

Research paper

## On *Dryopteris* site type forests in Estonia

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**Abstract.** Fern-rich forest communities are presented in Estonia in mesic or moderately humid nutrient-rich habitats, in areas of drained mire forests, on floodplains and lower parts of talus slopes of the North-Estonian limestone escarpment (klint). In the recent official forest typology only one site type has been distinguished and labelled by the ferns: the *Dryopteris* site type in the scope of boreo-nemoral forests. The aims of the current study were (i) to clarify whether distinguishing between two fern-rich forest site types, one among the full-drained forests group and another in the boreo-nemoral forests group, is reasonable, and if so, then (ii) what the main characteristics of both considered forest site types are, (iii) what the main environmental factors determining the structure of these communities are, and (iv) what the mutual relationship between those forests and other fern-rich forest communities is. Our results asserted a distinct difference between the full-drained and undrained *Dryopteris* site type forests distinguished by the former scholars. The undrained boreo-nemoral fern-rich stands have developed in the same place in harmony with habitat conditions, while drained forests have significantly changed. It seems that despite some vagueness due to long-lasting post-drainage succession, it is nevertheless justified to recognise the fern-rich drained stands in Estonian forest typology as representing an autonomous forest site type in the group of full-drained forests. To avoid confusion in nomenclature, in the future, the undrained fern-rich boreo-nemoral forests site type could be named according to the most conspicuous indicator species as the *Athyrium (filix-femina)* site type and fern-rich stands on full-drained peat soils as the *Dryopteris (expansa)* site type.

**Key words:** communities convergence, drainage impact, drained forests, indicator species.

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### Introduction

Fern-rich forest communities are spread over boreal and boreo-nemoral zones rather widely (e.g. Kielland-Lund, 1994; Dierßen, 1996; Buß, 1997; Vasilevic & Bibikova, 2002; Fedorchuk *et al.*, 2005; Heikurainen & Pakarinen, 1982; Laine, 1989).

In Estonia they are presented in mesic or moderately humid nutrient-rich habitats (Karu & Muiste, 1958; Katus & Tappo, 1965; Lõhmus, 1974, 2004), paludified and drained forest habitats (Hainla, 1957; Karu & Muiste, 1958; Katus & Tappo, 1965; Lõhmus, 1982), on floodplains (Paal *et al.*, 2007, 2008), as well as in forests covering the

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lower parts of talus slopes and the foot of the North-Estonian limestone escarpment (klint) (Paal, 2009).

Concerning the Estonian forest typology by Karu & Muiste (1958) the fern-rich forests belong to two forest site types. The first includes habitats with optimal moisture conditions and structured soils, having a slightly peaty humus horizon with a thickness of up to 25 cm; in the tree layer deciduous tree species are dominating, mainly *Betula pendula* Roth, *Alnus glutinosa* (L.) Gaertn. and *Populus tremula* L. The second site type comprises stands in excessively moist habitats situated on low sites, depressions or synclinal valleys, where the groundwater level is closer to the surface and the well-decomposed peat (decay) horizon is 20–30 cm thick; in the tree layer *Alnus glutinosa* and/or *Fraxinus excelsior* L. prevail. According to that forests of the first group were classified to the *Dryopteris* site type and the latter stands to the paludified *Dryopteris* site type. As a separate typological unit, the fern-rich forests were differentiated also within the forests of decayed-peat-mire site type divided according to *Myrtillus* and *Dryopteris* decayed-peat-mire pine forest, and *Oxalis* decayed-peat-mire pine and spruce forest types (Karu, 1957).

Katus & Tappo (1965) distinguished the *Dryopteris* site type in the group of boreo-nemoral forests, asserting that these are *Betula* spp. or *Alnus glutinosa* stands on gleyic soils or Gleysols; abundantly growing ferns are associated there with *Filipendula ulmaria* (L.) Maxim. and several nemoral forbs. These authors also recognised fern-rich forests among the decayed-mire forest site type, differentiating from *Oxalis* and *Vaccinium* variants the *Dryopteris* variant, arguing that all those variants have developed from swamp-like forests by successive paludification; initially the thickness of the peat horizon in these habitats can be 1.5–2 metres, after drainage it shrinks to 0.6–0.7 metres.

According to the forest site type clas-

sification proposed by Masing (1969), the fern-rich stands belong to the *Dryopteris* site type of nemoral forests (*Hainwälder* in Germany) on deep rich soil.

Löhmus (1974, 2004) also suggested only one *Dryopteris* site type and that among the boreo-nemoral forests. According to him, the respective habitats are located in alluvial and synclinal river valleys on various Gleysols, Histosols and Fluvisols. The tree layer is formed mostly by *Alnus glutinosa*, *A. incana* and *Betula* spp., whereas spruce stands occur in the less swampy or drained areas. Often *Fraxinus excelsior*, *Tilia cordata* Mill., *Ulmus glabra* Huds. or *U. laevis* Pall. and *Acer platanoides* L. are intermixed. Together with prevailing ferns, *Filipendula ulmaria* and numerous forbs of mesic and/or humic habitats can rather abundantly grow in the field layer, in some localities also *Urtica dioica* L. in the fern-rich drained forests on decayed peat. The fern-rich forest communities on drained areas represent a successional stage of relatively nutrition-rich drained swamp/fen forests which have not yet achieved a stable stage of decayed-mire *Oxalis* site type forests to which they typologically belong; therefore, it would be more justified to interpret them as lately or incompletely drained mire forests (Löhmus, 1981, 1982).

In the Estonian vegetation site types classification (Paal, 1997) *Dryopteris* site type forests are treated in the rich paludified forests type group but not indicated in the group of boreo-nemoral forests.

In neighbouring Latvia, fern-rich forests are likewise classified differently by various scholars. Saks (1966) distinguished between communities of *Dryopteris-Caricetum* in the group of forests on peat soils and drained peat soils. Later Bušs (1976) and Avis (1997) recognised *Dryopteriosa* type on wet mineral soils and *Dryopteriosacaricosa* type on wet peat soils, but within drained forests the fern-rich stands were not differentiated as a separate site type. In northwestern Russia Fedorchuk *et al.* (2005) discriminated between several types

or type variants of fern-rich forests on mineral soils as well as on drained areas within a group of drained shamrock-fern biogeocenoses (*Oxalidoso-Turfosa* and *Herboso-Oxalidoso-Turfosa* series).

The aim of the current study was (i) to clarify whether distinguishing between two *Dryopteris* forest site types, one among the undrained paludified forests group and another in the full-drained forests group, is reasonable, and if so, then (ii) what the main characteristics of both considered forest site types are, (iii) what the main environmental factors determining the structure of these communities are, and (iv) what the mutual relationship of these forests with other fern-rich forest communities is.

## Material and Methods

### Sample area and field data

A preliminary selection of studied forests was based on state forest maps (1:10,000). 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, southwestern Estonia and on the ancient Lake Peipsi basin between Tartu city and the western coast of Lake Peipsi, i.e. in regions where forest drainage has been the most extensive (Lõhmus, 1974). As for the *Dryopteris* site type forests, it is not indicated on the maps whether the forests are drained or not; therefore we carefully studied the maps regarding any drainage ditches in the neighbourhood 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. The sample included a total of 52 fern-rich stands without ditches in the neighbourhood of sample areas, and 38 stands where drainage ditches were discovered. The first forests were inter-

preted as representing undrained boreo-nemoral *Dryopteris* site type stands, whereas the second sample as belonging in the full-drained *Dryopteris* site type. Moreover, for reference we included in the analysed sample 14 relevés of fern-rich floodplains (Paal *et al.*, 2007, 2008) and 22 relevés of klint forests (Paal, 2009).

For vegetation description we used round sample plots with an area of 0.1 ha (radius 17.4 m), which fitted within a homogeneous forest stand. The tree layer was described by the canopy closure and by the basal area (DBH) of tree-trunks; the latter was estimated for every tree species at breast height (1.3 m) by means of the angle gauge. In every sample plot the basal area measurement was repeated in 4–5 random locations and averaged per site. Young trees, having a height below 5 m and/or a diameter at breast height of less than 5 cm were considered as saplings and registered 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. Shrub species outside the subplots were taken into account with number 1. For the field (grasses + herbs + dwarf shrubs) and moss layer vegetation the total species list was compiled and the cover-abundance rating of every species was conducted according to the scale: 0.1 (single specimens), 1 (average cover  $\leq 1\%$ ), 2 ( $\leq 5\%$ ), 3 ( $\leq 10\%$ ), 4 ( $\leq 25\%$ ), 5 ( $\leq 50\%$ ), 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), the names of bryophytes are taken from Ingerpuu & Vellak (1998) and the soils nomenclature from the IUSS Working Group WRB (2015).

