highest soil reaction and nitrogen content among the considered forests (Table 3).

Table 1. Centroids of community types (X ± SD)
Only species having abundance more than 0.5 at least in one community type are presented

Species	Community type (and the number of relevés)									
	1 (19)	2 (10)	3 (14)	4 (27)	5 (12)	6 (25)	7 (34)	8 (53)	9 (39)	10 (19)
Tree layer										
Alnus glutinosa	16.1 ± 10.3	9.2 ± 10.3	19.8 ± 15.7	9.4 ± 7.8	9.1 ± 5.7	16.7 ± 11.8	15.4 ± 9.3	14.6 ± 12.5	10.6 ± 8.8	11.2 ± 8.8
Alnus incana	0.1 ± 0.2	1.2 ± 2.4	0.6 ± 1.0	0.4 ± 1.3	-	-	< 0.1 ± 0.1	1.1 ± 4.0	0.1 ± 0.8	0.1 ± 0.2
Betula pubescens	7.0 ± 5.3	1.0 ± 1.4	1.2 ± 3.1	4.9 ± 4.8	3.9 ± 3.5	5.4 ± 4.4	8.7 ± 6.2	2.6 ± 3.6	6.1 ± 5.5	3.6 ± 3.7
Fraxinus excelsior	0.4 ± 0.9	0.8 ± 1.2	2.6 ± 5.8	0.9 ± 1.9	1.4 ± 1.9	-	< 0.1 ± 0.1	1.2 ± 2.3	0.1 ± 0.5	0.7 ± 1.5
Padus avium	-	-	0.3 ± 0.8	0.5 ± 1.2	0.8 ± 1.8	0.1 ± 0.6	-	0.1 ± 0.6	0.4 ± 0.8	1.3 ± 2.0
Picea abies	1.5 ± 2.5	0.7 ± 2.2	0.1 ± 0.3	2.4 ± 2.9	0.1 ± 0.3	1.4 ± 2.1	1.6 ± 2.2	0.4 ± 0.8	2.4 ± 3.3	1.5 ± 5.0
Pinus sylvestris	0.1 ± 0.2	0.7 ± 1.2	0.2 ± 0.9	0.3 ± 1.0	0.6 ± 1.2	1.1 ± 2.1	2.3 ± 4.6	0.2 ± 1.0	0.0 ± 0.2	-
Populus tremula	0.4 ± 0.8	0.2 ± 0.3	< 0.1 ± 0.1	0.9 ± 2.4	1.4 ± 4.9	1.7 ± 8.0	0.1 ± 0.3	0.8 ± 2.1	0.6 ± 1.1	0.5 ± 1.5
Quercus robur	0.1 ± 0.5	0.2 ± 0.6	-	< 0.1 ± 0.1	1.0 ± 1.3	-	< 0.1 ± 0.1	0.1 ± 0.5	0.2 ± 0.7	< 0.1 ± < 0.1
Ulmus glabra	0.1 ± 0.2	-	0.3 ± 0.6	0.1 ± 0.3	< 0.1 ± < 0.1	-	-	0.1 ± 0.5	0.1 ± 0.3	0.7 ± 1.2
Ulmus laevis	-	-	0.4 ± 1.3	0.3 ± 1.4	< 0.1 ± < 0.1	< 0.1 ± < 0.1	-	< 0.1 ± 0.2	-	0.9 ± 1.4
Regrowth and shrub layer										
Alnus glutinosa	0.4 ± 0.5	0.1 ± 0.3	0.3 ± 0.6	0.1 ± 0.5	0.9 ± 1.1	1.0 ± 1.2	1.2 ± 0.9	0.2 ± 0.5	0.6 ± 1.0	0.2 ± 0.7
Alnus incana	0.1 ± 0.2	-	0.2 ± 0.4	0.1 ± 0.4	-	0.2 ± 0.6	-	0.4 ± 1.0	0.1 ± 0.2	< 0.1 ± < 0.1
Betula pubescens	0.1 ± 0.5	-	0.1 ± 0.4	0.1 ± 0.4	0.3 ± 0.8	0.5 ± 0.7	0.5 ± 0.7	< 0.1 ± 0.3	0.1 ± 0.4	< 0.1 ± < 0.1
Corylus avellana	0.2 ± 0.7	1.3 ± 1.5	0.4 ± 1.3	0.9 ± 1.7	0.1 ± 0.3	-	-	0.4 ± 1.1	0.1 ± 0.3	0.6 ± 1.1
Frangula alnus	1.1 ± 2.1	1.4 ± 1.8	0.3 ± 0.6	0.3 ± 0.6	0.8 ± 0.9	0.6 ± 1.0	1.6 ± 1.3	1.1 ± 1.8	0.8 ± 1.1	0.0 ± 0.1
Fraxinus excelsior	0.6 ± 0.9	0.2 ± 0.6	0.5 ± 0.9	0.3 ± 0.7	0.6 ± 1.1	0.2 ± 0.6	0.1 ± 0.3	0.7 ± 1.4	0.8 ± 1.5	1.4 ± 1.8
Grossularia reclinata	-	0.7 ± 1.3	-	-	-	-	-	0.1 ± 0.3	-	< 0.1 ± < 0.1
Juniperus communis	-	0.8 ± 1.3	-	-	-	-	-	0.4 ± 0.8	-	< 0.1 ± < 0.1
Lonicera xylosteum	0.2 ± 0.5	1.7 ± 1.4	0.1 ± 0.3	0.1 ± 0.4	-	< 0.1 ± 0.2	-	0.2 ± 0.6	< 0.1 ± < 0.1	0.1 ± 0.3
Padus avium	1.0 ± 1.2	3.6 ± 1.4	2.8 ± 3.0	1.0 ± 1.6	< 0.1 ± < 0.1	0.5 ± 0.9	0.1 ± 0.5	3.0 ± 2.7	0.5 ± 0.8	1.9 ± 1.2
Picea abies	0.3 ± 0.6	-	0.2 ± 0.4	0.5 ± 0.9	0.3 ± 0.7	0.8 ± 1.0	1.3 ± 1.0	< 0.1 ± 0.3	0.9 ± 1.2	0.1 ± 0.3
Ribes nigrum	0.1 ± 0.3	1.2 ± 1.2	0.3 ± 0.8	0.7 ± 3.3	-	< 0.1 ± < 0.1	< 0.1 ± < 0.1	0.3 ± 0.8	0.1 ± 0.4	0.1 ± 0.3
Ribes rubrum	-	0.5 ± 0.8	0.2 ± 0.5	-	-	-	-	0.2 ± 0.6	< 0.1 ± < 0.1	< 0.1 ± < 0.1
Rosa sp.	< 0.1 ± < 0.1	0.2 ± 0.4	1.4 ± 5.4	-	-	-	-	0.1 ± 0.4	-	< 0.1 ± < 0.1
Sorbus aucuparia	0.3 ± 0.7	1.6 ± 1.3	0.8 ± 1.3	0.3 ± 0.7	0.1 ± 0.3	0.3 ± 0.6	0.5 ± 0.7	1.2 ± 1.4	0.1 ± 0.4	0.2 ± 0.6
Swida sanguinea	-	0.6 ± 1.3	-	-	-	-	-	0.1 ± 0.4	-	-
Tilia cordata	0.8 ± 1.8	-	-	0.5 ± 1.2	0.1 ± 0.3	-	< 0.1 ± 0.2	0.2 ± 0.5	0.3 ± 1.1	0.6 ± 1.2
Ulmus glabra	0.1 ± 0.3	< 0.1 ± < 0.1	< 0.1 ± 0.1	0.1 ± 0.4	0.1 ± 0.3	-	-	0.1 ± 0.4	-	0.5 ± 1.0
