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Diversity of old-drained forests in Estonia

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Abstract

Due to originating from various mire or paludified forests and consequently developing after drainage under different growth conditions, the drained forests are very heterogeneous and complex. In the official Estonian forest typology, the old-drained stands are divided into *Myrtillus* and *Oxalis* site types, but recently the validity of the autonomous *Dryopteris* (*expansa*) forest site type was again asserted. The aims of the current study were to (i) elucidate the main factors determining the structure and variation of the Estonian old-drained forests, (ii) elaborate the typology of these forests at the community level and, (iii) establish the indicator species of the established community types. 118 forest stands drained not less than 35–40 years ago were analysed. According to multivariate data analyses (cluster, ordination and variance analyses, multi-response permutation procedures, indicator species analyses) it appeared that the soil reaction, nutrients, and moisture content, assessed by the Ellenberg ecological indicator values for habitats are much more significant factors for plant growth and community structure than the thickness of soil/peat horizons. Nevertheless, the litter and peat horizons in soils of drained *Dryopteris* site type forests are significantly thinner than in *Oxalis* and *Myrtillus* site type stands. The *Dryopteris* site type forests can be divided into six, the *Oxalis* site type forests into three, and the *Myrtillus* site type forests into two types of communities. Each of the 11 established community types differ significantly ($p < 0.05$) from each other and have their own dominant and significant indicator species. When comparing the Estonian old-drained forests with analogous stands in neighbouring countries (Latvia, Finland, Sweden, northwestern Russia), we can find rather large similarities; the typological differences result mainly from the methodological approaches and geographical scope of countries.

Keywords: community types, drainage impact, *Dryopteris* forest site type, fern-rich forests, indicator species, Ellenberg indicator values, nutrition gradient

Introduction

Forest drainage started in Estonia already 200 years ago (Pikk 2000), with the first drainage ditches in forests dug in 1820 (Pikk 1997b). By the end of the 19th century, most paludified, swamp, and transitional mire forests on thin peat layer were already drained (Laasimer 1965). The extent and intensity of drainage abruptly increased following the introduction of machines in the 1950s (Lõhmus 1981). Estimations of the actual area of drained forests in Estonia are rather different; for example, according to Raudsaar et al. (2014), the drained swamp (decayed-mire) forests cover 328,300 ha or 14.8% of the total forest area, but Pikk (1997b, 2000) indicated a larger figure of 560,000 ha or 27% of the total forest area. The reason for this discrepancy seems to be linked to what specific forest lands or types were considered.

Drainage of forests causes extensive changes in their habitat conditions. Improved aeration of the peat layer enhances the activity of peat-decomposing microorganisms and invertebrates. An essential qualitative change in the post-drainage genesis of former mire soils is the formation of forest litter horizon typical of mineral soils. This horizon is followed by the well-decomposed horizon of decayed peat formed mainly from debris, under which a moderately to well-decomposed peat (decayed peat) horizon (AH) has formed. These changes in soil structure and chemistry increase their nutrition content and also induce substantial changes in plant cover (Lõhmus 1981, 1982, Paavilainen and Päivänen 1995).

Due to origination from different mire or paludified forests, and developing therefore in different growth conditions, the drained forests are very heterogeneous (Masing 1966, Lõhmus 1981, 1982, Reinikainen 1988). Karu (1957) classified the Estonian drained transitional mire areas according to the drainage intensity as: (i) *Myrtillus* decayed-mire pine forests on slightly decayed peat,

(ii) *Dryopteris* decayed-mire pine forests on well decomposed 10–25 cm thick peat and, (iii) *Oxalis* decayed-mire spruce or pine forests on thicker (25–40 cm) well-decomposed peat. All these anthropogenous ecosystems were treated as belonging to the decayed-peat-mire (*kõduturbasoo*) forest site type (ST) (Karu and Muiste 1958), or as variants of the decayed-mire (*kõdusoo*) forest ST (Katus and Tappo 1965).

In 1970, Marvet published a key book of the Estonian plant communities and described four distinct STs of decayed-peat forests: (i) *Vaccinium vitis-idaea* ST, (ii) *Dryopteris* ST, (iii) *Oxalis* ST, and, (iv) *Myrtillus* ST. Forests of *Vaccinium vitis-idaea* ST are mixed spruce and pine stands on nutrient-poor 25–50 cm thick decayed peat. In the field layer *Vaccinium vitis-idea* has the largest cover, followed by *Calluna vulgaris* and *V. myrtillus*; the other notable species are *Melampyrum pratense, Deschampsia flexuosa*, and *Lycopodium annotinum*. In the moss layer *Pleurozium schreberi, Hylocomium splendens*, and *Dicranum polysetum* dominate. The *Dryopteris* ST forests are situated on more nutrient-rich and thinner (< 40 cm) decayed peat. The tree layer is formed by birch, spruce, and black alder, the field layer resembles boreo-nemoral forests including abundant ferns *Dryopteris expansa, Dryopteris carthusiana, Athyrium filix-femina*, and species such as *Crepis paludosa, Cirsium oleraceum, Aegopodium podagraria*, and *Stellaria nemorum*. In the *Oxalis* ST forests, the decayed peat layer is thicker (> 40 cm), and dwarf shrubs are almost absent. In the field layer *Oxalis acetosella* is dominating, accompanied with *Maianthemum bifolium, Trientalis europaea, Luzula pilosa, Pyrola rotundifolia, Orthilia secunda*, and locally by *Rubus saxatilis*, whereas *Vaccinium myrtillus* and *V. vitis-idaea* are stunted and infrequent. In the tree layer, birch prevails, often intermixed with spruce, and seldom also with pine. The *Myrtillus* ST forests have also developed on a decayed peat layer thicker than 40 cm, and consist of pine or spruce/pine stands. In the field layer *Vaccinium myrtillus* is the most abundant species, the other typical species are *Trientalis europaea, Dryopteris carthusiana, Convallaria majalis, Mycelis muralis, Pyrola* spp., and *Huperzia selago*.

Lõhmus (1974) divided the decayed-peat-mire forest ST *sensu* Karu and Muiste (1958) into four subtypes according to whether they originated from swamps, fens, transitional mires, or raised bogs. In swamp and fen decayed-peat-mire subtypes the peat is well-decomposed, the field layer consists of species such as *Oxalis acetosella, Mycelis muralis, Paris quadrifolia, Urtica dioica, Rubus saxatilis, Aegopodium podagraria, Mercurialis perennis, Galeobdolon luteum, Circaea alpina* etc. Another characteristic of swamp and fen decayed-peat-mire subtypes is an abundance of ferns, including *Dryopteris carthusiana, D. expansa, Athyrium filix-femina*, and *Gymnocarpium dryopteris*. In the transitional mire decayed-peat-mire subtype, typical species are *Lycopodium annotinum, Pyrola rotundifolia, Maianthemum bifolium, Rubus saxatilis, Carex globularis, Equisetum sylvaticum*, while *Phragmites australis* and *Calamagrostis canescens* may have been locally preserved as relicts. The moss layer of the transitional mire decayed-peat-mire subtype mainly comprises *Pleurozium schreberi, Hylocomium splendens* and *Dicranum* spp., in patches *Rhytidiadelphus triquetrus, Plagiochila* spp., *Polytrichum* spp, and *Sphagnum* spp. may occur. If the peat horizon is less decomposed and contains less nutrients, *Vaccinium myrtillus* can dominate, less frequently other dwarf shrubs such as *Vaccinium vitis-idaea*, *V. uliginosum, Calluna vulgaris, Ledum palustre* can occur. The importance of the latter species increases in bog decayed-peat-mire subtype, where the moss layer is dominated by *Hylocomium splendens* and *Dicranum* spp., or with *Sphagnum* spp. in some patches. The tree layer of decayed-mire forests varies largely; in forests originating from swamps spruce prevails, often accompanied by *Betula pubescens* and *Alnus glutinosa*, in fen decayed-peat-mire forests both spruce or pine can dominate, whereas in transitional mire and bog-decayed-mire forests usually pine is the most abundant tree species.

Later Lõhmus (1981) adjusted the typology of drained forests; similarly to Sarasto (1961a,b) they were first divided into two groups: (i) drained-mire forests, encompassing stands of earlier post-drainage succession stages where their ground vegetation included hygrophilous mire plants to such an extent (i.e. cover exceeding 20%) that the original type of forests was recognisable and, (ii) decayed-peat forests, where succession had already reached the state of relatively stable equilibrium. The latter forests are also called as old-drained or full-drained (Etverk et al. 1995). The first group included four subtypes as in Lõhmus (1974). The second group was divided into *Oxalis* and *Myrtillus* peaty STs, for which the ground vegetation and whole community exhibits great similarity to the respective forest types on mineral soils (Figure 1). The present official Estonian forest typology (Lõhmus 2004) is based on stabilised old stands and only considers these two de-

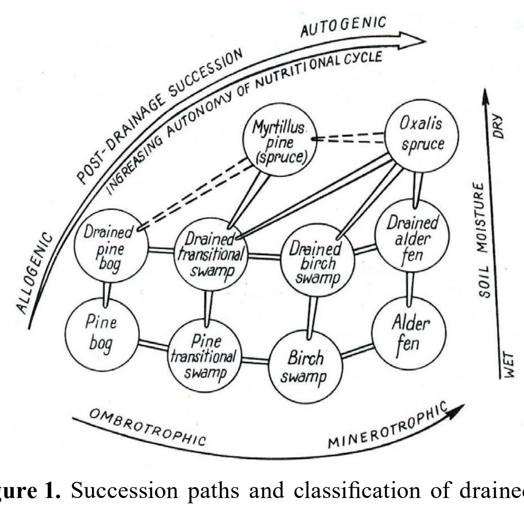

Figure 1. Succession paths and classification of drained peatland forests (Lõhmus 1981)

cayed-peat forests STs. The fern-rich drained *Dryopteris* ST forests were reclassified: according to Lõhmus (1982), these forests represent a successional stage of relatively nutrition-rich drained swamp/fen forests which have not achieved yet the stable stage of decayed-mire *Oxalis* ST type forests to which they typologically belong. The fern-rich *Dryopteris* ST forests growing in alluvial and synclinal river valleys were treated in the scope of the boreo-nemoral forests group. However, we recently disputed this opinion, arguing that it is justified to recognise the fern-rich drained forests as belonging to an autonomous *Dryopteris* (*expansa*) forest ST in the group of old-drained forests (Paal and Jürjendal 2019). More detailed analyses of the old-drained forest typology at the community level have so far not been conducted in Estonia. At the same time, an adequate and proper typology of forest communities is a presumption for better understanding their diversity, sustainable management and protection.

The aims of the current study were to (i) elucidate the main factors determining the structure and variation of the Estonian old-drained forests, (ii) elaborate the typology of these forests at the community level and, (iii) establish indicator species of the established community types.

Materials and methods

Sample area and field data

A preliminary selection of studied forests was based on state forest maps (1:10000). The sample plots were located all over Estonia, but the research was most intensive in northeastern Estonia (i.e. in the oil shale mining region), in southwestern Estonia, and on the ancient Lake Peipsi basin between Tartu city and the present western coast of Lake Peipsi (i.e. in regions where according to Lõhmus (1974) forest drainage has been the most extensive). As for the *Dryopteris* ST forests, it is not indicated on maps if they are drained or not, we always studied the maps carefully for drainage ditches in the vicinity of these forest subcompartments and investigated their surroundings concerning the presence of ditches in nature. According to the available documentation, but also by the state of drainage ditches in nature, all studied fern-rich forests were drained at least 35–40 years ago.

