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Vegetation patterns of boreal herb-rich forests in the Koli region, eastern Finland: classification, environmental factors and conservation aspects

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Academic dissertation

To be presented, with the permission of the Faculty of Forestry of the University of Joensuu, for public criticism in auditorium B1 of the University of Joensuu, Yliopistonkatu 7, Joensuu, on 6th October 2006, at 12 o'clock noon.

Title: Vegetation patterns of boreal herb-rich forests in the Koli region, eastern Finland: classification, environmental factors and conservation aspects

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Dissertationes Forestales 27

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ISSN: 1795-7389
ISBN-13: 978-951-651-142-2 (PDF)
ISBN-10: 951-651-142-2 (PDF)

Paper copy printed:
Joensuun yliopistopaino, 2006

Publishers:
The Finnish Society of Forest Science
Finnish Forest Research Institute
Faculty of Agriculture and Forestry of the University of Helsinki
Faculty of Forestry of the University of Joensuu

Editorial Office:
The Finnish Society of Forest Science
Unioninkatu 40 A, 00170 Helsinki, Finland
http:// www.metla.fi/dissertationes

Hokkanen, Päivi. 2006. Vegetation patterns of boreal herb-rich forests in the Koli region, eastern Finland: classification, environmental factors and conservation aspects. University of Joensuu, Faculty of Forestry.

ABSTRACT

The main aims of this thesis were to describe the vegetation patterns of herb-rich forests, herb-rich forest site types and the main underlying environmental factors, and to provide a classification of vegetation and analyse the pattern in species richness. A total of 101 herb-rich forest patches were studied in the Koli area, eastern Finland. Two-way indicator species analysis (TWINSPAN) and detrended correspondence analysis (DCA) were used for classifying the sites and species, canonical correspondence analysis (CCA) was used for identifying the main environmental gradients, and nestedness calculator and RANDNEST procedure for testing whether the species distribution showed a random occurrence. The main findings were as follows: 1) the vegetation composition of the studied site types corresponded relatively well to the previously described site types in eastern and northern Finland. 2) The multivariate ordination and classification methods used here complemented the classification. 3) An accurate classification was obtained when both vascular plants and bryophytes were used in the classification. 4) The compositional variation in the vegetation was mainly related to soil moisture and fertility. 5) Long-term human impacts had affected the composition of the vegetation and soil properties. 6) The soil of the studied sites was more acidic than those included in the earlier investigations. 7) Bryophytes reacted differently to topography and stand structure than vascular plants. 8) Large patches had more edaphically demanding and red-listed species than small ones, but a set of small patches supported more edaphically demanding species than a few large patches of the same total area.

The results show that the flora and vegetation groups had many characteristics specific for the Koli area, and therefore classification could not be generalised to other areas. Bryophytes seemed to play a minor role in the classification of herb-rich forests as compared with vascular plants. Most of the studied herb-rich forests had previously been managed and represented the middle stages of forest succession and recovery. Consequently, it is difficult to predict their future development, i.e. if they will develop into boreal herb-rich forest, herb-rich heath forest or herb-rich spruce mire. It is essential, in order to maintain vital plant populations, to conserve large areas, but small areas, such as woodland key-biotopes, are important to augment protected areas.

Keywords: edaphically demanding flora, forest site types, patch network, soil properties, terricolous bryophytes, vascular flora

ACKNOWLEDGEMENTS

First of all my deepest gratitude goes to my brilliant supervisor Jari Kouki, who has kindly helped me with numerous scientific problems and provided me excellent conditions in which to work. My warmest thanks also go to Kauko Salo for providing excellent data, helping with many dilemmas and supporting me throughout the entire process. I would like to thank Juha-Pekka Hotanen for his help with many statistical questions and for his valuable comments on the manuscripts and this summary.

I also wish to thank my collaborator Atte Komonen for his help with null models. I am grateful to Sirkka Hakalisto for her helpful information and advice about herb-rich forests and threatened plants. Many thanks to Lasse Lovén for the valuable information about the Koli National Park, and to Martti Ruuskanen for the valuable information about the woodland key-biotopes in the Koli area. I also thank Mekrijärvi Research Station, especially Taneli Kolström, for enabling me to complete this work.

Writing this thesis would not have been possible without the people who assisted me in the field and laboratory. Their contribution is acknowledged in the context of each paper. In addition, I wish to thank Riitta Jalkanen and Virva Rento for their help and company in looking for herb-rich forests in the Koli area during the first summer. I am also grateful to Rauni Oksman and Leena Kuusisto for their valuable advice and patience in the laboratory.

It has been a pleasure to work at the Finnish Forest Institute and the Faculty of Forestry in Joensuu and at the Mekrijärvi Research Station in Ilomantsi. I wish to thank the members of our research team for fruitful discussions in the group seminars, in particular Esko Hyvärinen, Kaisa Junninen, Jukka Kettunen, Harri Lappalainen and Olli-Pekka Tikkanen. I would also like to thank Veli-Pekka Ikonen, Harri Strandman, Mikko Mönkkönen, Kaisa Laitinen, Heli Peltola and Aija Ryyppö for their help with many other questions.

I thank Marja Kolström and Risto Virtanen for reviewing my thesis. Their comments were constructive and useful. I also thank John Derome for revising the language of the thesis.

I wish to express my gratitude to all my friends. I apologize that I cannot mention all my friends here by name. Special thanks to Hanna, Raimo, Pat and Virva for their help and interests in my work.

I am grateful to my mother, Raili for her continuous support in all my studies. I also wish to thank my siblings and Pirjo & Rick and Eila & Aarne for their support, and my in-laws for the extra family they have given to me. Special thanks go to Paula for searching and sending many scientific articles to me, and to Timo from whom I learned a lot of the scientific world.

My dearest gratitude goes to my husband Hannu for his support, friendship and love, and to our sweet children Salli, Janina, Leevi and Siiri.

This study carried out as a part of the Finnish Biodiversity Programme (FIBRE). Financial support from the Maj and Tor Nessling Foundation and the Finnish Forest Industries Federation is hereby acknowledged. The Academy of Finland (Centre of Excellence Programme 2000-2005, project No. 64308), the Graduate School for Forest Sciences and the Mekrijärvi Reseach Station also provided funding for the study. I express my thanks for this financial support.

LIST OF ORIGINAL ARTICLES

This thesis is a summary of the following papers, which are referred to in the text with Roman numerals I-IV:

I Hokkanen, P. 2003. Vascular plant communities in boreal herb-rich forests in Koli, eastern Finland. Annales Botanici Fennici 40: 153-176.

II Hokkanen, P. 2004. Bryophyte communities in herb-rich forests in Koli, eastern Finland: comparison of forest classifications based on bryophytes and vascular plants. Annales Botanici Fennici 41: 331-365.

III Hokkanen, P. 2006. Environmental patterns and gradients in the vascular plants and bryophytes of eastern Fennoscandian herb-rich forests. Forest Ecology and Management 229: 73-87.

IV Hokkanen, P., Kouki, J. & Komonen, A. Nestedness, SLOSS and conservation network of boreal herb-rich forests. Submitted manuscript.

P. Hokkanen participated planning the research, and in all studies she was responsible for conducting at least half of the field work and she made majority of the work in laboratory analyses, analysing the data and writing the articles.

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LIST OF SPECIFIC TERMS

Acidophilous species = species that favour acidic sites and they usually grow in boreal heath forests

Calciphilous species = calciphile species that favour calcium-rich substrate, but they are also able to grow on other substrates

Characteristic species = species that has both a strong presence and a relatively high mean coverage in a site type

Constant species = species that is frequently present and has a low coverage in a site type

Differential species = species that can be used for distinguishing site types, i.e. species that has a strong presence in a site type and which occurs abundantly or constantly only in few site types in the area

Edaphically demanding species = calciphiles and calcicoles and other species specific for the fertile sites

Hemerophilous species = culture-favouring species, their occurrence is related to human impacts, i.e. “man-made” habitats such as grazed forests, meadows etc.

Hygrophilous species = these species favour relatively high moisture content

Mesophilous species = species that have their optimum on mesic sites

Mor = raw humus; a type of humus, which occur largely in coniferous forest soils and the moor lands, characteristic for podzolic soils

Moder = humus, humified humus; a type of moderately humified humus, a transitional form of humus between mull and moder, characteristic for brown soils

Mull = a well humified organic matter, characterised by the neutral pH and it is typical for chestnut soils and soils under cultivation

Photophilous species = these species favour lightness and they usually suffer from shading

Sciophilous species = these species favour shading and they usually suffer from direct sunshine

Terricolous bryophytes = includes bryophytes (and lichens) that grew on mineral soil, ground litter, humus, small (height < 15 cm) stones and fine woody debris (d < 5 cm)

1 INTRODUCTION

1.1 Background

Boreal forests are often considered to be relatively homogeneous in the structure of their vegetation and simple in species richness. Closer inspection reveals, however, that conifer-dominated boreal forests comprise very different plant assemblages (Kuusipalo 1985). Specific forested biotopes, e.g. herb-rich forests within the boreal zone, may be especially diverse in terms of their species diversity (Kuusipalo 1984), yet they may cover only a fraction of the total forest area (Kuusipalo 1996, Airaksinen and Karttunen 2001). Such areas are especially important in order to maintain biological diversity in the boreal forests.

During the last 60 years, forestry has expanded and intensified in Fennoscandian forests (Esseen et al. 1997, Kouki et al. 2001). In Finland, more than 95% of the forested land is used for intensive timber production of which about 70% of the annual net growth is harvested (Peltola 2004). The fragmentation, habitat loss and habitat alteration may have negative effects on the persistence of many specific forest species (Esseen et al. 1997, Hanski et al. 1998). Isolation may also pose a real threat to plant assemblages in the forest patches while, simultaneously, the increased influence of edges may diminish habitat quality in the forest patches (Murcia 1995, Berglund and Johnsson 2003). The extent to which these species may survive and reproduce in small-sized forest fragments is still unclear. If the risk of extinction is highly increased in small fragments, species may also be at risk of extinct at the landscape or regional level (Berglund and Jonsson 2003). At the larger scale, the extinction of species may follow the habitat loss and fragmentation: species may disappear at the regional level after decades (Hanski 1999). Knowledge of the distribution pattern and species in relation to fragmentation is essential in order to develop a conservation strategy for the biological diversity of forests.

In conservation biology, the application of the theory of island biogeography (Simberloff and Abele 1976, 1982, Järvinen 1982, Quinn and Harrison 1988) and the species-area relationship have focused on the patterns of species richness (Worthen 1996). The SLOSS (a single large or several small) debate is an application of the island theory to the reserve network design. The main question in the issue is whether several small reserves support an equal number of species as a single large reserve, and thus could be equally valuable for conservation purposes. Species richness, however, overlooks the compositional aspects of species diversity, and thus it is not an adequate guiding principle for the selection of conservation areas.

Nested subset patterns of species assemblages focus on the compositional aspects of community assembly. Biotic communities are said to be nested when the species in species-poor sites are subsets of the species present at richer sites. Thus, perfect nestedness would indicate that a single large site contains all the species present in the network, while the species composition in several small sites would be smaller and comprise only the most common species (Cook 1995, Worthen 1996). The phenomenon of nestedness has largely resurrected the SLOSS debate (Boecklen 1997), although the focus is on the species composition, rather than on species richness. Analyses of nestedness can provide a useful complementary tool to address the SLOSS problem in conservation biology (Patterson and Atmar 1986, Patterson 1987, Wright and Reeves 1992, Cook 1995, Honnay et al. 1999, Patterson & Atmar 2000).

1.2 What are herb-rich forests?

According to Linkola (1916) and Cajander (1916, 1926), herb-rich forests (i.e. grass-herb forests) are characterised by herbaceous flora. Grasses and shrubs are also abundant, but dwarf-shrubs and terricolous lichens are normally rare or absent (Cajander 1926). The forest floor is sparsely covered by bryophytes (Kaakinen 1992). In terms of vegetation, herb-rich forests are the most luxuriant and species-rich forests in Finland (Alanen 1992, Kuusipalo 1984, 1996). The herb-rich tree stand can be composed of broad-leaved trees (e.g. *Corylus avellana* L., *Fraxinus excelsior* L., *Quercus robur* L., *Tilia cordata* Mill., *Ulmus glabra* Huds. and *U. laevis* Pall.), other deciduous trees (e.g. *Alnus incana* [L.] Moench, *A. glutinosa* [L.] Gaertn., *Betula pendula* Roth, *B. pubescens* Ehrh., *Populus tremula* L.), Norway spruce (*Picea abies* [L.] Karst.) and sometimes also Scots pine (*Pinus sylvestris* L.) (Valta and Routio 1990, Alanen et al.1996).

The differences between herb-rich and heath forests are mainly due to the properties of the soil: herb-rich forests have a fertile, relatively neutral (pH 5.5-7.0) brown soil with a thick mull (or moder) layer, whereas heath forests have acidic (pH < 5.0) podzols with a grey leached horizon (Aaltonen 1947, Kaakinen 1992, Kuusipalo 1996, Mälkönen and Tamminen 2003). The development of a mull layer presupposes a relatively high base cation (Ca^{2+}, Mg^{2+}) concentration in the underlying layer, which can be calciferous bedrock or mineral soil containing abundant fine-textured soil types, such as clay or silt (Valta and Routio 1990).