Viburnum opulus	0.3 ± 1.3	0.9 ± 1.0	0.1 ± 0.3	0.2 ± 0.5	0.1 ± 0.3	0.1 ± 0.3	0.1 ± 0.3	0.8 ± 1.3	< 0.1 ± < 0.1	0.1 ± 0.1
Field layer										
Aegopodium podagraria	< 0.1 ± 0.1	0.3 ± 0.7	13.6 ± 19.7	1.8 ± 4.9	-	-	-	0.2 ± 0.7	-	< 0.1 ± < 0.1
Allium ursinum	-	-	2.9 ± 9.8	0.1 ± 0.6	-	-	-	0.1 ± 0.8	-	-
Angelica archangelica	-	2.4 ± 7.5	-	0.2 ± 1.2	-	-	-	0.3 ± 2.2	-	< 0.1 ± < 0.1
Angelica sylvestris	< 0.1 ± 0.1	1.0 ± 2.2	0.1 ± 0.3	0.1 ± 0.4	< 0.1 ± < 0.1	< 0.1 ± < 0.1	< 0.1 ± 0.2	0.6 ± 1.9	< 0.1 ± 0.2	0.1 ± 0.5
Athyrium filix-femina	0.5 ± 1.1	0.1 ± 0.3	3.3 ± 5.2	1.4 ± 1.8	< 0.1 ± < 0.1	< 0.1 ± 0.2	0.4 ± 0.8	0.7 ± 1.9	4.4 ± 13.1	1.5 ± 1.9
Calamagrostis arundinacea	-	-	0.4 ± 1.3	0.3 ± 0.9	-	0.8 ± 1.2	< 0.1 ± 0.2	-	< 0.1 ± < 0.1	< 0.1 ± < 0.1
Calamagrostis canescens	0.1 ± 0.3	0.1 ± 0.4	0.3 ± 0.8	0.2 ± 0.6	1.4 ± 1.2	0.6 ± 1.1	1.8 ± 3.1	0.3 ± 0.9	2.1 ± 1.7	0.2 ± 0.6
Calla palustris	1.0 ± 2.4	-	-	-	-	-	0.4 ± 0.9	< 0.1 ± 0.2	0.1 ± 0.4	-
Caltha palustris	2.3 ± 2.7	1.5 ± 2.0	0.3 ± 0.6	0.6 ± 1.3	0.2 ± 0.4	0.1 ± 0.3	0.2 ± 0.5	1.7 ± 2.1	0.2 ± 0.4	0.1 ± 0.2
Calystegia sepium	-	0.5 ± 1.5	-	0.3 ± 1.5	-	-	-	0.2 ± 1.1	-	< 0.1 ± < 0.1
Carex acuta	0.9 ± 2.9	-	-	-	-	0.5 ± 1.4	0.4 ± 0.9	< 0.1 ± < 0.1	-	< 0.1 ± < 0.1
Carex acutiformis	3.9 ± 8.6	-	-	-	-	-	< 0.1 ± 0.2	< 0.1 ± 0.1	-	< 0.1 ± < 0.1
Carex appropinquata	0.1 ± 0.2	-	-	0.1 ± 0.4	-	0.1 ± 0.4	0.9 ± 0.3	-	-	-
Carex canescens	-	-	-	0.1 ± 0.4	-	-	0.6 ± 0.9	< 0.1 ± 0.3	-	< 0.1 ± < 0.1
Carex cespitosa	0.4 ± 1.4	-	-	0.9 ± 3.0	1.3 ± 2.0	0.1 ± 0.4	0.4 ± 0.8	0.3 ± 1.2	0.7 ± 1.4	-
Carex elata	-	0.4 ± 1.1	-	-	0.8 ± 1.4	0.2 ± 0.6	-	0.2 ± 0.8	-	-
Carex elongata	1.9 ± 6.6	-	0.3 ± 0.7	0.2 ± 0.5	-	0.1 ± 0.6	2.7 ± 5.5	0.4 ± 1.7	0.4 ± 0.9	0.2 ± 0.6
Carex lasiocarpa	0.1 ± 0.2	-	-	0.1 ± 0.3	0.5 ± 1.2	0.6 ± 1.4	0.1 ± 0.7	-	-	-
Carex vesicaria	2.0 ± 2.7	-	-	-	1.6 ± 2.1	0.8 ± 1.7	0.6 ± 1.0	0.4 ± 1.6	0.2 ± 0.7	-
Chrysosplenium alternifolium	0.2 ± 0.5	-	0.8 ± 0.9	0.2 ± 0.6	-	-	-	0.2 ± 0.9	0.3 ± 0.8	0.5 ± 0.8
Cirsium oleraceum	0.2 ± 0.8	-	0.4 ± 1.0	0.5 ± 1.2	-	-	< 0.1 ± 0.2	0.4 ± 1.1	0.2 ± 0.6	1.0 ± 3.2
Convallaria majalis	0.1 ± 0.3	0.9 ± 1.4	0.1 ± 0.5	0.8 ± 1.6	< 0.1 ± < 0.1	< 0.1 ± 0.2	0.1 ± 0.2	0.6 ± 1.1	0.1 ± 0.4	0.6 ± 0.8
Crepis paludosa	0.1 ± 0.5	< 0.1 ± 0.1	1.5 ± 2.9	1.5 ± 2.8	-	0.2 ± 0.7	0.1 ± 0.4	0.9 ± 2.9	0.1 ± 0.3	0.1 ± 0.4
Deschampsia cespitosa	< 0.1 ± 0.1	2.3 ± 1.6	1.2 ± 2.6	0.1 ± 0.4	-	< 0.1 ± 0.2	0.3 ± 0.5	3.7 ± 7.1	0.3 ± 0.8	< 0.1 ± < 0.1
Dryopteris carthusiana	0.2 ± 0.4	0.2 ± 0.6	0.5 ± 1.0	0.6 ± 0.8	-	0.2 ± 0.6	0.9 ± 0.8	0.3 ± 0.9	0.9 ± 1.1	-
Equisetum fluviatile	0.3 ± 0.9	-	0.1 ± 0.3	0.2 ± 0.4	0.9 ± 1.2	0.6 ± 1.2	0.3 ± 0.7	0.3 ± 1.0	0.1 ± 0.2	-
Equisetum pratense	0.2 ± 0.5	-	0.1 ± 0.2	0.7 ± 1.7	-	0.3 ± 0.9	-	0.3 ± 1.2	< 0.1 ± < 0.1	0.1 ± 0.2
Equisetum sylvaticum	< 0.1 ± 0.1	-	< 0.1 ± 0.1	0.5 ± 1.7	-	0.1 ± 0.3	0.5 ± 0.7	< 0.1 ± 0.1	0.1 ± 0.3	0.1 ± 0.3
Eupatorium cannabinum	0.2 ± 0.8	-	-	0.2 ± 1.0	-	-	-	0.3 ± 1.2	-	< 0.1 ± < 0.1
Filipendula ulmaria	4.4 ± 5.7	7.6 ± 6.4	10.5 ± 7.2	2.2 ± 3.4	4.4 ± 8.4	0.6 ± 1.0	0.7 ± 1.0	26.7 ± 15.4	3.4 ± 2.3	5.2 ± 3.8
Fragaria vesca	-	0.8 ± 1.5	-	-	-	< 0.1 ± 0.2	< 0.1 ± 0.2	< 0.1 ± 0.2	< 0.1 ± 0.2	< 0.1 ± < 0.1
Galeobdolon luteum	-	-	0.8 ± 1.6	1.0 ± 1.4	-	-	-	0.1 ± 0.7	0.4 ± 2.6	0.3 ± 1.1
Galium aparine	-	-	0.4 ± 1.6	0.2 ± 1.0	-	0.5 ± 2.6	-	-	-	< 0.1 ± < 0.1