To describe the vegetation, we used circular sample plots with an area of 0.1 ha (radius 17.4 m), which were fitted within a homogeneous forest stand. In total, 118 stands were analysed. The tree layer was described by the canopy closure and by the basal area (DBH) of tree trunks, estimated for every tree species at breast height (1.3 m), and only trees with diameter larger than 5 cm at breast height were registered. In every sample plot, the basal area measurement was repeated in 4–5 random locations and averaged per stand. Young trees, having a height below 5 m and/or a diameter less than 5 cm at breast height, were considered as saplings and were recorded together with the shrub layer. The forest understory was described by counting stems of all shrub species and tree saplings on five randomly placed subplots with a radius of 2 m. If there were shrub species outside the subplots, they were recorded with value 1. For the field (grasses + herbs + dwarf shrubs) and moss layer vegetation, a total species list was compiled and the cover-abundance rating of every species was conducted according to the scale: 0.1 (single specimen), 1 (average cover ≤ 1%), 2 (≤ 5%), 3 (≤ 10%), 4 (≤ 25%), 5 (≤ 50%), and 6 (> 50%). For the morphological description of soils and measuring the thickness of diagnostic horizons, a pit was dug in the middle of each sample plot. The nomenclature of vascular plant species follows Krall et al. (2010), and names of bryophytes are taken from 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). Before the cluster analysis, species occurring less than three times in the data were filtered out. The clusters (i.e. community types) were established on the basis of a dendrogram. Objectivity of relevés clustering on the ground of species content was tested by the multi-response permutation procedures (MRPP) (McCune and Mefford 1999), also considering correction for multiple comparisons. Differences between the mean values of environmental variables were checked by the one-way ANOVA using the Statistica data analysis software system, version 7.1 (StatSoft Inc. 2005).

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 weighted averaging (Schaffers and Sýkora 2000). Differences between mean values of environmental variables were checked by the one-way ANOVA (StatSoft Inc. 2005).

The species indicator values in community types were calculated by the Dufrêne and Legrendre (1997) method included in the program package PC-ORD (McCune and Mefford 2011). The statistical significance of the obtained indicator values were 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) was used. Species occurring in data less than three times were filtered out prior to the analysis.

Results

According to the cluster analysis dendrogram, all drained forests were on the level of remaining information 64% clearly divided into three groups, corresponding to the *Dryopteris, Oxalis*, and *Myrtillus* forest STs (Figure 2). Testing by the multi-response permutation proce-

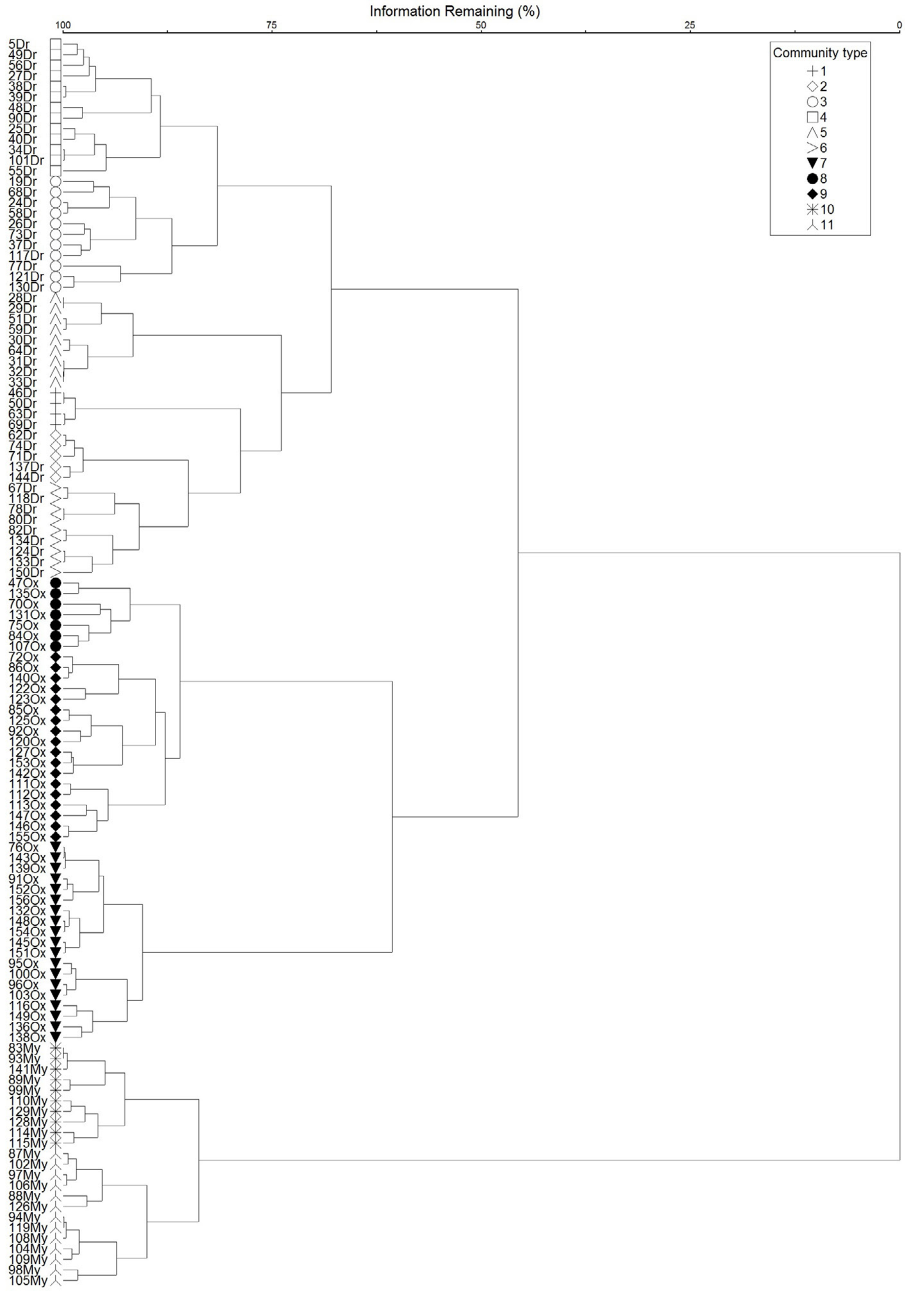

Figure 2. Cluster analysis dendrogram of old-drained forests

Dryopteris site type forests are indicated after sample plot number with letters 'Dr', *Oxalis* site type forests with letters 'Ox' and *Myrtillus* site type forests with letters 'My'.

dures confirmed that the species content in forests of all three STs was significantly different (Table 1). In accordance with those results, on the ordination plot the drained forests of considered STs were well-separated, with some overlapping appearing only between the *Dryopteris* and *Oxalis* ST stands (Figure 3). The variation of studied communities and differences between them were mainly described by the Ellenberg indicator values for soil reaction, nutrients availability, and moisture conditions, all being strongly positively correlated (Table 2) and decreasing significantly from *Myrtillus* to *Dryopteris* ST forests (Table 3). The total cover of the moss layer exhibited a very strong but negative correlation with those environmental factors, whereas the total cover of the field layer had a positive but weaker relationship.

Table 1. Comparison of old-drained forest site types (FSTs) species composition by the multi-response permutation procedures

Compared FSTs	*T*	*A*	*p*
Dryopteris vs. *Oxalis*	-22.09	0.048	<0.001
Dryopteris vs. *Myrtillus*	-39.40	0.157	<0.001
Oxalis vs. *Myrtillus*	-35.22	0.147	<0.001

Notations: T and A – calculated statistics, *p* – significance level.

It appeared that the soil reaction, nutrients, and moisture content, assessed by the Ellenberg indicator values for habitats, are much more important factors for plant growth and community structure than the actual thickness of soil/peat horizons. Here is important to keep in mind that the Ellenberg indicator values for habitats were calcu-

Table 2. Spearman rank order correlation coefficients between the old-drained forests environmental and structural variables. Significant ($p < 0.05$) coefficients are marked with asteriscs

Variables	O horizon	A horizon	AH horizon	H horizon	Cover field	Cover moss	Light	Moisture	Reaction
Nutrients	-0.10	0.19*	-0.08	-0.24*	0.58*	-0.88	0.55*	0.93*	0.94*
Reaction	-0.08	0.24*	-0.11	-0.30*	0.48*	-0.84	0.66*	0.90*	
Moisture	-0.10	0.20*	-0.10	-0.20*	0.56*	-0.90	0.74*		
Light	-0.07	0.15	-0.08	-0.17	0.31*	-0.72			
Cover moss	0.12	-0.11	0.11	0.08	-0.43*				
Cover field	-0.10	0.20*	0.09*	-0.25*					
H horizon	-0.04	-0.37*	-0.40*						
AH horizon	0.03	-0.43*							
A horizon	-0.14								

Notations: O horizon, A horizon, AH horizon and H horizon – thickness of respective soil diagnostic horizons; Light, Moisture, Reaction, Nutrients – Ellenberg indicator values; Cover field and Cover moss – total cover of field and moss layer.

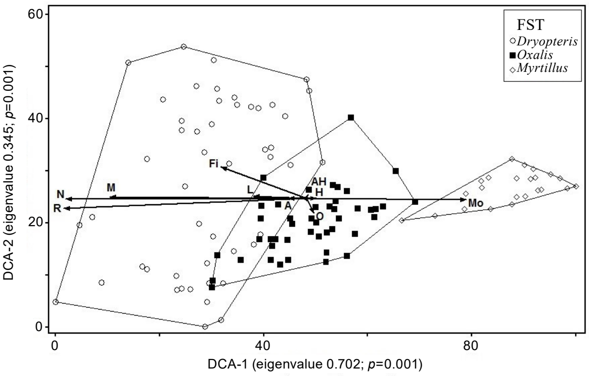

Figure 3. Ordination biplot of vegetation relevés (sample plots) and environmental characteristics of old-drained forests

Notations: FST – forest site type; O, A, AH and H – thickness of respective soil horizons; L, M, R and N – Ellenberg indicator values for light, moisture, reaction and nutrients conditions; Fi and Mo – total cover of field and moss layers.

Table 3. Average characteristics ± standard error of old-drained forest site types

Variable	Forest site type			p_{ANOVA}
	Dryopteris	*Oxalis*	*Myrtillus*	
O horizon	1.7±1.0^{a}	2.1±1.6^{ab}	2.6±2.0^{b}	0.041
A horizon	7.2±10.4	4.2±10.1	2.6±8.5	0.128
AH horizon	17.0±26.6	13.4±30.3	17.7±28.0	0.770
H horizon	7.7±17.2^{a}	31.2±37.9^{b}	13.3±21.0^{a}	<0.001
Light	3.8±0.5^{c}	3.6±0.6^{b}	3.2±0.5^{a}	<0.001
Moisture	5.8±0.8^{c}	5.0±0.7^{b}	3.4±0.5^{a}	<0.001
Reaction	4.6±0.8^{c}	3.9±0.7^{b}	2.1±0.4^{a}	<0.001
Nutrients	5.0±0.9^{c}	4.1±0.8^{b}	2.0±0.4^{a}	<0.001
Cover field	83.2±10.6^{c}	62.4±17.7^{b}	54.4±15.8^{a}	<0.001
Cover moss	15.4±14.9^{a}	28.4±19.4^{b}	63.8±20.9^{c}	<0.001
No tree spp	3±1^{a}	4±1^{b}	3±1^{a}	0.003
No shrub spp	6±2^{a}	8±3^{b}	5±2^{a}	<0.001
No field spp	25±11^{b}	26±8^{b}	15±8^{a}	<0.001
No moss spp	9±4^{a}	11±4^{c}	11±3^{b}	0.060
No total spp	44±14^{b}	49±10^{c}	34±12^{a}	<0.001

Notations: No tree spp, No shrub spp, No field spp, No moss spp, No total spp – number of species in respective layers; p_{ANOVA} – significance level by one-way ANOVA. Other notations as in Table 2. With upper-case letters are marked similar average values according to the Ficher LSD post-hoc tests.

lated only on the basis of vascular plant cover estimations, causing to some extent a *mortus circulo*. Nevertheless, the litter horizon in soils of the drained *Dryopteris* ST forests was significantly thinner than in *Oxalis* and *Myrtillus* ST stands (Table 3). The peat horizons was thinnest in communities of *Dryopteris* ST and thickest in *Oxalis* ST stands, where the peat horizon had always two or three subhorizons decomposed to different extents. A horizon was thickest in habitats of *Dryopteris* ST and thinnest in *Myrtillus* ST, but due to a large variation of this variable, the average values did not differ significantly. A remarkably large standard error was also observed for average values of thickness of decayed peat (AH) and undecomposed peat (H) horizons (Table 3). From the community structure variables, a total moss cover increase of more than four times between *Dryopteris* ST and *Myrtillus* ST communities was striking, accompanied at the same time by a significant decrease of field layer total cover in the opposite direction. The total number of species was highest in forests of *Oxalis* ST (Table 3).

