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VANTAAN TUTKIMUSKESKUS – VANTAA RESEARCH CENTRE

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Plant biology
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Academic dissertation

To be presented, with permission of the Faculty of Biosciences of the University of Helsinki, for public criticism in the auditorium of Arppeanum (Helsinki University Museum, Snellmaninkatu 3) on December 10th 2004 at 12 o'clock noon.

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To the memory of my father

Hannu Nousiainen, 2004

Contents

List of Original Publications

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

I Korpela, L. & Reinikainen, A. 1996. Numerical analysis of mire margin forest vegetation in South and Central Finland. Annales Botanici Fennici 3: 183-197.

II Korpela, L. & Reinikainen, A. 1996. Patterns of diversity in boreal mire margin vegetation. Suo - Mires and Peat 47(1): 17-28.

III Korpela, L. 1999. Diversity of vegetation in pristine and drained forested mire margin communities in Finland. International Peat Journal 9: 94-117.

IV Korpela, L. 2004. Structural and species diversity of boreal forested mire margin communities in South and Central Finland– effect of drainage. Silva Fennica (submitted manuscript).

Author's contribution

The initial idea of the study and the subject of the thesis is based on the suggestion provided by Lic. Sc Antti Reinikainen. His contribution to the planning and supervising the vegetation survey on the permanent sample plot network of the 8th National Forest Inventory (NFI 8, 1985–1986) was considerable. Leila Korpela participated in the fieldwork as one of the biologists in the 12 NFI field teams during 1985–1986. Leila Korpela and Antti Reinikainen are responsible for the planning and implementation of papers **I–II**. Leila Korpela is responsible for the planning and implementation of papers **III–IV.** Leila Korpela is responsible for for the data analysis and writing of the first drafts of papers **I–IV.**

Abstract

The study deals with the components and sources of plant diversity in pristine mire margin influenced forested sites and the effects of forest drainage on their diversity pattern. The study focuses on these mire types because (1) their position along the gradients between wetlands and forests results in high diversity, and (2) these sites have been strongly impacted by forest drainage. The study sites consist of paludified mineral soil forest, paludified mire margin forest, and forested spruce and pine mire sites, from the permanent sample plot data of the 8th National Forest Inventory (NFI 8, 1985-1986). The pattern of plant diversity and the effect of forest drainage on it have been approached from two main directions: (1) species diversity, and (2) structural diversity. Species diversity was measured using taxonomic units (species) as alpha-diversity and beta-diversity. The former was understood as species richness in the site (sample plot), and expressed by means of species number and diversity indices. The latter was understood as species diversity along ecological gradients and measured as the length of the gradients, dissimilarity in species composition, and the rate of compositional change along a gradient. Structural diversity, which means the vertical and horizontal architecture of a community, was measured by means of spatial dimensions. The results of this study revealed that species diversity remained relatively high after drainage, but the vegetation composition in the understorey changed towards mineral soil forest vegetation. The most drastic change in the composition and structure of the understorey vegetation after drainage was the clear decrease of *Sphagnum* species and their replacement by forest bryophytes. Also the structure and composition of the field layer showed increased abundance of the most common forest grasses and mesic forest herbs and forest dwarf-shrubs and by decrease of sedges after drainage. The structure and size distribution of the tree stands on forested mire margin sites remained uneven-aged and uneven-sized after drainage. Drainage changed the tree and shrub species composition and abundance in the different layers more clearly than the tree size distributions. The increased percentage cover of the dominant trees at all fertility levels and the increased percentage cover of deciduous trees, especially that of pubescent birch, were obvious.

Overall, the increase in the diversity indices of the understorey vegetation along the post-drainage succession gradient, as also the increased cover of deciduous trees in the overstorey, was seen to be mostly due to the increased number and cover of pioneer species (e.g. forest herbs, grasses, and bryophytes and pubescent birch in the overstorey), colonist species (e.g. forest dwarf shrubs, and carpet mosses), existing concurrently with decreased covers of mire species. The enrichment of nutrients after drainage caused an initial increase in diversity, but this was seen only as a transient phenomenon in the composition of the community. The drained forested mire margin communities change towards forest vegetation in which mesic and herb-rich forest species dominate but remnants of mire species are still found.

Keywords: biodiversity, vegetation diversity, forest ecology, mire ecolgy, forest vegetation, mire vegetation, forested peatland, forest drainage, boreal forest, spruce mires, mire margin, species diversity, structural diversity, forest structure.

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I express my warmest thanks to my supervisor at Metla, Lic.Sc. Antti Reinikainen, for suggesting the study subject, spruce mires (korpi in Finnish), and for his many comprehensive lectures in the field of community level vegetation research of forested mires and the effect of drainage, since the start of my master's thesis, and for his scientific guidance throughout the study. I would also like to thank him for being a co-author of the first two papers and for valuable comments on the thesis.

