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Vascular plant communities in boreal herb-rich forests in Koli, eastern Finland

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Herb-rich forests have aroused great interest in maintaining the biological diversity of boreal forests. The ecology and structure of these ecosystems are poorly known, and no systematic assessment of their characteristics has been made. In order to explore the structure of vascular plant communities, 101 sample plots in 57 herb-rich forest areas were studied in Koli, eastern Finland. The material was classified with two-way indicator species analysis (TWINSPAN) and ordinated with detrended correspondence analysis (DCA). The results suggest that many environmental variables; e.g. varying topography and bedrock affected the herb-rich forest vegetation. The most important compositional gradients were moisture, fertility and shading. According to species composition, the Koli area is an important patch for species dispersion from south to north. The study area is valuable for maintaining threatened forest flora and eastern elements. In particular, the unique *Diplazium sibiricum* communities and other taiga species deserve special attention. The site types (ecological groups) corresponded quite well to the herb-rich forest types described in literature.

Key words: biological diversity, classification, detrended correspondence analysis (DCA), ecology, herb-rich forests, threatened flora, two-way indicator species analysis (TWINSPAN)

Introduction

Herb-rich forests, the most luxuriant forest types in Finland, are characterized by herbaceous flora (Linkola 1916, Cajander 1926). Grasses and shrubs are often abundant (Kuusipalo 1996), but dwarf shrubs and lichens, which are typical for heath forests, are normally rare or absent (Cajander 1926). The moss carpet is sparse, but rich in species (Kaakinen 1992). Differences between groves and heath forests are mainly due to the properties of the soil: herb-rich forest soils are more fertile and less acid than heath forest soils (Kaakinen 1992).

Luxuriant herb-rich forests are rare in Finland for two main reasons: Firstly, conditions, e.g., cold climate and acid bedrock, are not convenient for the demanding herbaceous flora; and secondly, the best areas are taken into agricultural use (Alanen *et al*. 1996). Although groves cover less than one percent of the whole forest area in Finland (Alanen *et al*. 1996), they are

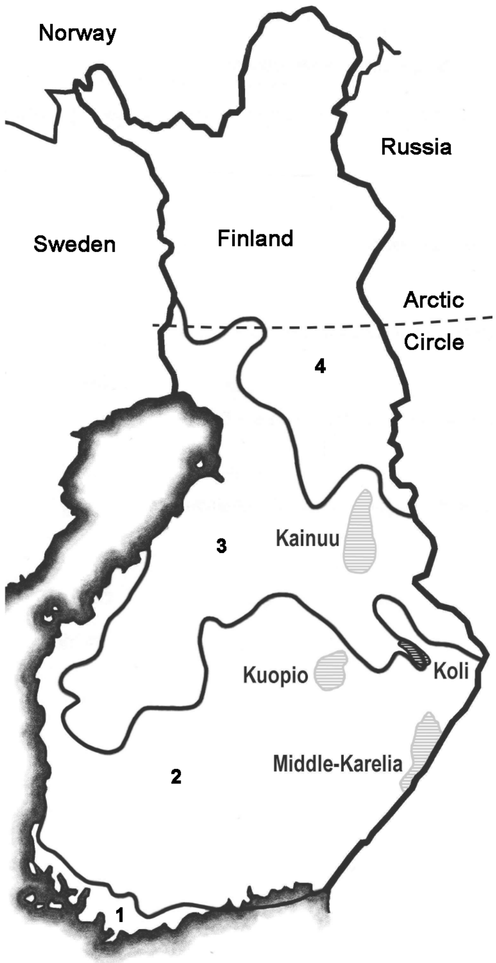

Fig. 1. Location of the study area and the nearest districts rich in grass-herb forests. Vegetation zones are after Ahti *et al.* (1968): 1 = hemiboreal zone, 2 = southern boreal zone, 3 = middle boreal zone, and 4 = northern boreal zone.

important for conservation, because 12% of all the threatened vascular plant species and 80% of the threatened forest-species occur primarily in these forests (Rassi *et al.* 2001). In southwestern Finland, herb-rich forests are characteristic, but in other parts of Finland, they are situated in specific areas with calciferous bedrock (Kaakinen 1982). These areas, called districts rich in grass-herb forests, are located in southern Tavastia, middle Karelia, Kuopio, Kainuu, southwestern Lapland, northern Kuusamo and Kittilä (Kaakinen 1982, Alapassi & Alanen 1988).

Finnish researchers have long traditions of studying herb-rich forests (Linkola 1916, Lukkala 1919). The vegetation and luxuriant areas are well known (Alanen 1992, Kaakinen 1992). However, systematic mapping of vegetation and research on Finnish herb-rich forests started as late as in 1982 (Alanen 1983). The aim of that study was to make a proposal for the protection of groves (Alanen & Alapassi 1988). Based on that proposal, the National Protection Program was launched in 1989 (Alanen 1992).

The Koli area, which is famous for its unique vegetation, is one of the best-studied areas in North Karelia. In particular, threatened flora is carefully mapped (Hakalisto 1987, Lyytikäinen 1991, Grönlund & Hakalisto 1998). Axelson (1902) was the first to describe the flora of the Koli area in the early 1900s. Sixty years later, Sonck (1964) mapped the vegetation in the whole Pielisjärvi and Lieksa area, including Koli. In the 1970s, vegetation was mapped extensively during the planning of Koli National Park (Pohjois-Karjalan seutukaavaliitto 1976). In the 1990s, most descriptions and mappings were done in the core-area of Koli National Park (Lyytikäinen 1991). However, herb-rich forests and their vegetation, especially the plant communities over the site types are still poorly known, and no systematic assessment of their characteristic has been made.

The main purposes of this study were: (1) To describe the herb-rich forest vegetation and forest site types in Koli, (2) to analyze and classify herb-rich forest vegetation by multivariate methods, and (3) to evaluate the herb-rich forest site types studied by comparing them to previously described site types.

Material and methods

Study area

The study area is located in Koli, North Karelia, eastern Finland (Fig. 1), which is characterized by high hills and open lakes (Lyytikäinen 1991, Antikainen 1993). The highest hills are 250 meters above the largest lake, Pielinen. Such high hills are rare in southern and middle Finland. Another unique feature is its location in the transition area between the southern and middle boreal zones (Ahti *et al.* 1968).

Koli is also situated between the pre-Karelian granite–gneiss area and Karelian schist zone (Simonen 1964, Kalliola 1973). Both formations are Precambrian; the granites and gneiss are 2700 million years old, and the metamorphous sedimentary rocks (conglomerates, quartzites) are 1750–1900 million years old (Simonen 1964, Piirainen *et al.* 1974). Granite–gneiss is typical in the eastern and northwestern parts of the study area, but metamorphous rocks are characteristic in the western and southern parts (Kohonen 1987). The highest hills consist mainly of durable quartzite (Kohonen 1987). Calcium-rich diabase occurs in intrusive bodies between metamorphous rocks on the eastern slopes (Piirainen *et al.* 1974, Grönlund & Hakalisto 1998). The mineral soils are mainly glacial moraine (Lyytikäinen 1991). Glacial sand and gravel occur in glacial formations, but silt and clay are rare. The hill slopes over 120 m above sea level are supra aquatic (Okko 1964). Moraine and eskers are glacial formations from the last glacial period about 10 000 years ago (Kalliola 1973).

The climate of this region is continental with long, cold winters and warm summers (Kalliola 1973). The mean annual temperature is 2 °C (Finnish Meteorological Institute 1991). The length of the thermal growing period is 150–155 days, and frost can occur at any time during the summer (Heino & Hellsten 1983). The sum of degree-days (threshold +5 °C) ranges from 1000 to 1100 (Atlas of Finland 1987). The mean annual precipitation is 600 mm and winter snowfall 60 to 70 cm (Heino & Hellsten 1983, Finnish Meteorological Institute 1991).

The dominating tree species are Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). Birches (*Betula pendula, B. pubescens*) and gray alder (*Alnus incana*) are common in the areas affected by slash and burn cultivation. Variable topography and post-glacial migration of the vegetation have created various plant communities (Grönlund & Hakalisto 1998). The sites are mainly medium fertile fresh heath (MT) and rich grove-like heath (OMT) forests (Antikainen 1993). The most luxuriant groves occur mainly on the eastern slopes or at the brook sides (Kärkkäinen 1994). Forest vegetation consists mainly of boreal dwarf-shrubs (*Vaccinium myrtillus* and *V. vitis-idaea*), forest ferns (*Dryopteris carthusiana* and *Gymnocarpium dryopteris*), low herbs (*Trientalis europaea* and *Maianthemum bifolium*) and forest grasses (*Deschampsia flexuosa, Luzula pilosa* and *Calamagrostis arundinacea*) (Kalliola 1973, Vanha-Majamaa 2001b).

Slash and burn cultivation was widely used in eastern Finland from the 1600s to the 1940s (Lyytikäinen 1991, Björn *et al.* 1997). At that time, the local people made their living from rye (*Secale cereale*) and turnip (*Brassica rapa*) cultivation as well as cattle raising (Antikainen 1993). As a result of slash and burn culture, views and forests became more open, which favored deciduous trees and meadow vegetation (Uutela 1939). After slash and burn cultivation, effective silviculture began to favor conifer forests. Since the 1950s deciduous forests and meadows have gradually changed to dark and closed spruce forests (Björn *et al.* 1997, Grönlund & Hakalisto 1998). Commercial forests are mainly privately owned, but forest companies also own some large forest areas. All conservation areas belong to the state. The protected forests include Koli National Park (3000 ha) and conservation programs (400 ha) for herb-rich and old forests (Alapassi & Alanen 1988, Rassi *et al.* 1992, 1994, Salo 1998).

Field procedures

The fieldwork for this study was carried out during the summers of 1996, 1997, 1999 and 2000. The mapping of the vegetation was started at Koli National Park, and in 1999 and 2000 the study was expanded to the surrounding protected herb-rich forests owned by companies and private citizens. Ecological survey studies were based on the earlier mappings of vegetation and other forest stand information made by Forest Research Institute and UPM. The pre-information was used to capture representative variation of vegetation. Based on the pre-information the 101 most representative grove stands were selected for the study. The groves represented the most common herb-rich forest site types of the area. In addition, the groves were also selected to represent different sizes and status; e.g. large protected grove-areas and small separated key-habitats in commercial forests.

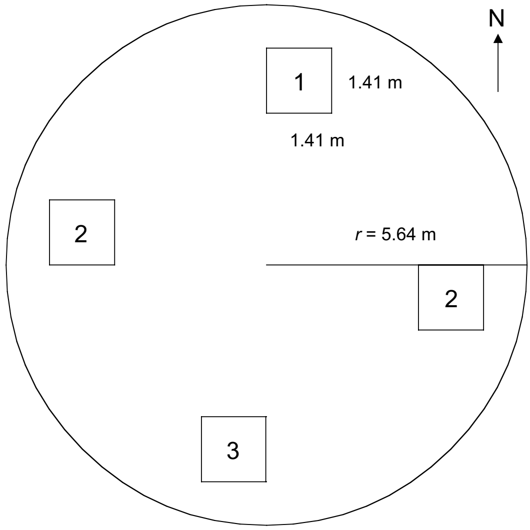

Fig. 2. Circular sample plot (100 m^2) and location of vegetation squares (2 m^2).