Table 1. (continued)

Species	Community type (and the number of relevés)									
	1 (19)	2 (10)	3 (14)	4 (27)	5 (12)	6 (25)	7 (34)	8 (53)	9 (39)	10 (19)
Galium palustre	0.8 ± 1.4	2.9 ± 4.2	0.3 ± 0.7	0.3 ± 0.7	< 0.1 ± < 0.1	0.1 ± 0.3	1.1 ± 1.1	1.3 ± 1.9	0.9 ± 1.0	0.1 ± 0.2
Galium uliginosum	0.8 ± 1.1	1.4 ± 3.3	0.5 ± 1.5	-	-	0.1 ± 0.7	-	0.8 ± 2.4	0.1 ± 0.7	< 0.1 ± < 0.1
Geum rivale	0.2 ± 0.3	8.7 ± 7.7	1.1 ± 2.5	1.5 ± 4.6	-	< 0.1 ± 0.1	0.1 ± 0.4	3.4 ± 5.3	0.2 ± 0.6	0.2 ± 0.5
Glyceria plicata	-	1.0 ± 2.1	-	-	-	-	-	0.9 ± 4.1	-	< 0.1 ± < 0.1
Humulus lupulus	0.2 ± 0.6	-	1.5 ± 5.1	0.3 ± 1.4	0.3 ± 1.2	-	-	0.3 ± 1.2	-	0.2 ± 0.6
Impatiens noli-tangere	0.1 ± 0.2	-	5.2 ± 8.6	1.1 ± 4.5	-	3.9 ± 14.4	-	0.2 ± 1.0	< 0.1 ± 0.1	< 0.1 ± < 0.1
Impatiens parviflora	-	< 0.1 ± 0.1	1.9 ± 4.8	0.2 ± 1.0	-	0.3 ± 1.0	-	1.5 ± 7.6	-	< 0.1 ± < 0.1
Iris pseudacorus	1.1 ± 1.4	1.9 ± 3.5	< 0.1 ± 0.1	-	< 0.1 ± < 0.1	0.6 ± 1.0	0.3 ± 0.6	0.3 ± 1.0	0.1 ± 0.3	-
Lunaria rediviva	-	-	5.5 ± 20.6	-	-	-	-	-	-	< 0.1 ± < 0.1
Lycopus europaeus	0.4 ± 0.6	0.5 ± 0.9	0.2 ± 0.4	0.1 ± 0.3	0.1 ± 0.3	0.1 ± 0.3	0.1 ± 0.3	1.0 ± 2.4	0.2 ± 0.5	< 0.1 ± < 0.1
Lysimachia thyrsiflora	0.3 ± 0.6	-	0.2 ± 0.3	< 0.1 ± 0.2	0.1 ± 0.1	0.4 ± 0.6	0.9 ± 0.9	0.3 ± 1.0	0.2 ± 0.6	0.1 ± 0.2
Lysimachia vulgaris	0.6 ± 2.0	2.8 ± 3.4	0.1 ± 0.2	0.3 ± 0.7	< 0.1 ± 0.1	0.5 ± 0.8	0.8 ± 0.7	2.0 ± 3.0	0.2 ± 0.5	-
Maianthemum bifolium	< 0.1 ± 0.1	0.7 ± 2.1	0.1 ± 0.2	0.2 ± 0.6	< 0.1 ± < 0.1	0.3 ± 0.5	0.7 ± 0.6	0.4 ± 1.0	0.3 ± 0.6	0.2 ± 0.4
Matteuccia struthiopteris	0.1 ± 0.5	-	0.2 ± 0.5	0.2 ± 0.7	-	-	-	0.4 ± 2.2	-	0.6 ± 1.0
Menyanthes trifoliata	0.9 ± 2.2	1.2 ± 3.1	-	0.3 ± 1.0	-	0.5 ± 1.0	0.3 ± 0.5	0.2 ± 1.0	-	-
Mercurialis perennis	0.4 ± 1.8	0.5 ± 1.5	2.9 ± 5.9	2.5 ± 5.0	-	-	-	0.2 ± 0.8	0.4 ± 2.7	1.3 ± 4.2
Milium effusum	-	0.5 ± 1.5	0.3 ± 1.0	0.1 ± 0.6	-	-	< 0.1 ± 0.2	< 0.1 ± 0.1	0.1 ± 0.3	-
Myosotis scorpioides	0.1 ± 0.5	0.5 ± 1.5	0.3 ± 1.0	0.1 ± 0.6	-	-	< 0.1 ± 0.2	0.2 ± 0.6	0.1 ± 0.3	< 0.1 ± < 0.1
Oxalis acetosella	0.2 ± 0.5	0.1 ± 0.2	1.1 ± 2.1	2.7 ± 4.7	-	0.5 ± 0.8	0.5 ± 0.9	0.6 ± 1.7	1.1 ± 1.3	1.0 ± 1.4
Paris quadrifolia	0.1 ± 0.1	0.2 ± 0.3	0.3 ± .8	0.3 ± 0.7	< 0.1 ± < 0.1	-	< 0.1 ± 0.1	0.5 ± 0.7	< 0.1 ± 0.1	< 0.1 ± < 0.1
Peucedanum palustre	0.1 ± 0.3	0.3 ± 0.6	< 0.1 ± 0.1	< 0.1 ± 0.2	< 0.1 ± < 0.1	0.2 ± 0.5	0.5 ± 0.6	0.2 ± 0.7	< 0.1 ± < 0.1	-
Phragmites australis	0.1 ± 0.2	0.1 ± 0.4	-	0.1 ± 0.4	10.3 ± 18.2	1.0 ± 1.4	0.7 ± 1.0	0.1 ± 0.4	0.4 ± 1.1	-
Poa palustris	0.1 ± 0.2	0.1 ± 0.3	0.1 ± 0.4	0.1 ± 0.2	-	-	0.2 ± 0.6	0.6 ± 2.2	-	< 0.1 ± < 0.1
Potentilla palustris	0.1 ± 0.2	< 0.1 ± < 0.1	-	0.1 ± 0.5	-	0.4 ± 0.7	0.6 ± 0.7	< 0.1 ± 0.3	0.1 ± 0.3	< 0.1 ± < 0.1
Ranunculus lingua	0.6 ± 1.0	-	-	-	< 0.1 ± < 0.1	0.2 ± 0.7	-	< 0.1 ± 0.3	-	0.2 ± 0.6
Ranunculus repens	4.0 ± 5.2	2.0 ± 2.5	0.3 ± 0.5	0.2 ± 0.6	0.3 ± 0.8	< 0.1 ± 0.2	0.1 ± 0.5	1.5 ± 2.9	0.1 ± 0.5	0.5 ± 0.9
Rubus caesius	0.4 ± 1.5	11.4 ± 9.8	-	0.5 ± 2.4	-	-	-	2.0 ± 4.2	-	< 0.1 ± < 0.1
Rubus idaeus	1.4 ± 2.7	2.7 ± 4.5	1.4 ± 3.3	0.2 ± 0.5	< 0.1 ± < 0.1	0.2 ± 0.6	0.3 ± 0.6	2.3 ± 5.6	0.1 ± 0.5	0.1 ± 0.5
Rubus saxatilis	0.3 ± 0.7	-	0.1 ± 0.2	0.9 ± 1.3	< 0.1 ± 0.1	0.4 ± .7	0.4 ± 0.7	0.1 ± 0.5	1.3 ± 1.1	0.3 ± 0.7
Scirpus sylvaticus	0.2 ± 0.5	-	1.1 ± 3.7	< 0.1 ± 0.1	-	0.8 ± 1.3	0.5 ± 1.1	0.2 ± 0.9	-	-
Scutellaria galericulata	0.3 ± 0.6	3.2 ± 4.8	0.5 ± 1.0	0.1 ± 0.5	-	< 0.1 ± < 0.1	< 0.1 ± 0.2	0.9 ± 1.7	0.1 ± 0.3	-
Solanum dulcamara	1.7 ± 2.3	1.8 ± 2.2	1.0 ± 3.4	< 0.1 ± 0.1	0.6 ± 2.0	0.5 ± 2.3	0.1 ± 0.4	1.7 ± 2.9	0.2 ± 0.6	0.1 ± 0.2