Herb-rich forests are rare forest site types with specific edaphic conditions. They characteristically occur as scattered, small patches in the boreal forest landscape (Alanen et al. 1996, Heikkinen 2002). They cover only 1.4% of the total forest area in southern Finland, while the herb-rich heath forests cover 23% (Kuusipalo 1996). Herb-rich forests are rare in the boreal zone, primarily because the cool climate and siliceous bedrock are not favourable for the demanding herbaceous flora (Cajander 1916, Valta and Routio 1990, Alanen et al. 1996). Secondly, the period of intensive slash-and-burn cultivation and forest grazing that lasted from the 17^{th} to 19^{th} centuries caused changes in the vegetation of the herb-rich forests (Heikinheimo 1915). Thirdly, the period of active slash-and-burn cultivation was followed by habitat loss and fragmentation due to the clearing of forest for agriculture, and this reduced the area of such forests (Alanen 1992). Fourthly, the intensive forestry practiced since the 1940’s has caused further fragmentation (Kaakinen 1992, Airaksinen and Karttunen 2001). Herb-rich forests are characteristic in the very southern and south-western parts of Finland owing to the favourable climate, but in other parts of Finland they are located in specific areas with calciferous bedrock (Pesola 1928, Kaakinen 1982, 1992, Valta and Routio 1990). These areas, called districts rich in grass-herb forests, are located in southern Häme, Central Karelia, Kuopio, Kainuu, south-western Lapland, northern Kuusamo and Kittilä, and in the Russian side in Sortavala (Kaakinen 1982).

1.3 Classification of herb-rich forests

Classification of forest vegetation in Finland is based on the forest site type system of Cajander (1909, 1926). In this system, individual communities are related to community types by certain characters of structural and compositional similarities (Kuusipalo 1985). In Fennoscandia, the forests are normally composed of a few tree species, each of them able to dominate a wide range of sites with different understorey associates (Kuusipalo 1985).

Table 1. Herb-rich forest site types after Kaakinen (1972), Heikkinen (1991), Alanen et al. (1996) and Kuusipalo (1996). Abbreviations for the site types: VFrT = *Vaccinium (vitis-idaea)—Fragaria (vesca),* VRT = *Vaccinium (vitis-idaea)—Rubus (saxatilis)*, GVT = *Geranium (sylvaticum)—Vaccinium (vitis-idaea),* MeLaT = *Melica (nutans)—Lathyrus (vernus),* OMaT = *Oxalis (acetosella)—Maianthemum (bifolium)*, GOMaT = *Geranium (sylvaticum)—Oxalis (acetosella)—Maianthemum (bifolium)*, GDT = *Geranium (sylvaticum)—(Gymnocarpium) dryopteris*, HeOT = *Hepatica (nobilis)—Oxalis (acetosella),* PuViT = *Pulmonaria (obscura)—Viola mirabilis*, ORT = *Oxalis (acetosella)—Rubus (saxatilis)* corresponding to OPaT = *Oxalis (acetosella)—Paris (quadrifolia)*, GORT= *Geranium (sylvaticum) —Oxalis (acetosella)—Rubus (saxatilis)* corresponding to GOPaT = *Geranium (sylvaticum)—Oxalis (acetosella)—Paris (quadrifolia)*, GT = *Geranium (sylvaticum)*, AthOT = *Athyrium (filix-femina)—Oxalis (acetosella)* corresponding to AthAssT = *Athyrium (filix-femina)—Assimilis (Dryopteris expansa)*, CiT (LaAth) = *Ciberbita alpina*—(*Athyrium filix-femina*), MatT = *Matteuccia (struthiopteris*), AthT = *Athyrium (filix-femina)*, OFiT = *Oxalis (acetosella*)—*Filipendula (ulmaria),* AT = *Aconitum septentrionale*, GOFiT = *Geranium (sylvaticum)—Oxalis (acetosella)—Filipendula (ulmaria)*, *DiplT* = *Diplazium (sibiricum)* and GFiT = *Geranium (sylvaticum)—Filipendula (ulmaria*).

VEG. ZONE	DRY moderately fertile	fertile	MESIC moderately fertile	fertile	MOIST moderately fertile	fertile
Southern boreal	VFrT* VRT	MeLaT	OMaT	HeOT PuViT ORT (OPaT)	(AthOT) AthAssT	MatT AthT OFiT AT
Middle boreal	VRT GVT		GOMaT	GORT (GOPaT)	AT AthAssT	MatT AthT GOFiT
Northern boreal	VRT GVT		GDT	GT	AthAssT CiT (LaAth)	MatT DiplT GFiT

* = An esker forest site type

Consequently, ground vegetation is a more sensitive indicator of the environment than the tree layer (Cajander 1909, 1926, Whittaker 1978, Kuusipalo 1985). According to the forest site type theory, the composition of the understorey vegetation reflects “the biological value”, i.e. the primary value or state of each site (Cajander 1926, Nieppola 1986). The site classification system was developed primarily for practical forestry and one aim was to keep the number of site types reasonable (Kuusipalo 1985, Nieppola 1986). However, a more accurate classification system is needed for conservation purposes, because the small-scale variation within a habitat site type is important for the occurrence of edaphically demanding species (Kontula and Raunio 2005).

Conventional classification of boreal herb-rich forests is mainly based on vascular flora (Kaakinen 1974, Alanen et al. 1996, Kuusipalo 1996) but other groups, such as bryophytes, may also be useful in the classifications (La Roi and Stringer 1976). Terricolous bryophytes are regarded as good indicators of site quality (Ulvinen et al. 2002) and environmental changes (Vellak et al. 2003, Mäkipää and Heikkinen 2003). Bryophytes, however, indicate other environmental factors than vascular plants (Carleton 1990, Ulvinen et al. 2002, Ingerpuu et al. 2003), and they are important for distinguishing boreal herb-rich forests from herb-rich spruce mires (Kuusipalo 1985, 1996, Eurola et al. 1984, Laine and Vasander 1998).

In Finland, a considerable number of herb-rich forest site types have been described (Alanen et al. 1996, see also Table 1). Herb-rich forests have traditionally been classified into dry, mesic and moist main groups (Linkola 1916), because site moisture has been considered the most important ecological environmental factor explaining the patterns of herb-rich forest vegetation (Linkola 1916, Kaakinen 1974, 1992, Alanen et al. 1996). Inside these three main groups, herb-rich forests are further divided into moderately fertile and fertile types (Alanen et al 1996), because soil acidity and fertility have been regarded as the second important environmental factor (Mäkirinta 1968). Classification of herb-rich forests has also been based on their topography and situation (Valle 1919). Classification is sometimes difficult, because the vegetation is rather varied, species number is high, and most herb-rich forests are still undergoing successional change resulting from human interference (Koponen 1967).

Although Finnish researchers have a long tradition of studying herb-rich forests (Linkola 1916, Valle 1919, Tuomikoski 1950), the ecology and flora of these forests are still poorly known (Kaakinen 1992). Especially, detailed descriptions of the plant communities over the site types are rare, and no systematic assessment of their characteristics has been made (Koponen 1967). However, a proper classification is needed both for forest management and for conservation purposes. An ecological classification of herb-rich forests, for instance, would be beneficial for ensuring an ecologically representative set of such forests in the forest conservation area network.

1.4 Conservation of herb-rich forests

In Fennoscandia, herb-rich forests are one of the focal biotopes in nature conservation (Saetersdal et al. 1993, Virkkala and Toivonen 1999, Airaksinen and Karttunen 2001). These forests are important ecosystems for maintaining biological diversity (Alapassi and Alanen 1988, Kaakinen 1982, 1992, Rassi et al. 2001), because they are floristically the most diverse of all boreal forests and harbour many edaphically demanding (calcicole and calciphile) and red-listed vascular plants (Virkkala and Toivonen 1999, Rassi et al. 2001, Heikkinen 2002). Although herb-rich forests cover less than one percent of the total forest area in Finland (Alanen et al. 1996), they are the primary habitat for over 20% of the threatened species, for over 10% of all vascular plant species, and over 55% of the threatened forest species (*see* Rassi et al. 2001).

In Finland, the first herb-rich forest reserve was established as early as 1925 and, since then, several other herb-rich forests have been protected (Alanen 1992). Despite early attempts to protect herb-rich forests, their total area declined as a result of intensive forestry and the clearing of forests for agriculture. In order to protect the most valuable sites, a national conservation programme for herb-rich forests was launched in 1989 (Alapassi and Alanen 1988). The programme was based on a nation-wide survey that was carried out in the 1970’s and 1980’s (Alanen 1992). The protection of herb-rich forests expanded during the 1990’s and 2000’s and, at present, some of them are also protected e.g. under the Forest

Act of Finland (1093/ 1996), Conservation Act of Finland (1096/ 1996) and the EU Habitats Directive (92/43/EEC).

Some herb-rich forests located outside the protected areas are classified as woodland key-biotopes and thus protected under the Forest Act (Meriluoto and Soininen 1998). The most valuable spruce-dominated herb-rich sites, i.e. Fennoscandian herb-rich forests with *Picea abies,* are partly protected under the EU Habitats Directive (Airaksinen and Karttunen 2001). These forest areas often belong to the Natura 2000 network, which covers mostly the previously protected areas, e.g. areas protected under the national conservation programmes, national parks and nature reserves. Hazel (*C. avellana*) and broad-leaved forests, which are the most valuable herb-rich forests in Finland, are protected under the Nature Conservation Act of Finland (Hietaranta and Vuorela 1997). However, in Finland their presence is limited to the southern coastal area, the hemiboreal zone. Intensive forestry and the planting of spruce are still the main threats to herb-rich forests (Airaksinen and Karttunen 2001).

1.5 Aims of the thesis

This thesis aims to describe the vegetation patterns of herb-rich forests, herb-rich forest site types and the main environmental factors related to the distribution of the vegetation, and to provide applicable information for classifying herb-rich forests in a certain area and maintaining species diversity in boreal herb-rich forests. The questions are addressed here more specifically:

1. What are the characteristic features of herb-rich forests in the Koli area and the vascular plant communities occurring in them? Does the composition of the vascular flora differ from the previously studied site types in other parts of Finland? (I)
2. What is the composition of the bryophyte flora in different herb-rich forest site types, and are bryophytes useful in classifying herb-rich forests? (II)
3. What are the environmental factors that are related to the distribution patterns of the vegetation in herb-rich forests, and do environmental variables vary between different herb-rich forest site types? (III)
4. Are the species occurrences non-random? Does the patch size relate to the richness of edaphically demanding and red-listed species, and does a set of small patches support more edaphically demanding and red-listed species than a few large patches of equal total area? (IV)

2 MATERIAL AND METHODS

2.1 Study area

The study area is located in the Koli region, province of North Karelia, eastern Finland (29°52' E and 63°04' N, in the transition area between the southern and middle boreal vegetation zones (Ahti et al. 1968) (Fig. 1).

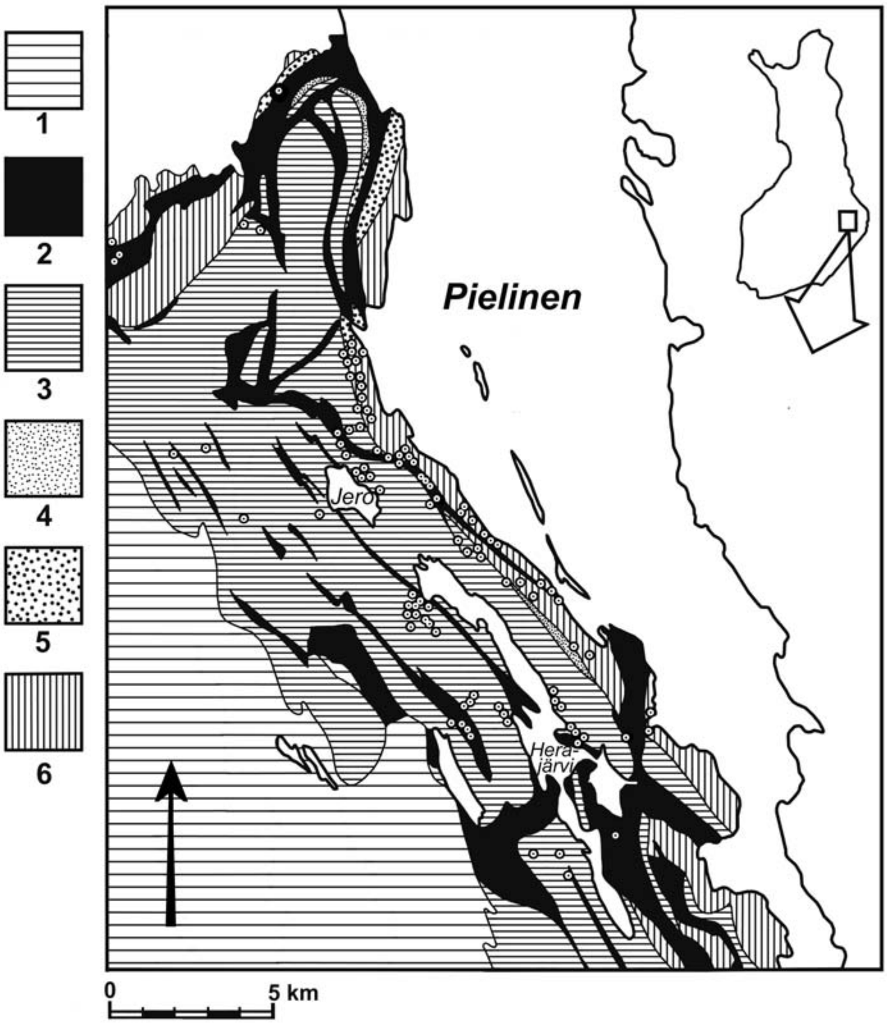

Figure 1. A map of the study area and location of the sample plots. The study area is located in Koli, eastern Finland (29°52' E and 63°04' N). The simplified lithographic map of the area is after Kohonen (1987). 1 = phyllite, mica schist and greywacke, 2 = diabase, 3 = conglomerate, quartzite and arkose, 4 = conglomerate and arkose, 5 = green schist (volcanic rock and sediment) and 6 = gneissose granite. White circles represent sample plots.