### Data processing

Cluster analysis was performed based on the field and moss layers data, using the

$\beta$ -flexible algorithm (McCune & Mefford, 2011) and the relative Sørensen distance as the measure of dissimilarity (McCune & Grace, 2002). Before the cluster analysis, species occurring in data less than three times were filtered out. The clusters (= community types) were established on the basis of a dendrogram. The objectivity of relevés clustering on the basis of species content was tested according to multi-response permutation procedures (MRPP) (McCune & Mefford, 2011), considering also correction for multiple comparisons.

For every stand the Ellenberg indicator values of habitat environment conditions (Ellenberg, 1979) were calculated on the basis of field layer species cover values and revised indicator values of species (Chytrý *et al.*, 2018) by weighted averaging (Schaffers *et al.*, 2000). Differences between mean values of environmental variables were checked by the univariate dispersion analysis (StatSoft Inc., 2005).

The species indicator values in community types were calculated by the Dufrêne and Legendre (1997) method included in the program package PC-ORD (McCune & 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 & Mefford, 2011) was used. Before the analysis, species occurring in data less than three times were filtered out.

## Results

Cluster analysis dendrogram (Figure 1) demonstrates that undrained and drained *Dryopteris* site type forests, as well as fern-rich floodplain forests are clustered not according to their forest site types or site type groups, but form clusters (dendrogram “branches”) of intermixed character, asserting ground vegetation convergence

and resemblance in considered habitats. Only fern-rich klint forest communities are merged in several cases into almost “pure” clusters where communities of other forest groups are not much intermixed.

The ordination analysis biplot (Figure 2) exhibits that, compared to other discussed forests, the forests of the drained *Dryopteris* site type have a remarkably larger ecological variation along the gradients designated by the vectors of ecological indicator values; they encompass almost totally all undrained *Dryopteris* site type stands and a large part of forests of two other groups. Fern-rich floodplain forests are essentially overlapping with forests of both *Dryopteris* site types, as well as with fern-rich klint forests. Overlapping of the fern-rich klint forest communities with forests of other groups is not so overwhelming but still extensive. According to the T-criterion of the MRPP test, both *Dryopteris* site type forests are the closest to each other and separated most noticeably from the klint forests. Nevertheless, the pairwise comparison of all considered forest groups asserted a significant difference between all of them (Table 1).

Variation in fern-rich forest communities in different habitats is mainly determined by the nutrient richness and reaction (pH) of habitats/soils; the soils of floodplain and klint forests are significantly less acidic and have a better supply of nutrients than the soils of both *Dryopteris* site type stands (Table 2). According to the ecological indicator values of habitats, the differences between undrained and drained *Dryopteris* site type forests are minute: this proceeds from the fact that these values were calculated on the basis of communities species content. A striking difference between undrained and drained *Dryopteris* site type forests appears in soils: the soils of the undrained forests do not have a peat horizon and the raw humus horizon (AH) is significantly thinner and the humus horizon (A) thicker than in drained forests (Table 2).

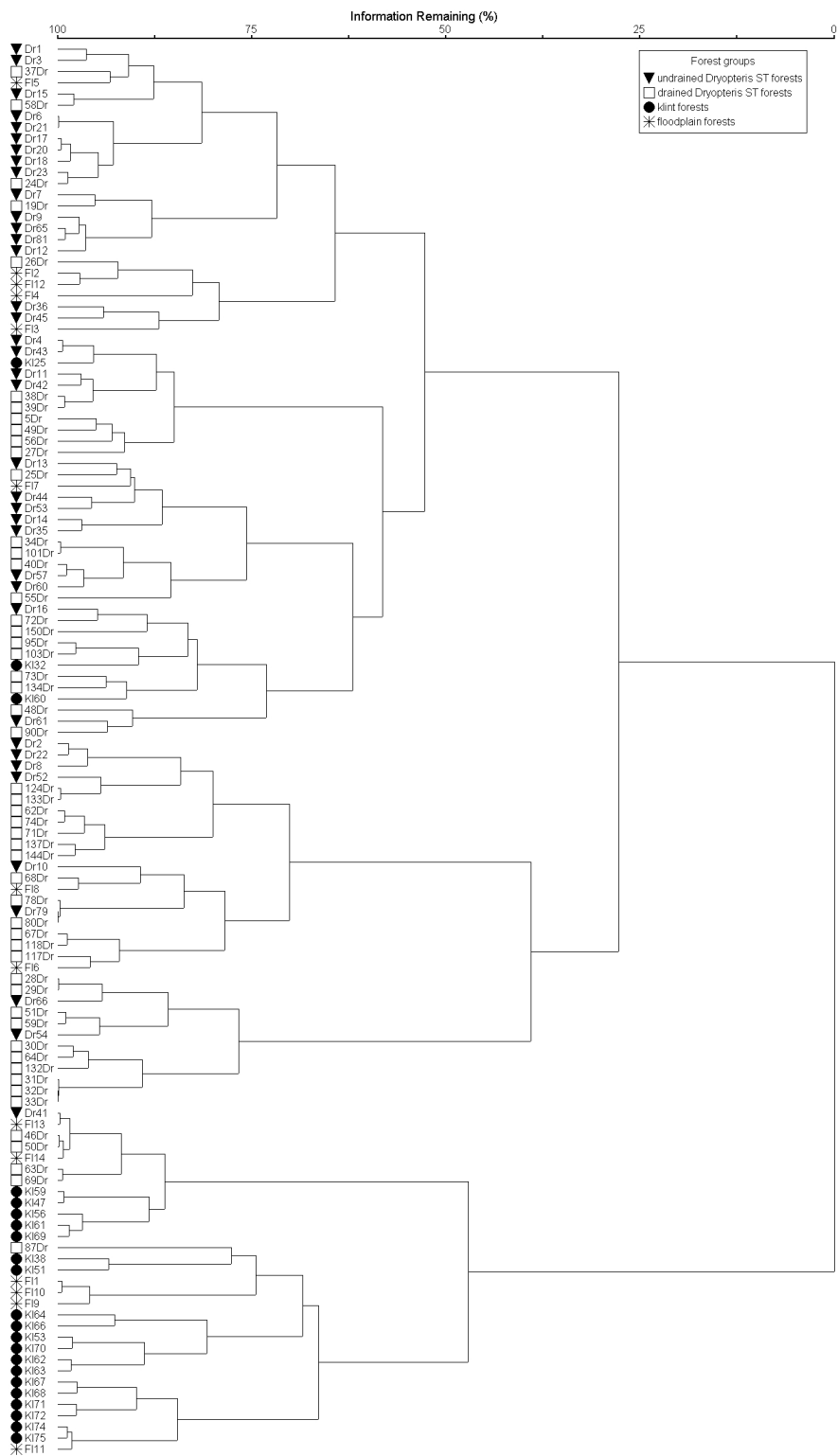


Figure 1. Cluster analysis dendrogram.