Stellaria holostea	-	-	0.7 ± 2.7	0.8 ± 2.5	-	-	< 0.1 ± < 0.1	0.1 ± 0.9	-	< 0.1 ± < 0.1
Stellaria nemorum	-	-	5.9 ± 5.4	2.8 ± 7.8	-	0.1 ± 0.3	< 0.1 ± 0.1	0.9 ± 3.7	0.1 ± 0.7	0.1 ± 0.4
Thelypteris palustris	4.8 ± 7.0	0.5 ± 1.4	0.2 ± 0.8	< 0.1 ± 0.2	-	0.1 ± 0.5	0.7 ± 1.1	0.1 ± 0.2	0.2 ± 0.6	< 0.1 ± < 0.1
Urtica dioica	< 0.1 ± 0.1	0.7 ± 2.3	9.2 ± 9.5	0.5 ± 1.1	< 0.1 ± 0.2	-	0.2 ± 1.4	1.2 ± 2.7	0.3 ± 1.1	0.3 ± 0.7
Vaccinum myrtillus	-	-	-	0.1 ± 0.3	< 0.1 ± < 0.1	1.0 ± 1.2	0.8 ± 0.8	-	-	-
Valeriana officinalis	0.3 ± 1.1	0.7 ± 1.6	-	< 0.1 ± 0.2	< 0.1 ± < 0.1	-	-	0.2 ± 0.7	-	< 0.1 ± < 0.1
Veronica beccabunga	-	-	-	-	-	-	-	0.3 ± 1.6	-	< 0.1 ± < 0.1
Viola canina	-	-	-	< 0.1 ± < 0.1	< 0.1 ± < 0.1	< 0.1 ± < 0.1	0.7 ± 3.8	-	-	< 0.1 ± < 0.1
Viola epipsila	0.1 ± 0.4	-	0.5 ± 1.3	0.5 ± 0.9	< 0.1 ± 0.1	0.1 ± 0.6	0.2 ± 0.7	0.8 ± 3.1	-	< 0.1 ± 0.1
Viola uliginosa	-	-	-	0.1 ± 0.4	0.3 ± 0.8	-	-	0.9 ± 5.8	0.1 ± 0.5	0.2 ± 0.6
					Moss layer					
Amblystegium riparium	0.2 ± 1.0	0.6 ± 1.9	-	-	-	-	< 0.1 ± < 0.1	< 0.1 ± 0.2	-	< 0.1 ± < 0.1
Brachythecium rivulare	-	0.4 ± 1.2	0.6 ± 1.4	0.6 ± 2.4	-	0.8 ± 3.3	0.1 ± 0.4	0.2 ± 0.6	< 0.1 ± < 0.1	< 0.1 ± 0.1
Brachythecium rutabulum	0.1 ± 0.2	3.1 ± 2.9	1.5 ± 1.9	0.6 ± 1.0	0.1 ± 0.2	0.8 ± 2.8	0.2 ± 0.3	1.6 ± 2.4	0.2 ± 0.5	0.3 ± 0.3
Calliergon cordifolium	0.3 ± 0.9	-	< 0.1 ± 0.1	0.1 ± 0.3	-	0.2 ± 0.8	1.5 ± 3.1	0.1 ± 0.7	0.2 ± 0.8	< 0.1 ± < 0.1
Calliergonella cuspidata	7.5 ± 7.0	1.9 ± 2.6	0.2 ± 0.5	0.2 ± 0.7	-	0.1 ± 0.3	0.6 ± 1.1	2.0 ± 3.3	0.2 ± 1.5	< 0.1 ± 0.1
Calypogeia integristipula	-	-	< 0.1 ± < 0.1	0.2 ± 0.6	0.1 ± 0.3	0.2 ± 0.6	< 0.1 ± 0.1	0.1 ± 0.4	1.8 ± 1.7	1.6 ± 1.5
Cephalozia bicuspidata										
Cirriphyllum piliferum	-	0.5 ± 1.7	-	0.3 ± 0.6	-	< 0.1 ± 0.1	-	< 0.1 ± 0.2	0.2 ± 0.7	< 0.1 ± 0.1
Climacium dendroides	0.6 ± 1.2	< 0.1 ± 0.1	0.1 ± 0.2	1.4 ± 1.6	0.4 ± 0.4	0.3 ± 0.4	1.3 ± 1.4	0.4 ± 0.9	2.3 ± 1.4	0.9 ± 1.2
Dicranum scoparium	< 0.1 ± < 0.1	-	-	0.3 ± 0.5	< 0.1 ± < 0.1	0.3 ± 0.4	0.6 ± 0.7	0.1 ± 0.5	0.4 ± 0.4	0.3 ± 0.3
Eurhynchium angustirete	< 0.1 ± < 0.1	0.1 ± 0.4	< 0.1 ± 0.1	1.8 ± 3.9	< 0.1 ± < 0.1	0.1 ± 0.4	-	0.1 ± 0.4	0.2 ± 0.3	1.1 ± 1.1
Eurhynchium hians	0.1 ± 0.4	0.9 ± 2.6	0.7 ± 1.4	0.1 ± .3	-	-	-	0.2 ± 1.1	-	0.3 ± 0.7
Eurhynchium pulchellum	-	1.3 ± 3.4	0.1 ± 0.2	< 0.1 ± 0.1	-	-	-	0.1 ± 0.4	-	0.1 ± 0.2
Homalia trichomanoides	-	-	< 0.1 ± < 0.1	0.3 ± 0.6	0.1 ± 0.2	-	< 0.1 ± 0.1	< 0.1 ± 0.1	0.2 ± 0.3	0.7 ± 0.8
Hylocomium splendens	0.1 ± 0.5	< 0.1 ± < 0.1	-	0.6 ± 1.6	-	0.7 ± 1.1	0.6 ± 0.8	0.1 ± 0.5	0.6 ± 0.9	< 0.1 ± < 0.1
Plagiomnium cuspidatum	< 0.1 ± 0.1	-	0.2 ± 0.4	0.5 ± 0.8	-	0.2 ± 0.6	< 0.1 ± 0.2	0.1 ± 0.3	0.4 ± 0.5	0.9 ± 0.7
Plagiomnium elatum	< 0.1 ± 0.2	0.4 ± 1.3	0.3 ± 0.6	1.9 ± 5.6	0.5 ± 1.2	0.2 ± 0.5	0.3 ± 0.8	0.6 ± 1.0	0.7 ± 0.8	0.2 ± 0.2
Plagiomnium ellipticum	0.9 ± 1.0	< 0.1 ± 0.1	0.3 ± 0.8	< 0.1 ± 0.2	0.1 ± 0.2	0.1 ± 0.3	0.3 ± 0.5	0.2 ± 0.6	0.2 ± 1.3	0.1 ± 0.2
Plagiomnium undulatum	-	0.8 ± 1.2	< 0.1 ± < 0.1	0.8 ± 1.6	-	-	-	0.7 ± 1.9	< 0.1 ± 0.2	0.2 ± 0.3
Pleurozium schreberi	0.1 ± 0.5	-	-	0.3 ± 0.6	0.2 ± 0.2	0.4 ± 0.7	0.7 ± 0.9	< 0.1 ± 0.1	0.2 ± 0.4	0.1 ± 0.2
Pseudobryum cinclidioides	0.3 ± 0.5	-	-	0.5 ± 0.8	-	0.2 ± 0.3	0.3 ± 0.3	0.1 ± 0.2	-	0.2 ± 0.3
Rhytidiadelphus triquetrus	0.6 ± 1.5	0.1 ± 0.2	-	0.7 ± 1.0	< 0.1 ± < 0.1	0.1 ± 0.3	1.0 ± 1.4	-	1.3 ± 1.2	0.2 ± 0.7
Sphagnum fallax	-	-	-	-	1.5 ± 2.2	0.1 ± 0.2	0.2 ± 0.4	-	-	-
Sphagnum girgensohnii	-	-	-	0.2 ± 0.8	-	0.8 ± 1.5	0.4 ± 0.6	-	-	-