Circular sample plots of 100 m^2 (radius = 5.64 m) were established in the middle of the grove stand. Vegetation coverage of the field layer was estimated from the sample plot by using three sample squares, each 2 m^2 (Fig. 2), located four meters from the center to the north (00°), east (90°), south (180°) and west (270°). Northern and southern squares were used on each plot, and eastern squares were preferred to western ones. Western was used only if it was impossible to use eastern (big stones, rocks etc.). Coverage of each species was estimated by the following percentage scale: 0.1, 0.5, 1, 2, 3, 4, 5, 7, 10, 15, 20, 25, … 90, 93, 95, 96, 97, 98, 99, 100. Species outside the square, but inside the circle plot received coverage of 0.1. Shrub coverage and all species in the field layer were determined from the circular sample plot. The shrub layer included tree saplings and shrubs lower than 150 cm. The nomenclature follows Hämet-Ahti *et al*. (1998).

Tree species and stand characteristics were determined from the circle sample plot. For each tree species, basal area (ba) was measured. Diameter (dbh), height and age were measured by using median size tree. The tree layer consisted of trees and shrubs over 150 cm tall.

A priori typification and description of herb-rich forest site types

Classification in the field was based mainly on Alanen *et al*. (1996) and Kuusipalo (1996), who divide groves into dry, mesic and moist types (Table 1). The herb-rich forest site types used in this study are described in the results. The tradi-

Table 1. Herb-rich forest sites types after Alanen *et al.* (1996) and Kuusipalo (1996). Abbreviations: VRT = *Vaccinium (vitis-idaea)–Rubus (saxatilis)*, OMaT = *Oxalis (acetosella)–Maianthemum (bifolium)*, GOMaT = *Geranium (sylvaticum)–Oxalis (acetosella)–Maianthemum (bifolium)*, PuViT = *Pulmonaria (obscura)–Viola mirabilis*, ORT = *Oxalis (acetosella)–Rubus (saxatilis)*, OPaT = *Oxalis (acetosella)–Paris (quadrifolia)*, GORT= *Geranium (sylvaticum)–Oxalis (acetosella)–Rubus (saxatilis)*, AthOT = *Athyrium (filix-femina)–Oxalis (acetosella)*, AthAssT = *Athyrium (filix-femina)*–Assimilis (*Dryopteris expansa*), OFiT = *Oxalis (acetosella)–Filipendula (ulmaria)*, MaT = *Matteuccia (struthiopteris)*, AthT = *Athyrium (filix-femina)*, GOFiT = *Geranium (sylvaticum)–Oxalis (acetosella)–Filipendula (ulmaria)*, GFiT = *Geranium (sylvaticum)–Filipendula (ulmaria)* and DiplT = *Diplazium (sibiricum)*.

Vegetation zone	SUBDRY	MESIC		MOIST	
	Medium fertile	Medium fertile	(Very) fertile	Medium fertile	(Very) fertile
Southern boreal	VRT	OMaT	PuViT ORT OPaT	AthOT AthAssT	OFiT MaT AthT
Middle boreal	VRT	GOMaT	GORT	AthAssT	GOFiT MaT AthT
Northern boreal	VRT			AthAssT	GFiT DiplT MaT AthT

tional Finnish forest site classification (Cajander 1926, Nieppola 1986) represents only the following herb-rich forest site types for North Karelia: *Oxalis–Maianthemum* type (OMaT), *Filices* type (FT), *Aconitum* type (AT), *Silene* type (LT) and *Vaccinium–Rubus* type (VRT).

Numerical analysis

PC-ORD software version 4 was used for multivariate analysis (McCune & Mefford 1999). Detrended Correspondence Analysis or DCA (Hill 1979, Hill & Gauch 1979) was applied for ordinating the sample plots and the vegetation data. The down weighting option was chosen to reduce the effect of rare species. In other options, default settings of DCA were used. Sample plots and species ($n = 167$) were also classified by TWINSPAN (Two-Way Indicator Species Analysis; Hill 1979). The default settings of TWINSPAN were used. Frequency and coverage of each species were calculated by data summarization of PC-ORD. Diversity index and species richness was determined for all sample plots. As a diversity index was used the estimated formula of Shannon-Weaver's entropy index, H' (Økland 1990).

Results

General features of vegetation

The most common vascular plant on the studied sites was *Maianthemum bifolium* (Table 2). Despite its high frequency, however, it was not very abundant on the sample plots. The most abundant species on the plots were *Athyrium filix-femina, Oxalis acetosella* and *Gymnocarpium dryopteris*. Constant species in almost all herb-rich forest site types studied were *Alnus incana, Angelica sylvestris, Dryopteris carthusiana, Geranium sylvaticum, Gymnocarpium dryopteris, Maianthemum bifolium, Melica nutans, Oxalis acetosella, Paris quadrifolia, Rubus idaeus, R. saxatilis, Sorbus aucuparia, Trientalis europaea* and *Viola selkirkii* (Tables 2 and 6).

The herb-rich forests studied were luxuriant and rich in species (Table 3). Groves were divided into three main groups on the ground of moisture and dominant species. These main groups were fresh low-herb-dominated groves (OMaT, ORT, GORT and PuViT), moist fern-rich groves (AthAssT, AthT, DiplT and MaT) and moist tall-herb-dominated groves (OFiT, GOFiT, GFiT). Low herbs and ferns, such as *Oxalis acetosella, Maianthemum bifolium, Rubus saxatilis* and *Gymnocarpium dryopteris*, were dominant in the fresh herb-rich forests. Characteristic species for the moist fern-rich groves were *Athyrium filix-femina*, *Phegopteris connectilis* and *Dryopteris expansa*. In addition, typical species for the most luxuriant fern-dominated sites were *Diplazium sibiricum* and *Matteuccia struthiopteris*. The moistest herb-rich forest patches were characterized by tall herbs, such as *Filipendula ulmaria, Geum rivale, Geranium sylvaticum* and *Crepis paludosa*.

Stands were mainly deciduous and mixed deciduous forests (Fig. 3). In addition, pure spruce (*Picea abies*) forests as well as spruce-dominated mixed forests were common in the

Table 2. Frequency and abundance (coverage) of the most common vascular plant species in the studied herb-rich forests.

Species	Frequency		Coverage (%)	
	Plots	%	Mean	SD
Maianthemum bifolium	98	95	3.4	3.6
Oxalis acetosella	95	92	9.7	9.7
Gymnocarpium dryopteris	94	91	9.6	9.3
Trientalis europaea	91	88	0.8	0.7
Geranium sylvaticum	82	80	2.2	4.2
Rubus idaeus	81	79	4.0	7.9
Melica nutans	77	75	0.6	1.4
Athyrium filix-femina	78	76	17.8	21.4
Rubus saxatilis	73	71	1.9	3.8
Paris quadrifolia	72	70	0.3	0.4
Phegopteris connectilis	68	66	5.7	7.6
Alnus incana	66	64	1.8	5.3
Sorbus aucuparia	66	64	1.0	2.0
Vaccinium myrtillus	62	60	1.4	4.7
Angelica sylvestris	62	60	0.6	1.7
Crepis paludosa	61	59	2.7	5.1
Calamagrostis arundinacea	58	56	1.9	5.2
Viola selkirkii	58	56	0.6	1.9
Filipendula ulmaria	58	56	6.4	9.9
Geum rivale	57	55	1.8	4.5
Prunus padus	54	52	1.1	2.6
Dryopteris carthusiana	53	51	2.0	4.0
Dryopteris expansa	49	48	9.6	16.5

area. Gray alder (*Alnus incana*), which usually grew together with spruce, was the most common deciduous tree. It also formed pure alder stands or mixed deciduous forests with downy birch (*Betula pubescens*) and European aspen (*Populus tremula*). Other typical tree species of the mixed forest were silver birch (*Betula pendula*), goat willow (*Salix caprea*) and Scots pine (*Pinus sylvestris*). However, pure pine, birch and willow forests were rare. Most of the stands were quite young (20–40 yr.), one third were mature (> 80 yr.) and only few stands were very young (< 20 yr.).

Description of herb-rich forest site types

Mesic sites

The *Oxalis acetosella–Maianthemum bifolium* group (OMa) included heterogeneous OMaT sites (3, 8, 16, 21, 29, 30, 32, 38, 43, 54, 56, 59, 67, 68, 71, 94, 100) and OMaT–VRT site (92). Most of these sites were dominated by *Gymnocarpium dryopteris, Maianthemum bifolium* and *Oxalis acetosella* (Table 6). Other characteristic species in the field layers were *Vaccinium myrtillus, Solidago virgaurea, Rubus saxatilis, Melica nutans, Convallaria majalis, Calamagrostis arundinacea, Viola riviniana* and *Luzula pilosa* (Tables 5 and 6). In addition, abundant species on some plots were also *Actaea spicata* and *Dryopteris expansa*. The sparse shrub layers consisted mainly of *Rubus idaeus, Sorbus aucuparia* and *Alnus incana* (Tables 4 and 6). The stands were mostly quite young, closed spruce-dominated mixed forests (Table 9).

The *Oxalis acetosella–Rubus saxatilis* group (OR) included GORT (39, 40, 53, 89), ORT (42, 62) and ORT–OMaT (76) sites. The field layers were dominated by *Oxalis acetosella, Rubus saxatilis* and *Maianthemum bifolium* (Table 6). Other characteristic species were *Viola mirabilis, Carex digitata, Fragaria vesca, Viola riviniana, Vaccinium vitis-idaea* and *Veronica officinalis* (Table 5). In addition, *Calamagrostis arundinacea, Vaccinium myrtillus, Geranium sylvaticum, Melica nutans, Paris quadrifolia* and *Viola selkirkii* were common species. Dominant species in the thick shrub layers were *Alnus incana, Prunus padus* and *Rubus idaeus* (Tables 4 and 6). The stands were mainly mature or quite young, spruce or alder forests (Table 9).

PuViT (14, 26), PuViT–OFiT (45) and PuViT–AthT (51) formed the *Dryopteris filix-mas–Viola mirabilis* group (PuV). These sites were quite similar in terms of species composition, except for the abundance of *Filipendula ulmaria* and *Athyrium filix-femina*. In addition, the plots had luxuriant vegetation (Tables 3,

Table 3. Number of sample plots, mean number of species (species/100 m^2) and mean diversity index (H') for the site type groups and TWINSPAN clusters (CLU). Total number of plots is 101, mean number of species in all plots is 29.7 and mean diversity index 2.15. Explanations for the clusters *see* Fig. 6 and for the groups *see* Fig. 4.