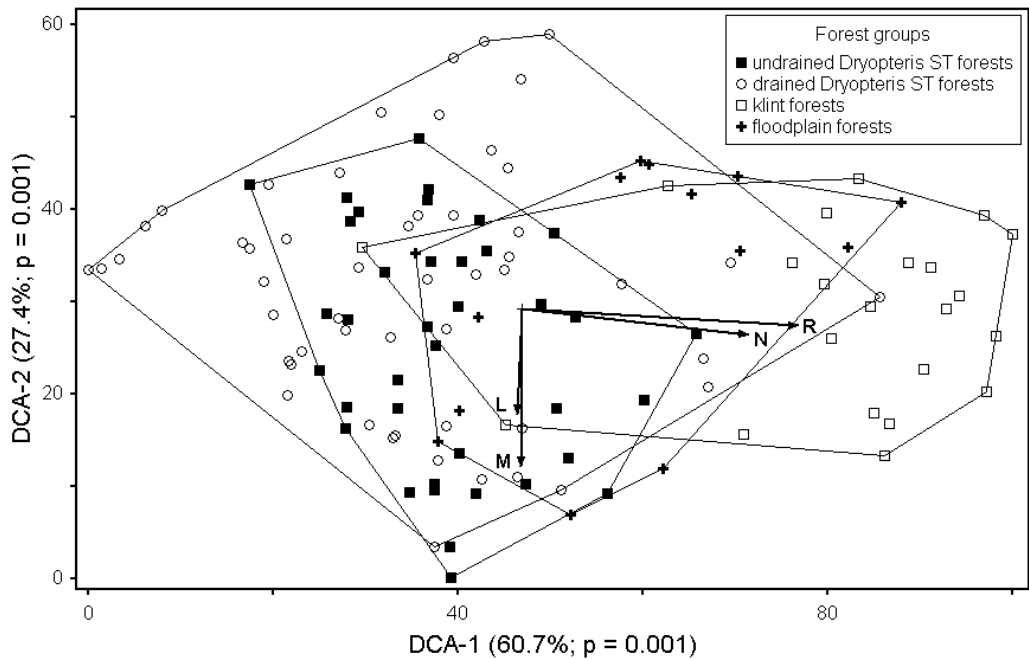


Figure 2. Ordination biplot of vegetation relevés (sample plots) and ecological indicator values of habitats. Notations: L, M, R and N – light, soil moisture, reaction (pH) and nutrition content indicator values of habitats, respectively.

Table 1. Results of the pairwise comparison of forest groups species content by multi-response permutation procedures. Notations: undr – undrained *Dryopteris* site type forests, dr – drained *Dryopteris* site type forests, kl – fern-rich forests on the talus slope of the klint, fl – fern-rich floodplain forests; *T* and *A* – test statistics, *p* – significance level, corrected for multiple comparisons according to Bonferroni procedure.

| Compared groups | <i>T</i> | <i>A</i> | <i>p</i> |
|-----------------|----------|----------|----------|
| undr versus dr  | -6.653   | 0.016    | <0.001   |
| undr versus kl  | -28.302  | 0.124    | <0.001   |
| undr versus fl  | -11.739  | 0.047    | <0.001   |
| dr versus kl    | -27.754  | 0.091    | <0.001   |
| dr versus fl    | -12.330  | 0.041    | <0.001   |
| kl versus fl    | -9.003   | 0.055    | <0.001   |

A particular nature of the considered forest groups is confirmed also by their numerous reliable indicator species (Table 3). For the undrained *Dryopteris* site type boreo-nemoral stands, *Athyrium filix-femina* (L.) Roth and *Dryopteris carthusiana* (Vill.) H.P.Fuchs are characteristic among ferns, *Crepis paludosa* (L.) Moench, *Paris quadrifolia* L. and *Rubus saxatilis* L. among forbs, and *Calamagrostis arundinacea* (L.) Roth among grasses. The presence of *Filipendula ulmaria*, *Cardamine amara* L. in the field layer and *Alnus glutinosa* in the tree layer suggests a good water supply in the habitats.

In drained *Dryopteris* site type forests the most prominent species is *Dryopteris expansa* (C.Presl) Fraser-Jenk. & Jermy, while low hummocks and root collars of trees are usually covered with *Oxalis acetosella* L., *Vaccinium myrtillus* L., *Maianthemum bifolium* (L.) F.W.Schmidt, *Trientalis*

Table 2. Ecological indicator values of habitats and the significance levels of their differences according to univariate ANOVA in fern-rich forest groups; similar groups of values by the Fisher LSD post-hoc test are marked with superscript letters. Notations:  $p$  – significance level of univariate ANOVA tests; Light, Moisture, Reaction, Nutrients – ecological indicator values (mean  $\pm$  standard error) of habitats, O ... A – thickness of respective soil horizons, nd – no data; other notations as in Table 1.

| Variable  | Forests group                |                              |                            |                             | $p$    |
|-----------|------------------------------|------------------------------|----------------------------|-----------------------------|--------|
|           | undr                         | dr                           | kl                         | fl                          |        |
| Light     | 3.9 $\pm$ 0.5                | 3.8 $\pm$ 0.5                | 3.6 $\pm$ 0.6              | 4.1 $\pm$ 0.7               | 0.089  |
| Moisture  | 5.8 $\pm$ 0.8                | 5. $\pm$ 0.8                 | 5.2 $\pm$ 0.9              | 5.7 $\pm$ 0.9               | 0.075  |
| Reaction  | 4.7 $\pm$ 0.6 <sup>a</sup>   | 4.6 $\pm$ 0.9 <sup>a</sup>   | 5.4 $\pm$ 0.9 <sup>b</sup> | 5.4 $\pm$ 0.8 <sup>b</sup>  | <0.001 |
| Nutrients | 4.9 $\pm$ 0.7 <sup>a</sup>   | 5.0 $\pm$ 1.0 <sup>a</sup>   | 5.8 $\pm$ 1.0 <sup>b</sup> | 5.4 $\pm$ 0.8 <sup>ab</sup> | 0.001  |
| O         | 1.4 $\pm$ 0.9 <sup>a</sup>   | 1.7 $\pm$ 1.0 <sup>a</sup>   | nd                         | nd                          | 0.215  |
| H total   | 0 <sup>a</sup>               | 7.4 $\pm$ 16.9 <sup>b</sup>  | nd                         | nd                          | 0.010  |
| H1        | 0 <sup>a</sup>               | 1.5 $\pm$ 3.7 <sup>b</sup>   | nd                         | nd                          | 0.016  |
| H2        | 0 <sup>a</sup>               | 3.9 $\pm$ 12.2 <sup>a</sup>  | nd                         | nd                          | 0.053  |
| H3        | 0 <sup>a</sup>               | 2.0 $\pm$ 8.3 <sup>a</sup>   | nd                         | nd                          | 0.151  |
| AH        | 6.1 $\pm$ 22.1 <sup>a</sup>  | 15.9 $\pm$ 25.1 <sup>b</sup> | nd                         | nd                          | 0.037  |
| A         | 20.0 $\pm$ 10.5 <sup>a</sup> | 7.6 $\pm$ 10.8 <sup>b</sup>  | nd                         | nd                          | <0.001 |

Table 3. Indicator value, relative abundance and relative frequency of species in fern-rich forest communities. Notations: tree-layer species are marked with asterisks; Max – forests group where the species indicator value is maximal,  $p$  – significance level; other notations as in Table 1.

| Species                          | Max | $p$    | Indicator value  |    |    |    | Relative abundance |    |    |    | Relative frequency |    |    |    |
|----------------------------------|-----|--------|------------------|----|----|----|--------------------|----|----|----|--------------------|----|----|----|
|                                  |     |        | Forest site type |    |    |    |                    |    |    |    |                    |    |    |    |
|                                  |     |        | ndr              | dr | kl | fl | ndr                | dr | kl | fl | ndr                | dr | kl | fl |
| <i>Crepis paludosa</i>           | ndr | <0.001 | 56               | 12 | 1  | 4  | 62                 | 23 | 7  | 7  | 89                 | 52 | 9  | 57 |
| <i>Brachythecium oedipodium</i>  | ndr | <0.001 | 53               | 33 | 0  | 0  | 63                 | 37 | 0  | 0  | 84                 | 88 | 9  | 7  |
| <i>Plagiomnium affine</i>        | ndr | <0.001 | 47               | 14 | 1  | 0  | 72                 | 25 | 4  | 0  | 66                 | 58 | 18 | 7  |
| <i>Athyrium filix-femina</i>     | ndr | <0.001 | 44               | 25 | 1  | 9  | 51                 | 30 | 9  | 10 | 87                 | 83 | 14 | 93 |
| <i>Equisetum sylvaticum</i>      | ndr | 0.001  | 43               | 20 | 0  | 3  | 56                 | 37 | 0  | 6  | 76                 | 54 | 0  | 43 |
| <i>Paris quadrifolia</i>         | ndr | 0.004  | 38               | 21 | 0  | 15 | 47                 | 29 | 3  | 21 | 82                 | 71 | 9  | 71 |
| <i>Calamagrostis arundinacea</i> | ndr | 0.005  | 40               | 3  | 0  | 1  | 84                 | 13 | 0  | 3  | 47                 | 25 | 0  | 21 |
| <i>Alnus glutinosa</i>           | ndr | 0.006  | 30               | 11 | 0  | 1  | 59                 | 32 | 0  | 9  | 50                 | 35 | 0  | 7  |
| <i>Filipendula ulmaria</i>       | ndr | 0.006  | 39               | 12 | 1  | 28 | 45                 | 19 | 3  | 33 | 87                 | 63 | 27 | 86 |
| <i>Alnus glutinosa</i> *         | ndr | 0.008  | 34               | 22 | 0  | 12 | 45                 | 32 | 4  | 19 | 76                 | 67 | 9  | 64 |
| <i>Dryopteris carthusiana</i>    | ndr | 0.010  | 39               | 33 | 0  | 2  | 48                 | 48 | 0  | 5  | 82                 | 69 | 0  | 50 |
| <i>Tilia cordata</i>             | ndr | 0.016  | 27               | 8  | 0  | 1  | 63                 | 28 | 0  | 9  | 42                 | 31 | 5  | 7  |
| <i>Luzula pilosa</i>             | ndr | 0.026  | 28               | 13 | 0  | 0  | 59                 | 38 | 2  | 1  | 47                 | 35 | 5  | 7  |