Table 1. (continued)

Species	Community type (and the number of relevés)									
	1 (19)	2 (10)	3 (14)	4 (27)	5 (12)	6 (25)	7 (34)	8 (53)	9 (39)	10 (19)
Sphagnum magellanicum	-	-	-	0.1 ± 0.8	0.5 ± 1.2	0.3 ± 0.9	0.5 ± 1.0	-	-	-
Sphagnum riparium	-	-	-	-	0.2 ± 0.4	0.6 ± 1.4	-	-	-	-
Sphagnum squarrosum	0.1 ± 0.4	-	-	< 0.1 ± 0.2	-	0.4 ± 0.9	2.0 ± 1.6	-	0.1 ± 0.2	-
Thuidium delicatulum	0.1 ± 0.4	< 0.1 ± 0.1	-	0.2 ± 0.3	< 0.1 ± < 0.1	0.2 ± 0.6	< 0.1 ± 0.2	0.1 ± 0.4	0.4 ± 0.5	0.5 ± 0.6

Table 2. Indicator species of community types and their relative frequency
Max type is the community type, where the species indicator value is maximal, *p* – significance level, T – tree layer

Species	Max type	*p*	Community type									
			1	2	3	4	5	6	7	8	9	10
Betula pubescens T	1	< 0.001	31	2	0	4	5	3	0	7	5	5
Calliergonella cuspidata	1	< 0.001	49	12	0	0	0	0	3	10	0	0
Caltha palustris	1	< 0.001	27	14	1	3	1	0	1	18	0	0
Carex acutiformis	1	< 0.001	36	0	0	0	0	0	0	0	0	0
Lysimachia nummularia	1	< 0.001	39	0	0	0	0	0	0	0	0	0
Plagiomnium ellipticum	1	< 0.001	34	0	3	0	1	1	5	2	0	0
Ranunculus repens	1	< 0.001	34	17	1	1	1	0	0	9	0	2
Thelypteris palustris	1	< 0.001	38	2	0	0	0	0	4	0	1	0
Carex vesicaria	1	< 0.001	25	0	0	0	14	3	3	1	0	0
Calla palustris	1	< 0.001	31	0	0	0	0	0	9	0	0	0
Veronica longifolia	1	0.001	25	0	0	0	0	0	0	0	0	0
Ranunculus lingua	1	0.003	16	0	0	0	0	3	0	0	0	2
Stachys palustris	1	0.010	16	0	0	0	3	0	0	0	0	0
Solanum dulcamara	1	0.012	19	14	4	0	1	1	0	12	0	0
Barbarea stricta	1	0.014	15	0	0	0	0	0	0	0	0	0
Carex riparia	1	0.028	14	0	0	0	0	0	0	0	0	0
Callitriche cophocarpa	1	0.035	10	0	0	0	0	0	0	0	0	0
Alisma plantago-aquatica	1	0.038	9	0	0	0	0	0	0	0	0	0
Galium uliginosum	1	0.042	14	11	3	0	0	0	0	6	0	0
Brachythecium populeum	2	< 0.001	0	25	0	0	0	0	0	0	0	0
Brachythecium rutabulum	2	< 0.001	0	37	13	3	0	1	1	13	1	2
Filipendula vulgaris	2	< 0.001	0	30	0	0	0	0	0	0	0	0
Fragaria vesca	2	< 0.001	0	33	0	0	0	0	0	0	0	0
Geranium sylvaticum	2	< 0.001	0	51	2	4	0	0	0	13	0	0
Grossularia reclinata	2	< 0.001	0	37	0	0	0	0	0	0	0	0
Lonicera xylosteum	2	< 0.001	2	48	0	1	0	0	0	1	0	1
Rubus caesius	2	< 0.001	0	80	0	0	0	0	0	5	0	0
Scutellaria galericulata	2	< 0.001	2	37	2	1	0	0	0	11	0	0
Swida sanguinea	2	< 0.001	0	35	0	0	0	0	0	0	0	0
Veronica officinalis	2	< 0.001	0	29	0	0	0	0	0	0	0	0
Eurhynchium pulchellum	2	< 0.001	0	33	1	0	0	0	0	1	0	0
Galium palustre	2	< 0.001	5	30	1	1	0	0	11	10	6	0
Sorbus aucuparia	2	< 0.001	2	24	7	2	0	2	6	12	1	1
Lysimachia vulgaris	2	< 0.001	3	27	0	2	0	3	9	15	1	0
Padus avium	2	0.001	4	22	15	3	0	1	0	17	2	13
Amblystegium varium	2	0.002	0	18	0	0	0	0	0	0	0	0
Polygonatum odoratum	2	0.002	0	19	0	0	0	0	0	0	0	0
Viburnum opulus	2	0.002	1	20	0	1	1	1	1	13	0	1
Ribes nigrum	2	0.003	0	25	3	3	0	0	0	2	1	1
Juniperus communis	2	0.003	0	20	0	0	0	0	0	7	0	0
Taraxacum sp.	2	0.004	0	18	4	0	0	0	0	3	0	0
Rhamnus catharticus	2	0.004	0	18	2	0	0	0	0	6	0	0
Aegopodium podagraria	3	< 0.001	0	0	49	2	0	0	0	0	0	0
Stellaria nemorum	3	< 0.001	0	0	47	8	0	0	0	1	0	0
Urtica dioica	3	< 0.001	0	1	58	1	0	0	0	4	0	0
Chrysosplenium alternifolium	3	< 0.001	1	0	24	3	0	0	0	2	1	8
Allium ursinum	3	0.002	0	0	20	0	0	0	0	0	0	0
Mnium hornum	3	0.003	0	0	16	0	0	0	0	1	0	0
Impatiens noli-tangere	3	0.005	0	0	25	2	0	3	0	0	0	0
Crepis paludosa	3	0.010	0	0	19	19	0	0	0	5	0	0
Mercurialis perennis	3	0.013	0	1	15	11	0	0	0	0	0	3
Sorbus aucuparia T	3	0.016	0	0	13	0	0	0	0	0	0	0
Acer platanoides T	3	0.036	0	6	10	3	0	0	0	0	0	0
Fissidens gracilifolius	3	0.037	0	0	10	0	0	0	0	0	0	1
Polygonatum multiflorum	3	0.048	0	0	9	0	0	0	0	0	0	3
Oxalis acetosella	4	0.004	1	0	7	24	0	2	3	2	7	6
Eurhynchium angustirete	4	0.004	0	0	0	25	0	0	0	0	2	19

Table 2. (continued)

Species	Max type	*p*	Community type									
			1	2	3	4	5	6	7	8	9	10
Milium effusum	4	0.013	0	0	4	16	0	0	0	1	1	0
Anemone nemorosa	4	0.017	0	0	0	15	0	0	0	2	0	4
Galeobdolon luteum	4	0.024	0	0	10	14	0	0	0	0	1	1
Tilia cordata T	4	0.033	2	0	0	15	0	0	0	1	1	0
Equisetum pratense	4	0.045	1	0	2	14	0	4	0	3	0	0
Phragmites australis	5	< 0.001	0	0	0	0	80	4	2	0	0	0
Quercus robur T	5	< 0.001	0	1	0	0	32	0	0	0	1	0
Sphagnum fallax	5	< 0.001	0	0	0	0	29	1	2	0	0	0
Equisetum fluviatile	5	0.003	2	0	0	1	21	10	4	1	0	0
Sphagnum capillifolium	5	0.008	0	0	0	0	17	0	13	0	0	0
Viola sp.	5	0.010	1	0	0	0	14	0	0	0	0	0
Carex cespitosa	5	0.013	2	0	0	5	16	0	2	1	5	0
Carex elata	5	0.016	0	5	0	0	12	2	0	1	0	0
Pohlia nutans	5	0.034	0	0	0	1	12	5	3	0	0	0
Calamagrostis arundinacea	6	0.001	0	0	2	4	0	19	0	0	0	0
Lycopodium annotinum	6	0.006	0	0	0	0	0	16	2	0	0	0
Drosera rotundifolia	6	0.007	0	0	0	0	0	16	0	0	0	0
Sphagnum girgensohnii	6	0.007	0	0	0	1	0	18	11	0	0	0
Carex appropinquata	6	0.009	1	0	0	0	0	15	5	0	0	0
Sphagnum riparium	6	0.013	0	0	0	0	4	12	0	0	0	0
Ptilidium pulcherrimum	6	0.018	0	0	0	8	0	14	2	0	10	1
Carex montana	6	0.031	0	0	0	0	0	11	0	0	0	0
Equisetum hyemale	6	0.033	0	0	0	0	0	10	0	0	0	0
Calluna vulgaris	6	0.034	0	0	0	0	0	11	0	0	0	0
Sphagnum centrale	6	0.034	0	0	0	0	0	11	8	0	0	0
Plagiothecium laetum	6	0.045	0	0	0	9	0	12	1	0	4	1
Betula pubescens T	7	< 0.001	1	0	0	3	0	12	46	0	0	0
Calliergon cordifolium	7	< 0.001	3	0	0	1	0	1	40	0	1	0
Carex canescens	7	< 0.001	0	0	0	0	0	0	34	0	0	0
Lysimachia thyrsiflora	7	< 0.001	3	0	2	0	2	7	29	4	2	0
Picea abies	7	< 0.001	3	0	1	5	2	9	26	0	10	1
Potentilla palustris	7	< 0.001	0	0	0	2	0	12	26	0	0	0
Sphagnum squarrosum	7	< 0.001	0	0	0	0	0	4	60	0	1	0
Vaccinium vitis-idaea	7	< 0.001	0	0	0	0	0	11	26	0	0	0
Vaccinum myrtillus	7	< 0.001	0	0	0	1	0	24	31	0	0	0
Carex elongata	7	0.002	16	0	1	1	0	0	29	1	1	0
Alnus glutinosa	7	0.003	5	0	2	1	10	12	19	1	5	0
Aulacomnium palustre	7	0.004	0	0	0	1	0	2	19	0	0	0
Calamagrostis canescens	7	0.004	0	0	1	1	17	3	21	0	21	0
Dicranum scoparium	7	0.004	0	0	0	8	0	8	21	0	13	11
Tetraphis pellucida	7	0.004	0	0	0	9	0	8	18	0	4	0
Peucedanum palustre	7	0.005	2	4	0	0	0	4	20	4	0	0
Vaccinium uliginosum	7	0.007	0	0	0	0	0	4	15	0	0	0
Cephalozia bicuspidata	7	0.008	0	0	0	2	0	0	14	0	2	1
Pleurozium schreberi	7	0.008	1	0	0	5	3	11	18	0	5	1
Dryopteris carthusiana	7	0.008	1	1	4	10	0	1	18	2	13	0
Pinus sylvestris T	7	0.012	0	4	0	1	4	8	18	0	0	0
Blepharostoma trichophyllum	7	0.014	0	0	0	0	0	1	14	0	3	0
Trientalis europaea	7	0.014	0	0	1	2	0	12	17	0	2	0
Betula pubescens	7	0.015	0	0	1	0	3	9	15	0	1	0
Frangula alnus	7	0.016	7	9	0	2	6	4	17	6	7	0
Sanionia uncinata	7	0.020	0	2	0	2	0	3	14	0	8	4
Equisetum palustre	7	0.024	0	0	0	0	0	2	14	1	1	0
Maianthemum bifolium	7	0.025	0	2	0	3	0	3	17	7	2	1
Sphagnum magellanicum	7	0.025	0	0	0	0	6	3	12	0	0	0
Equisetum sylvaticum	7	0.026	1	0	0	7	0	0	15	0	0	1
Juncus effusus	7	0.033	0	0	0	0	0	4	11	0	0	0
Dicranum polysetum	7	0.040	0	0	0	2	0	1	11	0	0	0
Hylocomium splendens	7	0.042	0	0	0	8	0	11	14	0	11	0
Luzula pilosa	7	0.045	0	0	0	0	0	0	12	0	0	0
Filipendula ulmaria	8	< 0.001	6	5	17	2	5	0	0	43	4	8
Deschampsia cespitosa	8	0.001	0	23	4	0	0	0	1	29	0	0
Paris quadrifolia	8	0.005	1	8	8	8	0	0	0	20	0	0
Lycopus europaeus	8	0.016	9	6	2	1	1	0	1	24	1	0
Ranunculus auricomus	8	0.016	0	0	0	0	0	0	0	15	0	0
Cratoneuron filicinum	8	0.046	0	0	0	0	0	0	0	13	0	0
Climacium dendroides	9	< 0.001	3	0	0	10	3	1	12	2	29	9
Rubus saxatilis	9	0.002	1	0	0	11	0	3	5	0	22	2