	Number of sample plots									Species		H'	
CLU	OMa	OR	PuV	AAs	Ath	Dip	Mat	OFi	Tot	Mean	SD	Mean	SD
1	4	1							5	29.2	8.0	2.30	0.28
2	1	3	1						5	25.2	8.0	2.22	0.31
3	10	3	1						14	26.6	7.7	2.23	0.27
4	3			18	7	3	2		33	26.5	7.7	1.96	0.35
5					1			5	6	41.8	7.0	2.56	0.33
6					3	7	2	1	13	32.1	3.9	2.05	0.44
7			2		3		6	3	14	28.4	4.2	2.15	0.25
8	1							10	11	37.9	6.0	2.42	0.27
Tot	19	7	4	18	14	10	10	19	101				
Sp.	25.8	31.1	27.8	25.1	31.1	30.6	27.9	37.3		29.7			
SD	8.1	5.7	7.4	8.0	4.8	7.2	4.3	7.7			8.1		
H'	2.19	2.34	2.22	1.89	2.12	1.84	2.22	2.45				2.15	
SD	0.28	0.21	0.26	0.34	0.31	0.43	0.32	0.27					0.36

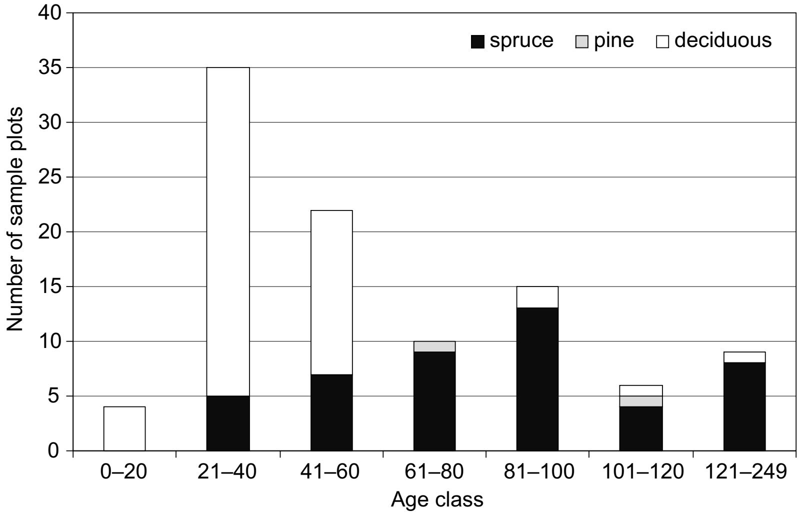

Fig. 3. Forests and their age-classes in the study area. Deciduous forests include pure deciduous stands (> 80% deciduous) and mixed deciduous stands (50%–80% deciduous). The most common deciduous tree species is gray alder (*Alnus incana)*. Other deciduous are birches (*Betula pendula, B. Pubescens*), European aspen (*Populus tremula*), mountain ash (*Sorbus aucuparia*) and goat willow (*Salix caprea*). Spruce forests include pure spruce (*Picea abies*) stands (> 80% spruce) and spruce–dominated mixed forests (50%–80% spruce). Pine forests include pine (*Pinus sylvestris*) -dominated stands (> 49% pine).

4 and 5). Characteristic for the group was the abundance of *Dryopteris filix-mas, Convallaria majalis, Viola mirabilis, Actaea spicata, Milium effusum* and/or *Stachys sylvatica* (Table 5). Other typical species in the field layers were *Dryopteris carthusiana, Melica nutans* and *Elymus caninus*

Table 4. Vegetation coverage (%) of the TWINSPAN clusters (numbers) and site type groups. Ferns (55.7%) and herbs (43.6%) are abundant on all studied sites. Dwarf-shrubs (Dwarf-shr.) have low coverage (1.4%). Explanations for the clusters, *see* Fig. 6 and for the groups, *see* Fig. 4. Here ferns** mean ferns, horsetails and club mosses, and grasses* mean grasses, sedges and rushes.

CLU/ Type	Shrubs		Dwarf-shr.		Ferns**		Herbs		Grasses*	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	6.5	8.9	13.4	12.9	23.2	19.9	48.7	19.2	13.7	9.8
2	20.4	32.2	0.4	0.6	40.9	22.2	46.0	20.0	4.9	4.0
3	3.3	4.3	3.5	5.8	28.9	17.1	45.0	16.6	9.2	7.7
4	5.0	4.8	0.5	0.8	79.1	24.0	30.5	17.8	3.6	4.3
5	8.0	12.8	0.5	0.6	51.1	36.9	59.2	15.3	4.8	2.8
6	6.3	6.8	0.1	0.2	82.9	30.8	34.4	19.0	1.4	1.5
7	3.3	5.9	0.0	0.0	50.8	27.5	56.9	22.4	4.0	4.8
8	12.5	10.4	0.4	1.1	17.7	15.7	63.4	32.3	6.9	10.7
OMa	4.8	7.2	4.2	8.1	34.4	15.3	41.0	19.3	41.0	19.3
OR	17.3	27.1	5.5	8.5	20.9	15.9	55.3	17.7	9.2	10.1
PuV	8.7	9.9	0.1	0.1	45.2	30.4	53.7	23.9	4.5	32.9
AAs	5.3	5.0	0.4	0.8	81.4	22.1	27.3	17.8	3.3	3.0
Ath	4.7	6.3	0.4	0.8	73.5	22.9	39.8	12.2	3.8	4.7
Dip	6.2	6.2	0.1	0.2	96.1	26.8	28.4	23.4	1.1	1.6
Mat	2.7	2.7	0.3	0.5	71.6	27.8	42.7	12.8	2.7	3.9
OFi	8.6	10.4	0.4	0.9	25.1	22.6	66.6	25.4	5.9	8.4
Tot.	6.5	10.1	1.4	4.5	55.7	34.2	43.6	23.3	5.1	6.5

(Tables 5 and 6). The shrub layers were sparse but diverse in species; e.g. *Daphne mezereum, Lonicera xylosteum* and *Ribes spicatum* (Tables 4 and 5). The stands were mainly dominated by young alders (Table 9).

Moist sites

The *Athyrium filix-femina–Dryopteris expansa* group (AAs) included AthAssT (19, 20, 22, 27, 48, 57, 61, 65, 66, 70, 72, 78, 80, 83, 85, 82), AthAssT–OPaT (17) and AthAssT–OMaT (24) sites. These sites were poor in species number (Table 3) and dominated by tall ferns, *Dryopteris expansa* and *Athyrium filix-femina* (Table 5). Under the tall ferns, typical species were *Phegopteris connectilis, Vaccinium myrtillus, Calamagrostis arundinacea, Rubus saxatilis, Luzula pilosa* and *Milium effusum* (Tables 5 and 6). Characteristic species of the sparse shrub layers were *Alnus incana, Rubus idaeus* and *Sorbus aucuparia* (Tables 4 and 6). Most of the stands were quite young, spruce-dominated forests (Table 9).

Sites dominated by *Athyrium filix-femina* (Ath) were classified in the field into the AthT (1, 25, 28, 75, 81, 87, 93, 95), AthT–OFiT (12, 23, 49), AthT–GORT (15) and AthT–OPaT (36, 88).

Table 5. Characteristic species composition ("indicator species") of the studied groups. Numbers represent frequencies (%) in each group. Mean coverages greater than 2% are identified as follows: ^{2} = 2.1%–5%, ^{3} = 5.1%–10%, ^{4} = 10.1%–20%, ^{5} = 20.1%–30%, ^{6} = 30.1%–40%, ^{7} = 40.1%–50%, ^{8} > 50.1%.

Species	OMa	OR	PuV	AAs	Ath	Dip	Mat	OFi
Actaea spicata	47	43	50	33	36	80	20	5
Athyrium filix-femina	37	43	50^{4}	100^{5}	100^{7}	100^{4}	100^{5}	74
Calamagrostis arundinacea	74	86^{2}	50	72	71	50	20	32
Calamagrostis purpurea	11	–	25	33	29	10	30	74
Carex digitata	40	86	–	22	29	30	–	21
Convallaria majalis	74	43	75^{3}	44	21	40	30	42
Crepis paludosa	16	–	25	61	93^{2}	90^{2}	90^{2}	79
Daphne mezereum	21	43	75	6	43	60	10	32
Deschampsia cespitosa	11	57	25	22	50	20	30	84
Diplazium sibiricum	–	–	–	–	–	100^{8}	–	–
Dryopteris expansa	58	43	50	100^{5}	36	50	30	11
Dryopteris filix-mas	32	43	75^{3}	17	21	–	–	11
Elymus caninus	–	29	50	6	36	50	50	21
Equisetum pratense	16	14	25	22	29	60	50	47
Equisetum sylvaticum	11	–	–	33	50	50	50	58
Filipendula ulmaria	5	43	50^{2}	28	86	90	80^{4}	100^{4}
Fragaria vesca	32	86	25	6	36	30	10	32
Galium triflorum	5	29	–	17	50	40	30	5
Geum rivale	16	57	25	22	79	80	70^{2}	100^{2}
Lonixera xylosteum	16	43	50	11	14	10	10	5
Luzula pilosa	58	57	50	61	36	20	–	63
Matteuccia struthiopteris	–	–	–	–	–	10	100^{5}	–
Milium effusum	42	–	50	56	21	20	40	11
Phegopteris connectilis	21	14	25	100^{3}	93^{3}	90^{3}	90^{3}	68
Ranunculus repens	5	29	50	6	21	20	70	68
Ribes spicatum	–	14	50	6	14	20	20	5
Solidago virgaurea	84	43	25	50	29	30	20	26
Stachys sylvatica	–	29	50	–	7	20	40	5
Vaccinium myrtillus	90	71	50	83	50	50	30	42
Vaccinium vitis-idaea	42	57	25	11	29	20	20	26
Veronica officinalis	11	57	25	11	7	10	–	16
Viola epipsila	16	–	–	17	64	20	60	79^{2}
Viola mirabilis	21	100	50	11	36	20	–	21
Viola riviniana	58	57	–	11	29	30	20	21

Vegetation seemed to be more luxuriant than in the former AAs group. Characteristic species in the upper field layers were *Athyrium filix-femina, Crepis paludosa* and *Filipendula ulmaria* (Tables 5 and 6). Typical species in the low-herb strata were *Phegopteris connectilis, Melica nutans, Paris quadrifolia, Geum rivale, Viola selkirkii* and *Galium triflorum*. The diverse shrub layers consisted mainly of *Rubus idaeus* and deciduous saplings (Tables 4 and 6). The stands were quite young, spruce-dominated mixed forests (Table 9).

The *Diplazium sibiricum* group (Dip) included DiplT (55, 60, 64, 74, 82, 84, 86) and DiplT–AthAssT (50, 52, 77) sites. On all these sites, the most abundant species was *Diplazium sibiricum*. Other typical, but less abundant species in the upper field layers were *Athyrium filix-femina, Crepis paludosa, Filipendula ulmaria, Elymus caninus* and, particularly on the DiplT–AthAssT sites, *Dryopteris expansa* (Tables 5 and 6). Characteristic species in the low-herb strata were *Phegopteris connectilis, Geranium sylvaticum, Geum rivale, Actaea spicata, Paris quadrifolia, Equisetum pratense* and *Viola selkirkii*. The diverse shrub layers consisted mainly of *Rubus idaeus, Prunus padus, Alnus incana, Daphne mezereum* and *Sorbus aucuparia* (Tables 4, 5 and 6). The stands were primarily young alder forests or mature spruce forests (Table 9).

The *Matteuccia struthiopteris* group (Mat) included MaT (6, 7, 63, 73), MaT–OFiT (9, 10, 11, 37) and MaT–AthAssT (18, 58) sites. These types were quite similar in terms of species, but MaT–AthAssT was characterized by *Dryopteris expansa*, which was rare in other types. The upper field layers were dominated by *Athyrium filix-femina* and *Matteuccia struthiopteris* (Table 5). Other characteristic species in the upper field layers were *Filipendula ulmaria, Crepis paludosa* and *Elymus caninus*. The species that best described the low-herb strata were *Phegopteris connectilis, Geum rivale, Ranunculus repens, Paris quadrifolia* and *Equisetum pratense* (Tables 5 and 6). The shrub layers were sparse and consisted mainly of *Rubus idaeus* and deciduous saplings (Tables 4 and 6). The stands were quite young spruce- or alder-dominated forests (Table 9).