The list of significant indicator species for old-drained *Dryopteris* ST forests proved to be remarkably long, including altogether 32 species (Table 4). Species such as *Urtica dioica, Galeobdolon luteum, Impatiens noli-tangere, I. parviflora, Mercurialis perennis, Stellaria nemorum, Matteuccia struthiopteris,* and *Chrysosplenium alternifolium* affirm the habitat nutrient richness, while *Alnus glutinosa, Filipendula ulmaria, Cardamine amara, Iris pseudacorus, Calamagrostis canescens*, and *Lycopus europaeus* conjointly confirm their relatively high moisture.

The list of indicator species for *Oxalis* ST forests (Table 4) mostly comprises species of mesotrophic habitats, such as *Oxalis acetosella, Carex digitata, Convallaria majalis, Mycelis muralis*, and *Rubus saxatilis*. Several indicator species whose Ellenberg indicator value for soil reaction were at least seven or higher (Chytrý et al. 2018), for example *Alnus incana, Rhamnus catharcticus, Daphne mezereum, Ribes alpinum, Viburnum opulus, Viola mirabilis*, and *Hepatica nobilis*, affirm the neutral reaction of soil.

For *Myrtillus* ST forests, many species of heaths and mires were specific, primarily the dwarf shrubs *Vaccinium myrtillus, V. vitis-idaea, V. uliginosum, Ledum palustre*, and *Chamaedaphne calyculata*, and species such as *Sphagnum angustifolium, S. capillifolium, S. magellanicum, S. fallax, S. russowii* in the moss layer. On hummocks and tree root collars, common forest bryophytes including *Dicranum scoparium, Hylocomium splendens, Pleurozium schreberi*, and *Ptilium crista-castrensis* were typical (Table 4).

Table 4. Significant ($p < 0.05$) indicator species, their indicator value, relative frequency and relative abundancy in old-drained forest site types

Species	*Max*	*p*	Indicator value			Relative frequency			Relative abundancy		
			Forest site type								
			Dr	Ox	My	Dr	Ox	My	Dr	Ox	My
ALNUS GLUTINOSA	Dr	<0.001	62	4	0	70	38	4	89	9	1
Alnus glutinosa	Dr	<0.001	34	0	0	36	2	0	95	5	0
Athyrium filix-femina	Dr	<0.001	70	10	0	82	67	9	85	15	0
Dryopteris expansa	Dr	<0.001	62	9	0	76	51	17	81	18	1
Galeobdolon luteum	Dr	<0.001	42	2	0	50	11	0	84	16	0
Impatiens noli-tangere	Dr	<0.001	42	2	0	46	18	0	90	10	0
Mercurialis perennis	Dr	<0.001	42	4	0	48	36	0	88	12	0
Ranunculus repens	Dr	<0.001	41	1	0	46	9	0	88	12	0
Stellaria nemorum	Dr	<0.001	47	5	0	56	31	0	85	15	0
Brachythecium oedipodium	Dr	<0.001	48	8	12	90	40	43	54	19	27
Brachythecium rutabulum	Dr	<0.001	39	1	0	44	11	0	88	12	0
Chrysosplenium alternifolium	Dr	<0.001	40	2	0	48	11	0	84	16	0
Equisetum sylvaticum	Dr	<0.001	44	4	2	56	29	22	79	12	9
Filipendula ulmaria	Dr	0.001	48	10	0	62	44	9	77	22	1
Urtica dioica	Dr	0.001	50	4	0	58	29	0	86	14	0
Milium effusum	Dr	0.002	35	8	0	50	27	4	70	29	1
Betula pubescens	Dr	0.005	44	30	13	92	84	78	48	35	16
Matteuccia struthiopteris	Dr	0.005	16	0	0	16	0	0	100	0	0
Cardamine amara	Dr	0.008	18	0	0	22	2	0	83	17	0
Ribes nigrum	Dr	0.010	23	2	0	30	13	4	76	18	5
Viola riviniana	Dr	0.016	17	0	0	18	2	4	95	2	3
Iris pseudacorus	Dr	0.018	12	0	0	12	0	0	100	0	0
Calliergonella cuspidata	Dr	0.023	12	0	0	12	0	0	100	0	0
Phegopteris connectilis	Dr	0.025	18	1	0	20	7	0	90	10	0
Calamagrostis canescens	Dr	0.026	25	2	0	30	22	4	83	8	9
Impatiens parviflora	Dr	0.028	14	0	0	14	2	0	99	1	0
Lycopus europaeus	Dr	0.029	15	1	0	18	4	0	81	19	0
Epilobium adenocaulon	Dr	0.040	10	0	0	10	0	0	100	0	0
Lysimachia vulgaris	Dr	0.041	27	5	0	34	24	4	79	20	1
Paris quadrifolia	Dr	0.041	31	30	0	72	58	4	44	52	5
Poa trivialis	Dr	0.047	10	0	0	10	0	0	100	0	0
Equisetum pratense	Dr	0.048	22	7	0	38	20	4	58	36	6
PADUS AVIUM	Ox	<0.001	3	41	3	16	58	30	19	71	11
Carex digitata	Ox	<0.001	3	44	2	28	60	13	10	74	16
Convallaria majalis	Ox	<0.001	1	56	2	18	69	17	8	81	11
Fragaria vesca	Ox	<0.001	1	54	4	22	71	26	6	77	17
Mycelis muralis	Ox	<0.001	2	66	0	28	76	9	8	87	5
Oxalis acetosella	Ox	<0.001	35	56	1	96	91	43	36	61	2
Rubus saxatilis	Ox	<0.001	12	56	2	58	82	22	21	68	11
Plagiomnium cuspidatum	Ox	<0.001	21	58	2	72	93	22	29	62	10
Rhytidiadelphus triquetrus	Ox	<0.001	5	54	6	36	76	43	15	72	13
Daphne mezereum	Ox	<0.001	2	32	1	10	44	13	18	73	9
Galium triflorum	Ox	<0.001	0	28	0	2	29	0	2	98	0
Viola mirabilis	Ox	<0.001	0	34	0	8	40	4	6	84	10
Ribes alpinum	Ox	0.001	2	35	0	14	47	4	17	75	8
Rhamnus catharticus	Ox	0.003	0	19	0	2	20	0	5	95	0
Eurhynchium angustirete	Ox	0.005	21	45	0	52	78	13	41	57	2
Gymnocarpium dryopteris	Ox	0.005	18	38	0	48	62	4	38	61	1
Circaea alpina	Ox	0.005	14	34	0	38	56	0	38	62	0
Viburnum opulus	Ox	0.007	3	22	0	12	29	4	21	77	2
Frangula alnus	Ox	0.008	3	45	16	40	69	61	9	65	26
Pyrola rotundifolia	Ox	0.008	0	20	2	0	27	9	0	76	24
Rhodobryum roseum	Ox	0.012	2	35	11	32	67	26	5	53	42
Solidago virgaurea	Ox	0.018	4	32	11	22	62	39	19	51	29
Luzula pilosa	Ox	0.023	5	35	24	30	73	65	16	47	37
ALNUS INCANA	Ox	0.023	0	14	0	2	16	0	11	89	0
Hepatica nobilis	Ox	0.026	8	25	0	22	40	0	38	62	0
Rubus idaeus	Ox	0.029	37	39	0	74	82	17	50	47	3
Deschampsia cespitosa	Ox	0.031	5	25	0	16	42	4	34	60	6
Moehringia trinervia	Ox	0.035	4	18	0	12	27	0	33	67	0
Acer platanoides	Ox	0.036	12	28	3	36	51	22	33	55	12
Brachythecium salebrosum	Ox	0.036	0	13	0	2	16	0	19	81	0
Actaea spicata	Ox	0.038	2	15	0	10	18	0	16	84	0
Brachythecium reflexum	Ox	0.039	0	9	0	0	9	0	0	100	0
Plagiomnium affine	Ox	0.042	25	29	0	56	53	0	45	55	0
Plagiomnium elatum	Ox	0.049	4	18	0	10	29	4	38	62	1
PINUS SYLVESTRIS	My	<0.001	5	4	50	30	36	70	18	11	71
Melampyrum pratense	My	<0.001	0	0	68	4	9	70	0	2	97
Vaccinium myrtillus	My	<0.001	0	5	90	24	60	100	2	8	90
Vaccinium vitis-idaea	My	<0.001	0	9	79	10	44	100	1	21	79
Dicranum majus	My	<0.001	0	0	38	4	2	39	0	1	98
Dicranum polysetum	My	<0.001	0	4	75	8	22	91	1	17	82
Hylocomium splendens	My	<0.001	1	15	80	26	80	100	2	18	80
Pleurozium schreberi	My	<0.001	1	8	87	38	67	100	1	12	87
Polytrichum longisetum	My	<0.001	1	2	38	12	13	52	10	17	73
Sphagnum girgensohnii	My	<0.001	0	0	48	0	2	48	0	0	100
Eriophorum vaginatum	My	<0.001	0	0	25	0	2	26	0	3	97
Vaccinium uliginosum	My	<0.001	0	0	25	0	4	26	0	3	97
Aulacomnium palustre	My	<0.001	0	1	26	0	4	30	0	16	84
Sphagnum angustifolium	My	<0.001	0	0	24	0	2	26	0	7	93

Table 4. Significant ($p < 0.05$) indicator species, their indicator value, relative frequency and relative abundancy in old-drained forest site types (continued)

Species	*Max*	*p*	Indicator value			Relative frequency			Relative abundancy		
			Forest site type								
			Dr	Ox	My	Dr	Ox	My	Dr	Ox	My
Sphagnum capillifolium	My	<0.001	0	0	34	6	0	35	3	0	97
Sphagnum magellanicum	My	<0.001	0	0	25	4	2	26	4	2	95
Sphagnum fallax	My	<0.001	0	0	17	0	2	17	0	0	100
Picea abies	My	<0.001	8	22	61	72	80	100	12	28	61
Calluna vulgaris	My	0.001	0	0	17	0	0	17	0	0	100
Sphagnum russowii	My	0.002	0	0	21	4	2	22	2	1	97
Ledum palustre	My	0.002	0	0	17	0	4	17	0	2	98
Chamaedaphne calyculata	My	0.003	0	0	17	0	2	17	0	3	97
Ptilium crista-castrensis	My	0.003	1	0	19	4	4	26	23	3	74
Deschampsia flexuosa	My	0.004	0	0	21	6	7	22	2	1	97
Salix cinerea	My	0.005	0	0	13	0	0	13	0	0	100
Sphagnum squarrosum	My	0.005	0	0	12	4	0	13	4	0	96
Oxycoccus palustris	My	0.007	0	0	13	0	0	13	0	0	100
Molinia caerulea	My	0.010	0	4	17	0	13	26	0	33	67
Betula pendula	My	0.010	5	1	26	20	13	39	23	9	67
Goodyera repens	My	0.011	0	0	11	2	0	13	13	0	87
Phragmites australis	My	0.015	0	2	17	4	11	22	9	15	76
Betula pubescens	My	0.015	1	9	26	14	31	39	5	28	67
Lycopodium annotinum	My	0.023	0	4	25	12	27	30	3	15	82
Orthilia secunda	My	0.028	0	3	20	8	20	26	6	17	77
Dicranum scoparium	My	0.034	5	20	31	24	49	78	19	42	39
Rubus chamaemorus	My	0.034	0	0	9	0	0	9	0	0	100
Chiloscyphus pallescens	My	0.036	1	3	18	8	18	26	13	18	68
Sphagnum centrale	My	0.038	0	0	9	0	0	9	0	0	100
Sphagnum flexuosum	My	0.038	0	0	9	0	0	9	0	0	100
Dicranum montanum	My	0.038	0	0	9	0	0	9	0	0	100
Carex globularis	My	0.041	0	0	9	0	0	9	0	0	100

Tree layer species are written with capital letters. Notations: Max – site type where the species indicator value is maximal, *p* – significance level; Dr, Ox and My – *Dryopteris, Oxalis* and *Myrtillus* forest site type, respectively.

The *Dryopteris* ST forests can be further divided into six, the *Oxalis* ST forests into three, and the *Myrtillus* ST forests into two types of communities (Figure 2). On the ordination plot (Figure 4) communities of most types are rather clearly separated, only communities of the fourth type of *Dryopteris* ST are considerably overlapping with communities of *Oxalis* ST. Nonetheless, the MRPP tests confirmed that all 11 community types established on the level of remaining information 61.3% differ reliably ($p < 0.05$) from each other, as well as all types have their own dominant and significant indicator species.