The Koli region is characterized by great altitudinal variation (90-340 m a.s.l.) and diversity of herb-rich forest vegetation (Lyytikäinen 1991, Kärkkäinen 1994). The climate is continental, the mean annual temperature is 2 ºC and the mean annual precipitation is 600 mm (Kalliola 1973, Heino and Hellsten 1983, Finnish Meteorological Institute 1991). The length of the thermal growing period is 150-155 days (Heino and Hellsten 1983). Herb-rich forests are usually situated on diabase-rich bedrock, while the rest of the area consists of siliceous rocks, e.g. granite-gneisses and different kinds of quartzite (Piirainen et al. 1974) (*see* Fig. 1). The mineral soils are mainly glacial till (Lyytikäinen, 1991). Dominant tree species are Norway spruce and Scots pine, but birches (*B. pendula, B. pubescens*), grey alder (*A. incana*) and aspen (*P. tremula*) are common particularly in the areas related to intensive, long-lasting slash-and-burn cultivation (Lyytikäinen 1991, Grönlund and Hakalisto 1998). Since the 1950's intensive forestry has caused further fragmentation of forests and increased the amount of coniferous forests (Grönlund and Hakalisto 1998).

2.2 '*A priori*' site types

Studied forests included eleven '*a priori*' herb-rich forest site types (*see* Table 1): 1) *Oxalis -Maianthemum* site type (OMaT), usually dominated by *Oxalis acetosella* L., *Maianthemum bifolium* (L.) F.W. Schmidt and *Gymnocarpium dryopteris* (L.) Newman, 2) *Oxalis-Rubus* site type (ORT), characterised by *O. acetosella, Rubus saxatilis* L. and *Viola mirabilis* L., 3) *Geranium-Oxalis-Rubus* site type (GORT), characterised by *O. acetosella, R. saxatilis, Geranium sylvaticum* L. *and Fragaria vesca* L., 4) *Pulmonaria obscura - Viola mirabilis* site type (PuViT), characterised by *Dryopteris filix-mas* (L.) Schott, *Convallaria majalis* L., *Actaea spicata* L. and *V. mirabilis*, 5) *Athyrium-Assimilis* (AthAssT) site type, dominated by *Dryopteris expansa* (C. Presl) Fraser-Jenk & Jermy and *Athyrium filix-femina* (L.) Roth, 6) *Athyrium filix-femina* site type (AthT), characterised by *A. filix-femina, Crepis paludosa* (L.) Moench and *Filipendula ulmaria* (L.) Maxim., 7) *Diplazium sibiricum* site type (DiplT), dominated by *Diplazium sibiricum* (Turcz. ex Kunze) Kurata, 8) *Matteuccia struthiopteris* site type (MatT), characterised by *Matteuccia struthiopteris* (L.) Tod. and *A. filix-femina,* 9) *Oxalis-Filipendula* site type (OFiT), characterised by *F. ulmaria, O. acetosella and Urtica dioica* L., 10) *Geranium-Oxalis-Filipendula* site type (GOFiT), characterised by *F. ulmaria, G. sylvaticum* and *O. acetosella,* and 11) *Geranium-Filipendula* site type (GFiT), characterised by *F. ulmaria, G. sylvaticum* and *Anthriscus sylvestris* (L.) Hoffm. For more detailed information about these types are available by Alanen et al. (1996) and Kuusipalo (1996). In the field, Heli Paatelainen (1996-1997) and Päivi Hokkanen (1999-2001) determined the herb-rich forest site types.

2.3 Concepts of a forest patch, stand and herb-rich forest site type

In the present study, stands and patches were used as synonyms depending on the context; in forestry a stand is more familiar (III) than a patch, and in conservation the term patch is more often used (IV). Both terms refer to a certain small forest area that differs in terms of vegetation from the surrounding forest. A forest stand is a basic unit for forestry management planning (e.g. Tonteri et al. 2005) and it is defined as a continuous forest area with homogeneous stand structure and soil properties. Although in practical forestry small stands (< 0.25 ha) are often combined into a larger stand, small woodland key-biotopes, such as boreal herb-rich forests, are separated into individual stands (Tonteri et al. 2005). A forest patch refers to a small forest area inside a larger (forest) area. In the study area, herb-rich forests in protected areas, i.e. forests in the Koli National Park or in other protected areas, were separated from the surrounding heath forests as individual stands but, because they often comprised several herb-rich forest site types, they were further divided into smaller units (patches) based on field inventories. Forest is a wider and more general term than a stand or patch but, because it refers to all the layers of vegetation, it was sometimes used as synonym for a stand and a patch. A site refers mainly to site characteristics and the lower layers of vegetation.

Concepts of "herb-rich forest site type" (III, IV) and "herb-rich vegetation group" (I-II) were used for describing the same kind of sites in terms of the composition of the ground vegetation. These concepts were used as synonyms. Vegetation groups were used when the purpose was to describe the vegetation only (I, II). Site types were used when the aim was to describe characteristics of the sites and vegetation (III), and further because it refers to the Finnish site type system (IV). However, the classification of herb-rich forests is based on classification of the vegetation (Alanen et al. 1996), which is not the principal aim of the traditional classification of forest site types (Cajander 1926, Nieppola 1986, Tonteri et al. 2005). The site type of herb-rich forest is also a narrower and more precise concept than the traditional forest site type. As the composition of the vegetation might also differ between the sites that correspond to each other in terms of nutrients and moisture, numerous site types of herb-rich forests have consequently been described in Finland. As a matter of fact, these types more resemble vegetation groups than site types. The herb-rich forest site type refers both to the understorey vegetation and soil properties, while the vegetation group or type refers more to the composition of the vegetation. Here vegetation type (II) is a wider concept than a vegetation group, and it refers to a group of similar habitats.

2.4 Herb-rich forest inventories (I, II, IV)

The study area was inventoried during the summers (from June to September) of 1996, 1997, 1999, 2000 and 2001 (*see* Table 2). A systematic inventory was used because the main aims were to obtain as representative sample as possible of the herb-rich forest types in the area, and to determine the size of each stand. The selection was based on earlier mappings of the vegetation and other forest stand information provided by the Finnish Forest Research Institute and the forest company UPM. Most of the study sites were in the Koli National Park, but some were situated in other conservation areas just outside the park, or in private forests in woodland key-biotopes protected by the Forest Act. The forests represented the most common herb-rich forest site types in the area, and their size varied from 0.05 ha to 6.93 ha. The majority of the stands (n = 68) were less than one hectare. A map of the stands was drawn, the area was digitized from the maps, and the size of each herb-rich stand was calculated by MAPINFO and Arc View computer programmes (IV).

Vascular plant species and the abundance (number of shoots of a species in a given area) of red-listed (threatened and near-threatened) species were recorded over the entire patch area (IV). The abundance was estimated using the following relative abundance scores: 1 = very rare; a species present but only as one or two individuals, 2 = rare; a species present but only as a few individuals, 3 = somewhat rare; individuals infrequently seen, with a low count and crown cover, 4 = scattered distribution, individuals frequently seen but with a low count and crown cover, 5 = frequent, a species not sharing dominance but has a significant role in the composition of the vegetation, 6 = abundant; dominance is shared by two to three other species, and 7 = very abundant; usually only dominant species. The vascular plants observed were assigned to the following three categories based on their conservation importance: 1) *Edaphically demanding species* included calciphile and calcicole species, and other demanding species in terms of nutrients (Hämet-Ahti et al. 1998). 2) *Red-listed species* included threatened and near-threatened species and the species mentioned in the EU Nature Directive (Annex II) (Rassi et al. 2001, Ilmonen et al. 2001). 3) *Weak indicators* were indicator species for herb-rich forests as indicated by Meriluoto and Soininen (1998), but excluded the above-mentioned *edaphically demanding* and *red-listed* species.

Vegetation cover (I, II) was estimated on a circular sample plot (r = 5.64 m) placed in the centre of each patch. Tree species and stand characteristics were determined on each circular plot (I, III). Basal area (m^2/ ha) was measured for each tree species and summed for the stand. Diameter at the breast high (cm) and forest age was measured by using a tree of medium diameter at the breast high. The tree layer was defined as consisting of trees over 1.5 m tall. The shrub coverage was determined on the circular sample plot. The shrub layer included shrubs and tree saplings up to 1.5 m high (genuine shrub species without an upper limit). The field and ground layer coverage was estimated on three quadrates, each 2 m^2 in size. Because the forest floor was often covered with small stones (height < 15 cm) and fine woody debris (d < 5 cm), all the bryophytes and lichens growing on ground litter, humus layer, small stones and fine woody debris were also recorded (II). The coverage of each species was estimated using 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 of the field and bottom layers that were found outside the quadrates, but inside the sample plot, received a percentage coverage of 0.1. In the vegetation analysis the mean cover values of species in the three quadrates was used. Inferred history of land use (III), such as slash-and-burn cultivation, forest grazing, selective felling and cuttings, was recorded. The duration of forest management was estimated on a scale from 0 (no management) to 4 (managed < 40 years ago). The vascular plant nomenclature follows Hämet-Ahti et al. (1998), that of the bryophytes Ulvinen et al. (2002) and that of the lichens Vitikainen et al. (1997). Classification of sites is based on Alanen et al. (1996) and Kuusipalo (1996).

Table 2. List of the field work and analyses that were carried out in the Koli area during the summers of 1996, 1997, 1999, 2000 and 2001. Abbreviations: FFRI = Finnish Forest Research Institute and UJo = University of Joensuu.

Type of activity	Sample units	1996 FFRI	1997 FFRI	1999 UJo	2000 UJo	2001 UJo
Herb-rich forest inventories	stands	-	-	x	x	x
Vegetation mappings	stands	-	-	x	x	x
	plots	x	x	-	x	x
Vegetation cover	quadrates	x	x	-	x	x
Soil samples	quadrates	x	x	-	x	-
Stand characteristics	stands, plots	x	x	-	x	-
Site characteristics	stands, plots	-	-	-	x	x
Laboratory analyses	soil samples	x	x	-	-	x

2.5 Soil sampling and laboratory analyses (III)

Soil samples (III) were taken in autumn 1996, 1997 and 2000 with a cylinder (d = 58 mm) from the organic layer at a depth of 0-10 cm. Soil subsample plots were located inside or close to the three quadrates used for vegetation analyses. The subsamples were combined for the chemical analyses. The type of humus was determined as mor, moder or mull, and in drained sites the organic layer was determined either as peat or peat mull. The site characteristics were recorded for each circular sample plot (100m^2 in size).

The intensity of water flow was estimated on a scale 0 to 2 (absent, occasional, continuous). Sites were classified according to the inclination of their slope as 0 = flat (inclination < 5°), 1 = gentle (inclination 5-9°), 2 = fairly steep (inclination 10-20°), and 3 = steep (inclination > 20°). The aspect of the slope was measured with a compass, and the location and altitude (m a.s.l.) was also determined. The site moisture (scored as 1 to 6) was estimated on the basis of 1) the occurrence and abundance of surface water, 2) depth to groundwater in a pit, 3) soil properties, e.g. type of humus, and 4) the abundance and frequency of hygrophytes and swamp vegetation (Kaakinen 1974, Tamminen and Mälkönen 1999).

Laboratory analyses (III) were done in the soil laboratory of the Finnish Forest Research Institute in 1996-1998, and in the soil laboratory of the Faculty of Forestry in Joensuu in 2001. Oven-dried samples were used for the analyses. The pH was measured from a water suspension (10: 25), and concentrations of the elements (Ca, Fe, K, Mg, Mn, P and Zn) were determined on the organic layer samples after ashing (3 hours 550° C), weighting and HCl-extraction (Halonen and Tulkki 1981). The concentrations of Ca, Fe, K, Mg, Mn and Zn were measured using a Hitachi Z-6000 polarised zeeman atomic absorption spectrophotometer. For P the molybdate-hydrazine method (Halonen and Tulkki 1981) and a Hewlett Packard 8453 spectrophotometer was used. The concentration of N was determined by the Kjeldahl method (Branstreet 1965). Nutrients are given g/ kg in oven-dry (dry-weight) soil.

2.6 Statistical analyses

2.6.1 Multivariate analyses

In the present study, the classification of sites is based on the abundance of the understorey vegetation. Two-Way Indicator Species Analysis (TWINSPAN) (Hill 1979) and an eigenvector method of ordination, Detrended Correspondence Analysis (DCA) (Hill and Gauch 1980), were used together to identify the vegetation gradients and groups (I, II). Both analyses were performed for vascular plants (I, n = 167), and separately for the following vegetation data (II): bryophyte data (n = 100), all vegetation data (n = 265) and vascular plant data (n = 165). Canonical correspondence analysis, CCA (Ter Braak 1986, 1987) was used to describe community variation with respect to environmental variables (III). The analyses were performed separately for the vascular plant (n = 165) and the bryophyte data (n = 100). In all the analyses, the number of sample plots was 101. Despite the fact that all these methods have been criticized (McCune and Grace 2002), they are widely used and very popular in plant ecology (Økland 1990, McCune and Grace 2002).

TWINSPAN is based on the concept that a group of samples which constitute a community type will have a corresponding group of species that characterize that type (indicator species) (Gauch 1982, Kuusipalo 1985, Økland 1990). It uses presence and absence data, but quantitative data are incorporated by considering that different abundance levels of the same species are different species, so called pseudo-species. The process is hierarchical, and therefore each of the new groups then undergoes the same process, until either a certain number of divisions have been reached or a group is too small to subdivide further. One problem of TWINSPAN is that it performs poorly with large heterogeneous data sets (McCune and Grace 2002). Another problem is that the early divisions might be decisive and can be affected too strongly by a low number of few species. In this study, the default settings (I), i.e. 0%, 2%, 5%, 10% and 20%, and the octave scale (II), i.e. 0%, 0.5%, 1%, 2%, 4%, 8%, 16%, 32% and 64%, were used as pseudo-species cut levels (*see* Hotanen 1990). The minimum group size for division was three, and the maximum number of species in the final table was 300. In other options, the default settings of the programme PC-ORD 4.0 (McCune and Mefford 1999) were used.