| Species                          | Max | $p$    | Indicator value  |    |    |    | Relative abundance |    |     |    | Relative frequency |    |    |    |
|----------------------------------|-----|--------|------------------|----|----|----|--------------------|----|-----|----|--------------------|----|----|----|
|                                  |     |        | Forest site type |    |    |    |                    |    |     |    |                    |    |    |    |
|                                  |     |        | ndr              | dr | kl | fl | ndr                | dr | kl  | fl | ndr                | dr | kl | fl |
| <i>Cardamine amara</i>           | ndr | 0.029  | 21               | 6  | 0  | 0  | 66                 | 29 | 5   | 1  | 32                 | 21 | 5  | 7  |
| <i>Rubus saxatilis</i>           | ndr | 0.030  | 31               | 19 | 0  | 11 | 43                 | 31 | 0   | 26 | 71                 | 62 | 0  | 43 |
| <i>Rhodobryum roseum</i>         | ndr | 0.031  | 25               | 6  | 0  | 3  | 68                 | 21 | 0   | 12 | 37                 | 31 | 0  | 21 |
| <i>Ranunculus auricomus</i>      | ndr | 0.041  | 12               | 0  | 0  | 0  | 93                 | 5  | 0   | 2  | 13                 | 2  | 0  | 7  |
| <i>Betula pubescens</i> *        | dr  | <0.001 | 44               | 45 | 0  | 0  | 50                 | 50 | 0   | 0  | 87                 | 90 | 0  | 0  |
| <i>Dryopteris expansa</i>        | dr  | <0.001 | 22               | 48 | 0  | 0  | 36                 | 64 | 0   | 0  | 61                 | 75 | 0  | 0  |
| <i>Oxalis acetosella</i>         | dr  | <0.001 | 23               | 53 | 3  | 9  | 24                 | 56 | 9   | 11 | 97                 | 94 | 32 | 86 |
| <i>Mycelis muralis</i>           | dr  | 0.002  | 1                | 30 | 0  | 0  | 7                  | 93 | 0   | 0  | 8                  | 33 | 0  | 0  |
| <i>Pinus sylvestris</i> *        | dr  | 0.002  | 1                | 31 | 0  | 0  | 5                  | 94 | 0   | 2  | 11                 | 33 | 0  | 7  |
| <i>Gymnocarpium dryopteris</i>   | dr  | 0.008  | 11               | 38 | 0  | 0  | 22                 | 76 | 0   | 1  | 50                 | 50 | 0  | 21 |
| <i>Trientalis europaea</i>       | dr  | 0.008  | 18               | 32 | 0  | 1  | 37                 | 60 | 0   | 4  | 50                 | 54 | 0  | 21 |
| <i>Picea abies</i>               | dr  | 0.012  | 26               | 39 | 0  | 3  | 34                 | 53 | 5   | 8  | 76                 | 73 | 9  | 36 |
| <i>Dicranum scoparium</i>        | dr  | 0.018  | 2                | 25 | 0  | 0  | 11                 | 87 | 1   | 1  | 16                 | 29 | 9  | 21 |
| <i>Maianthemum bifolium</i>      | dr  | 0.020  | 21               | 40 | 0  | 3  | 32                 | 57 | 4   | 7  | 66                 | 71 | 5  | 43 |
| <i>Vaccinium myrtillus</i>       | dr  | 0.023  | 1                | 25 | 0  | 0  | 7                  | 93 | 0   | 0  | 13                 | 27 | 0  | 0  |
| <i>Equisetum palustre</i>        | dr  | 0.023  | 1                | 18 | 0  | 0  | 15                 | 85 | 0   | 0  | 5                  | 21 | 0  | 0  |
| <i>Circea alpina</i>             | dr  | 0.025  | 9                | 24 | 0  | 0  | 28                 | 64 | 5   | 4  | 32                 | 38 | 5  | 7  |
| <i>Alnus incana</i> *            | kl  | <0.001 | 1                | 0  | 56 | 7  | 7                  | 0  | 78  | 15 | 8                  | 2  | 73 | 43 |
| <i>Sorbus aucuparia</i> *        | kl  | <0.001 | 0                | 0  | 41 | 0  | 0                  | 1  | 99  | 0  | 0                  | 2  | 41 | 0  |
| <i>Ulmus glabra</i> *            | kl  | <0.001 | 0                | 0  | 48 | 10 | 1                  | 4  | 71  | 24 | 8                  | 6  | 68 | 43 |
| <i>Lunaria rediviva</i>          | kl  | <0.001 | 0                | 0  | 45 | 0  | 0                  | 0  | 100 | 0  | 0                  | 0  | 45 | 0  |
| <i>Matteuccia struthiopteris</i> | kl  | <0.001 | 3                | 2  | 42 | 18 | 11                 | 12 | 52  | 25 | 24                 | 15 | 82 | 71 |
| <i>Amblystegium serpens</i>      | kl  | <0.001 | 0                | 0  | 65 | 0  | 0                  | 5  | 95  | 1  | 0                  | 6  | 68 | 7  |
| <i>Brachythecium rutabulum</i>   | kl  | <0.001 | 2                | 2  | 76 | 9  | 4                  | 5  | 80  | 10 | 34                 | 42 | 95 | 86 |
| <i>Chiloscyphus polyanthos</i>   | kl  | <0.001 | 0                | 0  | 41 | 0  | 0                  | 0  | 100 | 0  | 0                  | 0  | 41 | 0  |
| <i>Eurhynchium hians</i>         | kl  | <0.001 | 1                | 0  | 59 | 24 | 4                  | 0  | 62  | 34 | 29                 | 13 | 95 | 71 |
| <i>Fissidens gracilifolius</i>   | kl  | <0.001 | 0                | 0  | 64 | 0  | 0                  | 0  | 100 | 0  | 0                  | 0  | 64 | 0  |
| <i>Alnus incana</i>              | kl  | <0.001 | 1                | 1  | 43 | 16 | 5                  | 4  | 52  | 38 | 18                 | 12 | 82 | 43 |
| <i>Aegopodium podagraria</i>     | kl  | <0.001 | 3                | 1  | 52 | 14 | 4                  | 5  | 71  | 20 | 71                 | 29 | 73 | 71 |
| <i>Anomodon longifolius</i>      | kl  | <0.001 | 0                | 0  | 32 | 0  | 0                  | 0  | 100 | 0  | 0                  | 0  | 32 | 0  |
| <i>Conocephalum conicum</i>      | kl  | <0.001 | 1                | 0  | 32 | 0  | 11                 | 1  | 88  | 0  | 11                 | 8  | 36 | 7  |
| <i>Urtica dioica</i>             | kl  | 0.001  | 7                | 9  | 52 | 8  | 11                 | 16 | 61  | 12 | 63                 | 54 | 86 | 64 |
| <i>Pylaisia polyantha</i>        | kl  | 0.001  | 0                | 0  | 22 | 0  | 0                  | 0  | 97  | 3  | 0                  | 0  | 23 | 7  |
| <i>Brachythecium populeum</i>    | kl  | 0.003  | 0                | 0  | 18 | 0  | 0                  | 0  | 100 | 0  | 0                  | 0  | 18 | 0  |
| <i>Lonicera xylosteum</i>        | kl  | 0.004  | 4                | 3  | 34 | 3  | 12                 | 17 | 58  | 12 | 29                 | 17 | 59 | 29 |
| <i>Pseudoleskeella nervosa</i>   | kl  | 0.004  | 0                | 0  | 18 | 0  | 0                  | 0  | 100 | 0  | 0                  | 0  | 18 | 0  |
| <i>Amblystegium subtile</i>      | kl  | 0.004  | 0                | 0  | 14 | 0  | 0                  | 0  | 100 | 0  | 0                  | 0  | 14 | 0  |
| <i>Pohlia nutans</i>             | kl  | 0.006  | 0                | 0  | 14 | 0  | 0                  | 0  | 100 | 0  | 0                  | 0  | 14 | 0  |
| <i>Dryopteris austriaca</i>      | kl  | 0.006  | 0                | 0  | 20 | 6  | 0                  | 0  | 72  | 28 | 0                  | 0  | 27 | 21 |
| <i>Ribes nigrum</i>              | kl  | 0.011  | 7                | 3  | 34 | 0  | 20                 | 9  | 68  | 3  | 34                 | 29 | 50 | 14 |
| <i>Geranium robertianum</i>      | kl  | 0.013  | 0                | 0  | 17 | 0  | 0                  | 8  | 92  | 0  | 0                  | 6  | 18 | 0  |
| <i>Mnium hornum</i>              | kl  | 0.014  | 0                | 0  | 14 | 0  | 0                  | 0  | 100 | 0  | 0                  | 0  | 14 | 0  |
| <i>Taxiphyllum wissgrillii</i>   | kl  | 0.016  | 0                | 0  | 14 | 0  | 0                  | 0  | 100 | 0  | 0                  | 0  | 14 | 0  |
| <i>Pellia endiviifolia</i>       | kl  | 0.017  | 0                | 0  | 14 | 0  | 0                  | 0  | 100 | 0  | 0                  | 0  | 14 | 0  |