Starting from the *Dryopteris* ST, the tree layer of the 1st type communities mainly comprised *Alnus glutinosa* mixed with *Betula pubescens* and *Ulmus glabra*. Saplings of the latter species, together with *Padus avium*, were the most numerous and indicative species in the shrub layer. Total species number in the field layer (38) was the lowest among all established community types. In the field layer, *Matteuccia struthiopteris* was markedly dominating and

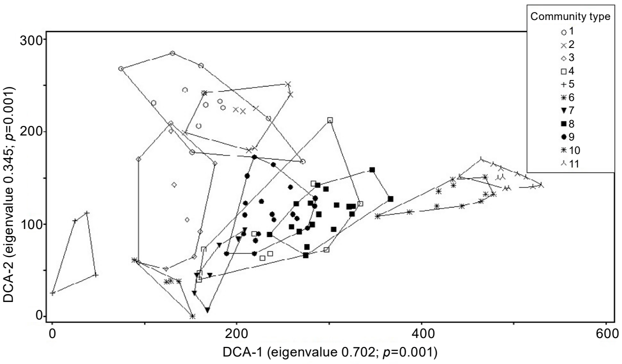

Figure 4. Ordination biplot of vegetation relevés (sample plots) and the mutual relationship of old-drained forests community types

indicative, this species was associated mainly with *Ranunculus ficaria, Mercurialis perennis, Stellaria nemorum, Galeobdolon luteum, Athyrium filix-femina*, and *Anemone nemorosa* (Table 5). The moss layer was very scarce, *Eurhynchium hians* and *Plagiothecium cavifolium* were there reliable indicator species (Table 6). Communities of this *Alnus glutinosa–Matteuccia struthiopteris–Ranunculus ficaria* type were related to habitats where soils were constantly moist or damp, weakly acidic to basic, and rather fertile. In these soils, the peat layer was fully decomposed and the A horizon was comparatively thick (Table 7).

Communities of the 2nd type represent *Betula pubescens* stands mixed with *Alnus glutinosa* and *Padus avium* in the tree layer. In the field layer, *Mercurialis perennis* had a striking dominance (Table 5), the other significant indicator species in the field layer was *Impatiens noli-tangere* (Table 6). Average cover of *Oxalis acetosella, Dryopteris carthusiana*, and *D. expansa* was 12.5, 5.8, and 3.7%, respectively. Average total cover of the species-poor moss layer was 11.7%; most abundant species were there *Cirriphyllum piliferum* and *Eurhynchium angustirete*. These *Betula pubescens–Mercurialis perennis–Dryopteris carthusiana* type communities have developed on soils without A horizon, but having a rather thick (19.2 cm on average) decayed-peat horizon enriched with humus. These soils were medium damp, moderately acidic, and fertile (Table 7).

In communities of the 3rd type, the tree layer was formed mainly by *Alnus glutinosa* and *Betula pubescens*. In the shrub layer, *Lonicera xylosteum, Padus avium, Sorbus aucuparia*, and saplings of *Fraxinus excelsior* and *Tilia cordata* were frequent. In the field layer, *Filipendula ulmaria* was prevailing and indicative, while the other most abundant species were *Athyrium filix-femina, Crepis paludosa, Cirsium oleraceum, Galeobdolon luteum, Urtica dioica, Oxalis acetosella*, and *Mercurialis perennis*

Table 5. Centroids of established community types (mean ± standard error of species abundance)

Species	Forest site type										
	Dryopters						*Oxalis*			*Myrtillus*	
	Community type										
	1	2	3	4	5	6	7	8	9	10	11
Number of relevés	4	5	10	13	9	7	19	10	18	11	12
Total number of species	88	85	144	155	102	140	155	156	184	143	92
Average number of species	39±17	44±4	51±10	45±13	32±14	49±18	47±9	47±11	52±11	39±14	30±9
Tree layer											
Closure of 1st sublayer	0.8±0.1	0.8±0.1	0.8±0.1	0.7±0.1	0.7±0.1	0.7±0.1	0.8±0.1	0.7±0.1	0.7±0.1	0.7±0.1	0.6±0.1
Closure of 2nd sublayer	0.2±0.2	0.4±0.1	0.3±0.2	0.2±0.1	0.2±0.1	0.4±0.3	0.3±0.2	0.4±0.1	0.3±0.1	0.4±0.1	0.2±0.1
Total number of species	7	6	7	8	6	11	12	11	10	7	6
Average number of species	4±1	4±1	4±1	4±1	3±1	4±1	3±1	4±1	4±2	3±1	3±1
Alnus glutinosa	14.5±15.0	9.9±10.9	12.3±12.6	11.4±14.3	8.2±12.4	0.8±1.7	0.9±1.7	1.2±1.3	1.1±2.3	0.3±1.1	<0.1±<0.1
Alnus incana	-	-	0.5±1.7	-	-	0.3±0.6	0.1±0.2	<0.1±<0.1	0.2±0.5	-	-
Betula pubescens	6.7±6.7	13.6±5.3	9.3±3.7	4.9±5.7	5.3±7.1	8.9±2.2	5.2±6.0	7.5±6.7	4.3±5.7	2.3±3.2	2.9±3.6
Fraxinus excelsior	0.5±0.6	-	0.6±0.9	0.1±0.4	-	0.9±1.9	<0.1±0.2	0.8±1.5	<0.1±<0.1	-	-
Padus avium	-	6.2±9.0	2.5±4.8	-	-	10.4±9.5	8.9±10.6	3.5±6.0	8.8±11.8	1.4±2.6	1.0±2.5
Picea abies	1.5±3.0	3.6±2.9	3.9±3.7	7.1±7.0	9.6±10.2	3.7±5.4	17.4±24.4	8.8±7.0	13.3±11.8	15.6±10.8	6.0±6.7
Pinus sylvestris	-	-	1.1±2.5	4.5±8.3	9.7±13.5	3.4±4.2	5.1±8.6	0.5±0.8	2.1±6.5	10.3±12.7	22.1±13.3
Populus tremula	-	-	2.3±7.3	1.4±4.0	0.1±0.4	0.1±0.3	1.0±3.8	2.2±3.2	0.2±0.6	1.7±5.0	0.2±0.8
Tilia cordata	0.3±0.5	0.5±1.2	0.2±0.3	0.1±0.3	-	0.1±0.3	<0.1±<0.1	0.1±0.4	-	0.1±0.4	-
Ulmus glabra	4.9±8.2	-	-	0.3±0.9	-	0.9±2.0	-	0.8±2.2	<0.1±0.1	-	-
Shrub layer											
Total number of species	13	16	20	18	14	17	22	22	23	21	16
Average number of species	7±3	7±1	8±1	6±2	5±2	8±2	8±3	8±3	8±3	7±2	5±2
Acer platanoides	0.7±0.6	0.8±0.8	0.4±0.9	<0.1±0.1	<0.1±0.1	1.1±1.2	1.0±1.5	1.0±2.0	0.2±0.3	0.3±0.7	<0.1±<0.1
Alnus incana	-	-	0.2±0.3	<0.1±0.3	-	0.6±0.9	0.1±0.3	0.1±0.2	0.2±0.5	<0.1±<0.1	<0.1±<0.1
Betula pendula	-	-	<0.1±<0.1	0.1±0.2	0.5±0.7	-	<0.1±0.1	<0.1±0.1	0.1±0.3	<0.1±<0.1	0.7±1.3
Betula pubescens	-	<0.1±<0.1	0.1±0.1	0.2±0.3	-	-	0.1±0.4	0.5±0.8	0.6±1.1	1.1±1.6	0.9±2.2
Corylus avellana	0.9±0.6	0.3±0.6	0.5±1.6	0.2±0.4	0.2±0.4	0.7±0.9	0.2±0.4	0.7±1.3	0.3±0.3	0.3±0.4	0.1±0.5
Frangula alnus	-	<0.1±<0.1	0.3±0.5	0.5±1.2	0.40±0.4	0.4±0.6	0.6±1.5	1.3±1.9	4.7±7.0	1.4±3.0	0.5±1.0
Fraxinus excelsior	0.2±0.3	1.3±1.2	1.5±3.0	0.1±0.3	0.16±0.4	0.7±0.7	0.8±1.6	1.9±2.3	0.3±0.7	<0.1±<0.1	<0.1±<0.1
Lonicera xylosteum	<0.1±0.1	0.2±0.3	1.3±2.3	<0.1±0.3	-	1.0±1.6	0.2±0.3	0.4±0.3	0.3±0.6	0.3±1.0	<0.1±<0.1