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Leila Korpela

1. Introduction

1.1. Background

Forest ecosystems are highly variable in structure, function and species diversity. This heterogeneity of habitats and species in time and space is a central component of biodiversity (Kouki 1994). Most of the forested area in Finland is silviculturally managed for timber production, and only about 3.1 % (Peltola 2003) of the forests has been set aside as reserves. Forestry is perhaps the most important single threat to animal and plant species diversity in Finland (Kouki 1994, see also Vanha-Majamaa and Reinikainen 2000, Ulvinen *et al.* 2002, Rautiainen *et al.* 2002). Forests are probably the most significant habitat in terms of nature conservation and the preservation of biodiversity (Kouki 1994, Haila and Kouki 1994). In managed forests, the loss of structural variation is one of the main problems in maintaining biodiversity. In temperate forests and Fennoscandian boreal forest environments, the role of the factors that cause natural disturbances and determine the characteristics of e.g. habitat mosaic, as forest fires, the proportion of broadleaved tree species, the amount of old-growth forests, and the amount of dead and decaying wood has decreased dramatically in recent decades (Esseen *et al.* 1992). Human activities are, at an accelerating rate, replacing natural disturbances in boreal forest (Esseen *et al.* 1997). In many regions, forest management has become the main driving force affecting forest dynamics. While the modification of forest structure to meet management goals, such as the production of timber, has often been successful in creating resource flow stability, this has taken place at the expense of biological diversity (Kouki 1994, Esseen *et al.* 1997, Linder and Östlund 1998, Siitonen 2001).

The general concern about the increasing loss of species caused by growing human activities (Wilson 1988, 1989) and the increasing concern about the preservation of the whole biosphere, have brought about a need to promote ecosystem research programs devoted to the dimensions of the biosphere (e.g. di Castri 1989, di Castri and Younes 1990, Solbrig 1991). Since the Rio 1992 Earth Summit, several countries, including Finland, have signed the agreement on the protection of biodiversity and the agreement on the principles of sustainable forest management (UNCED, Rio de Janeiro 1992). Consequently, after the ratification of the agreement in 1994, an agenda for research priorities for the conservation and sustainable use of biodiversity in Finland was published (Väisänen and Jäppinen 1994) and the National Program or Action Plan for Protecting and Preserving Biodiversity in Finland for the period 1997–2005 was prepared (Kangas *et al.* 1997). In today's forestry in Fennoscandia, ecological sustainability and care for biodiversity is claimed. As the new legislation on forestry and nature conservation came in to force, from the beginning of the year 1997, these aspects have to be taken into consideration in forest management practices in Finland (e.g. Annila 2001), and they are also included in the main criteria of sustainability and certification in European forestry (e.g. Parviainen 1996). Thus, preserving biodiversity in both natural and managed forests is the main goal of Finland in participating in the international commitments to preserve biodiversity in the world (Interim Report on… 1995, Anderson *et al.* 1997).

1.2. Concepts of biodiversity

Biodiversity refers to the variation at all different hierarchical levels of living nature. Thus, the concept of biodiversity is extremely wide and, when dealing with biological diversity, it is of utmost important to define which level and which part of biodiversity is in question. Biological diversity is usually divided into three main levels: genetic, species and ecosystem diversity (Wilson 1988). Genetic diversity refers to the genetic variation of individuals between and within populations. Species diversity describes species richness and changes in species composition. Ecosystem diversity is the widest term, and refers to the variation of ecosystem structures and habitat types (Wilson 1988).

The most studied aspect of biodiversity is species level diversity (e.g. Whittaker 1972, Hill 1973, Peet 1974, Kempton and Taylor 1976, Alatalo 1981, Kuusipalo 1985, Økland 1986, Ter Braak 1987a, Molinari 1989, Økland 1996...). Species level diversity is usually further divided into three levels, which are defined as alpha diversity, referring to species richness and abundance within an area (Whittaker 1972), beta diversity, describing the rate of species turnover along an environmental gradient (Whittaker 1972, 1977, Wilson and Shmida 1984), and gamma diversity, referring to the large number of species in a larger area with several habitat types (Whittaker 1972) thus making it a measure of species diversity at the landscape level. Already the early studies of Whittaker (1960, 1972) and MacArthur (1965) established the importance of identifying alpha and beta diversity as components of overall species diversity (Wilson and Shmida 1984).

The concept of structural diversity, i.e. the number of vertical layers present and the abundance of vegetation within them (commonly referred to as foliage height diversity), has been shown to be important in investigations on the relationships between plants and animals, such as early studies on the diversity of woodland bird communities (MacArthur and MacArthur 1961, Recher 1969, Wilson 1974, Moss 1978, Magurran 1988) and insect diversity studies (e.g. Southwood *et al.* 1979).