Table 2. (continued)

Species	Max type	*p*	Community type									
			1	2	3	4	5	6	7	8	9	10
Rhytidiadelphus triquetrus	9	0.002	3	0	0	8	0	1	11	0	24	0
Rhizomnium punctatum	9	0.025	0	0	0	6	3	0	5	0	14	8
Thuidium philibertii	9	0.032	0	0	0	0	2	0	0	0	10	0
Dicranum montanum	9	0.035	0	0	0	7	5	9	3	0	14	13
Galium rivale	9	0.036	2	0	0	0	0	0	0	0	11	0
Callicladium haldanianum	9	0.038	0	0	0	0	0	1	1	0	10	0
Calypogeia integristipula	10	< 0.001	0	0	0	1	1	1	0	0	34	34
Homalia trichomanoides	10	< 0.001	0	0	0	9	5	0	0	0	5	49
Orthotrichum affine	10	< 0.001	0	0	0	0	0	0	0	0	3	53
Plagiomnium cuspidatum	10	< 0.001	0	0	5	11	0	2	0	1	13	36
Radula complanata	10	< 0.001	0	0	0	6	0	0	0	0	7	42
Hypnum cupressiforme	10	< 0.001	0	0	0	7	5	3	0	0	18	25
Ulmus glabra T	10	< 0.001	0	0	6	1	0	0	0	1	0	26
Thuidium delicatulum	10	0.001	0	1	0	3	0	5	0	1	12	22
Ulmus laevis T	10	0.001	0	0	2	2	0	0	0	0	0	20
Anomodon longifolius	10	0.001	0	0	1	1	5	0	0	0	0	20
Frullania dilatata	10	0.002	0	0	0	3	2	0	0	0	3	17
Ulota crispa	10	0.002	0	0	0	1	1	0	0	0	8	16
Padus avium T	10	0.004	0	0	2	3	5	0	0	0	3	18
Ulmus glabra	10	0.006	4	0	1	1	1	0	0	1	0	18
Isothecium alopecuroides	10	0.009	0	0	0	4	0	0	0	0	0	13
Matteuccia struthiopteris	10	0.022	0	0	1	1	0	0	0	2	0	13
Lophocolea bidentata	10	0.026	0	0	0	0	0	0	0	0	0	10
Linnaea borealis	10	0.036	0	0	0	0	0	0	0	0	0	9
Brachythecium oedipodium	10	0.043	0	0	2	3	1	3	2	1	8	13
Fraxinus excelsior	10	0.044	6	0	4	1	4	1	0	5	6	14

Table 3. Ecological indicator values of community types

Community type	Indicator value				
	L	T	M	R	N
1	5.8 ± 0.3	5.2 ± 0.1	8.0 ± 0.7	5.9 ± 0.3	5.6 ± 0.4
2	5.9 ± 0.2	5.1 ± 0.2	7.1 ± 0.4	6.1 ± 0.4	5.7 ± 0.4
3	5.0 ± 0.4	5.1 ± 0.1	6.8 ± 0.5	6.3 ± 0.3	6.8 ± 0.5
4	4.8 ± 0.8	5.0 ± 0.1	6.6 ± 0.9	5.6 ± 0.6	5.6 ± 0.8
5	6.6 ± 0.5	5.0 ± 0.0	8.9 ± 0.5	5.9 ± 0.5	5.4 ± 0.4
6	5.9 ± 0.7	4.9 ± 0.2	7.6 ± 1.0	4.9 ± 0.9	4.8 ± 1.0
7	5.7 ± 0.4	5.0 ± 0.1	7.7 ± 0.5	4.8 ± 0.3	4.8 ± 0.4
8	5.7 ± 0.4	5.0 ± 0.1	7.5 ± 0.5	5,9 ± 0.3	5.6 ± 0.4
9	5.2 ± 0.6	5.0 ± 0.1	7.3 ± 0.6	5.4 ± 0.3	5.3 ± 0.5
10	4.9 ± 0.4	5.1 ± 0.1	7.0 ± 0.5	6.1 ± 0.3	5.8 ± 0.4
p_{ANOVA}	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

Notations: L – light, T – temperature, M – moisture, R – reaction, N – nitrogen, p_{ANOVA} – significance level by univariate ANOVA.

Table 4. Representation of community types in different regions

Region	Community type										Summary
	1	2	3	4	5	6	7	8	9	10	
Floodplains	15	-	2	-	1	-	-	12	1	1	32
Coastal dunes	-	2	4	1	-	-	-	15	-	-	22
Saaremaa Island	1	-	-	5	-	-	7	-	-	-	13
Klint foot, N Estonia	1	-	2	2	-	-	2	-	1	-	8
Agusalu NR, NE Estonia	-	-	5	2	-	2	-	1	1	-	11
Puhatu NR, NE Estonia	1	-	-	3	-	7	23	1	-	1	36
Muraka NR, NE Estonia	-	-	-	-	-	5	-	-	-	-	5
Järvamaa, C Estonia	-	-	1	9	11	11	2	5	36	17	92
Karula NP, S Estonia	1	8	-	1	-	-	-	19	-	-	29
Soomaa NP, SW Estonia	-	-	-	4	-	-	-	-	-	-	4
Summary	19	10	14	27	12	25	34	53	39	19	252

Notations: NR – nature reserve, NP – national park, NE – north-east, N – north, C – central, S – south, SW – south-west.

In the communities of the fourth type in the tree layer with *Alnus glutinosa*, also *Betula* spp., *Picea abies* and *Populus tremula* are intermixed, some single *Ulmus laevis* and/or *U. glabra* can occur. In the field layer, *Filipendula ulmaria*, *Stellaria nemorum*, *Mercurialis perennis* and *Oxalis acetosella* are found; in the moss layer, *Eurynchium angustirete* and *Climacium dendroides* are the most abundant species. As indicator species in these communities *Oxalis acetosella*, *Milium effusum*, *Galeobdolon luteum*, *Anemone nemorosa* and *Equisetum pratense* in the field layer and *Eurynchium angustirete* in the moss layer come forward (Table 2). The dense tree layer overshadows the ground vegetation considerably and the habitats are a bit dryer than in communities of other types (Table 3). These communities are widely presented all over Estonia (Table 4).