All the tall-herb-dominated sites were put together to form the *Filipendula* group (OFi). This group included the following herb-rich forest types: OFiT (41, 44, 46, 91, 99, 101), GOFiT (2, 4, 31, 33, 79, 97), GFiT (47, 96, 98), OFiT-AthT (13), OFiT–AthAssT (69), GOFiT–AthT (35) and GFiT–AthT (5). In this study, these were treated as one type, because differences between types were small and it was also difficult to separate them in the field. Species composition seemed to be

Table 6. Characteristic species composition ("constant" species) of the studied groups. Numbers represent frequencies (%) in each group. Mean coverages greater than 2% are identified as follows: ^{2} = 2.1%–5%, ^{3} = 5.1%–10%, ^{4} = 10.1%–20%, ^{5} = 20.1%–30%, ^{6} = 30.1%–40%, ^{7} = 40.1%–50%, ^{8} > 50.1%.

Species	OMa	OR	PuV	AAs	Ath	Dip	Mat	OFi
Alnus incana	60	86^2	100	67	71	60	60	58^2
Angelica sylvestris	63	71	50	33	64	60	60	84
Dryopteris carthusiana	58^2	43	100	28	71	10	50	69
Geranium sylvaticum	63	86	75	83	86	90	80	90^2
Gymnocarpium dryopteris	100^4	71^3	100^3	100^4	93^3	90^3	100^3	84^2
Maianthemum bifolium	100^2	100^2	100^2	100^2	100^2	100^2	90	90
Melica nutans	84	86	100	67	93	70	60	68
Oxalis acetosella	95^3	100^4	100^3	100^2	100^3	100^2	100^3	79^2
Paris quadrifolia	63	86	50	44	93	80	80	79
Picea abies	37	43	75	33	7	50	30	63
Prunus padus	21	57	50	50	64	70	60	68
Rubus idaeus	80	71^2	75	83	79^2	90	80	79
Rubus saxatilis	84	100^2	75	72	71	40	50	74
Sorbus aucuparia	90	29	75	78	57	60	40	63
Trientalis europaea	100	86	100	89	93	90	90	79
Viola selkirkii	58	86	50	33	71	80	40	58

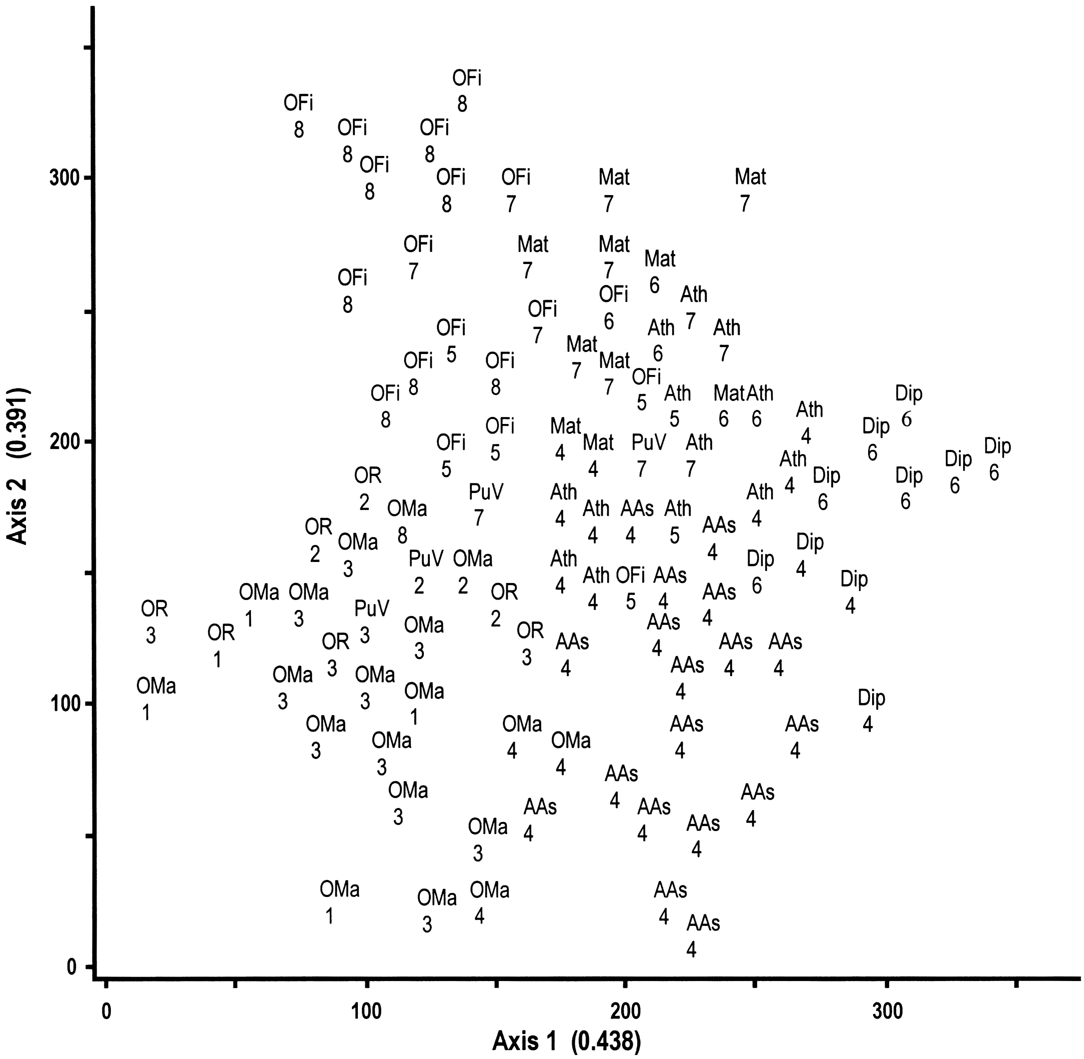

Fig. 4. DCA ordination of sample plots (total inertia is 3.933). Numbers (1–8) indicate TWINSPAN clusters and abbreviations site type groups. Abbreviations: OMa = *Oxalis acetosella–Maianthemum bifolium* group, OR = *Oxalis acetosella–Rubus saxatilis* group, PuV = *Dryopteris filis-mas–Viola mirabilis* group, AAs = *Athyrium filix-femina–Dryopteris expansa* group, Ath = *Athyrium* group, Mat = *Mateuccia struthipteris* group, Dip = *Diplazium sibiricum* group, OFi = *Filipendula ulmaria* group. For numbers *see* Fig. 6.

quite similar in different types, except that *Oxalis acetosella* was absent from the GFiT sites, and *Athyrium filix-femina* was abundant on the OFiT–AthAssT, GOFiT–AthT and GFiT–AthT sites.

Tall herbs and grasses e.g. *Filipendula ulmaria, Geum rivale, Angelica sylvestris, Deschampsia cespitosa, Crepis paludosa* and *Calamagrostis purpurea* were characteristics for the *Filipendula* group (Tables 4, 5 and 6). Other typical species were *Viola epipsila, Paris quadrifolia* and *Ranunculus repens*. The thick shrub layers were characterized by *Rubus idaeus* and tree saplings (Tables 4 and 6). The stands were mainly quite young deciduous forests (Table 9).

Multivariate analysis

DCA ordination

The moist Dip sites received the highest values for the first axis, whilst sub-dry OMa and OR

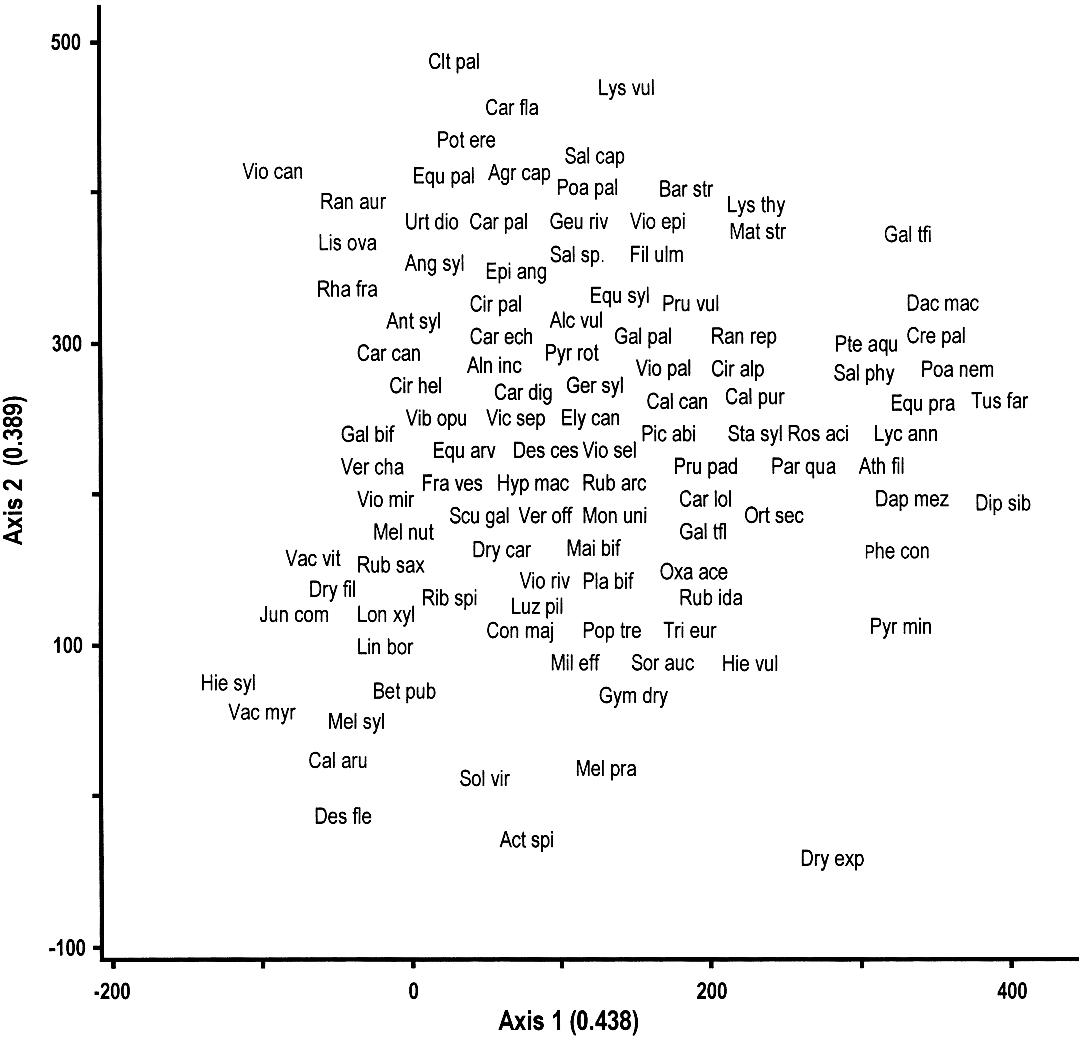

Fig. 5. DCA ordination of species (total inertia is 3.894). For abbreviations, *see* Appendix.

sites received the lowest values (Fig. 4). Almost all the fern-dominated sites (AAs, Ath, Mat) had higher values for the first axis than the herb-dominated (OMa, OR, PuV, OFi) sites. The *Filipendula ulmaria* dominated sites (OFi) had the highest values for the second axis, whilst the sites with abundance of *Dryopteris expansa* (some AAs and OMa sites) received the lowest values. However, the Mat sites also received high values for the second axis.