| Species                            | Max | $p$    | Indicator value  |    |    |    | Relative abundance |    |     |     | Relative frequency |    |    |    |
|------------------------------------|-----|--------|------------------|----|----|----|--------------------|----|-----|-----|--------------------|----|----|----|
|                                    |     |        | Forest site type |    |    |    |                    |    |     |     |                    |    |    |    |
|                                    |     |        | ndr              | dr | kl | fl | ndr                | dr | kl  | fl  | ndr                | dr | kl | fl |
| <i>Cratoneuron filicinum</i>       | kl  | 0.022  | 0                | 0  | 14 | 0  | 0                  | 0  | 100 | 0   | 0                  | 0  | 14 | 0  |
| <i>Anomodon viticulosus</i>        | kl  | 0.027  | 0                | 0  | 14 | 0  | 0                  | 0  | 100 | 0   | 0                  | 0  | 14 | 0  |
| <i>Ribes alpinum</i>               | kl  | 0.035  | 3                | 2  | 23 | 7  | 13                 | 12 | 50  | 25  | 24                 | 13 | 45 | 29 |
| <i>Mnium stellare</i>              | kl  | 0.039  | 0                | 0  | 9  | 0  | 0                  | 0  | 100 | 0   | 0                  | 0  | 9  | 0  |
| <i>Brachythecium velutinum</i>     | kl  | 0.040  | 0                | 0  | 9  | 0  | 0                  | 0  | 100 | 0   | 0                  | 0  | 9  | 0  |
| <i>Plagiochila porelloides</i>     | kl  | 0.040  | 0                | 0  | 9  | 0  | 0                  | 0  | 100 | 0   | 0                  | 0  | 9  | 0  |
| <i>Leptobryum pyriforme</i>        | kl  | 0.041  | 0                | 0  | 9  | 0  | 0                  | 0  | 100 | 0   | 0                  | 0  | 9  | 0  |
| <i>Brachythecium reflexum</i>      | kl  | 0.043  | 0                | 0  | 13 | 0  | 0                  | 0  | 95  | 5   | 0                  | 0  | 14 | 7  |
| <i>Bryum flaccidum</i>             | kl  | 0.044  | 0                | 0  | 9  | 0  | 0                  | 0  | 100 | 0   | 0                  | 0  | 9  | 0  |
| <i>Betula pendula</i> *            | fl  | <0.001 | 0                | 0  | 2  | 83 | 0                  | 0  | 11  | 89  | 0                  | 0  | 18 | 93 |
| <i>Fraxinus excelsior</i> *        | fl  | <0.001 | 4                | 1  | 14 | 43 | 11                 | 5  | 28  | 55  | 34                 | 13 | 50 | 79 |
| <i>Padus avium</i>                 | fl  | <0.001 | 10               | 8  | 9  | 53 | 16                 | 15 | 12  | 57  | 63                 | 52 | 73 | 93 |
| <i>Glechoma hederacea</i>          | fl  | <0.001 | 0                | 0  | 0  | 29 | 0                  | 0  | 0   | 100 | 0                  | 0  | 0  | 29 |
| <i>Polygonatum multiflorum</i>     | fl  | <0.001 | 0                | 0  | 0  | 43 | 0                  | 0  | 0   | 99  | 3                  | 2  | 0  | 43 |
| <i>Viola mirabilis</i>             | fl  | <0.001 | 1                | 0  | 0  | 44 | 16                 | 7  | 0   | 77  | 5                  | 6  | 0  | 57 |
| <i>Amblystegium varium</i>         | fl  | <0.001 | 0                | 0  | 0  | 33 | 0                  | 0  | 7   | 93  | 0                  | 0  | 5  | 36 |
| <i>Brachythecium salebrosum</i>    | fl  | <0.001 | 0                | 0  | 7  | 44 | 0                  | 12 | 37  | 51  | 0                  | 2  | 18 | 86 |
| <i>Drepanocladus revolvens</i>     | fl  | <0.001 | 0                | 0  | 0  | 36 | 0                  | 0  | 0   | 100 | 0                  | 0  | 0  | 36 |
| <i>Campanula latifolia</i>         | fl  | <0.001 | 0                | 0  | 0  | 29 | 0                  | 0  | 0   | 100 | 0                  | 0  | 0  | 29 |
| <i>Ranunculus cassubicus</i>       | fl  | <0.001 | 12               | 6  | 0  | 45 | 24                 | 18 | 0   | 57  | 50                 | 33 | 0  | 79 |
| <i>Poa nemoralis</i>               | fl  | <0.001 | 0                | 0  | 1  | 24 | 0                  | 0  | 32  | 68  | 0                  | 0  | 5  | 36 |
| <i>Carex vaginata</i>              | fl  | 0.001  | 0                | 0  | 0  | 21 | 0                  | 0  | 0   | 100 | 0                  | 0  | 0  | 21 |
| <i>Drepanocladus cossonii</i>      | fl  | 0.001  | 0                | 0  | 0  | 21 | 0                  | 0  | 0   | 100 | 0                  | 0  | 0  | 21 |
| <i>Ulmus laevis</i> *              | fl  | 0.002  | 0                | 0  | 0  | 21 | 0                  | 0  | 0   | 100 | 0                  | 0  | 0  | 21 |
| <i>Plagiomnium ellipticum</i>      | fl  | 0.002  | 2                | 4  | 2  | 37 | 20                 | 24 | 5   | 52  | 11                 | 17 | 36 | 71 |
| <i>Lysimachia nummularia</i>       | fl  | 0.002  | 0                | 0  | 0  | 21 | 0                  | 4  | 0   | 96  | 0                  | 2  | 0  | 21 |
| <i>Phegopteris connectilis</i>     | fl  | 0.002  | 0                | 0  | 0  | 21 | 0                  | 0  | 0   | 100 | 0                  | 0  | 0  | 21 |
| <i>Calliergon cordifolium</i>      | fl  | 0.002  | 0                | 0  | 0  | 21 | 0                  | 0  | 0   | 100 | 0                  | 0  | 0  | 21 |
| <i>Tilia cordata</i> *             | fl  | 0.003  | 1                | 1  | 0  | 31 | 7                  | 4  | 1   | 88  | 13                 | 15 | 5  | 36 |
| <i>Allium ursinum</i>              | fl  | 0.005  | 0                | 0  | 2  | 18 | 0                  | 0  | 18  | 82  | 0                  | 0  | 9  | 21 |
| <i>Lycopus europaeus</i>           | fl  | 0.007  | 1                | 2  | 0  | 23 | 6                  | 12 | 0   | 82  | 11                 | 15 | 0  | 29 |
| <i>Hypnum cupressiforme</i>        | fl  | 0.009  | 0                | 0  | 2  | 16 | 0                  | 0  | 44  | 56  | 0                  | 0  | 5  | 29 |
| <i>Carex nigra</i>                 | fl  | 0.010  | 0                | 0  | 0  | 14 | 0                  | 0  | 0   | 100 | 0                  | 0  | 0  | 14 |
| <i>Epilobium palustre</i>          | fl  | 0.010  | 0                | 0  | 0  | 14 | 0                  | 0  | 0   | 100 | 0                  | 0  | 0  | 14 |
| <i>Viola canina</i>                | fl  | 0.010  | 0                | 0  | 0  | 14 | 0                  | 0  | 0   | 100 | 0                  | 0  | 0  | 14 |
| <i>Brachypodium pinnatum</i>       | fl  | 0.010  | 0                | 0  | 0  | 14 | 0                  | 0  | 0   | 100 | 0                  | 0  | 0  | 14 |
| <i>Dryopteris cristata</i>         | fl  | 0.011  | 0                | 0  | 0  | 14 | 0                  | 0  | 0   | 100 | 0                  | 0  | 0  | 14 |
| <i>Phalaris arundinacea</i>        | fl  | 0.011  | 0                | 0  | 0  | 14 | 0                  | 0  | 0   | 100 | 0                  | 0  | 0  | 14 |
| <i>Valeriana officinalis</i>       | fl  | 0.011  | 0                | 0  | 0  | 14 | 0                  | 0  | 0   | 100 | 0                  | 0  | 0  | 14 |
| <i>Blepharostoma trichophyllum</i> | fl  | 0.012  | 0                | 0  | 0  | 14 | 0                  | 0  | 0   | 100 | 0                  | 0  | 0  | 14 |
| <i>Elymus repens</i>               | fl  | 0.012  | 0                | 0  | 0  | 14 | 0                  | 0  | 0   | 100 | 0                  | 0  | 0  | 14 |
| <i>Lophozia ventricosa</i>         | fl  | 0.012  | 0                | 0  | 0  | 14 | 0                  | 0  | 0   | 100 | 0                  | 0  | 0  | 14 |
| <i>Campylium stellatum</i>         | fl  | 0.013  | 0                | 0  | 0  | 14 | 0                  | 0  | 0   | 100 | 0                  | 0  | 0  | 14 |