Padus avium	3.8±4.3	1.6±1.2	0.8±0.7	<0.1±0.2	0.31±0.9	1.3±1.8	1.4±2.6	0.7±1.3	0.6±1.4	-	-
Picea abies	0.1±<0.1	0.2±0.2	0.2±0.3	0.8±1.5	0.37±0.5	0.6±1.6	0.7±0.8	2.3±1.6	1.6±1.6	2.3±2.3	3.2±7.2
Populus tremula	-	0.6±1.3	0.2±0.5	0.2±0.5	-	1.9±2.2	0.3±0.8	0.4±0.6	0.1±0.3	0.4±0.7	0.1±0.4
Ribes alpinum	-	<0.1±0.2	0.4±0.9	<0.1±0.1	-	0.4±0.6	0.7±1.5	0.2±0.5	0.5±1.0	0.1±0.4	-
Ribes nigrum	0.2±0.3	0.7±1.1	0.6±0.7	<0.1±0.2	<0.1±<0.1	-	<0.1±<0.1	<0.1±<0.1	<0.1±0.3	<0.1±0.1	-
Sorbus aucuparia	0.1±0.2	0.5±0.4	0.8±0.9	0.5±0.4	1.64±1.7	1.9±3.3	1.5±1.7	2.7±1.6	2.1±2.2	1.8±1.9	1.2±2.4
Tilia cordata	0.7±0.9	0.9±1.3	1.5±3.0	0.2±0.4	<0.1±0.1	0.3±0.5	<0.1±<0.1	0.2±0.6	-	<0.1±0.1	-
Ulmus glabra	1.3±1.8	0.3±0.6	0.4±1.0	-	-	0.9±2.0	<0.1±0.1	0.61.7	<0.1±<0.1	-	-
Field layer											
Total cover, %	84.8±5.2	77.2±13.7	77.1±27.1	87.3±6.8	87.1±9.0	74.2±11.7	71.2±14.6	60.8±13.8	56.3±12.7	48.0±14.7	60.3±15.0
Total number of species	38	46	84	96	58	87	85	87	112	78	41
Average number of species	20±8	23±3	29±8	27±10	18±11	29±17	25±7	24±7	28±10	20±9	11±6
Aegopodium podagraria	1.4±2.3	-	1.3±2.5	2.4±6.0	<0.1±0.1	0.2±0.5	0.6±2.7	0.6±1.5	0.1±0.4	0.1±0.3	-
Agrostis capillaris	-	-	2.7±6.2	-	-	0.2±0.5	<0.1±<0.1	-	<0.1±<0.1	0.41.3	<0.1±<0.1
Allium ursinum	-	-	<0.1±<0.1	<0.1±<0.1	-	<0.1±0.2	<0.1±<0.1	-	0.5±2.0	<0.1±<0.1	-
Anemone nemorosa	4.6±5.6	2.0±1.7	1.3±2.4	0.2±0.5	-	2.7±4.4	<0.1±0.2	2.4±3.8	1.0±2.2	0.7±1.7	-
Angelica sylvestris	<0.1±<0.1	-	0.3±0.8	0.7±1.7	<0.1±<0.1	0.1±0.2	0.1±0.3	1.0±1.9	0.3±0.7	<0.1±<0.1	<0.1±<0.1
Athyrium filix-femina	5.1±6.3	3.5±3.9	12.6±15.2	37.3±13.7	0.5±0.8	1.5±1.8	5.0±6.2	1.8±3.2	2.4±2.7	0.1±0.3	-
Calamagrostis arundinacea	-	<0.1±0.2	0.2±0.6	<0.1±0.2	<0.1±<0.1	0.3±0.6	<0.1±<0.1	8.1±12.4	1.7±2.9	3.6±6.5	1.1±2.4
Calamagrostis canescens	-	-	1.2±3.5	1.5±3.3	1.0±2.9	-	0.1±0.4	<0.1±0.1	<0.1±0.1	-	0.2±0.6
Caltha palustris	-	-	0.1±0.2	0.6±2.3	-	<0.1±<0.1	-	<0.1±0.1	<0.1±<0.1	0.1±0.4	-
Carex digitata	-	0.2±0.4	0.2±0.4	<0.1±0.1	<0.1±<0.1	0.4±0.4	0.2±0.3	1.5±1.3	0.9±1.3	0.3±0.8	-
Carex elongata	-	-	0.3±0.9	1.0±3.4	<0.1±<0.1	-	<0.1±<0.1	<0.1±0.1	-	<0.1±<0.1	-
Chrysosplenium alternifolium	0.6±0.6	0.1±0.2	0.8±1.1	1.4±4.3	<0.1±0.3	<0.1±0.1	<0.1±0.3	-	0.3±1.2	-	-
Circaea alpina	-	0.1±0.3	<0.1±0.1	0.5±0.8	0.3±0.5	0.5±1.0	1.3±1.7	-	0.4±0.4	-	-
Cirsium oleraceum	1.1±2.2	0.1±0.3	4.8±6.2	1.3±2.1	0.5±1.0	0.3±0.5	0.4±0.7	0.7±0.7	1.3±2.0	0.1±0.3	-
Convallaria majalis	-	0.5±0.8	0.5±1.2	<0.1±<0.1	0.7±2.0	1.0±1.4	1.7±3.2	2.4±4.1	5.7±6.7	1.0±1.6	-
Crepis paludosa	0.6±0.6	0.1±0.2	5.0±5.7	1.0±1.4	-	0.9±1.0	0.4±0.7	1.2±1.9	0.9±1.4	0.4±1.0	-
Deshampsia caespitosa	-	<0.1±<0.1	0.7±1.7	0.5±1.5	<0.1±<0.1	0.1±0.3	0.1±0.2	0.2±0.4	0.1±0.3	0.1±0.2	-
Deshampsia flexuosa	-	-	-	0.1±0.5	<0.1±<0.1	-	-	-	<0.1±0.1	0.2±0.6	3.1±8.8
Dryopteris carthusiana	-	5.8±6.0	2.1±3.3	10.9±16.3	2.0±3.3	2.4±3.2	5.6±6.1	3.3±5.5	2.7±2.4	1.1±2.5	2.5±4.7
Dryopteris expansa	0.1±<0.1	3.7±5.9	4.4±5.8	14.8±17.7	53.8±14.0	5.8±3.7	3.3±5.1	5.8±11.4	4.5±5.3	0.3±0.7	-
Dryopteris filix-mas	-	-	-	-	0.4±0.7	0.7±1.5	0.5±1.4	<0.1±<0.1	<0.1±<0.1	-	-
Equisetum pratense	0.9±1.5	0.2±0.5	0.7±1.7	2.0±3.8	0.3±0.8	0.4±1.0	<0.1±0.3	2.9±3.7	0.2±0.9	0.2±0.7	-
Equisetum sylvaticum	<0.1±0.1	<0.1±<0.1	2.6±3.4	2.0±3.8	0.4±1.0	1.0±1.9	<0.1±0.2	0.7±0.9	0.2±0.4	0.3±0.6	<0.1±<0.1
Eriophorum vaginatum	-	-	-	-	-	-	-	-	<0.1±0.2	0.5±1.5	0.8±1.8
Filipendula ulmaria	0.5±0.6	0.6±0.5	18.1±12.2	1.3±3.2	0.7±1.9	1.1±1.8	0.6±1.1	2.7±5.7	0.3±0.8	0.1±0.2	-
Fragaria vesca	-	-	<0.1±0.1	0.3±0.6	<0.1±<0.1	<0.1±<0.1	1.0±2.3	0.4±0.4	1.8±2.6	0.5±1.0	<0.1±<0.1
Galeobdolon luteum	5.7±3.8	3.4±5.2	4.5±5.9	1.1±2.5	0.1±0.3	7.1±5.4	0.2±0.6	0.3±0.8	<0.1±0.4	-	-
Galium odoratum	-	-	-	0.2±0.5	-	1.4±2.1	<0.1±<0.1	0.5±1.0	-	-	-
Geranium robertianum	-	<0.1±<0.1	<0.1±<0.1	-	-	0.5±1.2	1.1±3.5	-	-	-	-
Geum rivale	0.2±0.2	1.6±3.4	2.3±2.5	0.4±0.7	0.1±0.1	1.2±1.9	0.1±0.2	4.0±8.4	1.1±3.2	0.4±0.9	-
Geum urbanum	-	<0.1±<0.1	-	-	-	-	0.5±2.2	-	-	-	-
Gymnocarpium dryopteris	-	0.4±0.7	0.3±0.6	2.6±5.4	0.3±0.5	3.4±3.5	3.7±4.9	0.1±0.1	1.3±1.5	<0.1±0.1	-
Hepatica nobilis	-	0.2±0.3	4.0±9.0	0.5±1.6	-	9.4±5.5	1.4±3.5	0.8±2.0	1.0±2.1	-	-
Impatiens noli-tangere	0.4±0.5	5.5±9.9	0.9±2.5	0.3±0.4	2.8±8.2	2.0±3.5	0.4±1.5	0.1±0.2	<0.1±<0.1	-	-
Impatiens parviflora	-	0.2±0.5	-	0.8±2.2	2.0±5.5	-	<0.1±<0.1	-	-	-	-
Lathyrus vernus	-	<0.1±<0.1	<0.1±0.1	<0.1±<0.1	-	0.6±1.0	<0.1±0.2	0.4±0.8	0.2±0.5	<0.1±0.1	-
Ledum palustre	-	-	-	-	-	-	-	-	0.1±0.2	-	2.3±3.7
Linnea borealis	-	-	-	-	-	-	<0.1±0.2	0.2±0.5	0.6±1.8	0.4±1.0	<0.1±<0.1
Luzula pilosa	<0.1±<0.1	-	0.1±0.2	0.1±0.2	0.5±1.0	0.1±0.1	0.3±0.5	0.3±0.4	0.7±0.3	0.3±0.3	0.4±0.9
Lycopodium annotinum	-	-	<0.1±<0.1	0.4±1.2	<0.1±<0.1	-	0.3±1.2	1.2±2.6	0.5±1.25	0.9±2.0	4.6±9.7
Maianthemum bifolium	<0.1±<0.1	0.1±0.1	0.5±0.6	0.8±1.0	4.9±5.8	0.1±0.2	0.4±0.6	0.6±0.5	0.7±0.8	0.9±1.3	0.2±0.7
Matteuccia struthiopteris	56.3±3.1	-	1.0±3.3	1.0±3.5	-	1.2±3.0	-	-	-	-	-
Melampyrum pratense	-	-	-	<0.1±0.1	-	-	<0.1±<0.1	-	0.3±0.9	1.1±1.7	7.2±9.3
Mercurialis perennis	7.0±2.6	45.0±10.4	3.1±6.7	0.3±1.0	2.7±5.4	14.5±10.8	1.4±3.6	2.3±3.6	0.6±1.1	-	-
Milium effusum	-	-	0.1±0.2	0.5±0.6	0.3±0.6	0.2±0.4	0.2±0.3	0.1±0.2	<0.1±0.1	-	<0.1±<0.1
Molinea caerulea	-	-	-	-	-	-	<0.1±0.1	-	0.8±1.6	1.4±2.1	<0.1±0.1
Mycelis muralis	-	0.2±0.3	0.2±0.5	0.2±0.3	<0.1±<0.1	<0.1±<0.1	1.0±0.9	0.2±0.2	1.0±0.9	0.1±0.3	-