The tree layer in the communities of the fifth type is rather similar to that in previous types but here single *Quercus robur* can occur as well. The field layer is comparatively poor in species, in addition to the title species, *Carex vesicaria*, *Carex cespitosa* and *Sphagnum girgensohnii* could be mentioned (Table 1). Among indicator species, in addition to the dominant *Phragmites australis*, the most essential in the field layer are *Equisetum fluviatile*, *Carex cespitosa* and *C. elata*, and in the moss layer *Sphagnum fallax*, *S. capillifolium* and *Pohlia nutans* (Table 2). These communities have the highest light and moisture indicator values among the compared forests (Table 3); they were described mainly in central Estonia (Table 4).

In the communities of the sixth type *Betula* spp. are also quite common in the tree layer (Table 1). In the sparse field layer, sedges *Carex acuta*, *C. lasiocarpa*, *C. vesicaria* and *C. elata* together with *Phragmites australis* and *Scirpus sylvaticus* have a higher abundance in some respects, in the moss layer *Sphagnum girgensohnii*, *Brachythecium rivulare* and *B. rutabulum*. The significant indicator species in the field layer, besides *Calamagrostis arundinacea*, *Lycopodium annotinum*, *C. montana* and *Equisetum hyemale* are several mire species, such as *Carex appropinquata*, *Drosera rotundifolia*, *Sphagnum girgensohnii*, *S. riparium* and *S. centrale* (Table 2). The communities of this type have developed in habitats with comparatively low reaction and nitrogen content (Table 3). We described them in central and northeastern Estonia (Table 4).

The tree layer of the seventh type communities includes a quite large fraction of *Betula* spp., here then and there *Pinus sylvestris* and *Picea abies* are intermixed. In the field layer *Calamagrostis canescens*, *Galium palustre*, *Lysimachia vulgaris*, *Thelypteris palustris* and *Viola canina* are found, in the moss layer *Sphagnum squarrosum* and *Climacium dendroides* are comparatively abundant as well. The number of significant indicator species of this community type is remarkably large, altogether 34 species, of those 12 are bryophytes (Table 2). In the field layer, first of all *Carex canescens*, *C. elongata*, *Lysimachia thyrsiflora*, *Potentilla palustris*, *Calamagrostis canescens* and *Peucedanum palustre* should be mentioned among others; in the moss layer, *Calliergon cordifolium*, *Sphagnum squarrosum*, *Aulacomnium palustre*, *Tetraphis pellucida* and *Cephalozia bicuspidata* are distinguished. Soil in the habitats of these communities is rather acidic and poor in nitrogen (Table 3). These communities are common in Puhatu Nature Reserve in northeastern Estonia, but also on Saaremaa Island and other regions (Table 4).

In the communities of the eighth type, the field layer is overwhelmingly dominated by *Filipendula ulmaria*, *Dryopteris carthusiana*, *Geum rivale*, *Rubus idaeus*, *R. caesius*, *Lysimachia vulgaris*, *Solanum dulcamara* and *Caltha palustris*, in the moss layer *Calliergonella cuspidata* is the most frequent species. In addition to the abundant *Filipendula ulmaria*, these communities are distinguished by significant indicator species, such as *Deschampsia cespitosa*, *Paris quadrifolia*, *Lycopus europaeus*, *Ranunculus auricomus* and *Cratoneuron filicinum* (Table 2). According to the ecological indicator values, habitats of these communities have a medium quality among the studied sample (Table 3); the communities of this type are well presented in floodplains, between coastal dunes and in southern Estonia (Table 4).

In the communities of the ninth type, the prevailing species in the field layer are *Athyrium filix-femina*, *Filipendula ulmaria* and *Calamagrostis canescens*, in the moss layer *Climacium dendroides* and *Calypogeia integristipula* have the largest cover (Table 1). Indicator species in the field layer are *Rubus saxatilis* and *Galium rivale*, and *Climacium dendroides*, *Rhytidiadelphus triquetrus*, *Rhizomnium punctatum*, *Thuidium philibertii*, *Dicranum montanum* and *Callicladium haldanianum* (Table 2) in the moss layer. Habitats of a medium quality among the studied sample are characteristic of the communities of that type (Table 3). These communities are rather frequent in central Estonia (Table 4).

The communities of the last type have a comparatively large proportion of *Betula* spp., but also *Picea abies*, *Padus avium*, *Ulmus laevis* or *U. glabra* (Table 1) in the tree layer. Total cover of the ground layers is rather modest. The field layer is dominated by *Filipendula ulmaria*, besides of it only the cover of *Athyrium filix-femina* and *Mercurialis perennis* occupies more than one percent of their area here; in the moss layer only the cover of *Calypogeia integristipula* is more than one percent. Both *Ulmus* species together with *Padus avium* come forward as indicator species in the tree layer, *Fraxinus excelsior* in the regrowth, *Matteuccia struthiopteris* and *Linneae borealis* in the field layer; the other 13 significant indicator species are bryophytes, such as *Homalia trichomanoides*, *Ortotrichum affine*, *Plagiomnium cuspidatum*, *Radula complanata*, etc. (Table 2). The ground vegetation of these communities is considerably shadowed by the tree layer, the habitat indicator value of reaction is comparatively high (Table 3). Like the communities of the previous type, these communities are common in central Estonia (Table 4).

Considering the species abundance in different layers and their indicator values (Table 2), the community types could be titled as follows:

1. *Calliergonella cuspidata–Carex acutiformis–Thelypteris palustris–Alnus glutinosa*;
2. *Brachythecium rutabulum–Scutellaria galericulata–Rubus caesius–Alnus glutinosa*;
3. *Brachythecium rutabulum–Urtica dioica–Aegopodium podagraria–Alnus glutinosa*;
4. *Plagiomnium elatum–Galeobdolon luteum–Oxalis acetosella–Alnus glutinosa*;
5. *Sphagnum fallax–Filipendula ulmaria–Phragmites australis–Alnus glutinosa*;
6. *Sphagnum riparium–Vaccinium myrtillus–Impatiens noli-tangere–Alnus glutinosa*;
7. *Calliergon cordifolium–Lysimachia thyrsiflora–Carex elongata–Alnus glutinosa;*
8. *Calliergonella cuspidata–Deschampsia cespitosa–Filipendula ulmaria–Alnus glutinosa;*
9. *Climacium dendroides–Calamagrostis canescens–Athyrium filix-femina–Alnus glutinosa*;
10. *Calypogeia integristipula–Filipendula ulmaria–Ulmus laevis–Alnus glutinosa.*

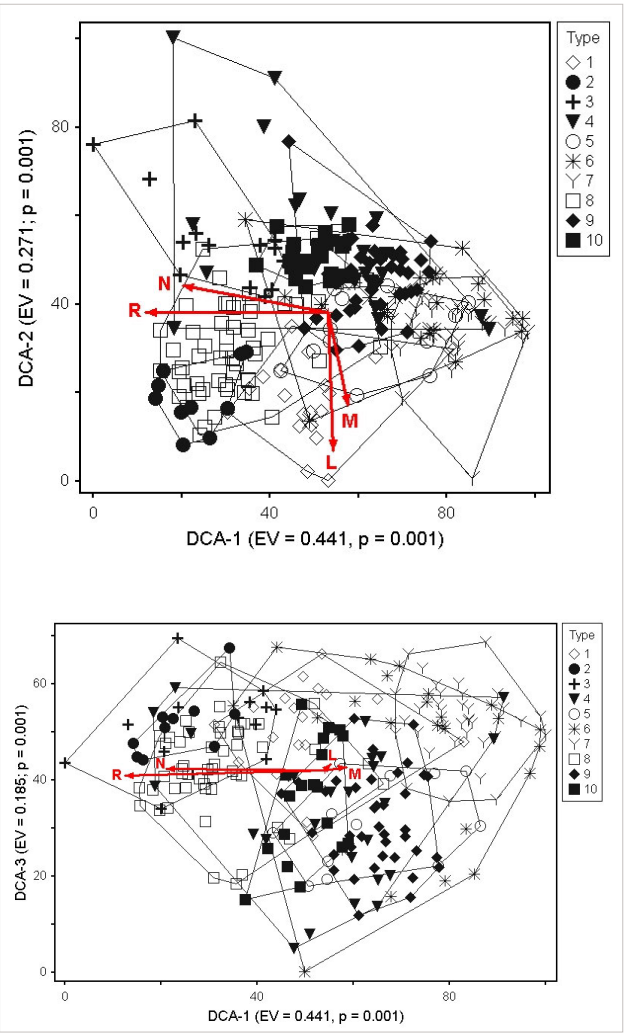

Figure 1. Ordination biplot of the analyzed swamp forest communities and their indicator values obtained by the detrended correspondence analysis

Notations: Type – community type, R – reaction, N – nitrogen, M – moisture, L – light.