| Species                        | Max | $\rho$ | Indicator value  |    |    |    | Relative abundance |    |    |     | Relative frequency |    |    |    |
|--------------------------------|-----|--------|------------------|----|----|----|--------------------|----|----|-----|--------------------|----|----|----|
|                                |     |        | Forest site type |    |    |    |                    |    |    |     |                    |    |    |    |
|                                |     |        | ndr              | dr | kl | fl | ndr                | dr | kl | fl  | ndr                | dr | kl | fl |
| <i>Brachythecium mildeanum</i> | fl  | 0.013  | 0                | 0  | 0  | 14 | 0                  | 0  | 0  | 100 | 0                  | 0  | 0  | 14 |
| <i>Carex pallescens</i>        | fl  | 0.014  | 0                | 0  | 0  | 14 | 5                  | 0  | 0  | 95  | 3                  | 0  | 0  | 14 |
| <i>Platanthera bifolia</i>     | fl  | 0.019  | 0                | 0  | 0  | 14 | 3                  | 2  | 0  | 95  | 3                  | 2  | 0  | 14 |
| <i>Quercus robur</i>           | fl  | 0.020  | 1                | 1  | 0  | 18 | 8                  | 10 | 0  | 82  | 11                 | 10 | 0  | 21 |
| <i>Ulmus glabra</i>            | fl  | 0.022  | 1                | 3  | 22 | 26 | 4                  | 15 | 40 | 41  | 21                 | 17 | 55 | 64 |
| <i>Homalia trichomanoides</i>  | fl  | 0.022  | 0                | 0  | 16 | 18 | 0                  | 0  | 58 | 42  | 0                  | 0  | 27 | 43 |
| <i>Fraxinus excelsior</i>      | fl  | 0.022  | 11               | 15 | 6  | 35 | 21                 | 31 | 11 | 37  | 50                 | 50 | 55 | 93 |
| <i>Lathyrus vernus</i>         | fl  | 0.024  | 8                | 3  | 0  | 23 | 37                 | 18 | 0  | 46  | 21                 | 19 | 0  | 50 |
| <i>Campylium sommerfeltii</i>  | fl  | 0.026  | 2                | 0  | 0  | 15 | 44                 | 0  | 5  | 51  | 5                  | 0  | 9  | 29 |
| <i>Equisetum pratense</i>      | fl  | 0.027  | 22               | 7  | 0  | 30 | 38                 | 18 | 2  | 42  | 58                 | 38 | 14 | 71 |
| <i>Atrichum undulatum</i>      | fl  | 0.029  | 4                | 0  | 0  | 17 | 51                 | 3  | 1  | 46  | 8                  | 4  | 5  | 36 |
| <i>Ranunculus ficaria</i>      | fl  | 0.045  | 0                | 1  | 0  | 12 | 0                  | 44 | 0  | 56  | 0                  | 2  | 0  | 21 |

europaea L., *Mycelis muralis* (L.) Dumort, *Equisetum palustre* L., *Circea alpina* L., etc. In the tree layer *Pinus sylvestris* L. is typical and in regrowth *Picea abies* (L.) Karst.

For fern-rich forest communities on the talus slope of the klint the significant indicator species in the tree layer are *Ulmus glabra* and *Alnus incana*, in the field layer above all *Matteuccia struthiopteris* (L.) Tod., *Lunaria rediviva* L., *Geranium robertianum* L. and *Aegopodium podagraria* L. In the moss layer of these forests numerous species growing on calcareous rocks are typical, e.g. *Fissidens gracilifolius* Brugg.-Nann. & Nyholm, *Anomodon longifolius* (Schleich. ex Brid.) Hartm., *Conocepalum conicum* (L.) Dumort, *Pseudoleskeella nervosa* (Brid.) Nyholm, *Taxiphyllum wissgrillii* (Garov.) Wijk & Margad., *Leptobryum pyriforme* (Hedw.) Wilson (Table 3). Those habitats have the highest light indices and the best supply of nutrients (Table 2).

Fern-rich floodplain forests include a long list of reliable indicator species (Table 3). In the tree layer *Ulmus laevis*, *U. glabra*, *Fraxinus excelsior*, *Quercus robur* L. and *Tilia cordata* can be noticed, in the field layer among ferns *Phegopteris connectilis* (Michx.) Watt and *Dryopteris cristata* (L.) A.Gray are characteristic, and among forbs *Glechoma hederacea* L., *Polygonatum multiflo-*

*rum* (L.) All., *Campanula latifolia* L., *Ranunculus cassubicus* L., *Allium ursinum* L., *Lycopodium europaeus* L., etc. are common. In the moss layer *Amblystegium varium* (Hedw.) Lindb., *Brachythecium salebrosum* (Hoffm. ex F.Weber & D.Mohr.) Schimp., *Drepanocladus revolvens* (Sw.) Warnst., *D. cossonii* (Schimp.) Loeske, *Plagiomnium ellipticum* (Brid.) T.J.Kop., etc. are remarkable indicator species. Floodplain habitats are the most shadowed by the dense tree layer, they have like klint forests a comparatively high soil reaction (pH) and a good nutrients supply (Table 2).