Table 5. Centroids of established community types (mean ± standard error of species abundance) (continued)

Species	Forest site type										
	Dryopters					*Oxalis*				*Myrtillus*	
	Community type										
	1	2	3	4	5	6	7	8	9	10	11
Oxalis acetosella	1.3±1.5	12.5±8.6	3.9±6.4	12.9±14.7	27.0±22.8	17.5±5.7	47.7±14.6	6.8±4.3	18.5±9.9	1.9±3.0	0.2±0.5
Phegopteris connectilis	-	0.2±0.4	<0.1±<0.1	<0.1±0.1	.	0.9±1.9	-	-	<0.1±<0.1	-	-
Pulmonaria officinalis	-	-	0.6±1.8	<0.1±0.3	-	<0.1±0.3	<0.1±<0.1	<0.1±<0.1	-	-	-
Pyrola rotundifolia	-	-	-	-	-	<0.1±<0.1	<0.1±<0.1	0.2±0.5	1.0±2.1	0.3±0.9	-
Ranunculus cassubicus	0.4±0.5	0.2±0.3	0.7±1.2	<0.1±0.1	-	0.3±0.5	<0.1±<0.1	0.1±0.2	0.2±0.6	<0.1±0.1	-
Ranunculus ficaria	8.1±16.2	-	-	-	-	-	-	-	-	-	-
Ranunculus repens	0.4±0.4	0.1±0.2	1.8±2.5	0.2±0.6	<0.1±0.28	0.2±0.4	-	-	0.1±0.3	-	-
Rubus idaeus	-	1.0±1.4	0.7±1.4	2.5±3.1	4.4±5.3	1.0±1.2	2.1±2.3	1.0±1.6	2.0±1.6	0.2±0.4	<0.1±<0.1
Rubus saxatilis	-	0.3±0.2	1.4±1.7	1.7±2.3	0.8±1.9	1.2±1.7	2.3±4.0	10.3±6.6	2.8±2.4	1.2±3.3	<0.1±0.2
Solidago virgaurea	-	-	0.1±0.3	0.7±1.6	<0.1±0.1	<0.1±<0.1	0.2±0.4	0.5±0.7	0.9±1.2	0.4±0.6	0.3±0.8
Stellaria holostea	0.2±0.4	-	<0.1±0.1	1.2±4.0	1.2±3.1	0.2±0.4	<0.1±<0.1	0.3±0.8	0.3±1.2	-	-
Stellaria nemorum	5.7±6.2	0.6±0.9	2.8±4.8	6.1±12.3	0.9±1.5	0.9±1.3	1.4±2.3	0.1±0.2	0.6±1.5	-	-
Trientalis europaea	-	<0.1±0.1	0.1±0.1	0.5±0.5	1.1±1.0	<0.1±<0.1	0.3±0.4	0.5±0.4	0.5±0.4	0.5±0.6	0.2±0.3
Urtica dioica	0.6±±0.6	0.3±0.4	5.5±14.6	1.4±2.5	0.2±0.5	0.9±1.8	0.8±1.9	-	0.1±0.2	-	-
Vaccinium myrtillus	-	-	<0.1±<0.1	0.2±0.4	3.0±5.8	<0.1±<0.1	0.4±0.7	6.0±6.4	4.7±6.3	28.5±11.7	38.0±17.3
Vaccinium vitis-idea	-	-	-	<0.1±<0.1	0.1±0.3	-	<0.1±0.2	0.8±1.7	2.3±6.2	2.2±2.7	5.7±5.2
Viola mirabilis	-	0.1±0.3	<0.1±<0.1	-	-	0.2±0.3	0.5±1.3	0.3±0.7	0.4±0.7	0.1±0.4	-
Viola palustris	-	-	<0.1±<0.1	<0.1±<0.1	-	0.3±6.0	0.7±1.7	0.2±0.6	0.2±0.4	<0.1±<0.1	-
Viola riviniana	-	-	0.3±0.9	0.8±1.8	<0.1±<0.1	-	-	-	<0.1±<0.1	<0.1±<0.1	-
Moss layer											
Total cover, %	3.4±3.3	11.7±15.0	16.3±11.8	13.1±13.7	6.8±6.5	25.0±13.3	21.1±18.6	34.1±19.0	40.2±16.0	63.1±20.1	63.7±21.5
Total number of species	30	17	33	33	24	25	36	36	39	37	29
Average number of species	9±9	9±3	10±3	9±3	6±4	9±4	11±4	10±4	12±5	10±4	12±3
Aulacomnium palustre	-	-	-	-	-	-	-	-	0.1±0.6	0.6±1.8	<0.1±<0.1
Brachythecium oedipodium	0.9±0.6	1.5±2.4	2.0±2.4	4.0±4.9	3.2±3.9	0.2±0.2	1.6±2.7	1.4±1.7	0.6±1.3	0.4±0.8	2.1±2.5
Brachythecium rivulare	0.2±0.4	-	1.6±3.7	-	-	-	-	-	-	-	-
Brachythecium rutabulum	0.3±0.3	0.2±0.3	0.9±1.4	0.3±0.6	<0.1±0.1	-	0.3±1.2	<0.1±<0.1	0.1±0.5	-	-
Bryum sp.	-	-	0.3±0.7	0.7±2.4	-	-	-	-	-	-	-
Calliergonella cuspidata	0.1±0.2	-	0.5±1.6	0.2±0.4	-	-	-	-	-	-	-
Cirriphyllum piliferum	0.1±0.2	4.7±10.2	1.9±1.8	1.0±2.9	<0.1±0.10	3.3±2.7	2.3±3.5	0.4±0.8	2.0±2.0	0.6±1.5	1.3±2.1
Climacium dendroides	0.3±0.6	0.2±0.4	1.0±2.0	0.2±0.4	<0.1±0.13	0.4±0.6	0.6±1.2	4.5±9.8	0.4±0.6	0.2±0.4	-
Dicranum majus	<0.1±<0.1	-	-	<0.1±<0.1	<0.1±0.13	-	-	0.3±0.9	-	0.6±1.6	6.5±7.7
Dicranum polysetum	-	-	-	-	<0.1±<0.1	0.2±0.4	-	<0.1±<0.1	1.0±1.7	2.8±4.2	1.1±0.9
Dicranum scoparium	-	-	0.3±0.7	-	<0.1±0.1	0.7±1.2	0.2±0.3	0.1±0.1	1.1±1.4	0.4±0.3	0.5±0.8
Eurhynchium angustirete	0.5±0.9	2.4±4.2	1.4±2.2	<0.1±0.1	0.2±0.4	8.1±10.7	2.6±5.8	2.4±2.5	2.2±3.0	0.2±0.3	-
Eurhynchium praelongum	<0.1±<0.1	-	<0.1±0.1	<0.1±0.1	<0.1±<0.1	-	-	0.4±0.9	-	-	0.7±1.6
Hylocomium splendens	<0.1±<0.1	0.2±0.2	<0.1±<0.1	0.6±2.0	-	1.2±2.2	4.1±5.8	2.3±2.1	8.2±7.2	34.4±17.6	10.9±8.2
Lepidozia reptans	-	-	-	-	<0.1±<0.1	-	-	-	-	1.7±5.5	-
Plagiochila asplenioides	<0.1±<0.1	<0.1±0.1	0.7±1.6	0.8±1.4	<0.1±0.1	1.1±1.1	0.4±0.8	2.6±3.3	2.7±4.7	4.4±8.1	<0.1±<0.1
Plagiomnium affine	0.1±0.2	0.4±0.5	1.5±1.6	0.8±1.0	0.3±0.8	0.1±0.9	0.8±1.8	1.1±1.6	1.1±1.6	-	-
Plagiomnium cuspidatum	0.4±0.2	1.0±0.9	1.4±1.8	1.3±2.0	1.0±1.5	1.4±1.4	2.8±3.6	2.6±2.5	4.0±5.1	0.9±1.5	<0.1±0.2
Plagiomnium elatum	-	0.1±0.2	-	-	-	8.7±11.1	0.9±1.6	0.1±0.2	3.2±7.0	<0.1±0.1	-
Plagiomnium ellipticum	<0.1±0.2	-	1.0±2.1	0.6±1.1	-	-	0.2±1.0	<0.1±0.1	1.1±3.1	0.5±1.7	0.1±0.4
Plagiomnium medium	<0.1±<0.1	-	0.5±1.1	10.6±36.2	-	-	0.5±1.5	0.3±0.8	0.9±2.6	-	-
Plagiomnium undulatum	0.5±0.9	0.8±1.4	0.3±0.8	<0.1±<0.1	-	<0.1±<0.1	0.1±0.4	0.5±1.4	<0.1±<0.1	-	-
Plagiothecium denticulatum	<0.1±<0.1	-	0.2±0.6	0.2±0.5	<0.1±<0.1	<0.1±<0.1	0.4±1.0	0.1±0.2	0.4±1.1	<0.1±<0.1	1.6±3.7
Plagiothecium laetum	-	-	0.1±0.3	0.2±0.6	0.5±1.1	-	-	<0.1±<0.1	<0.1±<0.1	-	0.4±0.9
Pleurozium schreberi	<0.1±0.2	-	0.1±0.1	0.1±0.1	0.1±0.2	1.3±2.3	0.8±1.9	0.8±1.4	4.0±3.8	9.0±6.4	20.5±11.7
Polytrichum longisetum	<0.1±<0.1	-	-	0.2±0.4	<0.1±0.1	<0.1±<0.1	0.1±0.3	0.4±0.8	0.1±0.4	0.3±0.5	0.7±1.1
Rhizomnium punctatum	<0.1±<0.1	-	0.3±1.0	<0.1±<0.1	-	0.2±0.4	0.1±0.6	-	0.6±1.7	-	-
Rhodobryum roseum	<0.1±0.2	0.1±0.2	0.1±0.1	<0.1±0.1	<0.1±<0.1	<0.1±0.2	0.2±0.3	0.8±1.0	1.1±1.3	1.1±1.6	<0.1±<0.1
Rhythidiadelphus triquetrus	0.1±0.3	0.3±0.5	1.2±2.5	0.4±1.5	0.2±0.7	2.5±3.2	1.5±3.2	11.9±13.8	4.8±5.2	1.6±2.5	<0.1±0.1
Sphagnum angustifolium	-	-	-	-	-	-	-	0.2±0.6	-	<0.1±<0.1	0.9±1.6
Sphagnum capillifolium	-	-	-	-	<0.1±0.1	<0.1±<0.1	<0.1±<0.1	-	-	<0.1±<0.1	1.0±1.4
Sphagnum centrale	-	-	-	-	-	-	-	-	-	0.9±2.8	-
Sphagnum fallax	-	-	-	-	-	-	-	-	<0.1±<0.1	2.2±5.5	0.2±0.8
Sphagnum flexuosum	-	-	-	-	-	-	-	-	<0.1±<0.1	0.7±1.5	-
Sphagnum girgensohnii	-	-	-	-	-	--	-	-	<0.1±0.3	4.2±8.0	10.1±13.0
Sphagnum magellanicum	-	-	-	-	<0.1±<0.1	-	<0.1±0.1	-	-	-	1.0±1.4
Sphagnum russowii	-	-	-	-	-	<0.1±<0.1	<0.1±<0.1	<0.1±<0.1	-	0.6±1.8	0.3±0.7

Only species with frequency > 3 in the data and with mean abundance > 0.5 at least in one community type are presented.

Table 7. Average thickness of soil diagnostic horizons (O, A, AH, H) and Ellenberg indicator values of established community types

Variable	Forest site type											p_{ANOVA}
	Dryopteris					*Oxalis*				*Myrtillus*		
	Community type											
	1	2	3	4	5	6	7	8	9	10	11	
O horizon	2.0±0.8^{abcd}	2.0±0.7^{abcd}	1.4±0.7^{a}	1.2±0.6^{a}	1.3±0.5^{a}	2.9±1.5^{cd}	1.7±1.5^{ab}	2.0±1.4^{abc}	2.6±1.8^{bcd}	3.5±2.2^{d}	1.9±1.5^{abc}	0.004
A horizon	11.0±12.7^{abcd}	-	12.1±11.7^{d}	8.8±10.4^{bcd}	0.9±2.7^{ab}	11.1±12.7^{cd}	3.5±10.4^{abc}	7.3±12.8^{abcd}	1.7±7.1^{a}	3.1±9.8^{abc}	2.2±7.8^{ab}	0.033
AH horizon	5.5±11.0	19.2±18.9	10.6±21.2	26.8±34.2	7.9±7.7	8.8±21.0	13.0±24.2	23.1±39.6	17.1±40.1	8.7±25.8	24.7±28.6	<0.001
H horizon	-	7.6±17.0^{ab}	2.0±6.6^{a}	1.5±2.8^{a}	30.3±26.2^{bcd}	4.7±14.0^{a}	35.6±37.0^{cd}	1.0±2.6^{a}	40.8±42.2^{d}	20.2±30.2^{abc}	8.0±7.1^{ab}	0.752
Light	4.1±0.2^{de}	3.7±0.4^{bcd}	4.4±0.5^{e}	3.8±0.7^{d}	4.0±0.3^{de}	3.5±0.5^{bcd}	3.4±0.5^{abc}	3.8±0.6^{cd}	3.4±0.5^{abc}	3.1±0.3^{a}	3.3±0.6^{ab}	<0.001
Moisture	6.4±0.5^{e}	5.7±0.8^{de}	6.0±0.4^{e}	5.8±1.1^{de}	5.8±0.6^{de}	5.3±0.6^{cd}	5.4±0.7^{d}	4.7±0.8^{bc}	4.5±0.4^{b}	3.3±0.4^{a}	3.4±0.6^{a}	<0.001
Reaction	6.1±0.3^{g}	5.2±0.5^{f}	4.9±0.5^{ef}	4.4±0.9^{d}	4.2±0.5^{cd}	4.5±0.3^{de}	4.1±0.6^{cd}	3.8±0.9^{bc}	3.5±0.5^{b}	2.1±0.4^{a}	2.1±0.3^{a}	<0.001
Nitrogen	6.3±0.4^{e}	5.5±0.7^{e}	5.0±0.7^{cd}	5.0±1.0^{cd}	4.8±0.8^{cd}	4.6±0.3^{c}	4.7±0.6^{c}	3.7±0.8^{b}	3.5±0.4^{b}	2.1±0.4^{a}	1.9±0.5^{a}	<0.001

Notations as in Table 2.

Table 6. Significant ($p < 0.05$) indicator species and their indicator values in old-drained forests community types