Species ordination was done for all species, but only selected species ($n > 3$) are shown in Fig. 5. Species that favored moisture and high fertility, e.g. *Diplazium sibiricum, Tussilago farfara, Crepis paludosa* and *Equisetum pratense* received the highest values for the first axis. However, the typical species for the less fertile and acid heat forests, e.g. *Hieracium sylvaticum* and *Vaccinium myrtillus* had the lowest values for the first axis. Furthermore, drought-tolerant species, e.g. *Juniperum communis, Vaccinium vitis-idaea* and *Dryopteris filix-mas* also received low values for the first axis. The light-tolerant meadow and eutrophic mire species, e.g. *Viola canina, Caltha palustris, Carex flava* and *Lysimachia vulgaris* received the highest values for the second axis, whilst the shade-tolerant species, such as *Dryopteris expansa* and *Actaea spicata*

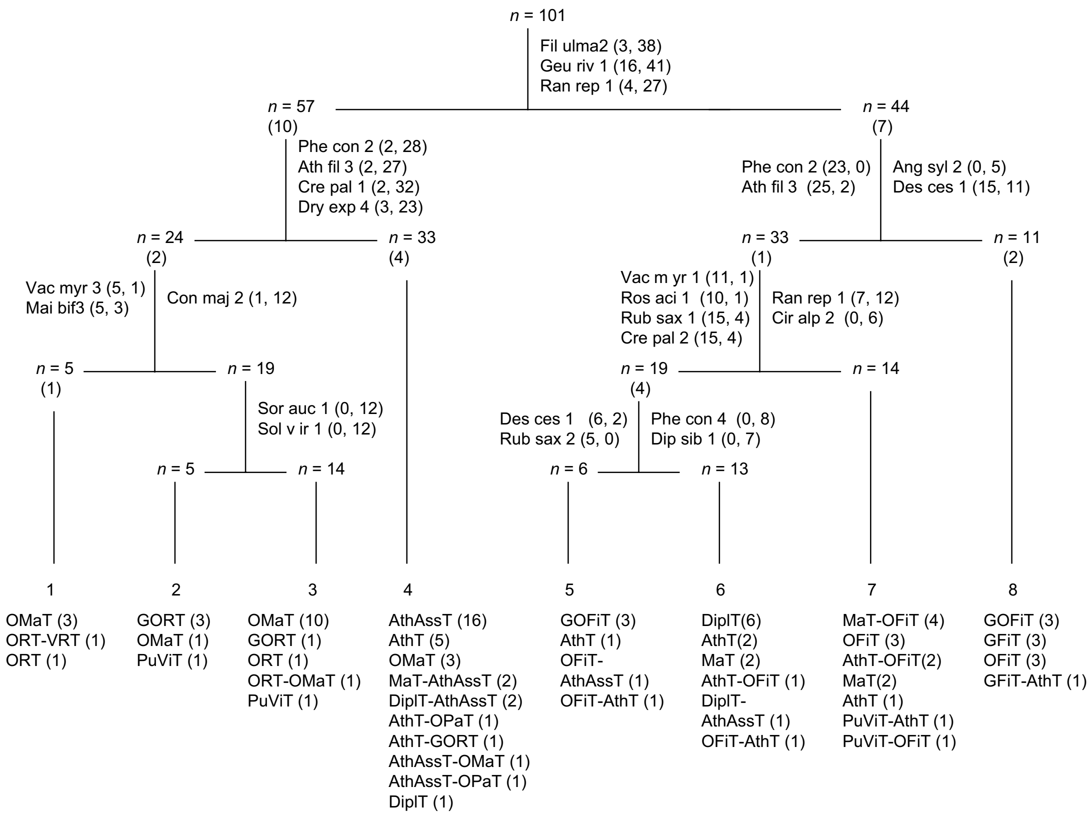

Fig. 6. TWINSPAN classification of the whole data set. Numbers of the misclassified sample plots are inside the brackets below *n*. Number after species (abbreviations see Appendix) gives coverage cut levels for indicator species/pseudospecies (1 = 0.1%–2%, 2 = 2%–5%, 3 = 5%–10%, 4 = 10%–20%, 5 > 20%). Frequencies are inside the brackets. Clusters are named after the most descriptive species. 1: *Vaccinium myrtillus–Maianthemum bifolium,* 2: *Oxalis acetosella–Rubus saxatilis*, 3: *Oxalis acetosella–Maianthemum bifolium*, 4: *Athyrium filix-femina–Dryopteris expansa*, 5: *Crepis paludosa–Phegopteris connectilis*, 6: *Athyrium filix-femina–Phegopteris connectilis,* 7: *Athyrium filix-femina–Ranunculus repens* and 8: *Filipendula ulmaria–Angelica sylvestris*.

and typical species for the heath forests, had the lowest values. The dominant species of the moist herb-rich forests, excluding *Dryopteris expansa*, received higher values for the second axes than dominant species of the mesic sites. According to the ordination, moisture and fertility seem to increase and acidity decrease along the first axis, while light and occurrence of culture-favoring species seem to increase along the second axis.

TWINSPAN classification

At the first level of the TWINSPAN, sample plots were divided into the mesic (*n* = 57) and moist sites (*n* = 44) (Fig. 6). Indicators for the right division were *Filipendula ulmaria, Geum rivale* and *Ranunculus repens*.

At the second level, the left subset was divided into low herb- (*n* = 24) and fern-dominated sites (*n* = 33). The fern-dominated sites formed the *Athyrium filix-femina–Dryopteris expansa* cluster (4) named after the dominant species. Indicators for this cluster were *Phegopteris connectilis, Athyrium filix-femina, Crepis paludosa* and *Dryopteris expansa*. Other species with certain abundance criteria were *Gymnocarpium dryopteris, Maianthemum bifolium, Calamagrostis arundinacea, Actaea spicata* and *Rubus idaeus* (Tables 7 and 8).

On the right (*n* = 44), moist sites were divided into fern-rich (*n* = 33) and herb-rich sites (n = 11). Indicator species of this division were *Phegopteris connectilis* and *Athyrium filix-femina* for the fern-rich sites, and *Angelica sylvestris* and *Deschampsia cespitosa* for the herb-rich sites. Moist herb-rich sites formed the *Filipendula ulmaria-Angelica sylvestris* cluster (8), which was also characterized by *Geum rivale, Viola epipsila, Crepis paludosa, Calamagrostis purpurea* and *Anthriscus sylvestris*.

At the third level, on the left, mesic sites were divided into dwarf-shrub (n = 5) and herb dominated sites (n = 19). The sites dominated by dwarf-shrubs formed the *Vaccinium myrtillus–Maianthemum bifolium* cluster (1). Typical species for the cluster one were also *Deschampsia flexuosa, Melica nutans, Sorbus aucuparia, Solidago virgaurea, Vaccinium vitis-idaea, Viola riviniana, Luzula pilosa* and *Veronica officinalis*.

At the third level, on the right, fern-rich sites were divided into the northern (n = 19) and southern forests (n = 14). The northern forests were characterized by northern and eastern species e.g. *Rosa acicularis, Diplazium sibiricum* and *Geranium sylvaticum*. The southern *Athyrium filix-femina–Ranunculus repens* cluster (7) was characterized by southern species, such as *Cir-*

Table 7. Characteristic species composition (“indicator” species) of the TWINSPAN clusters. Numbers represent frequencies (%) in each cluster. Mean coverages greater than 2% are identified as follows: ^{2} = 2.1%–5%, ^{3} = 5.1%–10%, ^{4} = 10.1%–20%, ^{5} = 20.1%–30%, ^{6} = 30.1%–40%, ^{7} = 40.1%–50%, ^{8} > 50.1%.

Species	1	2	3	4	5	6	7	8
Actaea spicata	40	20	57	70	–	54	21	–
Anthriscus sylvestris	40	20	–	–	–	15	36	64
Calamagrostis arundinacea	40	60	93^3	79	67	38	21	18
Calamagrostis purpurea	–	–	7	27	33	31	29	73
Carex digitata	40	60	57	27	67	15	7	–
Circaea alpina	–	20	–	6	–	8	50	18
Cirsium palustre	–	–	7	3	50	8	–	27
Convallaria majalis	40	20	93^2	39	50	46	14	55
Crepis paludosa	40	–	–	70	100^3	92^4	71	73
Daphne mezereum	20	20	36	18	50	62	29	18
Deschampsia cespitosa	20	60	7	21	100	15	50	100
Deschampsia flexuosa	80^2	40	36	15	33	8	14	9
Diplazium sibiricum	–	–	–	9	–	54^5	–	–
Dryopteris expansa	40	40	57	85^5	33	38	14	–
Dryopteris filix-mas	20	80^3	21	18	17	–	36	–
Elymus caninus	20	–	7	6	17	54	64	27
Equisetum pratense	–	–	21	21	50	70	43	46
Equisetum sylvaticum	20	–	–	27	50	77	43	64
Filipendula ulmaria	–	60	7	36	100^4	100^3	93^4	91^5
Fragaria vesca	20	60	50	18	67	15	7	46
Geum rivale	–	60	14	27	100	100	86	91^2
Phegopteris connectilis	60	–	7	94^3	100^3	92^4	71	46
Prunella vulgaris	20	–	7	6	67	23	–	18
Prunus padus	40	40	21	46	100	92	50	64
Ranunculus repens	20	20	7	3	50	31	79	73
Rosa acicularis	–	20	14	18	67	46	7	–
Solidago virgaurea	80	–	86	52	50	31	–	27
Stachys sylvatica	–	40	–	–	–	15	57	–
Vaccinium myrtillus	100^5	20	93	76	83	46	7	46
Vaccinium vitis-idaea	80	20	57	21	67	23	–	18
Veronica officinalis	60	20	14	6	17	8	14	18
Viola epipsila	20	–	7	24	83	38	64	82^2
Viola mirabilis	20	20	50	18	17	23	14	18
Viola palustris	–	–	–	9	50	8	21	27
Viola riviniana	80	40	50	30	50	8	7	27

caea alpina and *Stachys sylvatica*.

Most of the divisions at the fourth level seemed to be of minor ecological and phyto-sociological importance. The herb-dominated mesic sites ($n = 19$) were divided further into the *Oxalis acetosella–Rubus saxatilis* ($n = 5$) and *Oxalis acetosella–Maianthemum bifolium* clusters ($n = 14$). The *Oxalis acetosella–Rubus saxatilis* cluster (2) was characterized by the name species and *Dryopteris filix-mas, D. carthusiana, Gymnocarpium dryopteris, Alnus incana, Rubus idaeus, Fragaria vesca* and *Carex digitata*. Typical species for the *Oxalis acetosella–Maianthemum bifolium* cluster (3) including the name species were *Calamagrostis arundinacea, Convallaria majalis, Melica nutans, Rubus saxatilis, Carex digitata, Dryopteris expansa, Actaea spicata* and *Viola mirabilis*.