A more detailed comparison of only drained and undrained *Dryopteris* site type forests ascertained several more substantial indicator species for both communities. It appeared that for undrained forests also *Populus tremula* and *Fraxinus excelsior* in the tree layer and several nemoral species, such as *Pulmonaria officinalis* L., *Anemone nemorosa* L., *Ranunculus auricomus* L. and *Stellaria holostea* L. in the field layer are characteristic (Table 4). Drained forests stand out by a more abundant growth of *Frangula alnus* and *Padus avium* in the shrub layer, and *Rubus idaeus* in the field layer.

The main environmental factors determining the internal variation in both considered communities are the soil reaction

(pH) and nutrient content, but also the thickness of a slightly-decomposed peat horizon (H1; Figure 3). Thickness of the soil litter horizon and well-decomposed peat (decay) horizon are mutually positively correlated but their impact on the vegetation structure is weaker and almost independent from other mentioned factors.

## Discussion

Considering the issues discussed in the introduction, we can say that the *Dryopteris* site type forests with optimal moisture

conditions distinguished by Karu & Muiste (1958) correspond to the boreo-nemoral (undrained) *Dryopteris* site type described in the current paper, while their paludified *Dryopteris* site type stands have a great affinity with the *Tilia cordata*–*Mercurialis perennis* type of fern-rich floodplain forest communities (Paal *et al.*, 2007, 2008).

The *Dryopteris* site type forests characterised by Katus & Tappo (1965) also coincide rather well with the undrained *Dryopteris* site stands addressed by us, whereas the *Dryopteris* variant of decayed-mire forests established by them corresponds to the drained *Dryopteris* site type discussed in the recent paper. Lõhmus

Table 4. Indicator value, relative abundance and relative frequency of species in undrained and drained *Dryopteris* site type forests. Notations are as in Tables 1 and 3.

| Species                          | Max | $p$    | Indicator value  |    | Relative abundance |     | Relative frequency |    |
|----------------------------------|-----|--------|------------------|----|--------------------|-----|--------------------|----|
|                                  |     |        | Forest site type |    |                    |     |                    |    |
|                                  |     |        | ndr              | dr | ndr                | dr  | ndr                | dr |
| <i>Crepis paludosa</i>           | ndr | <0.001 | 65               | 14 | 73                 | 27  | 89                 | 52 |
| <i>Filipendula ulmaria</i>       | ndr | 0.001  | 61               | 19 | 70                 | 30  | 87                 | 63 |
| <i>Calamagrostis arundinacea</i> | ndr | 0.006  | 41               | 3  | 87                 | 13  | 47                 | 25 |
| <i>Populus tremula</i> *         | ndr | 0.014  | 29               | 4  | 80                 | 20  | 37                 | 17 |
| <i>Pulmonaria officinalis</i>    | ndr | 0.018  | 17               | 0  | 95                 | 5   | 18                 | 6  |
| <i>Plagiomnium affine</i>        | ndr | 0.019  | 49               | 15 | 74                 | 26  | 66                 | 58 |
| <i>Anemone nemorosa</i>          | ndr | 0.022  | 45               | 16 | 59                 | 41  | 76                 | 38 |
| <i>Eurynchium hians</i>          | ndr | 0.031  | 26               | 1  | 91                 | 9   | 29                 | 13 |
| <i>Ranunculus auricomus</i>      | ndr | 0.032  | 12               | 0  | 95                 | 5   | 13                 | 2  |
| <i>Fraxinus excelsior</i> *      | ndr | 0.037  | 24               | 4  | 70                 | 30  | 34                 | 13 |
| <i>Athyrium filix-femina</i>     | ndr | 0.042  | 54               | 31 | 63                 | 37  | 87                 | 83 |
| <i>Equisetum pratense</i>        | ndr | 0.046  | 39               | 13 | 67                 | 33  | 58                 | 38 |
| <i>Stellaria holostea</i>        | ndr | 0.049  | 25               | 5  | 68                 | 32  | 37                 | 15 |
| <i>Paris quadrifolia</i>         | ndr | 0.049  | 51               | 27 | 62                 | 38  | 82                 | 71 |
| <i>Mycelis muralis</i>           | dr  | 0.001  | 1                | 30 | 7                  | 93  | 8                  | 33 |
| <i>Oxalis acetosella</i>         | dr  | 0.003  | 29               | 66 | 30                 | 70  | 97                 | 94 |
| <i>Pinus sylvestris</i> *        | dr  | 0.003  | 1                | 31 | 5                  | 95  | 11                 | 33 |
| <i>Rubus idaeus</i>              | dr  | 0.006  | 12               | 59 | 20                 | 80  | 61                 | 73 |
| <i>Frangula alnus</i>            | dr  | 0.017  | 3                | 34 | 15                 | 85  | 24                 | 40 |
| <i>Padus avium</i>               | dr  | 0.027  | 0                | 15 | 0                  | 100 | 3                  | 15 |
| <i>Dicranum scoparium</i>        | dr  | 0.039  | 2                | 26 | 11                 | 89  | 16                 | 29 |
| <i>Equisetum palustre</i>        | dr  | 0.041  | 1                | 18 | 15                 | 85  | 5                  | 21 |

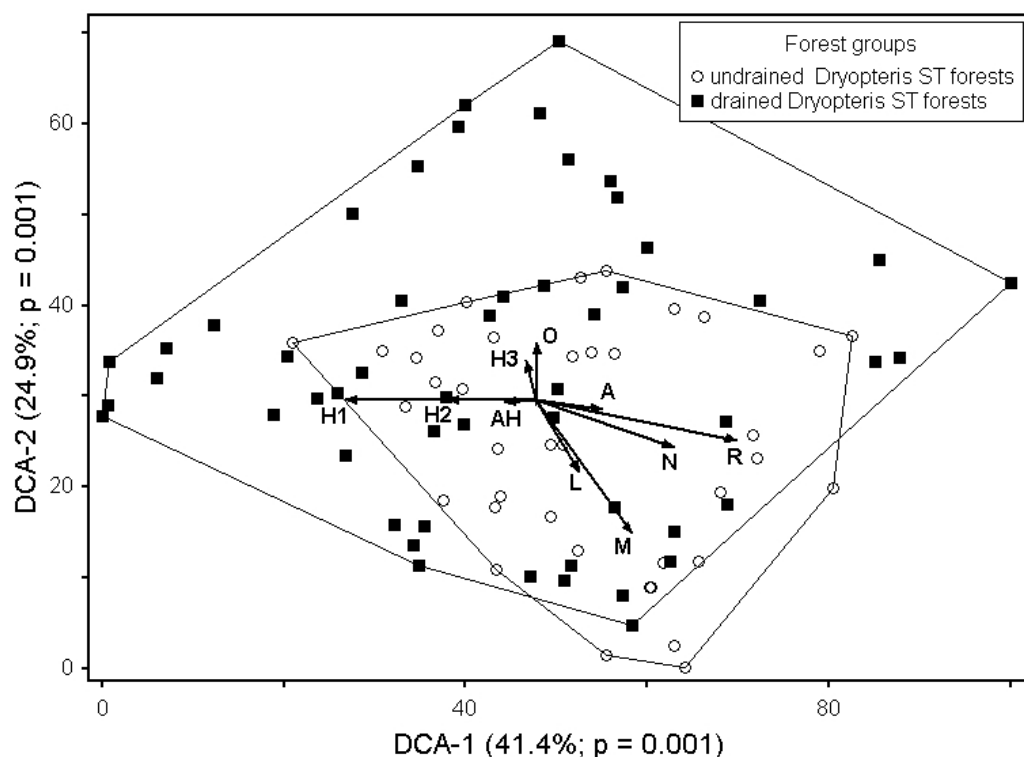


Figure 3. Ordination biplot of vegetation relevés (sample plots) and habitat characteristics values of undrained and drained *Dryopteris* site type forests. Notations: H1, H2 and H3 – thickness of the slightly, moderately and well-decomposed peat horizons, respectively, AH – thickness of the well-decomposed peat horizon enriched with humus (raw humus), O and A – thickness of the litter and humus horizons, respectively.

(1982) criticised those authors, pointing out that in their typology the essence of the drained forests habitat group remains unclear due to inconsistent data; although the authors have used for site types assignment the same names as Karu & Muiste (1965), the issue of paludified *Dryopteris* site type forests is not the same: according to Katus & Tappo (1965) these forests have not developed as a result of drainage but just from swamp-like forests by their successive paludification.