Species	*Max*	*p*	Community type										
			1	2	3	4	5	6	7	8	9	10	11
Matteuccia struthiopteris	1	<0.001	95	0	0	0	0	0	0	0	0	0	0
Ulmus glabra	1	0.003	39	2	2	0	0	7	0	3	0	0	0
ULMUS GLABRA	1	0.005	37	0	0	0	0	1	0	2	0	0	0
Eurhynchium hians	1	0.005	34	4	1	0	0	0	0	0	2	0	0
Galeobdolon luteum	1	0.010	28	7	14	2	0	19	0	0	0	0	0
Stachys sylvatica	1	0.014	28	2	0	0	0	3	0	0	1	0	0
Padus avium	1	0.032	31	13	6	0	0	17	6	2	2	0	0
Plagiothecium cavifolium	1	0.032	22	0	0	1	0	0	0	0	0	0	0
Ranunculus ficaria	1	0.033	25	0	0	0	0	0	0	0	0	0	0
Stellaria nemorum	1	0.033	29	1	9	15	2	3	3	0	1	0	0
ALNUS GLUTINOSA	1	0.034	24	13	15	14	6	2	1	1	0	0	0
Paris quadrifolia	1	0.037	20	3	17	9	1	6	9	5	4	0	0
Anemone nemorosa	1	0.049	24	11	5	0	0	11	0	14	4	2	0
Mercurialis perennis	2	<0.001	9	58	2	0	1	18	0	1	0	0	0
BETULA PUBESCENS	2	0.028	9	19	13	5	7	15	5	9	6	2	3
Impatiens noli-tangere	2	0.050	2	28	4	1	8	4	1	0	0	0	0
Filipendula ulmaria	3	<0.001	1	2	52	2	0	19	1	5	0	0	0
Cardamine amara	3	0.002	2	0	37	1	0	4	0	0	0	0	0
Cirsium oleraceum	3	0.003	2	0	40	7	2	3	2	4	9	0	0
Crepis paludosa	3	0.004	4	0	39	6	0	4	2	6	4	1	0
Scirpus sylvaticus	3	0.005	0	0	36	0	0	0	0	0	0	0	0
Ranunculus repens	3	0.006	9	2	38	3	0	7	0	0	1	0	0
Brachythecium rivulare	3	0.017	2	0	25	0	0	0	0	0	0	0	0
Equisetum sylvaticum	3	0.025	1	0	30	15	3	6	0	6	1	0	0
Myosotis scorpioides	3	0.031	0	0	22	1	0	2	0	0	0	0	0
Ribes nigrum	3	0.041	2	14	21	1	0	3	0	0	0	0	0
Athyrium filix-femina	4	<0.001	4	4	13	53	0	2	6	1	2	0	0
Epilobium adenocaulon	4	0.004	0	0	0	38	0	0	0	0	0	0	0
Alnus glutinosa	4	0.005	4	0	7	32	2	1	0	1	0	0	0
Conocephalum conicum	4	0.006	0	0	0	31	0	0	0	0	0	0	0
Plagiomnium medium	4	0.011	0	0	1	49	0	0	1	1	1	0	0
Milium effusum	4	0.022	0	0	2	26	18	5	5	2	1	0	0
Viola riviniana	4	0.033	0	0	8	26	0	0	0	0	0	0	0
Brachythecium oedipodium	4	0.046	5	7	9	23	18	1	4	5	1	1	6
Dryopteris expansa	5	<0.001	0	2	3	10	56	4	2	3	2	0	0
Maianthemum bifolium	5	0.001	0	1	4	6	52	1	3	5	7	6	1
Rubus idaeus	5	0.005	0	5	3	13	30	5	12	4	13	0	0
Trientalis europaea	5	0.011	0	1	2	7	24	0	4	13	12	10	3
Impatiens parviflora	5	0.047	0	2	0	6	22	0	0	0	0	0	0
Hepatica nobilis	6	0.007	0	0	8	1	0	35	3	2	3	0	0
Eurhynchium angustirete	6	0.015	1	11	3	0	1	34	10	9	9	0	0
Phegopteris connectilis	6	0.018	0	6	0	1	0	33	0	0	1	0	0
Galium odoratum	6	0.024	0	0	0	3	0	26	0	12	0	0	0
Plagiomnium elatum	6	0.037	0	0	0	0	0	25	3	0	7	0	0
Oxalis acetosella	7	<0.001	1	8	2	8	18	12	32	4	12	1	0
Circaea alpina	7	0.011	0	1	0	6	4	10	29	0	9	0	0
Galium triflorum	7	0.021	0	0	0	0	0	1	24	0	10	0	0
Rubus saxatilis	8	<0.001	0	1	4	5	1	4	8	46	11	2	0
Rhytidiadelphus triquetrus	8	0.001	0	0	2	1	0	7	4	42	16	5	0
Carex digitata	8	0.005	0	4	2	0	0	6	2	34	17	3	0
Calamagrostis arundinacea	8	0.011	0	0	0	0	0	1	0	37	10	18	3
Mycelis muralis	9	0.006	0	2	2	2	0	0	28	2	30	1	0
Frangula alnus	9	0.006	0	0	1	2	3	2	2	7	43	12	2
Fragaria vesca	9	0.007	0	0	0	3	0	0	13	9	37	7	0
Convallaria majalis	9	0.009	0	1	1	0	1	4	7	13	31	3	0
Pyrola rotundifolia	9	0.016	0	0	0	0	0	0	0	4	32	4	0
Dicranum scoparium	9	0.036	0	0	2	0	1	10	2	1	24	10	12
Rhodobryum roseum	9	0.036	0	1	1	0	0	1	3	15	26	12	0
Luzula pilosa	9	0.043	0	0	1	1	10	2	7	8	21	10	6
Plagiomnium cuspidatum	9	0.050	2	6	6	6	3	5	16	14	22	2	0
Hylocomium splendens	10	<0.001	0	0	0	0	0	1	4	4	13	53	21
Dicranum polysetum	10	0.003	0	0	0	0	0	1	0	0	9	45	22
Sphagnum fallax	10	0.0178	0	0	0	0	0	0	0	0	0	28	1
Molinia caerulea	10	0.024	0	0	0	0	0	0	0	0	10	23	1
Sphagnum flexuosum	10	0.044	0	0	0	0	0	0	0	0	0	20	0
Rubus chamaemorus	10	0.049	0	0	0	0	0	0	0	0	0	20	0
Sphagnum centrale	10	0.049	0	0	0	0	0	0	0	0	0	20	0
Melampyrum pratense	11	<0.001	0	0	0	0	0	0	0	0	1	5	72
Vaccinium myrtillus	11	<0.001	0	0	0	0	2	0	0	5	5	35	47
Pleurozium schreberi	11	<0.001	0	0	0	0	0	1	1	1	11	26	55
Sphagnum capillifolium	11	<0.001	0	0	0	0	0	0	0	0	0	0	49
Vaccinium vitis-idaea	11	<0.001	0	0	0	0	0	0	0	5	15	14	56
Dicranum majus	11	<0.001	0	0	0	0	0	0	0	1	0	0	57
Sphagnum girgensohnii	11	0.001	0	0	0	0	0	0	0	0	0	6	46
Sphagnum magellanicum	11	0.002	0	0	0	0	1	0	0	0	0	0	41
PINUS SYLVESTRIS	11	0.006	0	0	1	3	8	1	4	0	1	12	28
Chamaedaphne calyculata	11	0.011	0	0	0	0	0	0	0	0	0	0	30
Ledum palustre	11	0.012	0	0	0	0	0	0	0	0	0	0	30
Sphagnum angustifolium	11	0.013	0	0	0	0	0	0	0	3	0	0	30
Salix cinerea	11	0.014	0	0	0	0	0	0	0	0	0	0	23
Deschampsia flexuosa	11	0.048	0	0	0	1	0	0	0	0	0	1	27

Tree layer species are written with capital letters. Notations: Max – community type where the species indicator value is maximal, *p* – significance level.

(Table 5). Other significant indicator species identified were *Ranunculus repens, Cardamine amara, Scirpus sylvaticus*, and *Myosotis scorpioides* in the field layer, and *Brachythecium rivulare* in the moss layer (Table 6). The habitats were characterised as semi-shaded, moist, moderately acidic, and of intermediate fertility. In soils the A and decayed-peat horizons were of similar thickness (12.1 and 10.6 cm, respectively), but the undecomposed peat horizon was almost lacking (Table 7). This community type can be named as *Alnus glutinosa–Betula pubescens–Filipendula ulmaria–Athyrium filix-femina*.

In the tree layer of the 4th type communities, *Alnus glutinosa* prevailed (Table 5), and the shrub layer was modest or almost lacking. In the field layer, *Athyrium filix-femina* was overwhelmingly dominating and indicative. The other reliable indicator species in the field layer were *Epilobium adenocaulon, Milium effusum, and Viola riviniana* (Table 6). *Dryopteris expansa, D. carthusiana, Oxalis acetosella*, and *Stellaria nemorum* were also of comparative abundance. Average total cover of the field layer was high (87%). In the moss layer, *Plagiomnium medium* and *Brachythecium oedipodium* had the largest cover and significant indication value. These communities have developed in habitats where the average thickness of A horizon was 8.8 cm and the average thickness of the following decayed-peat horizon was 26.8 cm. According to the Ellenberg indicator values, the habitats were fresh or constantly moist, moderately acidic, and of intermediate fertility (Table 7). This community type can be named as *Alnus glutinosa–Athyrium filix-femina–Dryopteris expansa*.

The tree layer of the 5th type communities was mixed; almost evenly were represented *Pinus sylvestris, Picea abies*, and *Alnus glutinosa* (Table 5). In the shrub layer, *Sorbus aucuparia* was the most frequent species. The field layer was clearly dominated by *Dryopteris expansa*, under which *Oxalis acetosella* can grow abundantly. Other species identified as significant indicators were *Impatiens parviflora, Maianthemum bifolium, Rubus idaeus*, and *Trientalis europaea* (Table 6). The moss layer was developed only modestly; in that the trustful indicator species were lacking, but *Brachythecium oedipodium* was usually the most abundant species (Table 7). The soil A horizon of these communities was very shallow, while the thickness of decayed-peat and undecomposed peat horizons was on average 7.9 and 30.3 cm, respectively. Soils were fresh or constantly moist, slightly acidic, and of intermediate fertility. We name this community type as *Pinus sylvestris–Picea abies–Dryopteris expansa–Impatiens parviflora*.

Padus avium and *Betula pubescens* were the prevailing species in the tree layer of communities of the 6th community type. In the shrub layer, *Sorbus aucuparia, Padus avium*, and saplings of *Populus tremula* were the most frequent species. The field layer was dominated by *Oxalis acetosella* and *Mercurialis perennis*, but other trustworthy indicator species were *Hepatica nobilis, Phegopteris connectilis*, and *Galium odoratum*. In the moss layer, the most abundant and indicative species were *Plagiomnium elatum* and *Eurhynchium angustirete* (Tables 5 and 6). A horizon in soils in the respective habitats was rather thick (11.1 cm on average), followed by decayed-peat and undecomposed peat horizons of medium thickness. According to the Ellenberg indicator values, soils were of average dampness, moderate acidity, and medium fertility (Table 7). These communities belong to the *Betula pubescens–Padus avium–Oxalis acetosella–Phegopteris connectilis* type.

The next three community types represent the *Oxalis* forest ST. In the tree layer of the 7th type communities, *Picea abies* dominated, whereas *Padus avium, Betula pubescens*, and *Pinus sylvestris* were intermixed. In the shrub layer, *Sorbus aucuparia, Padus avium*, and *Acer platanoides* were the most frequent. In the field layer of these communities, *Oxalis acetosella* had the highest cover and indicator value, followed by *Athyrium filix-femina, Dryopteris carthusiana, Circaea alpina* and *Galium triflorum* (Table 5). The total cover of the moss layer was modest and no indicator species were ascertained (Table 6). The A horizon (3.5 cm on average) was followed by decayed-peat and undecomposed peat horizons with very varying thickness. Soils were fresh, modestly acidic, and of medium fertility (Table 7). We call this community type *Picea abies–Padus avium–Circaea alpina–Oxalis acetosella*.

Communities of the 8th type included mixed spruce (*Picea abies*) and birch (*Betula pubescens*) stands developed on soils with, on average, 7.3 cm thick A horizon, and 23.1 cm thick decayed-peat horizon. Soils were fresh, modestly acidic, and of medium fertility (Table 7). In the shrub layer, the most frequent species were *Sorbus aucuparia* and *Frangula alnus*, together with saplings of *Picea abies* and *Fraxinus excelsior*. In the field layer, the most abundant and indicative species was *Rubus saxatilis*, followed by *Carex digitata* and *Calamagrostis arundinacea* (Tables 5 and 6). *Dryopteris expansa, Oxalis acetosella*, and *Geum rivale* also had a relatively high cover. In the moss layer, *Rhytidiadelphus triquetrus* was indicative. The A horizon had an average thickness (7.3 cm), the decayed-peat horizon thickness was on average quite large but variable, and the undecomposed peat horizon was almost lacking. This community type can be titled as *Picea abies–Betula pubescens–Rubus saxatilis–Oxalis acetosella*.

In the 9th type communities, the tree layer was dominated by *Picea abies*, but *Padus avium* and *Betula pubescens* were also frequent. In the shrub layer, *Frangula alnus, Sorbus aucuparia*, and saplings of *Picea abies* were abundant. The total cover of the field layer was modest (56.3%). The most abundant species in the field layer were *Oxalis acetosella, Convallaria majalis, Vaccinium myrtilus*, and *Dryopteris expansa* (Table 5). Besides *Convallaria majalis*, significant indicator value had also *Mycelis muralis, Fragaria vesca, Pyrola rotundifolia*, and *Luzula pilosa* (Table 6). In the moss layer, *Hylocomium splendens, Rhytidiadelphus triquetrus, Plagiomnium elatum* and *P. cuspidatum* had the highest cover. The both mentioned *Plagiomnium species, Dicranum scoparium* and *Rhodobryum roseum* were identified as reliable indicator species for this community type (Table 6). Soil A horizon for this group was shallow (usually less than 2 cm) but the undecomposed peat horizon of these communities was the thickest (40.8 cm in average) among the compared community types (Table 7). Soils were fresh, rather acidic, and only of modest fertility. This type of communities can be named as *Picea abies–Padus avium–Convallaria majalis–Oxalis acetosella*.

The two final community types belong to the *Myrtillus* ST, which comprises communities where the habitats' Ellenberg indicator values of moisture, reaction, and nutrient content were remarkably lower than for the other considered communities (Table 7). On the ordination scheme (Figure 4), the drained *Myrtillus* ST forests are distinctly separated from others.