From the viewpoint of population biology, Harper (1977) describes four forms of diversity that contribute to the structural diversity of plant communities. First of all there is the somatic polymorphism of the parts of a genet (or functional individual). For instance the same plant may have different leaf forms on its juvenile and mature branches, at different times of the year or on its flowering and non-flowering parts. The second is the diversity of age stages within a community. Old and young plants of the same species often have markedly different growth forms. Trees are good example of plants which vary greatly in their growth form, as well as in their ecological role, during the different phases of their life. The third concerns the genetic variants within a species. The diversity of microsites within a habitat is the fourth, and is a very important form of variety. Variation in soil texture, drainage, exposure and countless other environmental factors can influence the intensities and abundances of species found in a particular habitat (Harper 1977, Magurran 1988).

In community ecology, the species richness, species composition and species dominance of plant communities are greatly affected by the availability of their limiting resources (Tilman 1997). Disturbances create spatial and temporal variance in the availability of limiting resources. So, for example, losses of biomass and density caused by natural disturbances have an effect on diversity (Tilman 1997). The average rate of resource supply and the spatial variance in supply are important determinants of plant community diversity (Tilman 1982).

From the ecosystem point of view, high variation in the vegetation structures of sites provides, because plant communities are the primary autotrophic component of terrestrial biodiversity (Austin 1999), an opportunity for high diversity of all other species (organisms) as well (Huston 1994, Rescia *et al.* 1994, Larsen 1995). Diversity is both a measure of the chance of having certain species present in a system and a measure of variation in species traits in an ecosystem. Diversity impacts the structure, dynamics, and functioning of ecosystems (Tilman 1999).

Since human activities have a strong effect on biodiversity, a population/community level approach is considered to be the level that can help in exploring the responses of the whole ecological system to various kinds of disturbance (e.g. Hanski and Gilpin 1991, Barbault and Hochberg 1992). It has been stressed that special attention should be paid to habitat disturbances in biodiversity research because the populations of many species are being turned into metapopulations as a result of habitat fragmentation (e.g. Hanski and Gilpin 1991). This landscape ecological level view has become a central focus point in conservation biology and biodiversity research (e.g. Hanski and Gilpin 1991). In the ecosystem level approach, multiscale heterogeneity, chance events, nonequilibrium dynamics and 'complexity' are nowadays seen as fundamental characteristics of forest ecosystems, where individual species are embedded in interactive communities of micro-organisms, plants and animals (Attiwill 1994, Pickett *et al.* 1997, Hunter 1999, Kuuluvainen 2002).

1.3. Importance of forested mire margins for the overall biodiversity of boreal forests and mires

Swamp forests have been found to be natural centres of biodiversity within the boreal forest landscape in Fennoscandia (Ohlsson 1990, Kuusinen 1996, Ohlsson *et al.* 1997), as well as wetland forest communities in the hemiboreal landscape in North-Eastern Europe (Prieditis 1999). Even at the southern border of the distribution of *Sphagnum* mires in Europe, the *Picea abies* dominated mire margin communities show high species diversity (Kutnar and Martinčič 2003). Special attention has been focused on nutrient-rich and herb-dominated swamp forests (Ohlsson *et al.* 1997) because they are the most vascular plant species rich forest sites (e.g. Ohlsson 1990) and also have a high forest (timber) productivity after drainage (Malmström 1928, Holmen 1964, Hånell 1988). In Finland these biotopes were recognised to be the most potential wetland forest sites (e.g. Lukkala 1929) and, to date, a high proportion of them have been drained (Hökkä *et al.* 2002). They have also been extensively exploited in Sweden (Ohlsson *et al.* 1997). Detailed inventories and protection of the remaining fragments of old-growth swamp forests have become a highly important reference points for managed forests (Hanski and Hammond 1995). The most fertile sites of forested mire margin communities (the most fertile swamp forest sites) are nowadays also considered as threatened biotopes, which should be protected in Finland (Heikkilä 1994ab, Heikkilä and Lindholm 2000).