The northern fern-rich forests ($n = 19$) were further divided into the *Crepis paludosa–Phegopteris connectilis* ($n = 6$) and *Athyrium filix-femina–Phegopteris connectilis* clusters ($n = 14$). The *Crepis paludosa–Phegopteris connectilis* cluster (5) was also characterized by *Deschampsia cespitosa* and *Rubus saxatilis* as well as hydrophilous species, such as *Filipendula ulmaria, Geum rivale, Viola epipsila, V. palustris, Cirsium palustre* and *Equisetum pratense*. Other typical species were *Prunus padus, Geranium sylvaticum, Paris quadrifolia, Prunella vulgaris* and *Rosa acicularis*. Characteristic species for the *Athyrium filix-femina–Phegopteris connectilis* cluster (6) including the name species were *Diplazium sibiricum, Crepis paludosa, Filipendula ulmaria, Geranium sylvaticum, Geum rivale* and *Prunus padus*. Other describing species were *Equisetum pratense, Daphne mezereum, Elymus caninus* and *Rubus idaeus*.

Discussion

Description of herb-rich forests

The diversity of the herb-rich forest site types is high in the study area for many reasons: Firstly, Koli is located in the transition area between the southern and middle boreal zones. Consequently, vegetation includes both northern and southern features. Secondly, the topography of the area offers many different habitats. Thirdly, the alkaline rocks, such as diabase, maintain calciphilous and relict flora.

The field classified site types were combined into the eight main ecological types as follows:

- Mesic, low-herb-dominated sites:
  Oxalis acetosella–Maianthemum bifolium group (OMa)

Table 8. Characteristic species composition ("constant" species) of the TWINSPAN clusters. Numbers represent frequencies (%) in each cluster. Mean coverages greater than 2% are identified as follows: ^{2} = 2.1%–5%, ^{3} = 5.1%–10%, ^{4} = 10.1%–20%, ^{5} = 20.1%–30%, ^{6} = 30.1%–40%, ^{7} = 40.1%–50%, ^{8} > 50.1%.

Species	1	2	3	4	5	6	7	8
Alnus incana	40	100^2	64	70	83	46	64	64
Angelica sylvestris	60	60	79	42	83	70	50	91^2
Athyrium filix-femina	60	80^2	14	97^5	100^4	100^5	86^5	55
Dryopteris carthusiana	40	80^3	50	39	50	38	71	82
Geranium sylvaticum	60	60	71	82	100	100^2	71	91^2
Gymnocarpium dryopteris	80^2	100^3	93^4	97^4	100^2	100^2	100^2	73
Luzula pilosa	80	60	50	58	83	31	36	46
Maianthemum bifolium	100^4	100^2	100^2	100^2	100^2	100	100^2	82
Melica nutans	100	60	93	67	83	92	71	64
Oxalis acetosella	80^3	100^5	100^4	97^2	100^3	100^2	100^3	64
Paris quadrifolia	40	60	57	73	100	77	57	100
Rubus idaeus	40	100^2	79	85	67	92	64	91^2
Rubus saxatilis	80^3	100	86	73	83^3	70	29	73
Sorbus aucuparia	100	–	79	73	83	62	43	55
Trientalis europaea	100	100	93	94	83	100	79	82
Viola selkirkii	60	60	71	42	67	77	64	46

Oxalis acetosella–Rubus saxatilis group (OR)
Dryopteris filix-mas–Viola mirabilis group (PuV)

- Moist, fern-rich sites:
  Athyrium filix-femina–Dryopteris expansa group (AAs)
  Athyrium filix-femina group (Ath)
  Diplazium sibiricum group (Dip)
  Matteuccia struthiopteris group (Mat)
- Moist, tall-herb-dominated sites:
  Filipendula ulmaria group (OFi)

Sample plots were grouped by TWINSPAN as follows:

Vaccinium myrtillus–Maianthemum bifolium cluster (1)
Oxalis acetosella–Rubus saxatilis cluster (2)
Oxalis acetosella–Maianthemum bifolium cluster (3)
Athyrium filix-femina–Dryopteris expansa cluster (4)
Crepis paludosa–Phegopteris connectilis cluster (5)
Athyrium filix-femina–Phegopteris connectilis cluster (6)
Athyrium filix-femina–Ranunculus repens cluster (7)
Filipendula ulmaria–Angelica sylvestris cluster (8)

On the whole, the classification methods used here complemented each other. The ecological groups were based on an *a priori* typification. Multivariate analyses brought new points for classification, such as southern and northern aspect. The aim was to find enough clear and large vegetation groups to describe the characteristic features of the flora.

Specific features of vascular plant communities in Koli

The Koli area offers different habitats for many species. Cold and moist eastern and northern slopes are ideal habitats for arctic and taiga species. Eastern calcium rich slopes, in particular, maintain demanding northern, eastern and southern flora (Kalliola 1973). Moist and shaded forest valleys offer sites for hydrophilous herbs, ferns and sedges. Southern species grow mainly on warm and sub-dry western and southern slopes.

Northern and eastern species and features were characteristic for the herb-rich forests studied. A rare northern taiga species, *Diplazium sibiricum*, was abundant on the luxuriant fern-rich sites of the eastern slopes. Other characteristic species for the eastern herb-rich forests, such as *Rosa acicularis*, *Viola selkirkii, Crepis paludosa, Equisetum pratense* and *Actaea spicata* (Kalliola 1973), were common on the studied plots. In addition, *Geranium sylvaticum* and *Gymnocarpium dryopteris* were abundant on many sites, which is typical for the northern forests (Sepponen *et al*. 1982, Alanen *et al*. 1996, Kuusipalo 1996). However, other rare eastern taiga species, *Glyceria lithuanica* and *Carex rhynchophysa* (Ruotsalo 1958, Tuomikoski 1958a, Hakalisto 1987, Lyytikäinen 1991), occurred sporadically in the study area (Appendix). According to Sonck (1964), these species usually grow together and they have only a couple of habitats in Koli.

The data included the following southern species for which the northernmost habitat is Koli: *Tilia cordata, Aegopodium podagraria, Epipactis helleborine, Galium odoratum, Mycelis muralis, Stachys sylvatica, Scrophularia nodosa, Vicia sylvatica* and *Poa remota* (Jalas 1958, 1965d, 1980c, 1980d, Roivainen 1958, Kujala 1965, Skult 1980, Suominen 1980, Hakalisto 1987). These species, except for the quite abundant *Stachys sylvatica*, occurred sporadically on the plots (Appendix). However, other southern species, e.g. *Lonicera xylosteum, Dryopteris filix-mas, Matteuccia struthiopteris, Circaea alpina* and *Viola mirabilis* were quite common on the plots. These species occur in the middle boreal zone, but not as abundantly as in the southern boreal zone (Tuomikoski 1958c, 1958e, Hämet-Ahti 1980b, Jalas 1980b, 1980e).

Vascular plants as site indicators

The results of this study referred that moisture, shading and nutrients were the most important factors in classifying and ordinating the sample plots.

In fact, the classification of boreal forests is based mainly on moisture and fertility (Kuusipalo 1985, Lahti & Väisänen 1987). Moisture is the most important, and fertility the second important factor in classifying herb-rich forests (Huttunen 1982a, 1982b, Lahti & Väisänen 1987, Kaakinen 1992).

The first axis of DCA indicates probably the moisture gradient. The vegetation changed gradually from the mesic to the moist sites (Fig. 5). Drought-tolerant species, e.g. *Vaccinium vitis-idaea* and *Dryopteris filix-mas* received lower values than hydrophilous ferns, such as *Phegopteris connectilis, Athyrium filix-femina* and *Matteuccia struthiopteris* (Hämet-Ahti *et al*. 1998). However, hydrophilous herbs, e.g. *Potentilla erecta, Anthriscus sylvestris, Cirsium palustre* and *Cirsium helenioides* received lower values than the hydrophilous ferns. It might be due to that these herbs reflect other factors, e.g., earlier land use, more than moisture (Linkola 1916, Jalas 1953).

However, the axes are ecologically complex factors and they have more than one interpretation. Thus, the first axis of DCA might also indicate soil fertility or acidity. In this study, species specialized in the herb-rich forests received higher values for the first axis than the typical species for the heath forests, except for *Dryopteris carthusiana* (Fig. 5). Owing to the very wide habitat amplitude, *D. carthusiana* is able to success on different site types (Nousiainen 2001). Abundance of the species specialized in the herb-rich forests often indicates high fertility (Huttunen 1982b). In the Koli area, these species include *Daphne mezereum, Lonicera xylosteum, Rosa acicularis, Elymys caninus, Glyceria lithuanica, Milium effusum, Diplazium sibiricum, Dryopteris expansa, Equisetum pratense, Matteuccia struthiopteris, Actaea spicata, Circaea alpina, Epipactis helleborine, Galium triflorum, Listera ovata, Paris quadrifolia, Stachys sylvatica, Viola mirabilis* and *V. selkirkii* (Hakalisto 1987, Kärkkäinen 1994).

Species favoring springs and brook-sides, e.g. *Tussilago farfara* and *Crepis paludosa* as well as calciphilous species, e.g. *Diplazium sibiricum* and *Daphne mezereum* also received higher values for the first axis than other typical species for the herb-rich forests (Fig. 5). Abundance of *Daphne mezereum, Crepis paludosa* or *Diplazium sibiricum* might indicate high calcium content on the soil surface (Pankakoski 1939, Kalliola 1958, Dahlskog 1980). Calciferous bedrock has an effect on vegetation, particularly if the soil layer above is thin enough. Moreover, flowing water (brooks, springs) might have a calcium-like-effect (Pesola 1929).

The second axis of DCA probably indicates light conditions. Pioneers, such as meadow species and other sun plants received higher values for the second axis than shade plants (Fig. 5.). Photophilous plants, e.g. *Carex flava, Matteuccia struthiopteris, Epilobium angustifolium, Filipendula ulmaria, Geum rivale, Potentilla erecta* and *Viola canina* (Palmgren 1958, Tuomikoski 1958e, 1965, Jalas 1965b, Hämet-Ahti *et al*. 1998, Silfverberg 2001b, Vanha-Majamaa 2001a) seemed to be the most abundant on young deciduous forests or open sites. Sciophilous plants, e.g. *Actaea spicata, Dryopteris expansa, Circaea alpina, Linnaea borealis* and *Platanthera bifoliata* (Cedercreutz 1958, Tuomikoski 1958b, Jalas 1965a, 1980b, Salemaa 2001a) favored spruce-dominated forests and eastern slopes. However, *Circaea alpina* received higher values than other shade plants. It might be due to its habit to grow under the tall ferns (Jalas 1980b).

Additional interpretation of the second axis could be earlier land use (agriculture, slash-and-burn culture, woodland pastures and hay-meadows). Some culture-favoring species, such as *Potentilla erecta, Ranunculus auricomus, Urtica dioica, Anthriscus sylvestris* and *Epilobium angustifolium* (Marklund 1965, Pettersson 1965, Hämet-Ahti 1980a, Silfverberg 2001b, Vanha-Majamaa 2001a), had relatively high values for the second axis. In the Koli area, the following species are culture-favoring: *Alchemilla* sp., *Anthriscus sylvestris, Deschampsia cespitosa, Fragaria vesca, Prunella vulgaris, Ranunculus acris, R. auricomus, Urtica dioica* and *Veronica officinalis* (Kärkkäinen 1994). In this study, however, the coverage of these species was quite low.