The mixed tree layer in communities of the 10th type has been formed by *Pinus sylvestris* and *Pices abies*, but the pine has a dominating position. In the shrub layer, spruce saplings are comparatively frequent, as well as stems of *Frangula alnus* and *Sorbus aucuparia*. The total cover of the field layer was less than 50%. The most abundant species there was *Vaccinium myrtillus*, the abundance of other species was far lower (Table 5). In the field layer, *Molinia caerulea* and *Rubus chamaemorus* were identified as significant indicator species, while the other reliable indicator species occurred in the well-developed moss layer (i.e. *Hylocomium splendens, Dicranum polysetum, Sphagnum fallax*, and *S. flexuosum* – Table 6); rather common species were there also *Pleurozium schreberi* and *Plagiochila asplenioides* (Table 5). Ground vegetation in these comunities was comparatively shaded, soils were rather dry, strongly acidic, and relatively infertile (Table 7). We name this community type as *Picea abies–Pinus sylvestris–Molinia caerulea–Vaccinium myrtillus.*

In the tree layer of the 11th type communities, *Pinus sylvestris* clearly dominated, intermixed with spruce. In the shrub layer, spruce saplings were the most frequent, but some saplings of *Betula pendula* were also found. In the field layer, *Vaccinium myrtillus* had the highest cover, followed by *Melampyrum pratense, Vaccinium vitis-idaea, Lycopodium annotinum, Deschampsia flexuosa, Dryopteris carthusiana*, and *Ledum palustre* (Table 5). Besides of *Vaccinium myrtillus*, the highest indicator values had *Melampyrum pratense, Chamaedaphne calyculata* (in eastern and central Estonia), and *Ledum palustre* (Table 6). In the dense moss layer, which mainly comprised species such as *Pleurozium schreberi, Hylocomium splendes*, and *Sphagnum girgensohnii*, the presence of *Dicranum majus, Plagiothecium denticulatum, Sphagnum capillifolium*, and *S. angustifolium* was also noteworthy (Table 5). The soil reaction in these forests was as acidic as for communities of previous type, but the fertility was even lower (Table 7). This community type can be named as *Pinus sylvestris–Ledum palustre–Vaccinium myrtillus.*

Discussion

Though several forests studied by us were drained less than 60 years ago, a post-drainage period of 35 to 40 years seems to be sufficient for decomposition of the uppermost part of peat layer, and for formation of enough decayed soil horizon to achieve a new equilibrium of ground vegetation. Only in forests of *Alnus glutinosa–Betula pubescens–Filipendula ulmaria–Athyrium filix-femina* type, the fen/swamp species *Filipendula ulmaria* could in some cases have a projective cover of over 20%, postulated by Lõhmus (1981) as a criteria for discrimination of comparatively resently and old-drained forests. We presume that the drainage network in these stands was not sufficiently dense, or did not work effectively enough. In other forests of *Dryopteris* ST, even the total cover of all mire species will not exceed the pointed critical value. Soils of all *Dryopteris* ST forests described in the current study had already formed the litter horizon, as well as a remarkably thick decayed peat horizon which are additional important criterions for old-drained forest communities (Lõhmus 1981, 1982).

According to Pikk (1997a), in drained mire forests in Orajõe forestry, southwestern Estonia, where the peat layer was previously up to 60 cm thick, 42 years after drainage, the peat had decomposed and totally disappeared from large areas. In forests of Paasvere forestry, eastern Estonia, where the peat layer was 40–50 cm thick in the 1950s before drainage, after 40 years nothing remained of it, and gleyey sand or sandy clay was covered only by a thin horizon of forest litter (Pikk 1997a, Pikk and Seemen 2000). In Finland, where the climate is harsher than in Estonia and the peat decomposition intensity therefore lower, if the drainage system is sufficiently efficient, forests drained more than 25–40 years ago acquire the final stage of succession (Heikurainen and Pakarinen 1982, Хейкурайнен 1983). Also in forests of northwestern Russia, if the drainage system has been effective, the ground vegetation, as well as other components of the ecosystem, have been found to achieve a relatively stable state 40 years after the beginning of the drainage (Федорчук и др. 2005).

When comparing the Estonian old-drained forests with analogous stands in neighbouring countries, we can find rather large similarities according to expectation; the typological differences accrue mainly from the methodological approaches and geographical scope of countries. In Latvia, Sakss (Сакс 1966) distinguished *Sphagnum, Comarum palustre* (= *Potentilla palustre*), *Carex–Phragmites*, *Filipendula*, and *Dryopteris–Carex* STs on drained peat soils, coinciding with forest STs in excessively moist habitats on peat soils. Later, Bušs (Буш 1976, Bušs 1981, 1997) divided the drained forests first by the thickness of peat layer: (i) forests on drained mineral soil, where the peat thickness is < 20 cm (this group includes drained *Callunosa* mel. (i.e. meliorated), *Vacciniosa* mel., *Myrtillosa* mel. and *Mercurialiosa* mel. STs) and, (ii) forests on drained peat soil, comprising drained forests where the peat layer is > 20 cm thick (incorporating *Calluno-*

sa turf. mel., *Vacciniosa* turf. mel., *Myrtillosa* turf. mel. and *Oxalidosa* turf. mel. STs). A good correspondence of the *Myrtillosa* turf. mel. and *Oxalidosa* turf. mel. STs of drained peat forests with the respective Estonian STs was pointed at already by Lõhmus (1982), while the remaining two STs include forests where many bog species have been preserved in the ground vegetation, and those are dealt in Estonian forest typology among the drained bog forests.

In Finland, the post-drainage forests were divided into three groups according to time since drainage and its impact on vegetation: (i) recently drained mires (*ojikko*), (ii) transforming drained mires (*muuttuma*) and, (iii) transformed or old drained mires (*turvekankaat*) (Sarasto 1961ab, Heikurainen 1964, Paavilainen and Päivänen 1995). The latter forests "are characterised by a rather stable ground vegetation which clearly differs from that on virgin peatlands, resembling more the vegetation associated with mineral soil forests" (Heikurainen and Pakarinen, 1982) and they were classified into four STs considering their origin and fertility: (i) herb-rich ST, (ii) *Vaccinium myrtillus* ST, (iii) *Vaccinium vitis-idaea* ST and, (iv) *Ledum–Empetrum* ST. On the basis of multivariate cluster analysis of old peatland forests, Reinikainen (1988) also established seven STs: (i) eutrophic hardwood-spruce forests, (ii) herb-rich hardwood-spruce swamps, (iii) *Myrtillus* spruce swamps, (iv) herb-rich sedge pine swamps, (v) ordinary sedge pine swamps, (vi) cottongrass sedge pine bogs, (vii) low-shrub pine bogs. Furthermore, Laine (1989) adjusted the typology of old-drained Finnish peatland forests and distinguished: (i) herb-rich ST, where communities have developed from the most fertile spruce mires; ground vegetation is characterised by tall ferns and herb species; in southern Finland *Oxalis acetosella* is typical; (ii) *Vaccinium myrtillus* ST I which develops from genuine forested spruce mires, where *V. myrtillus* and *V. vitis-idaea* dominate the field layer, and *Trientalis europaea* and *Dryopteris carthusiana* are indicator species; (iii) *Vaccinium myrtillus* ST II originates from mesotrophic treeless and composite pine or spruce mires; indicator species are largely the same as for ST I, but tree stand and peat characteristics differ; (iv) *Vaccinium vitis-idaea* ST I develops from less fertile spruce mires and minerotrophic genuine pine mires; dwarf shrubs typical for pine mires (*Ledum palustre, Vaccinium uliginosum*) grow scattered amongst *Vaccinium myrtillus* and *V. vitis-idaea* which dominate the community; (v) *Vaccinium vitis-idaea* ST II develops from treeless and composite types of oligotrophic tall-sedge mires; in younger communities *Betula nana* usually dominates, whereas the more stabilised communities are rather similar to those in type I, major differences become evident in the peat properties; (vi) dwarf-shrub ST originates mainly from ombrotrophic pine bogs; *Ledum palustre* and *Vaccinium uliginosum* usually dominate the field layer; and (vii) *Cladina* ST develops from the most nutrient-poor bogs; *Sphagnum fuscum* along with lichens dominate the moss layer, *Calluna vulgaris, Empetrum nigrum*, and *Eriophorum vaginatum* prevail in the field layer.

There is rather good agreement between the respective *Vaccinium myrtillus* STs in Finland and Estonia. Due to the comparatively long south-north gradient of habitat conditions in Finland, the variation of these stands is much pronounced there and, e.g. *Molinia caerulea* does not have a noticeable position in those communities. At the same time, the diversity of old-drained *Oxalis* and *Dryopteris* ST forests in Estonia is remarkably larger than that of herb-rich STs in Finland, therefore the respective Estonian stands have certain affinity mainly with the herb-rich old-drained stands in southern Finland. The drained *Vaccinium vitis-idaea* ST forests distinguished by Marvet (1970) occur in Estonia only fragmentarily on the verges of drained bog forests and there is no reason to accept them as constituting a separate ST (Lõhmus 1982).

Drained *Myrtillus* ST pine and spruce forests in Sweden (Holmen 1964) are quite similar with corresponding forests in Estonia, while the Swedish drained *Maianthemum* and *Oxalis* ST spruce forests resemble Estonian drained *Oxalis* ST spruce stands.

In the forest typology of northwestern Russia (Федорчук и др. 2005), the relatively sustainable old-drained pine stands are treated in *Ledum-Vaccinium* drained biogeocenoses group, including (a) dwarf-shrub communities – *Fruticuloso-Turfosa*, where thickness of peat layer is more than 1.5 m, dominant species of ground vegetation are *Vaccinium vitis-idaea, Calluna vulgaris, Ledum palustre, V. uliginosum, Chamaedaphne calyculata, Dicranum polysetum, Pleurozium schreberi* and *Sphagnum* spp., and (b) bilberry-cowberry communities – *Vaccinioso-Turfosa*, where thickness of peat layer is > 30 cm, ground vegetation is dominated by *Vaccinium myrtillus, V. vitis-idaea, Calluna vulgaris, Ledum palustre, Betula nana, Pleurozium schreberi, Dicranum* spp. and *Hylocomium splendens*; those communities are often located along the drainage ditches as belts 20 metres in width. Old-drained spruce and potentially spruce forests are considered in (i) bilberry drained biogeocenoses group, comprising bilberry communities – *Myrtilloso-Turfosa*, where peat layer thickness is 20–150 cm; dominant species in the field layer are *Vaccinium myrtillus*, sometimes *Equisetum sylvaticum* or *Lycopodium annotinum, Trientalis europaea, Dryopteris expansa, Rubus idaeus, Carex globularis, Molinia caerulea* and, (ii) shamrock-fern drained biogeocenoses group, including (a) shamrock communities – *Oxalidosa-Turfosa*, where dominant species of ground vegetation are *Maianthemum bifolia, Trientalis europaea, Rubus saxatilis, Luzula pilosa, Oxalis actosella, Dryopteris carthusiana, Linnaea borealis, Melampyrum sylvaticum, Orthilia secunda, Phegopteris connectilis, Circaea alpina* and *Plagiomnium medium*; when more than 30 years have passed since drainage, *Melica nutans, Carex digitata, Pyrola rotundifolia, Paris quadrifolia, Veronica officinalis, Milium effusum, Dryopteris filix-mas, Anemone nemorosa, Rhodobryum roseum* will also appear, and single specimens of *Oxycoccus palustris, Chamaedaphne calyculata, Vaccinium uliginosum, Sphagnum girgensohnii, S. capillifolium, S. magellanicum, Polytrichum commune, Aulacomnium palustre, Potentilla palustris, Menyanthes trifoliata, Equisetum fluviatile, Carex lasiocarpa* and *Phragmites australis* may be preserved as relicts, (b) herb-shamrock communities (*Herboso-Oxalidoso-Turfosa*); *Alnus glutinosa* is always present in the tree layer, in the field layer species of *Maianthemum*, ferns, and *Filipendula* groups dominate, with *Oxalis acetosella* prevailing in stands of high density.

On the grounds of the short characterisation above, we can recognise a pretty good correspondence of *Vaccinioso-Turfosa* and *Myrtilloso-Turfosa* communities with the Estonian *Myrtillus* ST forests, while the *Oxalidosa-Turfosa* communities have great affinity with our *Oxalis* ST stands, and *Herboso-Oxalidoso-Turfosa* communities with Estonian *Dryopteris* ST forests.

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