DCA is an indirect ordination method that arranges sites so that sites with a similar species composition are situated near each other in the ordination space (Hill and Gauch 1980). DCA as well as correspondence analysis (CA), is based on the assumption that the data have a unimodal response to an underlying gradient. DCA and non-metric multidimensional scaling (NMDS) are the best ordination methods to use when there are no environmental data, despite the fact that DCA has been criticized by McCune and Grace (2002). The weaknesses of the DCA are, e.g. the method used for correcting the arch effect and compression (Minchin 1987), the instability problem (Oksanen and Minchin 1997), and the tongue effect caused by its tendency to minimize variation in the higher axes (Minchin 1987, Økland 1990). To avoid some of these problems, Økland (1990) recommends that 50 sample plots should be a minimum if there is more than one gradient. In this study, the down-weighting option was chosen to reduce the effect of rare species. In other options, the default settings of the programme PC-ORD 4.0 were used.

Canonical correspondence analysis, CCA, is based on developing linear combinations of two sets of variables that maximize the linear combination between those sets (Ter Braak 1986, 1987). It focuses on the relationships between species and measured environmental variables and, according to McCune and Grace (2002), it considers community structure only if it is related to the environmental variables. CCA is the most appropriate for community data sets where species responses to the environment are unimodal, and the most important environmental variables have been measured (McCune and Grace 2002). However, the results obtained are dependent on the sets of selected explanatory variables (Ter Braak 1986, 1987, Økland and Eilertsen 1994). Therefore it is important to select “the right” variables, i.e. environmental variables that are the most important for explaining the variation in species abundances (Økland and Eilertsen 1994), and to remove some of the inter-correlated variables (Ter Braak 1986). The hypothesis of non-significant deviation of variation explained by a variable from that explained by a random variable was tested by the Monte Carlo test in 100 unrestricted permutations of the constraining variable (Økland and Eilertsen 1994). The Monte Carlo test was also used to assess the significance of each individual environmental variable by taking one variable at a time (Økland and Eilertsen 1994). Only variables significant at the probability level of $P \leq 0.05$ were included in the final analysis. In this study, the option "optimize columns" (species) were selected, i.e. species scores were weighted by the mean site scores (alpha = 0). This was chosen for optimizing the configuration of species in the ordination. In other options, the default settings of the programme PC-ORD 4.25 were used.

2.6.2 Nested subset analyses

Nested subset analyses (IV) were used to measure the order in an ecological system, referring to the order in which the number of species is related to area (Atmar and Patterson 1993). Species are commonly distributed across fragmented landscapes as "nested subsets", where the species in smaller biotas comprise a proper subset of those in richer assemblages. To test whether the species distribution in the herb-rich forest patches was nested, two procedures (RANDNEST, NESTCALC) which are based on different metrics and underlying null models (Atmar and Pattersson 1993, Jonsson 2001) were used.

RANDNEST is based on a null model where species are drawn in proportion to their frequency of occurrences in the observed matrix, while the probability of occurrence across the sites is considered to be equiprobable. The underlying assumptions of the model are that the observed species frequency is an estimate of the probability of occurrence for the particular species, and all sites are equal. In the procedure, the species are first ranked by frequency, and sites are ranked by species richness. After that the discrepancy (*d*), which is the number of occurrences that needs to be changed in each ordered matrix in order to obtain a perfectly nested matrix, is calculated. The discrepancy measure *d* is affected by matrix size, and thus matrices of different size cannot readily be compared. Statistical significance of the matrix-wide discrepancy is obtained using a Monte-Carlo permutation test, i.e. comparing the observed *d* against a set of 1000 simulated values using a one-sided t-test (Jonsson 2001). To test whether patch area was related to the nested subset pattern, a second set of analyses with the RANDNEST procedure in which the sites were ordered by area was run (*see* Berglund & Jonsson 2003).

In NESTCALC, species are represented in columns and sites in rows. The matrix temperature (*T*) is related to the concept of entropy, i.e. the thermodynamic measure of order and disorder. A perfectly nested matrix is described as maximally “cold” (T = 0˚), and a completely random matrix is labelled as maximally “hot” (T =100˚). The observed *T* was compared to the average temperature of 1000 randomly ordered matrices using a Monte-Carlo permutation test. In contrast to RANDNEST, the underlying null model in NESTCALC retains site richness. NESTCALC is argued to be very sensitive to type I error, whereas the RANDNEST procedure is considered to be a more conservative test of nestedness (Fischer and Lindenmayer 2002, Sætersdal et al. 2005). The NESTCALC was used because it allows comparisons between matrices of different size (McAbendroth et al. 2005).

Nestedness was calculated for *edaphically demanding* and *red-listed* species for all the selected forests in the patch network (n = 90) and for the selected herb-rich forest site types (n=6) separately. To examine the SLOSS issue, the nestedness analysis was accompanied by the analysis of “Saturation Index” (SI; Quinn and Harrison 1988). This index is the ratio between the area under the cumulative species-area curve for sites ordered from small to large, and the area under the curve for sites ordered from large to small. Index values > 1 indicate that a set of several small sites supports more species than a single large site of the same total area. Selected site types were 1) the AAs (n = 18) including AthAssT sites, 2) the Ath (n = 14) including AthT sites, 3) the Dip (n = 10) including DiplT sites, 4) the Mat (n = 10) including MatT sites, 5) the OFi (n = 19) including OFiT, GOFiT and GFiT sites and 6) the OMa (n = 19) including OMaT sites. The OR (n=7) and PuV (n=4) site types were not included in the analyses because forest patches of these types were relatively rare (n ≤ 10) in the area.

2.6.3 Other analyses (I-IV)

Frequency and coverage of each species were calculated with the data summarization of PC-ORD 4 program package (I, II). The diversity index, such as the estimated formula of the Shannon-Weaver's entropy index, H' (Økland, 1990) and species richness was also determined for all the sample plots (n = 101). The non-parametric Kruskall-Wallis test was used to analyse the differences in the soil chemical properties, the other site properties, the land use history and the structural characteristics of the forests among the different site types (III). SPSS 10.1 for Windows was used for the calculations. Site types used here included the above described six types, and the OR including ORT and GORT sites and the PuV including PuViT sites. Correlations between environmental variables were calculated with the Pearson's product moment correlation coefficients (III). The species-area relationships (IV) were calculated with the Spearman's rank correlation test (IV).

3 RESULTS AND DISCUSSION

3. 1 General description of the herb-rich forests in the Koli region

3.1.1 Site characteristics and stand structure (I, III, IV)

The herb-rich forests studied here were primarily situated on steep, easterly diabase-rich slopes, characterised by the presence of erratic boulders (I, III). Over half of the herb-rich forest stands were situated along brooks or ditches. In northern and eastern Finland herb-rich forests are usually situated on calcium-rich slopes and/ or along brooks (Kaakinen 1974, Ratia and Timonen 1975, Huttunen 1978, Tuovinen 1979, Soini 1982).

The ground surface was usually covered by stones and a thick slightly acidic organic layer (III). Mull and moder were the prevailing types of humus. The average pH value of the organic layer was 5.1, but it varied considerably between the sites (pH 3.8-6.3). The soils were considerably more acidic than those studied previously in eastern Finland (Huttunen 1978, Tuovinen 1979), Russian Karelia (Brandt 1933, Pankakoski 1939), Kainuu, Kuusamo (Kaakinen 1972, 1974) and southern Finland (Aaltonen 1947, Koponen 1967, Hinneri 1972, Kuusipalo 1985, Heikkinen 1991), where the pH value varied from 5.0 to 7.0. In North Karelia the soils are often very acidic because acid bedrock (quartzite, granites, and gneisses) is prevailing and basic rocks are rare (Lehtinen et al. 1998).

The majority of the stands were smaller than one hectare (IV), which represents the typical size of woodland key biotopes protected under the Forest Act (Alanen et al. 1996, Meriluoto and Soininen 1998). Over half of the herb-rich stands were relatively young, 21- to 60-year-old deciduous or mixed deciduous forests (I). One third was over 60-year-old spruce or spruce-dominated mixed forests. Mature deciduous forests and pine forests were rare. The most common deciduous tree species was grey alder, which usually formed mixed stands with Norway spruce. Forest management practises had a marked impact in the studied herb-rich forests: 65% of all the stands had been cut 20-80 years ago, 38% had been subjected to intensive slash-and-burn cultivation, 12% had been planted with spruce, and only 6 % were unmanaged (III). The effect of human impact has been relatively strong in herb-rich forests in southern (Tapio 1953, Koponen 1961, 1967) and eastern Finland (Ratia and Timonen 1975, Huttunen 1978, Tuovinen 1979, Soini 1982), Russian Karelia (Karelia ladogensis) (Brandt 1933, Pankakoski 1939, Hiitonen 1946) and Kainuu (Kaakinen 1974). However, there are still some native herb-rich forests in Kuusamo (Kaakinen 1974).

3.1.2 Vegetation (I, II, IV)

Herb-rich forests in the study area had a luxuriant, diverse vegetation. Altogether 215 vascular plant species, of which 165 were found on the plots, and 100 terricolous bryophytes and lichens, were recorded. The mean number of vascular plants per acre (plot) was 30 (I), which is a typical number for herb-rich forests in the southern boreal zone (Kuusipalo 1996). The mean number of bryophytes was 13 (II). The mean diversity index for vascular flora was 2.15 and for bryophytes 1.64 (I, II). The field layer was luxuriant and the mean coverage of herbs was as high as 100% of the projection. This is a noticeably high coverage (*see* Tonteri et al. 2005). Shrubs, grasses and dwarf-shrubs had a relatively low mean coverage: 7%, 5% and 1% of the projection, respectively (I). The bottom layer was usually sparse (II), which is typical for herb-rich forests (Cajander 1926, Kaakinen 1974, Alanen et al. 1996). Bryophyte flora consisted mainly of mosses that covered an average of 23% of the projection, while *Sphagna*, hepatics and lichens each covered less than 1% of the projection.

The most common vascular plant species was *M. bifolium* (I), and the most common bryophytes were *Brachythecium reflexum* (Starke) Schimp. and *B. oedipodium* (Mitt.) A.Jaeger (I, II). Despite the high frequency, they usually had a relatively low mean coverage (< 5 %) on the plots. The most abundant species were *A. filix-femina*, *O. acetosella* and *G. dryopteris*; each covered more than 10% of the projection. Other regularly occurring species were *A. incana*, *Rubus idaeus* L., *Sorbus aucuparia* L., *Angelica sylvestris* L., *G. sylvaticum*, *Paris quadrifolia* L., *R. saxatilis*, *Trientalis europaea* L., *Viola selkirkii* Purch ex Goldie, *Melica nutans* L., *Brachythecium salebrosum* (Hoffm. ex F.Weber & D.Mohr) Schimp., *Plagiomnium cuspidatum* (Hedw.) T.J.Kop. and *Plagiothecium laetum* Schimp. In eastern Finland *Viola selkirkii* occurs in all kinds of herb-rich sites (Huttunen 1978, Kärkkäinen 1994), but in Kainuu (Mikkola 1937, Kaakinen 1972) it is the most common in mesic herb-rich forests, and in central Häme (Mäkirinta 1968) and in Kuusamo (Kaakinen 1974) it grows mostly on moist herb-rich sites. The abundance of *R. idaeus, A. filix-femina, A. sylvestris, P. quadrifolia, Brachythecium* spp. and *Plagiomnium* spp. indicates the herb-rich forest site (Tonteri et al. 2005).

The diversity of the vegetation in the study area was higher than that in the surrounding heath forests (*see* Pitkänen 1998), and there were many reasons for this. First, the study area was located in the transition area between the southern and middle boreal vegetation zones. Consequently, the vascular plant vegetation included many eastern, northern and southern features (I, II). Second, the variable topography of the area offered a wide range of different habitats. Third, the basic bedrock (e.g. diabase) maintained calciphilous and relict flora (I, IV). Fourth, the intensive, long-lasting slash-and-burn cultivation and forest grazing had a marked influence on the stand structure and species composition (I, II).

Characteristic species for the eastern herb-rich forests (Kalliola 1973), e.g. *Rosa acicularis* Lindl., *A. spicata*, *Crepis paludosa* (L.) Moench. and *V. selkirkii* were common in the studied sites (I). Rare eastern species, e.g. *Carex rhyncophysa* Fisch., C.A.Mey. & Avé-Lall. and *Glyceria lithuanica* (Górski) Górski (Jalas 1958, Hämet-Ahti et al. 1998) had a relatively low frequency (I, IV). Northern taiga species (*see* Hiitonen 1946, Jalas 1958, 1980), such as *Diplazium sibiricum* (Turcz. ex Kunze) Kurata formed abundant patches on some very fertile sites, while *Lactuca sibirica* (L.) Maxim. had few occurrences and *Calypso bulbosa* (L.) Oakes had only one small population. *C. bulbosa* is a threatened species, and classified as a vulnerable (VU) (for classes *see* Rassi et al. 2001). *C. bulbosa* and *D. sibiricum* deserve special attention because of their rarity in the entire EU area (Ilmonen et al. 2001). The above mentioned species are edaphically demanding (Pankakoski 1939, Jalas 1958, 1965, 1980, Hämet-Ahti et. al. 1998, Meriluoto and Soininen 1998), and in the study area they primarily occurred in herb-rich forests and sometimes in other fertile habitats e.g. eutrophic, hardwood-spruce mires and eutrophic fens (Hokkanen et al. 2003).

Southern species (Jalas 1958, 1965, 1980, Hämet-Ahti et al. 1998) e.g. *Lonicera xylosteum* L., *Circaea alpina* L., *D. filix-mas, M. struthiopteris, Stachys sylvatica* L., *V. mirabilis* and *Atrichum undulatum* (Hedw.) P.Beauv. and *Cirriphyllum piliferum* (Hedw.) Grout. were relatively common, but e.g. *T. cordata, Viburnum opulus* L., *Epipactis helleborine* (L.) Crantz, *Mycelis muralis* (L.) Dumort., *Scrophularia nodosa* L. and *Poa remota* Forselles had a relatively low frequency in the studied forests (I, II). The above-mentioned species except for the bryophytes are also regarded as edaphically demanding (e.g. Pankakoski 1939, Jalas 1958, 1965, 1980, Kujala 1964, Hinneri 1972). However, *D. filix-mas* is not very demanding in terms of nutrients (Jalas 1958), but as a southern species it demands edaphic condititions as when it occurs in the northern parts of its distribution area (Kujala 1964, *see* also Pesola 1928). *M. muralis* and *P. remota* are regionally threatened (RT) species, and in Northern Karelia they are rare species (Hakalisto 1987).