1.3.1. Definitions of forested mire margin sites

According to the Finnish mire site type classification (Eurola *et al.* 1984), swamp forests are part of forested mire margin vegetation communities. Mire margin vegetation communities, forested sites that are typically situated in the transition zone between mineral soil forests and open peatlands, include mire margin forests (paludified mineral soil forests and paludified mire margin forests) and forested, minerotrophic spruce and spruce-pine mires (Lumiala 1937, Tuomikoski 1942). Paludified mire margin forests and forested spruce and pine mires are so-called genuine forested mire sites, which are characterised by hummock and intermediate level vegetation resembling forest vegetation, especially at the more nutrient-rich end of the vegetation continuum. These sites have often developed from the paludification of mineral soil forests. The more nutrient-rich types are called spruce mires (spruce swamps) or hardwood-spruce mires (hardwood-spruce swamps) (*korpi* in Finnish), with vegetation characterised by shade tolerant herbs and dwarf shrubs. The sites with lower nutrient levels are usually called pine mires with characteristic hummock dwarf shrub vegetation (Laine and Vasander 1996). In this study, the term spruce mire includes all spruce mires, and not only the more nutrient-rich hardwood-spruce mires. According to environmental characterisations, mire margin vegetation occurs on sites with a thin peat layer. The average thickness of the peat layer of mire margin sites varies from under 20 cm in the thinnest-peated, paludified mire margin forests to about 1m in the fen-like spruce swamps (Ilvessalo 1956, 1957, Ruuhijärvi 1960, Eurola 1962) that receive a supplementary input of mineral nutrients from the surrounding mineral soil and are thus minerotrophic (Eurola *et al.* 1984). The importance of this external nutrient flow is strongly related to topography and slope (Backman 1919, Lukkala 1929) and the inflow of oxygen-rich surface or spring water (e.g. Havas 1961, Persson 1961ab, Eurola *et al.* 1984, Tahvanainen *et al.* 2003). The active functioning of micro-organisms and favourable conditions for the existence of mycorrhizas are also included in the spruce mire and mire margin influence (Ruuhijärvi 1960, Nurminen 1964). The existence and origin of spruce mire and mire margin influenced vegetation are also affected by the peat chemistry, especially the proportions of mineral nutrients such as calcium, potassium and phosphorus (Heikurainen 1957, Ruuhijärvi 1960). The proportions of phosphorus are generally higher in spruce mires than in open peatlands (e.g. Valmari 1956, Heikurainen 1979, Reinikainen *et al.* 1984, Kaunisto and Paavilainen 1988, Eurola *et al.* 1995b, Laine *et al.* 2004). As a result, the decomposition rates and fluxes of mineral nutrients are also more stable than in mires in general (e.g. Ruuhijärvi 1981). This Finnish mire margin classification differs from the other Scandinavian interpretations (Sjörs 1983, Økland 1989, 1990), according to which the marginal pine forests of bogs, despite being ombrotrophic, are also included in mire margin sites. The Finnish definition (e.g. Eurola *et al.* 1984) of the mire margin concept is used in this study (Fig. 1).

1.3.2. Special characteristics of forested mire margins - the biodiversity viewpoint

The above-mentioned environmental features, which are included in the mire margin influence, induce the richness of species in pristine (natural) swamp forests (spruce swamps). The small-scale hydro-topographic variation (typical for spruce

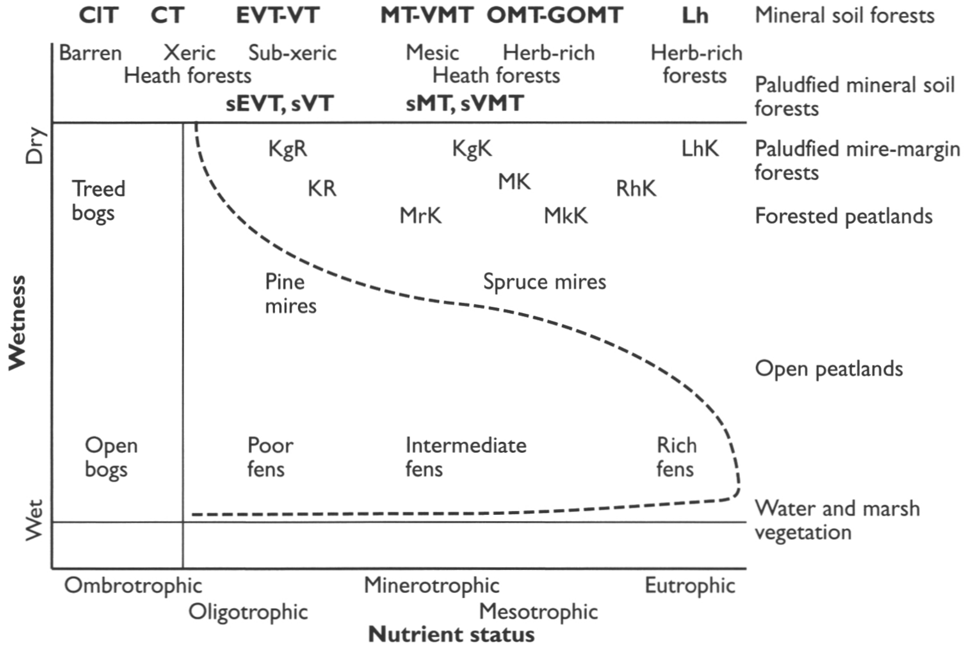


Fig. 1. An idealized two-dimensional ordination of boreal forest and wetland sites. The studied paludified mineral soil and mire site types are marked with their Finnish symbols (see Table 1.). Dotted curve = border between mire margin and mire expanse influenced site types.