Evaluation of herb-rich forest site types

Constant and indicator species

Constant species are common, but not very abundant in the region (Kuusipalo 1996).

Indicator species should reflect site properties reliably (abundance) and they should also be constant enough (frequency) for describing the region (Kuusipalo 1985). In this study, the most describing indicator species were chosen by TWINSPAN (*see* Fig. 6). These species were e.g., *Dryopteris expansa* and *Phegopteris connectilis* at abundance level four (coverage > 10%), *Vaccinium myrtillus* at abundance level three (coverage 5.1%–10%), *Filipendula ulmaria, Angelica sylvestris, Convallaria majalis* and *Circaea alpina* at abundance level two (coverage 2.1%–5%) and *Deschampsia cespitosa, Solidago virgaurea* and *Rosa acicularis* at abundance level one (coverage 0.1%–2%).

Dryopteris expansa and *Vaccinium myrtillus* had the highest coverage on the poorest spruce-dominated slopes of the OMa and AAs groups (Tables 5, 9 and 10). Abundance of these species indicated primarily moderate shading. They might also indicate soil acidity, because both species favor acidic, shaded sites and avoid calciferous, very fertile sites (Tuomikoski 1958b, Salemaa 2001b). *Dryopteris expansa* is a typical species for the moderate fertile, shaded rocky sites (Tuomikoski 1958b) and *Vaccinium myrtillus* for the closed, spruce-dominated heath forests (Kuusipalo 1996).

Phegopteris connectilis was characteristic for the moist fern-dominated sites and *Angelica sylvestris, Deschampsia cespitosa* and *Filipendula ulmaria* for the moist herb-dominated sites (Tables 5 and 7). Abundance of *Phegopteris connectilis, Angelica sylvestris, Deschampsia cespitosa* and *Filipendula ulmaria* indicated at least moderate fertility and moisture. In addition, *Phegopteris connectilis* reflected shading, whilst *Angelica sylvestris, Deschampsia cespitosa* and *Filipendula ulmaria* reflected openness. These species are quite demanding in terms of nutrients and moisture (Tuomikoski 1958d, Jalas 1965b, 1980a, Silfverberg 2001a). In addition *Angelica sylvestris*, *Deschampsia cespitosa* and *Filipendula ulmaria* favor open, fertile and culture-affected sites, such as meadows, young deciduous forests and moist clear-cutting areas (Jalas 1965b, 1980a, Silfverberg 2001a). *Phegopteris connectilis* is a type plant for the moist herb-rich forests (Alanen *et al*. 1996), and it is also demanding in terms of shading (Tuomikoski 1958d).

Convallaria majalis was the most abundant on the mesic OMa and luxuriant PuV sites, but *Solidago virgaurea* was typical for all OMa sites (Tables 5 and 7). In this study, both species indicated primarily mesic conditions and secondarily early succession stages. In addition, abundance of *Convallaria majalis* might also indicate moderate fertility, because in the middle boreal vegetation zone it is the most abundant in the luxuriant herb-rich forests (Tonteri 2001a). However, *Convallaria majalis* is common, but light green and sterile in young and open heath forests. *Solidago virgaurea* is typical for the sunny sites,

Table 9. Dominant tree species and succession stages of the studied groups (%). Numbers represent frequencies (%) in each group. Succession stages: I = initial stage (0–20 years); mainly saplings, II = intermediate stage (21–80 years); young or almost mature forests, III = climax (80–250 years); mature, over mature and old forests.

Dominant tree sp.	OMa	OR	PuV	AAs	Ath	Dip	Mat	OFi
Alnus incana	21	57	75	39	29	40	30	42
Betula pendula	–	14	25	–	29	20	–	–
Betula pubescens	5	–	25	22	7	–	20	37
Picea abies	68	57	50	50	57	40	40	26
Pinus sylvestris	11	14	–	–	14	–	–	5
Populus tremula	21	–	–	11	–	10	–	–
Sorbus aucuparia	5	–	–	–	–	–	–	–
Salix caprea	–	–	–	–	–	–	10	–
Forest age								
I) 0–20 yr.	5	–	25	–	–	–	10	16
II) 21–80 yr.	68	43	50	72	79	60	60	68
III) 81–250 yr.	26	57	25	28	21	40	30	16

especially for the grove-like heath forests (OMT) (Tonteri 2001b). Both species are common in young and open heath forests (Kuusipalo 1996).

Circaea alpina was typical for the southern and *Rosa acicularis* for the northern fern-rich forests (Table 7). The first one seemed to indicate primarily southern features (long growing season, warm conditions) and the second one northern features (short growing season, cold and humid conditions). *Circaea alpina* is a typical species for the southern fern-rich forests (AthT, MaT), but it occurs sporadically in the middle- and northern-boreal zones (Jalas 1980b, Meriluoto & Soininen 1998). In Finland, *Rosa acicularis* is a quite demanding eastern and northeastern species in terms of nutrients and moisture (Jalas 1965c). In eastern Fennoscandia, it is common only in North Karelia, eastern Finland and in Aunus in the neighboring Karelian Republic, Russia (Jalas 1965c).

Comparison between forest site types and multivariate analyses

Interpretation of the results was based on the field classification and multivariate analyses. The multivariate methods bring supplementary, objectivity to the analyses and to the presentation of the results. The methods can be used as tools; e.g. in order to pay more attention to certain species and abundance criteria when specifying and identifying more traditional vegetation types. Some degree of subjectivity is needed in defining the program parameters, as well as in the final compilation of results (Oksanen 1984). As pointed out by Oksanen (1984), the classifier must be responsible for his results; he cannot hide behind "objective" methods.

DCA ordination of the whole data set (Figs. 4 and 5) yielded quite low eigenvalues. In addition, the eigenvalues did not differ a lot between different site types and there was no clear main gradient. This might indicate that a large number of environmental factors have an effect on herb-rich forest vegetation (Heikkinen 1991). Low eigenvalues might suggest that random variation in species composition play a relatively significant role (Gauch 1982, Heikkinen 1991). However, the field-classified site types and the ordination results corresponded quite well to each other's (Fig. 4). The clearest correspondence between the ordination results and the site typification occurred in the case of *Diplazium sibiricum* site types. Another clear correspondence was between the moist herb-rich forest types and the ordination results.

For example, TWINSPAN brought out an aspect of northern and southern forest site types that was not taken into consideration in the site typification. Moreover, classification in the field was quite difficult, because many types were "mixed" with diverse vegetation or representing intermediate succession stages (Tables 9 and 10).

Table 10. Dominant tree species and succession stages of the TWINSPAN clusters. Numbers represent frequencies (%) in each cluster. Succession stages: I = initial stage (0–20 years); mainly saplings, II = intermediate stage (21–80 years); young or almost mature forests, III = climax (80–250 years); mature, over mature and old forests.

Dominant tree sp.	1	2	3	4	5	6	7	8
Alnus incana	20	60	29	30	17	38	43	55
Betula pendula	–	–	7	–	–	23	7	–
Betula pubescens	–	–	21	17	17	15	36	36
Picea abies	60	80	64	64	50	38	29	–
Pinus sylvestris	40	–	7	3	17	–	–	9
Populus tremula	–	–	21	9	–	8	–	9
Sorbus aucuparia	–	–	–	3	–	–	–	–
Salix caprea	–	–	–	–	–	–	7	–
Forest age								
I) 0–20 yr.	–	–	7	–	–	–	7	27
II) 21–80 yr.	60	80	57	61	67	85	79	64
III) 81–250 yr.	40	20	36	39	33	15	14	9

Especially, it was difficult to classify the moist tall-herb-dominated sites with high abundance of ferns. In addition, differences between sub-dry and mesic OMaT sites were small. TWINSPAN divided the heterogeneous OMa group into the sub-dry, luxuriant mesic and moderate fertile mesic sites (Fig. 6). In addition, the traditional OMaT sites include a wide range of mesic herb-rich forests (Alanen *et al*. 1996, Kuusipalo 1996). Nevertheless, TWINSPAN did not separate *Diplazium sibiricum*-dominated sites into the own group despite of high coverage of *Diplazium sibiricum* in these sites.

Comparison between earlier and previous forest site types

The *Oxalis acetosella–Maianthemum bifolium* group (OMa) as well as the *Oxalis acetosella–Maianthemum bifolium* cluster (3) were quite similar to the traditional OMaT (Alanen *et al*. 1996, Kuusipalo 1996). However, the studied sites were more luxuriant in vegetation in terms of specialized herb-rich forest species, such as *Dryopteris expansa* and *Actaea spicata*. These species are not typical for the traditional type (Cajander 1926, Kuusipalo 1996). Furthermore, the *Vaccinium myrtillus–Maianthemum bifolium* cluster (1) corresponded quite well to the traditional OMaT. This cluster also had some features of the VRT (Alanen *et al*. 1996).

The *Oxalis acetosella–Rubus saxatilis* group (OR) corresponded well to the earlier described GORT (Kuusipalo 1996). In addition, a typical species for the PuViT sites, *Viola mirabilis* was characteristic for the OR group. Nevertheless, the *Oxalis acetosella–Rubus saxatilis* cluster (2) reminded more the described ORT than GORT (Alanen *et al*. 1996). The *Dryopteris filix-mas–Viola mirabilis* group (PuV) corresponded well to the *Pulmonaria-Viola* site type (PuViT) described in literature (Alanen *et al*. 1996). However, TWINSPAN divided the sites of the PuV group into the *Oxalis acetosella–Rubus saxatilis* (2), *Oxalis acetosella–Maianthemum bifolium* (3) and *Athyrium filix-femina-Ranunculus repens* (7) clusters (*see* Fig. 6).

In this study, all sites dominated by *Dryopteris expansa* were included to the *Athyrium filix-femina–Dryopteris expansa* group (AAs). The group and the *Athyrium filix-femina–Dryopteris expansa* cluster (4) reminded each other, and their vegetation composition corresponded quite well to the earlier described AthAssT (Kärkkäinen 1994, Alanen *et al*. 1996). Typical species to the AthAssT, such as *Scrophularia nodosa* and hydrophilous herbs, did not occur on the studied sites (Alanen *et al*. 1996, Kuusipalo 1996). However, the TWINSPAN cluster was more luxuriant than the type described in literature. In fact, it reminded the AthAssT of Tohmajärvi excluding *Aconitum septentrionale, Stellaria nemorum* and *Aegopodium podagraria* (Ratia & Timonen 1975).

The *Athyrium filix-femina* group (Ath) reminded both AthT and AthOT sites described in literature (Alanen *et al*. 1996, Kuusipalo 1996). The *Crepis paludosa–Phegopteris connectilis* cluster (5) was quite similar to the AthT, although it had many features of the GOFiT. The studied sites were more luxuriant in vegetation than the traditional AthT or AthOT. Nevertheless, typical southern species of the AthT, such as *Stellaria nemorum* and *Scrophularia nodosa*, did not occur on the studied plots (Alanen *et al*. 1996, Kuusipalo 1996). The TWINSPAN cluster (5) also corresponded well to the *Filipendula ulmaria–Phegopteris connectilis* group of the earlier study in Koli (Kärkkäinen 1994). However, TWINSPAN divided the most sites of the *Athyrium filix-femina* group into the *Athyrium filix-femina-Dryopteris expansa* cluster (4) (Fig. 6).