Other edaphically demanding species included e.g. *Alnus glutinosa,* (L.) Gaertn., *Daphne mezereum* L., *Rosa majalis* Herrm., *Cirsium helenioides* (L.) Hill, *Coeloglossum viride* (L.) Hartm., *Cypripedium calceolus* L., *D. expansa, Epilobium montanum* L., *Epipogium aphyllum* Sw., *Equisetum pratense* Ehrh., *Galium triflorum* Michx., *Listera ovata* (L.) R.Br., *Moehringia trinervia* (L.) Clairv., *P. quadrifolia, Platanthera bifolia* (L.) Rich., *Tussilago farfara* L., *Urtica dioica* L. ssp. *sondenii* (Simmons) Hyl., *Valeriana sambucifolia* J.C.Mikan, *Carex flava* L., *Elymus caninus* (L.) L., *Milium effusum* L. and *Poa nemoralis* L. (e.g. Jalas 1958, 1965, 1980). However, *E. aphyllum* might also occur in fertile and old-growth heath forests (Jalas 1958). Although *D. expansa* is a mesotrophic species (Pankakoski 1939, Jalas 1958), it is regarded as edaphically demanding because, in the study area, it primarily occurred in herb-rich forests (Hokkanen et al. 2003). *C. calceolus* and *E. aphyllum* are vulnerable species, and *U. dioica* ssp. *sondenii* is a regionally threatened species (Rassi et al. 2001). Hemerophilous species that were related to slash-and-burn cultivation or forest grazing, such as *Botrychium lunaria* (L.) Sw., *Campanula glomerata* L., *Knautia arvensis* (L.) Coult. and *Pimpinella saxifraga* L. (Grönlund et al. 1998), had a relatively low frequency in the studied sites (I, IV). *B. lunaria* is both near threatened (NT) and regionally threatened species (Rassi et al. 2001).

3.2 Description of the herb-rich forest site types

3.2.1 Formation of the vegetation groups (I-IV)

In this study, eleven '*a priori'* site types (*see* Table 1) described in Material, and their 16 'variants' were found. Here a variant refers to a type which has elements of two or more site types. For example, OMaT-VRT is a variant for OMaT, and it consists of a larger OMaT patch and a smaller VRT patch. Based on the vascular plant composition eight (I) vegetation groups (herb-rich forest site types) which were named after dominant or characteristic species, were formed: 1) The *Oxalis acetosella—Maianthemum bifolium* (OMa) group (n=19) included sites that were classified in the field as OMaT and OMaT-VRT, 2) the *Oxalis acetosella—Rubus saxatilis* (OR) group (n=7) included GORT, ORT and ORT-OMaT, 3) the *Dryopteris filix-mas—Viola mirabilis* (PuV) group (n=4) included PuViT, PuViT-AthT and PuViT-OFiT, 4) the *Athyrium filix-femina—Dryopteris expansa* (AAs) group (n=18) included AthAssT, AthAssT-OMaT and AthAssT-OPaT, 5) the *Athyrium filix-femina* (Ath) group (n=14) included AthT, AthT-OFiT, AthT-GORT and AhtT-OPaT, 6) the *Diplazium sibiricum* (Dip) group (n=10) included DiplT and DiplT-AthAssT, 7) the *Matteuccia struthiopteris* (Mat) group (n=10) included MatT, MatT-OFiT and MatT-AthAssT and the *Filipendula (ulmaria)* group (n=19) included OFiT, GOFiT, GFiT, OFiT-AthT, OFiT-AthAssT, GOFiT-AthT and GFiT-AthT. Based on the bryophyte composition (II), the OFi was dived into the *Oxalis acetosella—Filipendula ulmaria* (OFi) group (n=8) including OFiT, and the *Geranium sylvaticum—Filipendula ulmaria* (GFi) group (n=11) including GOFiT and GFiT. However, when using the term site type, three groups were named as follows (III, IV): 3) the *Pulmonaria obscura—Viola mirabilis* site type (PuV), 4) the *Athyrium—Assimilis* site type (AAs) and 8) *Oxalis-acetosella—Filipendula ulmaria* site type (OFi). The main differences in the vegetation composition are represented briefly in Tables 3 and 4. The pH values of the studied vegetation groups and site types are represented in Tables 5 and 6.

3.2.2 Sub-dry and mesic vegetation types (I-IV)

Sub-dry and mesic herb-rich forests, such as the *Oxalis acetosella—Maianthemum bifolium* (OMa) group, the *Oxalis acetosella—Rubus saxatilis* (OR) group and the *Dryopteris filix-mas—Viola mirabilis* (PuV) group, were primarily situated on steep, north-eastern slopes. The ground surface was usually covered by stones and a relatively thin organic layer (III). Almost half of the studied forests had been cut 20 to 80 years ago, while the rest had been subjected to intensive slash-and-burn cultivation 80 to 200 years ago. The OMa and OR stands were mainly 55- to 130-year-old spruce-dominated forests, whereas the PuV stands were usually 10- to 40-year-old alder forests. The vegetation composition (I, II) differed only slightly between these groups, although the *edaphically demanding* species did not occurred as frequently in the OMa sites as in the OR or PuV sites (Tables 3 and 4). The vegetation structure, however, differed less between the OR and OMa groups than between the OR and PuV groups (I, II). In terms of moisture, acidity and nutrient status, these groups did not differ significantly from each other. However, the pH values were higher on the OR and PuV plots (MD = 4.9) than on the OMa plots (MD = 4.5) (Table 5). Furthermore, the OR and PuV sites were usually dryer than the OMa sites.

Characteristic species of the OMa group were *M. bifolium, O. acetosella* and *G. dryopteris*, but *A. spicata, D. expansa*, *Melampyrum sylvaticum* L., *Solidago virgaurea* L., *Viola riviniana* Rchb. and *Calamagrostis arundinacea* (L.) Roth. were also typical (I). Herbs, small ferns and grasses were relatively abundant, and they covered an average of 41%, 34% and 9% of the projection, respectively. Dwarf-shrubs, especially *Vaccinium myrtillus* L. was also characteristic, although it had a relatively low mean coverage (4%). The shrub layer was sparse (the mean coverage of 5%) and poor in species. Altogether 125 vascular plant species, of which 32 were regarded as edaphically demanding, were found in the OMa stands (IV). The mean number of vascular plant species per plot was 26. However, in terms of vegetation the OMa group was relatively heterogeneous, as found previously (Kärkkäinen 1994). The bottom layer was relatively sparse and relatively poor in species; the mean coverage was 24% of the projection, and the mean number of species per plot was 13 (II). The most common dominants were *B. oedipodium*, *B. reflexum* and *Hylocomium splendens* (Hedw.) Schimp., and the other characteristic bryophytes included *Dicranum scoparium* Hedw., *P. cuspidatum, Pleurozium schreberi* (Willd. ex Brid.) Mitt. and *Rhytidiadelphus triquetrus* (Hedw.) Warnst. The organic layer was moderately fertile (the mean pH value was 4.7), and moder and mull were the prevailing types of humus (III). The sites were the least fertile of all the studied sites (Table 5). The patch size varied from 0.1 ha to 6.9 ha, while the mean size was 1.5 ha (IV).

The OR sites were often dominated by *O. acetosella*, *R. saxatilis* and *M. bifolium* (I). Other characteristic species were *A. spicata, Fragaria vesca* L., *G. sylvaticum, S. virgaurea, Veronica officinalis* L., *V. mirabilis, V. riviniana, C. arundinacea* and *Carex digitata* L. Small ferns, herbs and grasses were relatively abundant, and they covered an average of 55%, 21 % and 9 % of the projection, respectively. Dwarf-shrubs, such as *V. myrtillus* and *V. vitis-idaea* L., were also typical, but they had a relatively low mean coverage (6%). The shrub layer was denser (the mean coverage of 17 %) than in the OMa group, and edaphically demanding shrubs, such as *D. mezereum* and *L. xylosteum*, were typical. Altogether 133 vascular plant species, of which 29 were regarded as edaphically demanding, were found in the OR stands. The mean number of vascular plant species on the plots was as high as 31. The bottom layer was denser (the mean coverage was 35% of the projection) than in the OMa, but relatively poor in species (the mean number of species was 13) (II). Dominating bryophytes included *B. reflexum*, *P. cuspidatum* and *P. schreberi*, but *B. salebrosum, H. splendens, Rhizomnium punctatum* (Hedw.) T.J.Kop. and *R. triquetrus* were also characteristic (II). The organic layer was moderately fertile – relatively fertile (the mean pH value was 4.9), but the pH values varied considerably between the sites (Table 5). The prevailing types of humus were moder and mull (III). The patch size varied from 0.4 to 0.8 ha, while the mean size was 0.7 ha.

Characteristic species of the PuV group were *D. flix-mas, Convallaria majalis* L., *A. spicata* and *V. mirabilis*, but *D. mezereum, L. xylosteum, Ribes spicatum, S. sylvatica, E. caninus* and *M. effusum* were also typical (I). Herbs and ferns had relatively high coverage; the mean coverage was 54% and 45% of the projection, respectively. Nevertheless shrubs, grasses and dwarf-shrubs were sparsely distributed, and they covered an average of 9%, 5% and 0.1% of the projection, respectively. Altogether 121 vascular plant species, of which 32 were regarded as edaphically demanding, were found in the PuV stands. The mean number of vascular plants per plot was 28. In terms of vascular flora, the PuV sites are very important in maintaining the edaphically demanding and red-listed flora in the Koli region. The bottom layer was sparser and poorer in species than in the other groups; the mean coverage was only 18% of the projection, and the mean number of species per plot was 8 (II). Characteristic bryophytes were *B. reflexum, B. rutabulum* (Hedw.) Schimp., *B. salebrosum, Dicranum fuscescens* Turn., *P. cuspidatum* and *R. triquetrus*. The organic layer was moderately fertile – relatively fertile (the mean pH 4.8), but the pH values varied considerably between the sites (Table 5). The prevailing type of humus was moder (III). The patch size varied from 0.5 ha to 0.9 ha, and the mean size was 0.7 ha.

Table 5. The differential (characteristic and constant) species for the studied vegetation groups. Explanations: D, differential = recorded ≥ 50% stands, "characteristic" or "constant" ≤ 4 groups; C, characteristic = recorded ≥ 40% stands, the mean coverage ≥ 2% (vascular plants) or ≥ 1% (bryophytes) in a group; +, constant = recorded ≥ 40% stands, the mean coverage ≤ 2% in a group.

Species	OMa	OR	PuV	AAs	Ath	Dip	Mat	OFi
Daphne mezereum		+	D		+	D		
Lonicera xylosteum		D	D					
Ribes spicatum			D					
Vaccinium vitis-idaea	+	D						
Actaea spicata	c	c	D			D		
Diplazium sibiricum						D		
Dryopteris filix-mas		+	D					
Equisetum pratense						D	D	D
Fragaria vesca		D						
Galium triflorum					D	+		
Melampyrum sylvaticum	D	D						
Ranunculus repens			D				D	D
Solidago virgaurea	D	D		D				
Stachys sylvatica			D				+	
Veronica officinalis		D						
Viola epipsila					D		D	D
Viola mirabilis		D	D					
Viola riviniana	D	D						
Calamagrostis purpurea								D
Carex digitata	+	D						
Deschampsia cespitosa		D			D			D
Elymus caninus			D			D	D	
Milium effusum	+		D	D				
Brachythecium rutabulum	+		D		+			
Cirriphyllum piliferum				+		D		
Climacium dendroides					D	+	+	D
Dicranum fuscescens			D					
Plagiothecium denticulatum				D		D		
Rhodobryum roseum	c					D	D	
Rhytidiadelphus triquetrus	c	D	D	+				
Lophocolea heterophylla				D		+		

Table 4. Characteristic (and constant) species of the studied vegetation groups. Symbols and abbreviations see Table 3 and the main text.