swamps) creates a mosaic-like vegetation structure where the range of microsites (or microhabitats) varies from dry hummocks and the base of trees to permanently water filled hollows (Tuomikoski 1942, Heikurainen 1954, Eurola *et al.* 1984, Ohlsson 1990, Hörnberg *et al.* 1998). The diversity value of spruce mire vegetation is often increased by the appearance of ground and surface water influenced vegetation. The relatively great importance of spruce mires and mire margin vegetation communities to forest biodiversity is partly due to the fact that they often occur as ecotones lying between mineral soil forests and open peatlands or water bodies. The vegetation composition therefore always reflects features derived from the surrounding areas (Tolvanen 1994, Sjöberg and Ericson 1997).

As is the case in forested ecosystems, decaying wood plays an important role as a habitat or in ecological processes in pristine spruce mires (Saaristo 1998, Siitonen 1998, Siitonen and Saaristo 2000). Spruce mires have been found to be important environments also for many threatened Polypore species (Kotiranta and Niemelä 1996). The diversity of epiphytic lichens is higher in spruce mires than in mineral soil forests (Kuusinen 1996). The moist, shady environment of spruce mires is also ideal for epixylic bryophytes (e.g. Laaka 1992).

Similarly as for vascular plant species, the composition of invertebrate species living in spruce mires reflects the ecotonal nature of the sites (Aapala 2001). Most of the invertebrate species are generalist forest species, but there is a group of species that favours spruce mire habitats (Saaristo 1998, Siitonen and Saaristo 2000). Spruce mires are also important habitats for many forest-dwelling fowls (e.g. Sjöberg and Ericson 1997).

In Finland 422 plant taxa (415 species), including vascular plants, *Bryidae*, *Sphagnum* mosses and ground lichens, frequently occur on mire sites (Eurola *et al.* 1995a). About 70 % of these species favour mire margin influenced sites (Korpela and Reinikainen 1996a). In spruce mires, the bryophyte species composition of the ground layer varies, according to the nutrient level (from oligotrophy to meso-eutrophy) and hydrology of the sites, from hummock level forest mosses (carpet or cushion mosses) to the intermediate level *Sphagnum* mosses and, as the nutrient level increases, the number of intermediate level *Sphagnum* and *Mniaceae* species rises (Eurola *et al.* 1995a, Ohlsson *et al.* 1997).

There are no vascular plant species in Finland that thrive only in spruce mires, but spruce mires are the optimum habitats for many vascular plant species. These include many mesotrophic *Carex* species. The total number of vascular plant species found in spruce mires in Finland is more than 250 (Aapala 2001). The vascular plant species composition of spruce mires reflects the ecotonal nature of these sites. In oligotrophic spruce mires the vascular plant species composition is scanty, and is mostly dominated by dwarf shrubs, while meso-eutrophic spruce mires are dominated by species-rich herb and grass vegetation. According to Ohlsson (1990), 60 % of all vascular plant species living in the forests of Sweden are present in pristine nutrient-rich spruce mires, the area of these biotopes being only 5 % of the total forest area.

The species composition of mire margins or spruce mires can be divided into different ecological species groups such as forest, spruce mire, pine mire (or bog), poor fen, rich fen, spring and marsh species groups (see Fig. 2, according to Korpela and Reinikainen 1996a).

1.3.3. Structure and dynamics of the tree stands on forested mire margins

In Finland, most of the studies carried out on the tree stand structure and dynamics of pristine (undrained) spruce mires have primarily concentrated on the forest management point of view and considered as a part of all types of peatland forest stand, and in many cases they are based on National Forest Inventories (Gustavsen and Päivänen 1986, Mattila and Penttilä 1987, Paavilainen and Tiihonen 1988, Uuttera *et al.* 1996, 1997, Norokorpi *et al.* 1997). In Sweden, most of the studies concentrating on the tree stand structure and dynamics of pristine spruce mires alone have been carried out relatively recently (Hörnberg 1995, Hörnberg *et al.* 1995, 1997). In addition to spruce, deciduous trees dominate the tree species composition of spruce mires. Deciduous trees dominate on nutrient-rich spruce mire sites, and spruce and a mixture of spruce and pine on nutrient-poorer sites (Gustavsen and Päivänen 1986). According to the third Finnish National Forest Inventory (1951–1953), the proportion of deciduous trees (mostly birch) was about one third of the total tree stand volume in pristine spruce mires (Gustavsen and Päivänen 1986). In a case study of pristine, old growth spruce mires in the northern part of the middle boreal zone in Finland (Kuhmo), the proportion of Norway spruce was the highest (75–95 %) and that of birch was only 5–18 % (Saaristo 1998). Other deciduous tree species present in spruce mires, in addition to birch (mostly *Betula pubescens*), are alder (*Alnus incana* and *A.*