The *Diplazium sibiricum* group (Dip) corresponded well to the DiplT sites of literature (Alanen *et al*. 1996, Kuusipalo 1996). Some typical species for the DiplT, such as *Stellaria nemorum* and *Cinna latifolia*, were not found from the studied sites. The *Athyrium filix-femina–Phegopteris connectilis* cluster (6) also reminded the DiplT, although *Diplazium sibiricum* did not occur on all the plots. However, the cluster (6) had many features of the GOFiT sites. Furthermore, the Dip group and the cluster corresponded well to the *Diplazium sibiricum–Athyrium filix-femina* group of the earlier study in Koli (Kärkkäinen 1994).

The *Matteuccia struthiopteris* group (Mat) was similar to the MaT sites described in literature (Alanen *et al*. 1996). The following characteristic species of the MaT were not found from the studied plots: *Stellaria nemorum, Glyceria lithuanica, Poa remota* and *Cinna latifolia* (Kuusipalo 1996). Vegetation composition of the *Athyrium filix-femina–Ranunculus repens* cluster (7) reminded the MaT, although *Matteuccia struthiopteris* did not occur on all plots. The cluster (7) also had features of the OFiT and AthT. In addition, the group and cluster corresponded well to the *Matteuccia struthiopteris–Ranunculus auricomus* group of the previous study in Koli (Kärkkäinen 1994). *Ranunculus repens*, however, was more common on the studied plots than *Ranunculus auricomus*.

The *Filipendula ulmaria* group (OFi) corresponded well to the OFiT and GOFiT described in literature (Alanen *et al*. 1996, Kuusipalo 1996). Moreover, culture-favoring species were abundant on some plots, which is quite typical to the herb-rich forests of the Koli area (Kärkkäinen 1994). The *Filipendula ulmaria–Angelica sylvestris* cluster (8) reminded the GOFiT and GFiT sites described in literature (Kuusipalo 1996) and the *Aconitum-Filipendula* sites (AT) of Kitee and Tohmajärvi (Ratia & Timonen 1975). However, some typical species to the AT, such as *Aconitum septentrionale* and *Aegopodium podagraria*, did not occur on the studied sites.

Conclusions and prospects for future work

Boreal herb-rich forests are important ecosystems for maintaining biological diversity in Finnish forests. They differ from hemiboreal deciduous forests and herb-grass forests in many ways, because they have unique features due to the northernmost habitats of the specialized herb-rich forest species. For example, spring herbs are rare or absent from the northern parts of the southern boreal zone. Boreal herb-rich forests are also more luxuriant and richer in vascular plant species than boreal heath forests. Moreover, most of the threatened forest plants (80%) grow in the herb-rich forests, which cover less than 1% of the total forest area in Finland. Due to rarity and biological diversity, it is important to preserve existing herb-rich forests vitality and large enough by protection and legislation.

In eastern Finland, most herb-rich forests centered to the surroundings of Kuopio, Kitee and Tohmajärvi. Koli is an important interarea between these two districts and a significant patch for species dispersion from middle Karelia to Kainuu. The quite high variation of vegetation is mainly due to variable topography and bedrock. In addition, herb-rich forests of the Koli area are significant for maintaining eastern and northern taiga species, such as *Diplazium sibiricum, Glyceria lithuanica, Carex rhynchophysa, Viola selkirkii* and *Rosa acicularis*. The *Diplazium sibiricum* communities should deserve special attention, because they are rare in the whole EU area, excluding Kuusamo and middle Karelia.

This study should be seen as a basic work for describing herb-rich forest vegetation in the Koli area. The next important task is to explore reasons for the variation in vegetation. For this purpose, it might be essential to study the effects of soil total nutrients and acidity on the vegetation structure.

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Appendix. All vascular plant species on the sample plots in the study area, abbreviations and frequences. Number of sample plots is 101 and total number of species 167.

Species	Abbr.	Freq.
Actaea spicata	Act spi	36
Aegopodium podagraria	Aeg pod	1
Agrostis capillaris	Agr cap	10
Agrostis stolonifera	Agr sto	2
Alchemilla sp.	Alc sp.	3
Alchemilla vulgaris	Alc vul	8
Alnus incana	Aln inc	66
Andromeda polifolia	And pol	1
Angelica sylvestris	Ang syl	62
Anthoxanthum odoratum	Ant odo	1
Anthriscus sylvestris	Ant syl	16
Athyrium filix-femina	Ath fil	78
Barbarea stricta	Bar str	3
Betula pubescens	Bet pub	8
Botrychium lunaria	Bot lun	1
Calamagrostis arundinacea	Cal aru	58
Calamagrostis canescens	Cal can	11
Calamagrostis purpurea	Cal pur	28
Calla palustris	Cal pal	1
Caltha palustris	Clt pal	9
Campanula glomerata	Cam glo	1
Campanula rotundifolia	Cam rot	1
Carex buxbaumii	Car bux	1
Carex canescens	Car can	10
Carex cespitosa	Car ces	1
Carex digitata	Car dig	29
Carex echinata	Car ech	3
Carex elongata	Car elo	2
Carex flava	Car fla	4
Carex globularis	Car glo	1
Carex loliacea	Car lol	7
Carex pallescens	Car pal	8
Carex rhynchophysa	Car rhy	1
Carex sp.	Car sp.	2
Carex vaginata	Car vag	1
Circaea alpina	Cir alp	13
Cirsium helenioides	Cir hel	8
Cirsium palustre	Cir pal	9
Convallaria majalis	Con maj	46
Corallorhiza trifida	Cor tri	1
Crepis paludosa	Cre pal	61
Cypripedium calceolus	Cyp cal	2
Dactylis glomerata	Dac glo	2
Dactylorhiza maculata	Dac mac	4
Daphne mezereum	Dap mez	30
Deschampsia cespitosa	Des ces	38
Deschampsia flexuosa	Des fle	22
Diplazium sibiricum	Dip sib	10
Dryopteris carthusiana	Dry car	53
Dryopteris cristata	Dry cri	2
Dryopteris expansa	Dry exp	49
Dryopteris filix-mas	Dry fil	20
Elymus caninus	Ely can	24
Epilobium angustifolium	Epi ang	18
Epilobium montanum	Epi mon	2
Epipactis helleborine	Epi hel	2
Epipogium aphyllum	Epi aph	1
Equisetum arvense	Equ arv	5
Equisetum fluviatile	Equ flu	1
Equisetum palustre	Equ pal	6
Equisetum pratense	Equ pra	33
Equisetum sylvaticum	Equ syl	36
Festuca ovina	Fes ovi	1
Filipendula ulmaria	Fil ulm	58
Fragaria vesca	Fra ves	29
Galeopsis bifida	Gal bif	13
Galium boreale	Gal bor	1
Galium palustre	Gal pal	3
Galium trifidum	Gal tfi	11
Galium triflorum	Gali tfl	21
Galium uliginosum	Gal uli	2
Geranium sylvaticum	Ger syl	82
Geum rivale	Geu riv	57
Glyceria lithuanica	Gly lit	2

Appendix. Continued.

Species	Abbr.	Freq.
Gymnocarpium dryopteris	Gym dry	94
Hieracium pilosella-coll.	Hie pil	1
Hieracium sylvatica-coll.	Hie syl	7
Hieracium vulgata-coll.	Hie vul	4
Huperzia selago	Hup sel	2
Hypericum maculatum	Hyp mac	11
Impatiens glandulifera	Imp gla	1
Juniperus communis	Jun com	5
Lathyrus pratensis	Lat pra	1
Linnaea borealis	Lin bor	11
Listera ovata	Lis ova	12
Lonicera xylosteum	Lon xyl	16
Luzula pilosa	Luz pil	51
Lycopodium annonitum	Lyc ann	22
Lycopodium clavatum	Lyc cla	1
Lysimachia thyrsiflora	Lys thy	4
Lysimachia vulgaris	Lys vul	6
Lythrum salicaria	Lyt sal	1
Maianthemum bifolium	Mai bif	98
Matteuccia struthiopteris	Mat str	11
Melampyrum pratense	Mel pra	9
Melampyrum sylvaticum	Mel syl	28
Melica nutans	Mel nut	77
Mentha arvensis	Men arv	1
Menyanthes trifoliata	Men tri	1
Milium effusum	Mil eff	31
Moehringia trinervia	Moe tri	1
Moneses uniflora	Mon uni	4
Mycelis muralis	Myc mur	1
Orthilia secunda	Ort sec	28
Oxalis acetosella	Oxa ace	95
Paris quadrifolia	Par gua	72
Parnassia palustris	Par pal	1
Peucedanum palustre	Peu pal	2
Phegopteris connectilis	Phe con	68
Picea abies	Pic abi	41
Pinus sylvestris	Pin syl	1
Platanthera bifolia	Pla bif	4
Poa nemoralis	Poa nem	4
Poa palustris	Poa pal	3
Poa remota	Poa rem	1
Poa sp.	Poa sp.	1
Poa trivialis	Poa tri	2
Populus tremula	Pop tre	10
Potentilla erecta	Pot ere	7
Potentilla palustris	Pot pal	1
Prunella vulgaris	Pru vul	14
Prunus padus	Pru pad	54
Pteridium aquilinum	Pte aqu	13
Pyrola minor	Pyr min	19
Pyrola rotundifolia	Pyr rot	6
Ranunculus acris	Ran acr	1
Ranunculus auricomus	Ran aur	8
Ranunculus repens	Ran rep	31
Rhamnus frangula	Rha fra	9
Ribes rubrum	Rib rub	2
Ribes spicatum	Rib spi	9
Rosa acicularis	Ros aci	20
Rosa majalis	Ros maj	1
Rubus arcticus	Rub arc	5
Rubus idaeus	Rub ida	81
Rubus saxatilis	Rub sax	73
Rumex acetosa	Rum ace	1
Salix caprea	Sal cap	6
Salix pentandra	Sal pen	1
Salix phylicifolia	Sal phy	6
Salix sp.	Sal sp.	3
Scirpus sylvaticus	Sci syl	1
Scrophularia nodosa	Scr nod	1
Scutellaria galericulata	Scu gal	3
Silene dioica	Sil dio	2
Solidago virgaurea	Sol vir	43
Sorbus aucuparia	Sor auc	66
Stachys sylvatica	Sta syl	12
Stellaria media	Stel med	2
Trientalis europaea	Tri eur	91
Tussilago farfara	Tus far	8
Urtica dioica	Urt dio	12
Vaccinium myrtillus	Vac myr	62
Vaccinium vitis-idaea	Vac vit	29
Valeriana sambucifolia	Val sam	1
Veronica chamaedrys	Ver cha	7
Veronica officinalis	Ver off	14
Viburnum opulus	Vib opu	7
Vicia sepium	Vic sep	5
Viola canina	Vio can	3
Viola epipsila	Vio epi	38
Viola mirabilis	Vio mir	23
Viola palustris	Vio pal	13
Viola riviniana	Vio riv	31
Viola rupestris	Vio rup	2
Viola selkirkii	Vio sel	58