Species	OMa	OR	PuV	AAs	Ath	Dip	Mat	OFi
Alnus incana	+	c	+	+	+	+	+	c
Prunus padus		c	+	+	+	+	+	+
Rosa acicularis						+		
Rubus idaeus	c	c	c	c	c	c	c	c
Sorbus aucuparia	c		+	+	+	+	+	+
Vaccinium myrtillus	c	c	+	+	+	+		+
Angelica sylvestris	+	+	+		+	+	+	c
Athyrium filix-femina		+	c	c	c	c	c	c
Convallaria majalis	c	c	c	+		+		
Crepis paludosa				c	c	c	c	c
Dryopteris carthusiana	c	c	c		c		c	+
Dryopteris expansa	c	+	+	c		c	c	
Filipendula ulmaria		+	+		c	+	c	c
Geranium sylvaticum	c	c	c	+	+	c	+	c
Geum rivale		+			+	+	c	c
Gymnocarpium dryopteris	c	c	c	c	c	c	c	c
Maianthemum bifolium	c	c	c	c	c	c	c	c
Oxalis acetosella	c	c	c	c	c	c	c	c
Paris quadrifolia	+	+	+	+	+	+	+	+
Phegopteris connectilis				c	c	c	c	c
Rubus saxatilis	c	c	+	+	c	+	+	c
Viola selkirkii	+	+	+		+	+	+	c
Calamagrostis arundinacea	c	c	c	+	+	+		
Deschampsia cespitosa		+			+			+
Brachythecium oedipodium	c	c	+	c	c	c	c	c
Brachythecium reflexum	c	c	c	c	c	c	c	+
Brachythecium salebrosum	+	c		+	c	+	+	
Dicranum scoparium	c	+	+	+	c	+	+	
Hylocomium splendens	c	c	+		+	+		
Plagiomnium cuspidatum	c	c	c	c	c	+	+	+
Plagiomnium ellipticum	+			+	+	+	c	c
Plagiomnium medium		+		c	c	+	+	c
Pleurozium schreberi	c	c		+	+			c
Rhizomnium punctatum		c		+	+	c	+	

Table 5. The pH values on the organic layers of the studied herb-rich forest vegetation groups. The median (MD), mean, standard deviation (SD) and range with the lowest and highest values are given.

pH	OMa	OR	PuV	AAs	Ath	Dip	Mat	OFi
MD	4.6	4.9	4.9	4.8	5.1	5.7	5.4	5.,6
Mean	4.7	4.9	4.8	4.9	5.1	5.7	5.2	5.4
SD	0.5	0.7	0.7	0.5	0.4	0.3	0.8	0.5
Range	3.9-5.6	4.0-6.0	4.0-5.5	4.3-5.9	4.3-5.7	5.2-6.1	3.8-6.0	4.6-6.3

3.2.3 Mesic-moist and moist vegetation types (I-IV)

Mesic-moist and moist herb-rich forests included the *Athyrium filix-femina—Dryopteris expansa* group (AAs), the *Athyrium filix-femina* group (Ath), the *Diplazium sibiricum* group (Dip), the *Matteuccia struthiopteris* group (Mat) and the *Filipendula (ulmaria)* (OFi) group (I, II). The fern-rich sites were often situated on stony, eastern (NE, E) slopes, along brooks. The ground surface was usually covered by numerous of stones (III). Sites dominated by large herbs were primarily situated below western (SW, W, NW) slopes, along ditches. The ground surface was almost free of stones. The AAs, Ath, Dip and Mat stands were either over 80-year-old spruce-dominated forests or 30- to 60-year-old alder-dominated forests. The OFi stands were usually 20- to 60-year-old deciduous forests. Vegetation, especially ferns and herbs were luxuriant, and they grew in several layers. Dwarf-shrubs covered an average of less than 0.5% of the projection (I). Shrubs covered an average of 1% of the projection, and grasses covered an average of 9% of the projection. The bottom layer was relatively sparse, and the mean coverage varied from 21% to 24% (II), but in the Dip group the mean coverage was 32 % of the projection. The mean number of bryophyte species per plot varied from 13 to 14. In all the groups, *B. oedipodium* and *B. reflexum* were among the dominant bryophytes.

The AAs sites were dominated by *D. expansa* and *A. filix-femina*, and the other characteristic species were *C. paludosa, G. dryopteris, O. acetosella*, *Phegopteris connectilis* (Michx.) Watt, *S. virgaurea*, *M. effusum* and *R. idaeus*. The vegetation composition had many similarities with the Ath group, but the AAs group had less edaphically demanding species (I, IV). The mean coverage of ferns was as high as 81% of the projection, while the mean coverage of herbs was only 27 % of the projection (I). Altogether 115 vascular plant species, of which only 22 were regarded as edaphically demanding, were found in the AAs stands (IV). The mean number of vascular plants per plot was 25 (I). The number of edaphically demanding species was the lowest of all the studied sites. Typical bryophytes included *P. cuspidatum*, *P. medium* (Bruch & Schimp.) T.J.Kop., *Plagiothecium denticulatum* (Hedw.) Schimp., *P. schreberi* and *Lophocolea heterophylla* (Schrad.) Dumort. (II). The AAs stands were often situated on mesic-moist, middle and upper slopes (III). The organic layer was usually moderately fertile (the mean pH value of 4.9), and moder was the prevailing type of humus (III). Almost two thirds of the stands had been cut 30 to 80 years ago, and the rest had been subjected to intensive slash-and-burn cultivation over 80 years ago (III). The patch size varied from 0.1 ha to 3.3 ha, while the mean size was 1.0 ha (IV).

Table 6. The pH values on the organic layers of the studied parallel site types (GORT, ORT, OFiT, GOFiT and GFiT). The median (MD), mean, standard deviation (SD) and range with the lowest and highest values are given.

pH	GORT	ORT	OFiT	GOFiT	GFiT
MD	4.9	4.9	5.5	5.6	5.2
Mean	4.8	5.0	5.4	5.5	5.2
SD	0.5	1.0	0.5	0.3	0.6
Range	4.2-5.3	4.0-6.0	4.6-6.3	5.1-5.9	4.7-5.8

The most abundant species on the Ath sites were *A. filix-femina* and *P. connectilis*, but *G. triflorum, Viola epipsila* Ledeb. and *Deschampsia cespitosa* (L.) P.Beauv., *C. paludosa, Dryopteris carthusiana* (Vill.) H.P.Fuchs, *Equisetum sylvaticum* L. and *F. ulmaria* were also typical (I). Ferns and herbs were abundant, and they covered an average of 74% and of 40 % of the projection, respectively. Altogether 137 vascular plant species, of which 30 were regarded as edaphically demanding, were found in the Ath stands (IV). The mean number of vascular plants per plot was as high as 31 (I). Characteristic bryophytes were *B. salebrosum, Climacium dendroides* (Hedw.) F.Weber, *P. cuspidatum* and *P. medium* (II). The Ath sites were often situated on lower, mesic-moist or moist slopes (III). The organic layer was relatively fertile – fertile (the mean pH value of 5.1), and the prevailing type of humus was moder. Almost all the stands had been cut 20 to 80 years ago, some of them had been drained and planted with spruce (III). The patch size varied 0.3 ha to 1.5 ha and the mean size was 0.8 ha (IV).

D. sibiricum was a dominant species on the Dip sites, and it formed abundant patches on diabase-rich, eastern, lower slopes (I, III). *A. filix-femina, P. connectilis* and *G. dryopteris*, *D. mezereum, R. acicularis, A. spicata, C. paludosa, D. expansa, E. pratense* and *E. caninus* were also typical (I). The mean coverage of ferns was 96% of the projection, and the mean coverage of herbs was 30% of the projection. Altogether 116 vascular plant species, of which 31 were regarded as edaphically demanding, were found in the Dip stands (IV). The mean number of vascular plants per plot was as high as 31 (I). Characteristic bryophytes were *C. piliferum* , *P. denticulatum, R. punctatum* and *Rhodobryum roseum* (Hedw.) Limpr. (II). The ground surface was usually mesic-moist, and covered by a thick and fertile organic layer (the mean pH value of 5.7) (III). The prevailing type of humus was mull but on the wettest sites the organic layer composed of peat mull. Most of the forests had been cut (by selection felling) over 80 years ago. The patch size varied from 0.1 ha to 2.4 ha and the mean size was 0.7 ha (IV).

A. filix-femina and *M. struthiopteris* were dominant species on the Mat sites. In addition, *E. pratense, Ranunculus repens* L., *V. epipsila* and *E. caninus,* and *C. paludosa, D. carthusiana, D. expansa, Geum rivale* L., *F. ulmaria* and *P. connectilis* were also characteristic (I). The vegetation composition had many similarities with the Ath but hygrophilous species were often more abundant on the Mat than on the Ath sites. *M. struthiopteris* formed small but abundant patches on the terraces of the middle and upper slopes (III, IV). The mean coverage of ferns was 72% of the projection, while the mean coverage of herbs was 43% (I). Altogether 117 vascular plant species, of which 29 were regarded as edaphically demanding, were found in the Mat stands (IV). The mean number of vascular plants on the plot was 28 (I). Characteristic bryophytes included *Plagiomnium ellipticum* (Brid.) T.J.Kop. and *R. roseum* (II). The ground surface was usually moist and covered by a thick and fertile (the mean pH value of 5.2) organic layer, which was composed mainly of peat mull (III). The stands had been cut over 40 years ago and some of them had been planted with spruce. The patch size varied from 0.1 ha to 0.9 ha, and the mean size was 0.4 ha (IV).

The *Filipendula (ulmaria)* (OFi) group was dominated by *F. ulmaria*, but other large herbs, such as *A. sylvestris, C. paludosa, G. sylvaticum* and *G. rivale*, were also relatively abundant (I). Other typical species were *E. pratense, P. connectilis, R. repens, V. epipsila, Calamagrostis purpurea* (Trin.) Trin. and *D. cespitosa*. In the OFi and GFi groups, the vascular plant composition (II) and site properties were almost identical (Table 6). Consequently these groups are described here as a one, the *Filipendula (ulmaria)* group (OFi). Herbs covered an average of 67% of the projection, while ferns covered an average of 25% of the projection. Altogether 170 vascular plant species, of which 29 were regarded as edaphically demanding, were found in the OFi stands (IV). The mean number of vascular plants on the plot was 37, which was the highest of the studied groups. Despite the high total number of vascular plants, these sites did not support relatively well red-listed flora (IV). Typical bryophytes were *P. cuspidatum*, *P. ellipticum* and *P. medium*, but in the GFi sites *C. dendroides, P. schreberi, R. punctatum* and *R. roseum* were also typical (II). The ground surface was usually moist or wet, and covered by a thick and fertile (the mean pH value of 5.4) organic layer (III). Half of the sites had been drained of over 40 years ago, and on these sites the organic layer was composed of peat mull. On mineral soils the prevailing humus type was moder. Almost all the stands had been cut 20 to 60 years ago, and some of them had been planted with spruce. The patch size varied from 0.1 ha to 2.7 ha, and the mean size was 0.7 ha (IV).

3.2.4 Evaluation of the vegetation groups (I-III)

The vegetation composition (I, II) of the groups studied here (I, II) corresponded relatively well to previously studied herb-rich forest site types in eastern (Ratia and Timonen 1975, Huttunen 1978, Tuovinen 1979, Kärkkäinen 1994) and northern Finland (Kaakinen 1972, 1974) and in Russian Karelia (Brandt 1933, Pankakoski 1939), and on the eskers in southern boreal zone (Heikkinen 1991), but they corresponded to a lesser extent to the herb-rich forests in the southern boreal zone (e.g. Valle 1919, Tapio 1953, Mäkirinta 1968) and in the hemiboreal zone (e.g. Koponen 1961, 1967, Hinneri 1972). However, as the flora and vegetation groups had many specific characters for the Koli area, classification could not be generalised to the other areas. It is noticeable that the vegetation of the studied groups had southern, northern and eastern features. For example, the abundance of *G. dryopteris* and *G. sylvaticum* indicates northerly features (Kaakinen 1974). Many southern species typical of the described southern types (Tapio 1953, Koponen 1961, 1967, Mäkirinta 1968, Hinneri 1972), such as *Ribes alpinum* L., *Anemone nemorosa* L., *Chrysosplenium alternifolium* L., *Corydalis* spp. Vent., *Hepatica nobilis* Schreb., *Lathyrus vernus* (L.) Bernh., *Pulmonaria obscura* Dumort., *S. nodosa* and *Stellaria nemorum* L., were absent or rare on the studied sites. Eastern species (*see* Hiitonen 1946, Kalliola 1973), except for *Aconitum lycoctonum L.* were characteristic in the study area. *A. lycoctonum* is typical of the herb-rich forests in Central Karelia (Ratia and Timonen 1975) and in Sortavala district in Russian Karelia (Hiitonen 1946, Jalas 1958).

The soils of the studied forests were considerably more acidic (III) than those studied previously (Aaltonen 1947, Pesola 1928, Pankakoski 1939, Koponen 1967, Hinneri 1972, Kaakinen 1974, Huttunen 1978, Tuovinen 1979, Heikkinen 1991). The lower pH values might be primarily a result of the different parent rock; herb-rich forests in the Koli region occur on diabase-rich bedrock, which contains less calcium than e.g. dolomite-rich parent rock (Lehtinen et al. 1998). A second reason might be the different intensity of the land use history, e.g. long-term human impacts, primarily a very intensive period of slash-and-burn cultivation. During the first few years after burning soil acidity can decrease by 0.5-2.0 pH units, but during the following decades, the acidity of soils returns to its original level (Kivekäs 1939, Mälkönen 2003). Thus burning probably created suitable habitats for many edaphically demanding species, and some of them are still present on these sites despite the increased acidity of the soil. These sites have been classified on the basis of the vegetation into herb-rich forests, although their soil properties (acidity, a thin layer of mor or moder, genetic horizons down the layered soil profile) corresponded better to those of heath forests. These kinds of forests might be earlier succession stages of spruce-dominated heath forests (Mannerkoski 2005, *see* also Cajander 1916). Furthermore, herb-rich forests on drained sites are often "man-made" sites, and part of them may gradually revert back to some kind of herb-rich wooded mires (Mannerkoski 2005).

3.3 Classification and ordination of the sites

3.3.1 Vascular plants and bryophytes in the site classifications (I-II)

Classification and description of herb-rich forests are primarily based on vascular flora, because they are predominant and more abundant in herb-rich forests than bryophytes. The results indicated that bryophytes brought different aspects to the classification than vascular plants (II). This pattern was revealed by using multivariate analyses, such as TWINSPAN and DCA (I, II). The multivariate methods brought supplementary objectivity to the analyses, and the methods were used as tools (*see* Oksanen 1984). On the whole, the classification methods used here complemented each other. The aim was to find enough clear and large vegetation groups to describe the characteristic features of the vegetation structure.

Based on the TWINSPAN classifications and DCA ordinations, vascular plants seemed to be more informative in classifying herb-rich forests than bryophytes (*see* also Huttunen 1978), because vascular plants formed clearly separated groups, whereas bryophytes did not (I, II). These separated groups (Table 7) corresponded well to the field-classified and '*a priori*' site types (Table 8). However, the multivariate analyses brought new features to the classification, such as southern and northern aspects (I, II). Bryophytes classified sites according to the topography, stand structure and exposition, but these groups did not correspond at all to the field-classified or '*a priori*' site types. Thus bryophytes alone were not sufficiently useful for classification, but when combined with vascular plants, the classification became very detailed and the groups corresponded well to the field classified and '*a priori*' site types. The TWINSPAN clusters, studied vegetation groups and their corresponding '*a priori*' site types are given in Tables 7 and 8.