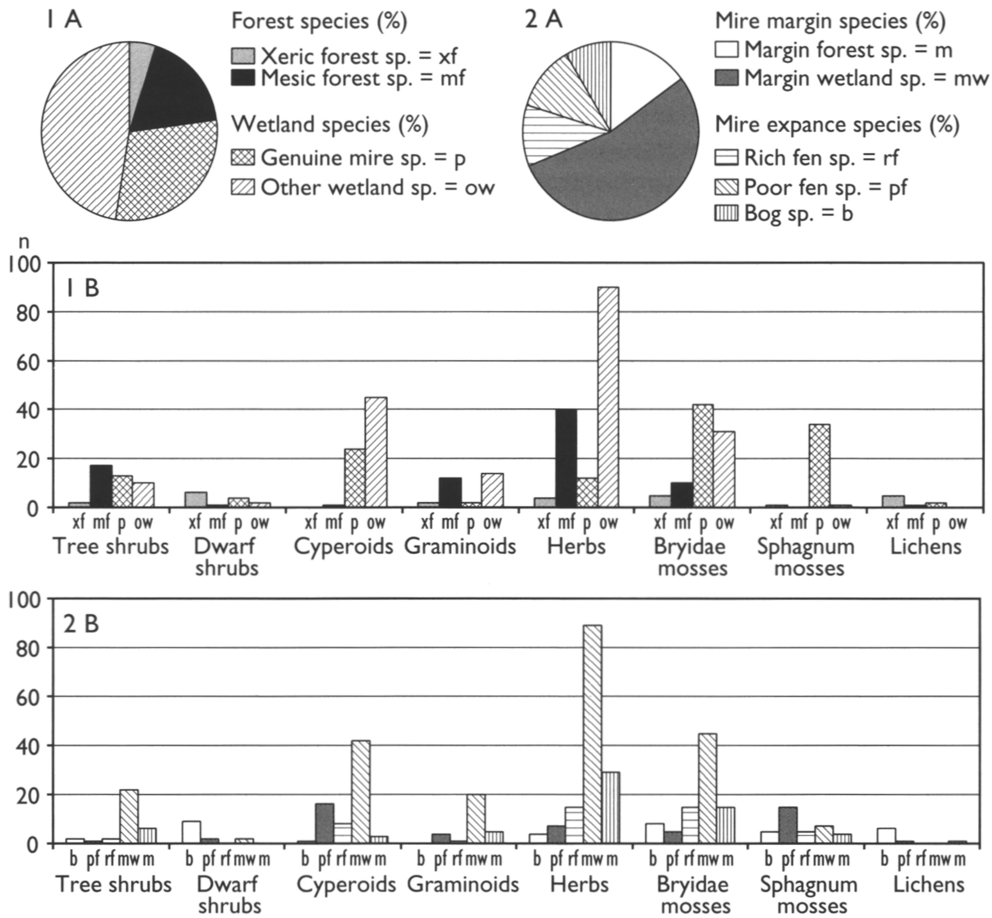


Fig. 2. Distribution of the Finnish mire flora (422 taxa) between different ecological guilds (1A, 2A) and the number of species of the ecological guilds in different life forms (1B, 2B). Drawn according to the list of Eurola *et al.* (1995a).

glutinosa), tree-like *Salix* species (*Salix caprea*, *S. pentandra*) and aspen (*Populus tremula*). According to palaeoecological studies, varying proportions of deciduous broad-leaved trees have been continuously present in swamp forests during their life history (Segerström *et al.* 1994, 1996, Ohlson and Tyrterud 1999). One common feature of spruce mires in Finland is that the proportion of alder (*Alnus*), especially black alder (*Alnus glutinosa*) has diminished over time (Aapala 2001).

The old-growth *Picea abies* -swamp forests are, in the short term perspective, characterized by an all-aged structure and small-scale disturbance dynamics, where individual trees reach senescence, die, and fall to the ground (Hörnberg *et al.*1995). According to tree stand size distribution analyses, the structure of undrained peatland forests is, according to the data of a Finnish inventory in the 1950's, uneven-aged with a wide range of tree diameters (Heikurainen 1971, Gustavsen and Päivänen 1986, Norokorpi *et al.* 1997). In uneven-aged stands, most of the trees are concentrated in small diameter classes and the shape of the diameter distribution is usually a reversed

'J' (Gustavsen and Päivänen 1986, Norokorpi *et al.* 1997). In Kuhmo (see above), eastern Finland (Saaristo 1998), the stem number distribution was found to be only a slightly reversed J shape. Stem numbers have been found to vary according to the spruce mire site type and geographical region (e.g. Gustavsen and Päivänen 1986). Stem numbers on nutrient-rich spruce mire sites are much higher than on nutrient-poorer spruce mire sites (e.g. Gustavsen and Päivänen 1986). The tree stand dynamics of spruce mires differs from that of the mineral soil forests. Spruce mires do not necessarily require large scale disturbances like forests fires for natural regeneration as they have all-age structured and small-scale disturbance dynamics (Hörnberg *et al.*1995).