Masing (1969) recognised the fern-rich forests only in the scope of one *Dryopteris* site type of nemoral forests, i.e. as undrained forests. Nowadays, the term 'nemoral' must be replaced here by 'boreo-nemoral', because Estonia belongs in the boreo-nemoral vegetation zone (Moen,

1999). Lõhmus (1974, 2004) who also accepted the *Dryopteris* site type only among the undrained boreo-nemoral forests, obviously kept in mind the fern-rich floodplain stands like the paludified *Dryopteris* site type of Karu & Muiste (1958), but possibly also analogous stands on the talus slopes of the klint, i.e. the *Ulmus glabra*–*Alnus incana*–*Matteuccia struthiopteris* type and *Alnus glutinosa*–*Athyrium filix femina*–*Impatiens noli-tangere* type (Paal, 2009).

The difference between the *Dryopteris* site type forests on the one hand, and fern-rich floodplain and klint forests on the other hand is convincing already based on their landscape peculiarities and, therefore, both of the latter forests are segregated to a separate group of forest site types (Paal, 1997). The validity of that differentiation

is additionally confirmed in the current study by the habitats indicator values and by the comparatively long list of reliable indicator species.

Our present results also assert persuasively a distinct difference between the two *Dryopteris* site type stands on flat landscapes. First of all these forests have a different development history: when undrained boreo-nemoral stands have developed on the same place in harmony with habitat conditions and without a considerable anthropogeneous impact, in drained forests the growth conditions have very crucially changed by the lowering of the water level which initiated large changes in the soil properties and forest structure. That is also the reason behind a remarkably larger variation in the drained fern-rich forests: their species content and other structural characteristics depend much on the initial type and state of drained forests, and on the stage of succession achieved after the construction of the drainage system. Though after stabilization of the initialised secondary succession the ground vegetation of drained *Dryopteris* site type forests has due to convergence acquired a rather great affinity with undrained *Dryopteris* site type stands, they both still have a discrepant list of significant indicator species; even more conspicuous is the distinction by soil properties.

We cannot agree with the statement of Lõhmus (1981, 1982) that differentiation of the fern-rich drained forests as a separate forest site type is not justified because those stands do not represent full-drained forests but just post-drainage successional stages developing towards the full-drained *Oxalis* site type being the final stage of this succession. In his study Lõhmus (1981) used as examples of old-drained forests 20 stands drained 60–155 years ago but also established the criteria for distinguishing between the earlier post-drainage stages of drained mire forests and full-drained (decayed peat) forests. In forests of the first group the total cover of hygrophilous mire

plants in ground vegetation exceeds 20% and on that basis the original type of drained forests is recognizable. Full-drained (decayed peat) forests have reached the state of a relatively stable equilibrium and there the total cover of hygrophilous plant species is less than 20%; in these forests the occurrence of forest litter and a thin layer of fine textured (granular) well-decomposed peat underneath is typical of soils. Though the drained *Dryopteris* site type forests analysed in the current study were drained in some areas only 35–40 years ago, they already correspond to the criteria of full-drained stands above. As it appears from the table of indicator species (Table 3), in the sample of drained forests the mire species were almost lacking and the forest litter horizon was even a bit thicker than in undrained forests (Table 2). The results of research carried out by Pikk (1997) showed that in Orajõe forest area the initially 60 cm thick peat layer was almost totally decomposed 42 years after drainage.

The closeness of drained fern-rich stands analysed in the current study to the subclimax state is indirectly confirmed with the Finnish approach (Heikurainen & Pakarinen, 1982; Laine, 1989) of the drained forests typology. There drained forests are divided into three main groups: (i) newly (15–30 years ago) drained swamps where the total cover of preserved mire bryophytes is over 25%, (ii) drained stands where the characteristics of the original forest type are still discernible and, (iii) old forests drained more than 15–30 years ago where the total cover of mire bryophytes is less than 25% and where the ground vegetation has already stabilised (Heikurainen, 1964). According to this classification, forests drained more than 40 years ago can be interpreted as fully drained (Heikurainen, 1983); forest communities in the older drainage areas are traditionally classified into four drained peatland site types, where the herb-rich type (*ruohoturoekangas* in Finnish) is characterised *inter alia* by the abundance of ferns *Athyrium filix-femina*,

*Dryopteris expansa*, *Matteuccia struthiopteris* and *Thelypteris phegopteris* (= *Phegopteris connectilis*) (Laine, 1989; Paavilainen & Päivänen, 1995). However, taking into account the fact that in the studied drained *Dryopteris* site type forests pine dominated in the tree layer, the regrowth was formed mainly by spruce, the post-drainage succession is surely not finished yet and we can expect certain changes in the last stages of succession: an increase in spruce abundance in the tree layer, further acidification of the litter horizon and perhaps an increase in *Oxalis acetosella* abundance in the field layer, as well. The current subclimax state of the analysed forests obviously explains also the comparatively large variation in the species content of drained fern-rich forests, which totally covers the variation amplitude in undrained *Dryopteris* site type forests. In the Estonian peatlands classification comparatively few site types have been established and for that reason the variation in the conditions within site types is rather large and, therefore, the same site type may include forests with great differences in the peat decomposition rate (Pikk & Seemen, 2000). Considering the results and facts discussed above, it seems that despite some vagueness in discriminating fern-rich drained forests as a separate typological unit, it is nevertheless justified to recognise them in Estonian forest typology as an autonomous forest site type in the group of full-drained forests. To avoid confusion in nomenclature, undrained fern-rich boreo-nemoral forests site type could in the future be named according to the most conspicuous indicator species as the *Athyrium (filix-femina)* site type and fern-rich stands on full-drained peat soils as the *Dryopteris (expansa)* site type.

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# Sõnajala kasvukohatüübi metsadest Eestis

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## Kokkuvõte

Metsi, kus alustaimestus domineerivad sõnajalad, esineb Eestis nii mõõdukalt niisketes kui soostunud toiterikastes kasvukohtades, jõelammidel, klindi rusukalletel, samuti kuivendatud soometsades (kõdusoometsades). Kasvukohtade laia ökoloogilise muutlikkuse tõttu on erinevad autorid (Karu & Muiste, 1958; Katus & Tappo, 1965; Lõhmus, 1974, 2004; Paal, 1997) neid metsi rühmitanud kasvukohatüüpidesse ja -tüübirühmadesse mitmel viisil. Meie töö eesmärgiks oli selgitada, 1) kas on põhjendatud sõnajalarikka *Dryopteris* kasvukohatüübi eristamine nii kõdusoometsade kui ka salumetsade tüübirühmas, 2) kui see on nii, siis millised on mõlemasse kasvukohatüüpi kuuluvate metsakoosluste peamised tunnused, 3) mis on nende koosluste struktuuri määravad olulisemad keskkonnatingimused ja 4) milline on nende kasvukohatüüpide metsade seos/suhe lammidel ja klindi rusukalletel kasvavate sõnajalarohkete metsakooslustega. Ehkki

pikaajalise kuivendusjärgse suktsessiooniprotsessi tõttu on sõnajalarohke alustaimestuga kõdusoometsade eristamine omaette kasvukohatüübina mõneti problemaatiline, erinevad kuivenduse mõjul oluliselt muutunud keskkonnas kujunenud kõdusoometsad suhteliselt stabiilsetes tingimustes arenenud kuivendamata kasvukohtade kooslustest märkimisväärselt nii mulla diagnostiliste horisontide kui ka taimkatte indikaatorliikide poolest. Seega on kahe sõnajalarohke alustaimestuga metsakasvukohatüübi eristamine Eesti metsatüpoloogias põhjendatud. Nomenklatuurse segaduse vältimiseks võiks kuivenduse mõjul kujunenud sõnajalarikaste kõdusoometsade rühma nimetada kõige iseloomulikuma alustaimestu liigi järgi *Athyrium (filix-femina)* kasvukohatüübiks, inimtegevuse poolest muutmata tingimustes arenenud sõnajalarikaste salumetsade rühma aga *Dryopteris (expansa)* kasvukohatüübiks.

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