Table 7. Names for the TWINSPAN clusters of the different data sets and options. The clusters are named after dominant, indicator or other descriptive species.

vascular, default settings:	vascular, octave scale:	whole data set, octave scale:	bryophytes, octave scale:
Vd1) *Vaccinium myrtillus-Maianthemum bifolium*	Vo1) *Oxalis acetosella-Fragaria vesca*	T1) *O. acetosella-Deschampsia cespitosa*	B1) *Rhytidiadelphus triquetrus-Cirriphyllum piliferum*
Vd2) *O. acetosella-Rubus saxatilis*	Vo2) *M. bifolium-Gymnocarpium dryopteris*	T2) *G. dryopteris-V. myrtillus*	B2) *Brachythecium reflexum-Plagiothecium curvifolium*
Vd3) *O. acetosella-M. bifolium*	Vo3) *O. acetosella-R. saxatilis*	T3) *O. acetosella-R. saxatilis*	B3) *B. reflexum-Plagiothecium cuspidatum*
Vd4) *Athyrium filix-femina-Dryopteris expansa*	Vo4) *D. expansa-Equisetum sylvaticum*	T4) *D. expansa-O. acetosella*	B4) *Pleurozium schreberi-Dicranum scoparium*
Vd5) *A. filix-femina-Phegopteris connectilis*	Vo5) *A. filix-femina-Actaea spicata*	T5) *A. filix-femina-P. connectilis*	B5) *Plagiomnium medium-Brachythecium oedipodium*
Vd6) *Crepis paludosa-P. connectilis*	Vo6) *D. expansa-A. filix-femina*	T6) *D. expansa-Sphagnum girgensohnii*	B6) *Climacium dendroides-Pseudobryum cinclioides*
Vd7) *A. filix-femina-Ranunculus repens*	Vo7) *Diplazium sibiricum-Geranium sylvaticum*	T7) *G. sylvaticum-A. filix-femina*	B7) *Plagiomnium ellipticum-Sphagnum russowii*
Vd8) *Filipendula ulmaria-Angelica sylvestris*	Vo8) *F. ulmaria-O. acetosella*	T8) *A. filix-femina-Filipendula ulmaria*	
	Vo9) *F. ulmaria-A. sylvestris*	T9) *Geum rivale-A. sylvestris*	

3.3.2. Main environmental gradients and the distribution patterns of vegetation (I-III)

Based on both DCA (I, II) and CCA (III) analyses, the most important environmental variable classifying vascular plant and bryophyte communities in herb-rich forests was site moisture, as found previously (Linkola 1916, Tapio 1953, Koponen 1967, Mäkirinta 1968, Kaakinen 1974, 1992, Huttunen 1978, Tuovinen 1979, Kuusipalo 1985, Kärkkäinen 1994, Alanen et al. 1996). The next most important factors explaining the distribution of vegetation were soil acidity and the intensity of water flow (III), as also reported previously (Linkola 1916, Pesola 1928, Pankakoski 1939, Mäkirinta 1968, Kaakinen 1974, 1992, Huttunen 1978, Kärkkäinen 1994, Alanen et al. 1996). The intensity of water flow, however, is closely related to soil acidity. Running water has a “calcium-like-effect”, i.e. running water has a similar effect to soil like calcium because it brings nutrients (e.g. base cations) and thus enables many edaphically demanding species to grow on relatively acidic soils along brooks (Cajander 1916, Pesola 1928). In the study area, this might explain the abundance of *M. struthiopteris* on some relatively acidic plots (*see* Table 5).

Other important environmental factors, such as the type of organic layer, stoniness and major topographic features (e.g. slope inclination, altitude and exposure), were related to the vascular plant and bryophyte communities primarily through the site moisture, as also found previously (Valle 1919, Whittaker 1956, Kalliola 1973, Wikum and Wali 1974, Kuusipalo 1985, Heikkinen 1991, Quian et al. 2003).

Table 8. The vegetation groups and TWINSPAN clusters, and their corresponding '*a priori*' site types (Kaakinen 1974, Kuusipalo 1996, Alanen et al. 1996). The comparison is based primarily on vascular plants (groups, Vd1-8, Vo1-9, and T1-9) and secondarily on bryophytes* (B1-7). Explanations: for the vegetation groups and 'a priori' site types *see* Table 1, and for the TWINSPAN clusters see Table 7.

	SUB-DRY AND MESIC		MOIST		PALUDIFIED
	mod. fertile	fertile	mod. fertile	fertile	
Southern	OMa ~ OMaT	PuV ~ PuViT;	AAs ~ AthAssT	Ath ~ AthT	Vo4 ~ LhK
boreal	Vd2 ~ OMaT	~ MelaT	Vd4 ~ AthAssT	Vd5 ~ AthT	T6 ~ LhK
	Vo2 ~ OMaT	Vd3 ~ ORT	Vo6 ~ AthAssT	Vo5 ~ AthT	
	T2 ~ OMaT		T4 ~ AthAssT	T5 ~ AthT	
	Vd1 ~ OMaT		B3* ~ AthAssT	Mat ~ MatT	
	dry variant			Vd7 ~ MatT	
				Vo8 ~ MatT	
				T8 ~ MatT	
				OFi ~ OFiT	
Middle	Vo3 ~ GOMaT	OR ~ GORT		GFi ~ GOFiT	
boreal	T3 ~ GOMaT	~ GOPaT		Vd8 ~ GOFiT	
	B2* ~ GOMaT	Vo1 ~ GOPaT		Vo9 ~ GOFiT	
	B4* ~ GOMaT	T1 ~ GOPaT		T9 ~ GOFiT	
		B1* ~ GOPaT		B5* ~ GOFiT	
				B7* ~ GOFiT	
Northern				Dip ~ DiplT	
boreal				Vd6 ~ DiplT	
				Vo7 ~ DiplT	
				T7 ~ DiplT	
				GFi ~ GFiT	
				Vd8 ~ GFiT	

It is noticeable that bryophytes reflected the water (moisture) content of the organic layer better than the vascular plants (II, III). Vascular plants were more closely related to earlier land use and forest management (I, III), as also found previously (Ingerpuu et al. 2003). The tree characteristics were indirectly related to the vascular flora through shading and disturbance, as reported previously (Kuusipalo 1985, Heikkinen 1991, *see* also Nieppola 1986). Bryophytes seemed to be more sensitive to the soil water content because they lack a root system and have no mechanisms for water storage (Busby et al. 1978). On the other hand, bryophytes are more independent of soil moisture and nutrients than vascular plants because they are able to take up water and nutrients directly from the rainwater, and some species are capable of fixing nitrogen (Longton et al. 1992). Nevertheless, the nitrogen concentration of the organic layer did not correlate significantly with the organic matter content (III), as assumed on the basis of the DCA analyses (II) and its dependence on the soil organic matter content (Tamm 1991).

The first two axes of the CCA analyses explained only 10.5% of the variance in the vascular plant data and 8.3% of the variance in the bryophyte data (III). Moreover, all of the significant ($P \leq 0.05$) variables explained 51.8% (l=20) of the vascular plant data and 40.5% of the bryophyte data (l= 14) when the variables were taken one at a time. In addition, both DCA (I, II) and CCA (III) ordinations of all the data sets yielded relatively low eigenvalues. This suggests that a large number of environmental factors are related to the herb-rich forest vegetation (Gauch 1982, Heikkinen 1991). Other factors might be random variation in the species composition, competition, dispersal capability, patch size and edge effect.

3.3.3 Species indicating the site properties (I-III)

Plant species tend to form groups that are characterized by similar resource requirements and tolerance limits (Cajander 1926, Tilman 1982, Kuusipalo 1985). Thus, some species might reliably reflect site properties if they are constant enough throughout the region (Kuusipalo 1985). In this study, the species formed several groups according to the most important environmental variables, moisture and acidity (inverse of fertility). Forming the species groups was based on the multivariate analyses, CCA, DCA and TWINSPAN. In addition, these “indicative” species should be evidently well spaced-out in the niche space, and abundant enough on these sites. This means here that, using the abundance scale 1-7 (Alanen et al. 1996), the species occurred at least scattered in the patches or had a cover of over 1 % (shrubs), 5% (vascular plants in the ground layer) or 2.5% (bryophytes) of the projection when sample plots or vegetation quadrates were used. As a summary the four groups were formed.

The “sub-dry” group included the “drought-tolerating” and acidophilous species, such as *V. myrtillus V. vitis-idaea, F. vesca* and *D. filix-mas.* These species thrived well on the sub-dry sites but had a low coverage on the moist sites, as recorded previously (Pesola 1928, Jalas 1958, 1965, Reinikainen et al. 2001). *V. myrtillus and V. vitis-idaea* L. grew abundantly on the sub-dry and mesic, moderately fertile sites, where the pH varied from 4.0 to 4.8. *F. vesca* and *D. filix-mas* usually occurred on the sub-dry, moderately fertile or fertile sites, where the pH varied from 4.5 to 5.9. However, *F. vesca* is the most abundant on sites where the pH is over 5.0, as found previously (Pesola 1928, Pankakoski 1939, Jalas 1965). In southern Finland and in Kuopio district *D. filix-mas* primarily occurs on moderately fertile sites (Tapio 1953, Kujala 1964, Huttunen 1978).

The "mesic" group included the mesophilous species, e.g. *L. xylosteum, A. spicata, D. expansa, M. effusum* and *V. mirabilis*, and *S. virgaurea, B. rutabulum*, *H. splendens* and *Hylocomiastrum umbratum* (Ehrh. ex Hedw.) M.Fleisch. The first-mentioned species are regarded as edaphically demanding, while the rest are typical of the moderately fertile heath forests or eutrophic spruce mires (Jalas 1958, 1965, 1980, Nitare 2000, Reinikainen et al. 2001, Ulvinen et al. 2002). All these species had their optimum on the mesic and mesic-moist sites, but *V. mirabilis* also grew on the sub-dry sites, as recorded previously (e.g. Tapio 1953, Jalkanen and Hokkanen 2003). The edaphically demanding species favoured the fertile sites, where the pH varied from 4.8 to 5.7. *D. expansa* and *M. effusum* also thrived well on the moderately fertile sites (pH of 4.0-4.8), as also recorded previously (Pankakoski 1939, Kaakinen 1974, Huttunen 1978). However, in Russian Karelia and in Kuopio district *M. effusum* has been recorded only on sites where the pH is of over 5.6 (Pankakoski 1939, Huttunen 1978). *S. virgaurea, H. splendens* and *H. umbratum* grew abundantly on the moderately fertile sites (pH of 4.3-5.0), where the concentrations of calcium (< 10 g/kg) and magnesium (< 2g /kg) were relatively low. *B. rutabulum* had a relatively wide amplitude in terms of acidity, and it grew on sites where the pH varied from 4.1 to 5.9. *H. umbratum* was the most abundant on the sites that had earlier been subjected to intensive slash-and-burn cultivation or forest grazing.

The "moist group" included the hygrophilous "ditch- and brook-side species" that were the most abundant on the fertile and moist sites along ditches, but which had a very low coverage on the mesic and sub-dry sites. These species also avoided acidic sites, where the pH values were less than 4.5. The hygrophilous "ditch-side species" included *A. sylvestris, G. rivale, V. epipsila, C. dendroides*, *P. ellipticum, P. medium* and *Pseudobryum cinclioides* (Huebener) T.J.Kop, which tolerate a relatively high moisture content and occasional flooding (Jalas 1980, Reinikainen et al. 2001, Ulvinen et al. 2002). The hygrophilous "brook-side species" included *R. acicularis, C. alpina, C. paludosa, D. sibiricum*, *M. struthiopteris, S. sylvatica, C. piliferum, Hylocomiastrum pyrenaicum* (Spruce) M.Fleisch. and *Rhytidiadelphus subpinnatus* (Lindb.) T.J.Kop. The last-mentioned species are demanding in terms of nutrients (Pesola 1928, Jalas 1958, 1965, 1980, Nitare 2000, Ulvinen et al. 2002), and in the study area they occurred abundantly on fertile sites (pH of over 5.0) along brooks. Particularly, *D. sibiricum* and *S. sylvatica* favoured very fertile (pH of over 5.5) and calcium-rich (Ca concentration of over 8 mg/ g) sites, as also found previously (e.g. Pesola 1928, Pankakoski 1939, Hinneri 1972, Huttunen 1978). *C. piliferum* and *R. subpinnatus* grew abundantly on the sites that had earlier been subjected to intensive slash-and-burn cultivation and forest grazing, whereas *D. sibiricum* and *M. struthiopteris* occurred primarily on the unburned sites.

The "wet group" included the mire species, *Viola palustris* L., *C. flava, C. loliacea* L., *Aulacomium palustre* (Hedw.) Schwägr., *Rhizomnium pseudopunctatum* (Bruch & Schimp.) T.J.Kop. and *Sphagna* (*S. girgensohnii* Russow, *S. russowii* Warnst. and *S. squarrosum* Crome) (Eurola et al. 1990, Ulvinen et al. 2002), which occurred abundantly only on the paludified herb-rich sites, and thus their abundance indicated paludification (II, III). These species occurred most abundantly on the earlier (40-80 yr. ago) drained sites, but *S. girgensohnii* and *S. squarrosum* had the highest coverage on the undrained sites.

3.4 Patterns of nestedness, species area relationships and conservational aspects (IV)

In this study, the exhibition of a nested subset pattern varied to a larger extent than would be expected on the basis of the underlying null model and to a lesser extent on the herb-rich forest site type. For example, when a conservative RANDNEST procedure was used, the edaphically demanding and red-listed vascular plant species in herb-rich forests did not generally exhibit nested subset patterns. On the other hand, when the less conservative NESTCALC procedure was used the edaphically demanding and red-listed vascular plants generally showed nestedness patterns. However, these analyses focused on the species group that is in need of conservation, and thus the generalists did not contribute towards significant nestedness.

The richness of edaphically demanding and red-listed species increased with patch size in the whole patch network and in all except one herb-rich forest site type, but nestedness was not linked with a patch size. The occurrence patterns of edaphically demanding and red-listed species had a large variation that could not be predicted by the patch size alone. The small-scale variation is probably due to variations in soil chemical properties and moisture, which are strongly related to the species composition and species richness (Lahti and Ranta 1985, Lahti et al. 1991, Pausas and Austin 2001, Berglund and Jonsson 2003).