1.4. Effect of drainage on the diversity of boreal forests and mires

The drained peatland area in Finland amounts to almost 6 million hectares (drained during the period 1950–1990, Tomppo 1999, Hökkä *et al.* 2002), which is more than half of the total peatland area in Finland. Most of the peatlands drained for forestry are currently undergoing a transforming (middle) phase of the post-drainage succession phases (Tomppo 1999, Hökkä *et al.* 2002).

Compared to the early 1950's only one half, and in southern and central Finland only one quarter, of the area of forested mire margin sites have remained undrained (Ilvessalo 1957, Eurola *et al.* 1991, Hökkä *et al.* 2002). In their undrained condition these forested mire margin habitats have retained a relatively natural stand structure and ground vegetation, although they have been often subjected to some degree of silvicultural management. Thus, on the community and species level, they are assumed to be important for local and regional diversity.

Most of the studies on the effect of forest drainage on vegetation have concentrated either on sparsely forested pine mires (pine bogs) (Laine and Vanha-Majamaa 1992, Laine *et al.* 1995, Vasander *et al.* 1997, Laiho *et al.* 2003) or on a broader scale on all peatland sites, also including treeless mires (Sarasto 1957, 1961, Pienimäki 1982, Reinikainen 1988, Hotanen and Vasander 1992, Hotanen *et al.* 1999). After drainage, with the subsequent change in the growth substrate and tree layer, the composition of the lower vegetation layers also changes drastically. Plant species adapted to wet habitats are the first to disappear, while hummock-dwelling species (e.g. dwarf shrubs) and forest species may benefit from drainage (Sarasto 1961, Eurola *et al.*1984, Laine *et al.* 1995, Laiho *et al.* 2003). Only a few studies have concentrated on the effect of drainage on mire margin influence (e.g. Eurola *et al.* 1995b).

Despite partial cuttings, which are usually carried out in connection with drainage (Paavilainen and Päivänen 1995), the shape of the diameter distribution has been found to remain negatively skewed for up to 30–50 years after drainage (Keltikangas *et al.* 1986, Hökkä and Laine 1988). This has been explained on the basis of the post-drainage growth of seedlings and on the greater release growth of smaller trees compared to larger ones as a response to the drawdown of the water level and subsequent improvement of growth conditions (Hånell 1984, Hökkä and Laine 1988). However, when the stand structure is analysed using characteristics other than the shape of the tree stand distribution, such as the proportions of different tree species, the effect of drainage and cuttings can be clearly seen in the structure and dynamics of peatland forests (Uuttera *et al.* 1996, 1997). In recent years, structural or physiognomic-structural vegetation classification (e.g. ground, field, shrub and tree layers) (Küchler 1967, Küchler and Zonneveld 1988) methods have proved to be useful in the classification of old growth forests (Lindholm and Tuominen 1989, Tuominen 1994, Leppäniemi *et al.* 1998) and also for assessing structural diversity (Korpela 2004).

1.5. Approach and aims of the study

The aim of the study arose from the clear lack of statistically tested information about the floristic state and importance of forested mire margin communities as sources of biodiversity in Finland. The availability of the unique, systematic vegetation sample and tree stand data covering the whole of the forest land area of Finland made the statistical testing possible. As one of the key topics for research on the management of biodiversity is to determine the differences in biodiversity indicators between undisturbed and managed forests, a comparison of pristine and drained forested mire margin sites is one of the main objectives of this study. The general objective of the study was to describe and analyse the species and community level vegetation diversity of the forested mire margin sites in the present landscape of managed forests in Finland, and the effect of drainage on their diversity pattern.

The approach of the study was first to examine the prevailing community and species level vegetation diversity by analysing the species richness and the main ecological gradients in vegetation composition of those forested mire margin sites that are still undrained, and thus more or less pristine (natural) (I, II). The second phase was to analyse the changes in the vegetation diversity caused by drainage, by comparing the vegetation of the undrained remnants to the corresponding sites drained for forestry (III, IV). The hypothesis was that drainage has decreased the diversity. This has been found in other peatland forest studies carried out in Finland, but has not been studied before using the systematically sampled large area data and by paying special attention to spruce mire and mire margin influenced vegetation communities. The diversity pattern of the spruce mire and mire margin influenced vegetation communities and the effect of forest drainage on it has been approached from two main directions: (1) species diversity, and (2) structural diversity (both alpha and beta levels).