According to the ordination biplot, the largest internal variation occurs in the communities of *Sphagnum riparium–Vaccinium myrtillus–Impatiens noli-tangere–Alnus glutinosa* and *Plagiomnium elatum–Galeobdolon luteum–Oxalis acetosella–Alnus glutinosa* (6th and 4th) types, whereas the most homotoneus are the *Brachythecium rutabulum–Scutellaria galericulata–Rubus caesius–Alnus glutinosa*, *Calypogeia integristipula–Filipendula ulmaria–Ulmus laevis–Alnus glutinosa* and *Brachythecium rutabulum–Urtica dioica–Aegopodium podagraria–Alnus glutinosa* (2nd, 10th and 3rd) types. The mutual position of the communities is clearly correlated with the main ecological gradient determined by the habitats reaction and nitrogen content (Figure 1). Extensive overlapping of communities of different types indicates the similarity of their species content.

Discussion

Swamp forests of the *Alnus glutinosa–Athyrium filix-femina–Impatiens noli-tangere* type, distinguished by us earlier on the foot of scree of the North-Estonian Klint and on the adjacent coastal plain (Paal 2009), are in the recent more comprehensive classification embraced by the *Brachythecium rutabulum–Urtica dioica–Aegopodium podagraria–Alnus glutinosa* type, whereas the coastal swamp forests flooded by seawater are more diverse (Paal and Rooma 2001): they are represented mainly in the *Calliergonella cuspidata–Deschampsia cespitosa–Filipendula ulmaria–Alnus glutinosa*, *Brachythecium rutabulum–Urtica dioica–Aegopodium podagraria–Alnus glutinosa* and *Climacium dendroides–Calamagrostis canescens–Athyrium filix-femina–Alnus glutinosa* types, some also in the *Brachythecium rutabulum–Scutellaria galericulata–Rubus caesius–Alnus glutinosa* and *Plagiomnium elatum–Galeobdolon luteum–Oxalis acetosella–Alnus glutinosa* types.

The black alder swamps and forests of Finland are classified by Mäkinen (2018) into 14 community types; two of them are presented in the alluvial forests site type group, five in the herb-rich forests site type group, while seven forest types belong to the swamp forests site type group. They are the following:

1. *Phragmites australis–Alnus glutinosa*,
2. Paludified *Carex–Alnus glutinosa*,
3. *Equisetum fluviatile–Alnus glutinosa*,
4. *Thelypteris palustris–Alnus glutinosa*,
5. *Iris pseudacorus–Alnus glutinosa*,
6. *Athyrium filix-femina–Calla palustris–Alnus glutinosa*,
7. *Scirpus sylvaticus–Alnus glutinosa*.

The first of them corresponds rather well to our *Sphagnum fallax–Filipendula ulmaria–Phragmites australis–Alnus glutinosa* type and the *Thelypteris palustris–Alnus glutinosa* type to our *Calliergonella cuspidata–Carex acutiformis–Thelypteris palustris–Alnus glutinosa* type; the paludified *Carex–Alnus glutinosa* type has some similarity with our *Calliergonella cuspidata–Carex acutiformis–Thelypteris palustris–Alnus glutinosa* type, whereas with the remaining Finnish swamp forests we cannot find a considerable congruity.

In the neighbouring Latvia, Prieditis (1993) has classified the *Alnus glutinosa* swamp forests according to the Braun-Blanquet methodology into three associations: 1. *Carici elongatae–Alnetum* (with subassociations (i) *Carici elongatae–Alnetum typicum*, (ii) *Carici elongatae–Alnetum thelypteridetosum*, (iii) *Carici elongatae–Alnetum urticetosum*, (iv) *Carici elongatae–Alnetum caricetosum elatae*); 2. *Sphagno squarrosi–Alnetum*; and 3. *Circaeo–Alnetum*. We can assert certain similarity between the Latvian subassociation *Carici elongatae–Alnetum typicum* and our *Calliergonella cuspidata–Carex acutiformis–Thelypteris palustris–Alnus glutinosa* community type, but in the latter also *Thelypteris palustris* is one of the dominant species which in the Latvian classification is a diagnostic species of the second subassociation *Carici elongatae–Alnetum thelypteridetosum*.

The Latvian *Carici elongatae–Alnetum urticetosum* subassociation corresponds rather well to our *Brachythecium rutabulum–Urtica dioica–Aegopodium podagraria–Alnus glutinosa* type. For the Latvian *Carici elongatae–Alnetum caricetosum elatae* subassociation we do not have a good counterpart among Estonian forest types: *Carex elata* had the highest average cover (0.8% only) in communities of the *Sphagnum fallax–Filipendula ulmaria–Phragmites australis–Alnus glutinosa* type, whereas the two other important diagnostic species of the considered Latvian subassociation, *Carex acutiformis* and *Scirpus sylvaticus*, are not presented at all.

Neither can we find a satisfactory match for the Latvian *Sphagno squarrosi–Alnetum* and *Circaeo–Alnetum* associations among the Estonian classification units, where *Sphagnum squarrosum* has the highest average cover (2.0%) and significance as an indicator species in communities of the *Calliergon cordifolium–Lysimachia thyrsiflora–Carex elongata–Alnus glutinosa* type, but in communities of this type *Peucedanum palustre*, *Comarum palustre*, *Calla palustris*, *Menyanthes trifoliata*, *Vaccinium myrtillus* and *Pleurozium schreberi* what are the dominating and diagnostic species of the *Sphagno squarrosi–Alnetum* association occur only with a modest abundance.

To the *Circaeo–Alnetum* association resemble to some extent communities of our *Plagiomnium elatum–Galeobdolon luteum–Oxalis acetosella–Alnus glutinosa* type, though in the field layer of the respective Latvian communities grow rather abundantly *Malachium aqyaticym* (= *Myosoton aquaticum*), *Urtica dioica*, *Ranunculus repens*, *Geum rivale*, *Mercurialis perennis*, *Cardamine amara*, *Equisetum sylvaticum*, *Dryopteris spinulosa* and *Crepis paludosa*, in the moss layer *Plagiominum undulatum*, *Eurynchium angustirete*, *Climacium dendroides*, *Cirriphyllum piliferum* and *Brachythecium curtum*. In the Estonian corresponding communities *Mercurialis perennis* and *Oxalis acetosella* dominate together with *Filipendula ulmaria* and *Stellaria nemorum* in the field layer, while in the moss layer the most abundant species are *Plagiomnium elatum*, *Eurynchium angustirete* and *Climacium dendroides*.

In the compared Latvian classification, the communities, where the field layer is dominated by *Phragmites australis* or *Rubus caesius*, are not represented, as well as the communities with abundant *Carex acutiformis* in them.

In the bogs of northwestern Russia, Boch and Smagin (1993) have distinguished, according to the Braun-Blanquet methodology, only two associations of *Alnus glutinosa* swamp forests: 1. *Carici elongatae–Alnetum medioeuropaeum*, and 2. *Alnetum glutinosae–Sphagnosum*, both with two subassociatons: (i) *typicum* and (ii) *calletosum*. We cannot find any acceptable match between these syntaxa and community types established in the recent study. The same appears by comparison of later results with the classification of forests of northwestern Russia (Fedorchuk et al. 2005) established also using the Braun-Blanquet methodology.

The comparatively large variation of *Alnus glutinosa* dominated forests in a small country like Estonia proceeds not only from the peculiarities of their habitats, but the compared results depend largely on the methods of classification used for establishing the community types. Though the Braun-Blanquet approach has several advances (e.g. Whittaker 1962), it often ignores the smaller classification units distinguished by cluster analyses even if their objectivity is statistically verified. It seems like when using the abovementioned methodology, sometimes the typological diversity of studied samples cannot be fully discovered. In the current study, we tried to avoid, when processing obtained data, the moments sometimes criticized by the followers of employing cluster analysis: we used the complete list of recorded species but not only a selection of them and exploited as a measure of dissimilarity between the relevés the relative Sørensen distance which does not overestimate the value of the most abundant species: relativization shifts the emphasis of the analysis to proportions of species in a sample unit rather than absolute abundances (McCune and Grace 2002).

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