The results showed that a set of several small herb-rich forest patches have a higher cumulative richness of edaphically demanding species than a set of large patches of equal size. Similar observations with plant communities have been found previously (Simbeloff and Abele 1976, Järvinen 1982, Lahti and Ranta 1985, Quinn and Harrison 1988, Virolainen et al. 1998, Honnay et al. 1999). This indicates that a patch size could not be a sole meaningful indicator of conservation priority in herb-rich forest vegetation. However, the large herb-rich areas in the Koli area often consist of a mosaic of different herb-rich forest site types, which increases their conservation importance for red-listed species. For example, red-listed orchids were primarily found in these large areas, but they did not occur at all in small isolated woodland key biotopes. Although, small patches harbour a representative set of edaphically demanding species, the populations in these patches may be too small and thus vulnerable to extinction resulting from environmental and demographic stochasticity (Saetersdal 1994, Hanski et al. 1998). In the study area, both large and continuous herb-rich forest areas and small woodland key biotopes are needed to cover species diversity and to maintain viable populations of different plant species, as has also been found in previous studies (Forman 1995, Virolainen et al. 1998, Honnay et al. 1999, Berglund and Jonsson 2003).

4 IMPLICATIONS FOR CLASSIFYING HERB-RICH FORESTS

In the field, classifying herb-rich forests into types was sometimes very difficult. For instance, the composition of the vegetation might primarily be typical to one type, but the occurrence of certain “type” species or soil properties might indicate another type. Furthermore, most of the herb-rich forests in the study area had earlier been intensively managed, and thus the vegetation is still undergoing successional change. The main tree species and land use history were strongly related to the composition of the vegetation and soil properties, as also found previously (e.g. Linkola 1916, Koponen 1967, Kuusipalo

1985, Kiirikki et al 1992, Smolander and Priha 2003, Tonteri et al. 2005). As a result, the composition of the vegetation and soil properties might vary considerably within a type, which makes classification even more difficult. In the Koli area, as in the other parts of southern Finland, there are relatively few real native herb-rich forests (Koponen 1967). Thus, classification of herb-rich forests has remained largely tentative and there are no detailed descriptions for all the types (*see* Alanen et al. 1996). It is important to find suitable indicator species, and take soil properties, main tree species and land use history into the consideration (Fig. 2). Indicator species should reliably reflect the site properties and they should also be constant enough throughout the region (Kuusipalo 1985). Classification should be based more on “indicative” or “differential” species than on dominant species alone It is also important to recognize regionally constant species, because they might not always be suitable for distinguishing site types.

In this study, some of the sites classified in the field as OMaT were problematic because their soil properties (pH < 4.5 and a thin mor or moder layer) corresponded better to those of herb-rich heath forests (*Oxalis-Myrtillus*-type, OMT) (III). The vegetation had similarities with both OMaT and OMT (I, II). However, *V. myrtillus* was never among the dominant species, while *D. expansa* was often among the dominant species and edaphically demanding species, especially *A. spicata* and *P. quadrifolia*, were typical (I). In addition, dwarf shrubs covered 1- 10 % of the projection, while ferns and herbs covered 40% - 80 % of the projection (*see* Kuusipalo 1996, Tonteri et al. 2005). These forests included alder- or spruce-dominated mixed forests, which had earlier been subjected to intensive slash- and -burn cultivation (III). At the present time, the soil acidity is gradually returning to its original level; the pH of the organic horizon is lower than that of the subsoil (C horizon). Therefore these forests are probably earlier succession stages of herb-rich heath forests (*see* also Mannerkoski 2005).

Furthermore, some of the other sites classified in the field as OMaT were problematic because of a relatively high pH (> 5.2), abundance of edaphically demanding species, and dominance of type species for OMaT (I, III). The OMaT forests are normally defined as moderately fertile, mesic herb-rich forests that are characterised by *O. acetosella* and *M. bifolium*, whereas the edaphically demanding shrubs and herbs are rare or absent (Alanen et al. 1996). These problematic sites might have been misclassified, because the high pH and abundance of edaphically demanding species, especially *L. xylosteum* and *V. mirabilis* indicate relatively high fertility. It would be desirable to put these sites into the OR group and reclassify them in the field as GOPaT, GORT or ORT. However, Kärkkäinen (1994) suggests that all mesic herb-rich forests in the Koli area should put together and classify them as OMaT (*see* also Mikkola 1937, Kalela 1952).

It is noticeable that there are only a few detailed descriptions for GORT (GOPaT) and ORT (OPaT) forests (Kaakinen 1972, 1974, Huttunen 1978, Tuovinen 1979, Leivo 1983). In the Koli area distinguishing ORT and GORT from GOMaT and OMaT was very difficult, because these types had a lot of similar features (I, II, III), as recorded peviously (Kärkkäinen 1994). In the study area, the acidity of some of the ORT and GORT sites was, however, probably due to the earlier land use history and stand structure (Mannerkoski 2005); originally they were herb-rich heath forests, where the herb-rich forest stage represented a succession stage of heath forest. These sites were burned and then changed into deciduous herb-rich forests, which later changed to spruce forests. The soil profile was typical for podzols with a grey leached (Ae) horizon (III), but the composition of the vegetation was typical for ORT or GORT, except that edaphically demanding species were rare (I). The stand structure and main tree species are strongly related to soil properties (e.g.

Kiirikki et al. 1992). For instance, the pH values of the organic layer in a spruce forest can be 0.5 to 1.0 pH units lower than in a deciduous forest (Smolander and Priha 2003).

Classification of fern-rich sites was based on the dominant and characteristic species. These were no notable differences between the AAs, Ath and Mat groups, but it is reasonable to separate these sites into their own site types because each type had specific characters of its own (*see* Kaakinen 1974). However, sites classified in the field as AthOT were combined with AthT because their vegetation composition corresponded very well with each other (Hokkanen et al. 2003). Classification of variants was very difficult, but in these sites classification should be based on type or differential species rather than on dominants. Based on the species composition and land use history, sites dominated by *F. ulmaria* (OFi) might be either earlier succession stages of fern-dominated forests or "man-made" herb-rich forests, which may eventually revert back to herb-rich spruce mires (Mannerkoski 2005).

ELEMENTS OF CLASSIFYING HERB-RICH FORESTS

1. Stand structure
   - stand age (e.g. sapling, young forest, closed forest, old-growth forest)
   - density (sparse, moderate, dense)
   - main tree species (pine, spruce, deciduous)
   - age range and number of canopy layers

4. Dominant species
   - dwarf-shrubs and small herbs
   - small herbs and ferns
   - tall ferns and/ or tall herbs
   - sedges and grasses

2. Organic layers and soil
   - type of organic layer (mor, moder, mull, peat mull, peat)
   - type of soil (podzol soil – brown soil)
   - soil chemical properties (acidity)

5. Characteristic species
   - abundant enough
   - constant enough throughout the region
   - not generalists, not constants

3. Land use history
   - natural (no stumps, no signs)
   - semi-natural (slash-and burn cultivation, forest grazing and selective felling)
   - intensively managed (drained, tilling, felling, planting, old fields)

Figure 2. The most important elements of classifying herb-rich forests. The classification of herb-rich forests is based on vegetation, mainly on dominant and characteristic (type) species, but it is also useful to take stand structure, soil properties and land use history into the consideration.

5 IMPLICATIONS FOR CONSERVATION

In order to maintain vascular plant species diversity in Fennoscandian boreal forests, it is essential to protect the different site types of herb-rich forests. The number of red-listed species that occurs primarily in the herb-rich forests is high (Rassi et al. 2001), and many edaphic species, such as *D. sibiricum* and *M. struthiopteris*, occur mainly in specific site types of herb-rich forests. In any region, the herb-rich forests seem to form a complicated habitat network that has a very rich biodiversity (Kaakinen 1992, Alanen 1992, Heikkinen 2002). This presents challenges for successful regional conservation of herb-rich forests. However, the high heterogeneity and the spatial context of different herb-rich site types should be taken into account first (*see* also Honnay et al. 2001). In addition, small-scale environmental factors within a habitat site type are likely to produce important variation that affects the occurrence of edaphically demanding and red-listed species. Making inventories of the entire patch network are essential before efficient conservation actions can be planned. Effective conservation solutions should be based on a sound knowledge of species distribution patterns and on regional planning where the contribution of each patch to conservation goals can be evaluated at the species level (Heikkinen 2002).

Most of the herb-rich forests in the study area are situated in the Koli National Park, and some in other protected areas or in small woodland key-biotopes protected by the Forest Act. The most suitable areas for red-listed flora occur inside the Koli National Park. Other protected areas and woodland key-biotopes usually consist of small, distinct patches, which are often fragmented and intensively managed in the surrounding forests. Areas belonging to conservation programmes have diverse and valuable flora, but clear cuttings next to protected areas may diminish the quality of the habitat though an increasing edge effect (changes in light conditions) and drainage (leaching of nutrients) (e.g. Murcia 1995). In the study area, the woodland key-biotopes do not seem to support red-listed flora. They might be too small and too isolated, and are often affected by strong disturbance and edge effects. A buffer zone might reduce the negative impacts from the surroundings, and thus prevent the decline in habitat quality and also reinforce the protection of the small forest areas (e.g. Thorell 2003).

Habitat fragmentation, shrinkage of the area and land transformation increases habitat loss and isolation (Forman 1995, Hanski et al. 1998). Because environmental heterogeneity is highly scale-dependent (Honnay et al. 1999, Pausas and Austin 2001), small patches should be though of as a supplement to, but not a replacement for large patches (Forman 1995). For instance, woodland key-biotopes can provide a support for maintaining regional biodiversity (Heikkinen 2002). However, subpopulations have a greater risk of local extinction in small, isolated and low-quality patches than in large or high-quality ones (Forman 1995, Hanski et al. 1998). An optimum patch network includes large protected areas supplemented with small patches (Forman 1995), but patches are also needed to be connected to each other (Thorell 2003).

6 FUTURE RESEARCH NEEDS

Although several studies have been carried out on the vegetation in herb-rich forests (e.g. Linkola 1916, Valle 1919, Pesola 1928, 1934, Brandt 1933, Mikkola 1937, Mäkelä 1937, Pankakoski 1939, Hiitonen 1946, Kalela 1952, Tapio 1953, Koponen 1961, 1967, Mäkirinta 1968, Hinneri 1972, Kaakinen 1972, 1974, Ratia and Timonen 1975, Huttunen 1978, Tuovinen 1979, Soini 1982, Alanen 1983, Kärkkäinen 1994, Jalkanen and Hokkanen 2003), detailed descriptions of the plant communities over the site types are still rare, and the ecology, succession, human impacts, soils and macrofungi of these forests are also poorly known (*see* Tuomikoski 1950, Koponen 1967, Kaakinen 1992, Ohenoja 1992, Sippola et al. 2005). In addition, there are only few studies on the differences between the herb-rich forests and herb-rich heath forests (*see* Tonteri et al. 2005). The differences between the herb-rich forests and herb-rich heath forests are crucial for evaluating the value of the site, e.g. whether the site is a woodland key-biotope protected by the Forest Act of Finland (1996) or not. This also requires comprehensive studies of the soil in herb-rich forests. Most of the studies concentrate on the hemiboreal zone and the districts rich in grass-herb forests, in southern Häme, Central Karelia, Kuopio, Kuusamo and Kainuu, but studies on the herb-rich forests in other districts and Lapland are rare.

As a summary, future research work should include the following studies in herb-rich forests:

1. Studies should incorporate more study areas, particularly outside the districts rich in herb-rich forests and in northern Finland, and detailed descriptions of the plant communities over the site types are also needed.
2. Exploring the succession, and searching for suitable and real native reference areas is essential. This includes studies and/ or experiments on the human impacts (e.g. restoration, forest management) and history of herb-rich forests to reveal the post human impacts, and detailed descriptions of soil profiles, soil chemical and physical properties, and soil formation.
3. Detailed descriptions of the differences between the herb-rich forests and heath forests.
4. Population studies on small patches, for conservation purposes.

7 CONCLUDING REMARKS

Finally, my studies suggest the following concluding remarks:

1. Herb-rich forests are biodiversity “hotspots” for vegetation, particularly for vascular plants, in the boreal zone (Kuusipalo 1984, Valta and Routio 1990, Virkkala and Toivonen 1999), as also found here.
2. Boreal herb-rich forests are unique ecosystems and very different from the nemoral forests in the temperate zone, or deciduous herb-rich forests in the hemiboreal zone. For example, the spring aspect, i.e. herbs flowering during spring time, are absent in the middle and northern parts of the boreal zone.

3. In eastern Finland, Koli is a valuable and to some extent unique herb-rich area that maintains rare eastern and northern flora (e.g., *D. sibiricum* communities).
4. Classification of herb-rich forests can be largely based on vascular flora, but bryophytes are useful for more accurate classifications.
5. Although vascular plants well predicted the soil nutrient status, the herb-rich forest site types did not form clear groups along the fertility gradient.
6. Classification of herb-rich forests is more the classification of vegetation than the classification of sites.
7. Classification of herb-rich sites is primarily needed for conservation purposes in order to find both valuable habitats and specific species assemblages, and not for predicting timber production.
8. The conservation value of each herb-rich site should also be estimated on the grounds of edaphically demanding and red-listed flora. “Man-made” herb-rich forests should only be included in the conservation network if they are “high-quality” sites rich in edaphically demanding or red-listed species. However, management e.g. burning, grazing or the removal of small spruces, may be necessary in order to maintain the valuable characteristics of these sites.
9. Although several small patches supported more edaphically demanding species than a set of large patches of equal size, red-listed orchids were primarily found in large heterogeneous areas.
10. The classification of herb-rich forests still remains somewhat unclear; the grouping of herb-rich sites into types is difficult, descriptions of some types are insufficient or missing, and a classification system that covers all herb-rich forest site types in Finland is still lacking.

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