The specific aims of the thesis were:

- to explore the structure of the vegetation of forested mire margins located in south and central Finland, using ordination and classification techniques (I),
- to test the hypothesis that species and structural diversity on pristine sites typically peaks in communities located in the transition zone between forest and mire (II),
- to describe and analyse the changes caused by drainage on species and community level vegetation diversity in forested mire margin sites (III),
- to detect changes in structural diversity caused by drainage, by taking all the structural layers of the vegetation into account (IV), and
- to test the hypothesis that forested mire margin sites become more uniform, both in the understorey vegetation and in the forest structure, after drainage (IV)

2. Material and methods

2.1. Study area and study sites

2.1.1. Description of the study area

Biogeographically, the sampled area extends from the northernmost border of the hemiboreal zone to the southern parts of the northern subzone of the boreal zone (Ahti *et al.* 1968). The study area comprises three forest vegetation subzones: the coastal area of Finland, southern Finland, and the western, central and eastern parts of Finland (Kalela 1961). The border between the zones of raised bogs and aapa fens runs through the area (Ruuhijärvi 1982). The mean annual temperature (for the period 1961–1980) within the study area ranges from +1 to +5°C; the effective temperature sum (threshold +5°C) from 850 to 1 350 degree days, d.d. (Heino and Hellsten 1983); the mean annual precipitation from 500 to 600 mm; the duration of the growing season from 135 to 180 days; Conrad's continentality index from 24 to 34; and Thornthwaite's index of humidity from 20 to 50 (Tuhkanen 1980). The study area and distribution of the studied sample plots are shown in Fig. 3.

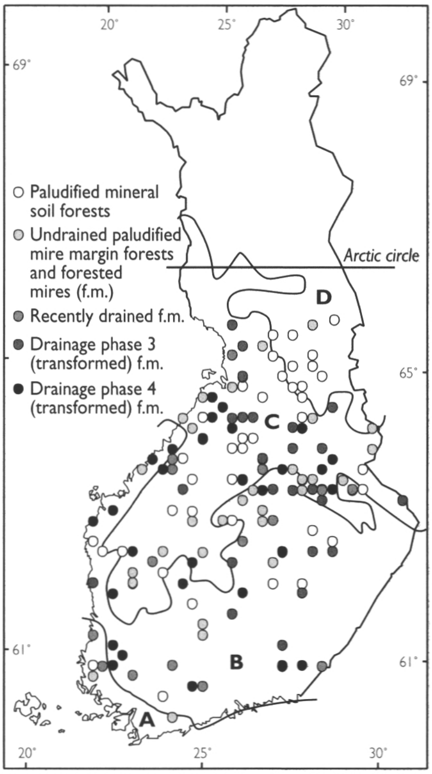
2.1.2. Sample plots

The material of the study is derived from the data of the permanent sample plot network of the 8th National Forest Inventory (8th NFI). The field data were collected by 12 NFI crews during late May - September 1985–1986. This sample plot network, established for monitoring tree vitality (Salemaa *et al.* 1991), ground vegetation (Tonteri *et al.* 1990), and deposition (Ruhling *et al.* 1987), included 3 009 permanent plots (Fig. 4) covering the entire forested land area of Finland (see Reinikainen 1990, Tomppo *et al.* 1997). Circular plots were located systematically: four circular plots in one cluster (a sample plot tract) in each 16 × 16 km grid square in southern and central Finland (S of 66°N; 2 618 plots, Fig. 4a), and three circular plots in one cluster in 24 × 32 km grid in northern Finland (N of 66°N, 391 plots, Fig. 4b). On each of the circular plots (300 m^2) there were from three to six, mostly four, 2 m^2 vegetation sample quadrats (Fig. 4c) (for a more detgailed description, see Heikkinen and Reinikainen 2000).

The first criterion was that the sample plots situated south of the 66°N latitude (in total 2 618 sample plots) are to be included. The study was restricted to the area of south and central Finland (south of latitude 66°N) because of the more intensive sample plot network, differences in determining the paludified mineral soil forest vegetation in southern and in northern Finland, and the fact that spruce mires are more common in southern and central Finland than in northern Finland.

The second criterion in selecting a subset of the 2 618 sample plots was that each plot should consist of only one site type in order to obtain as reliable a description of the site type in question as possible. The third criterion was that the plot site type should have been classified in the field into each of the forested mire margin sites (paludified mineral soil forest, paludified mire margin forest or mire margin spruce or pine mire sites in undrained and drained phases) as described in the introduction. The assessment of the original site type before drainage in the field, corresponding to

Fig. 3. Distribution of sample plots within A = hemiboreal, B = southern boreal, C = middle boreal and D = northern boreal subzones. The boreal subzones are drawn according to Ahti *et al.* (1968).



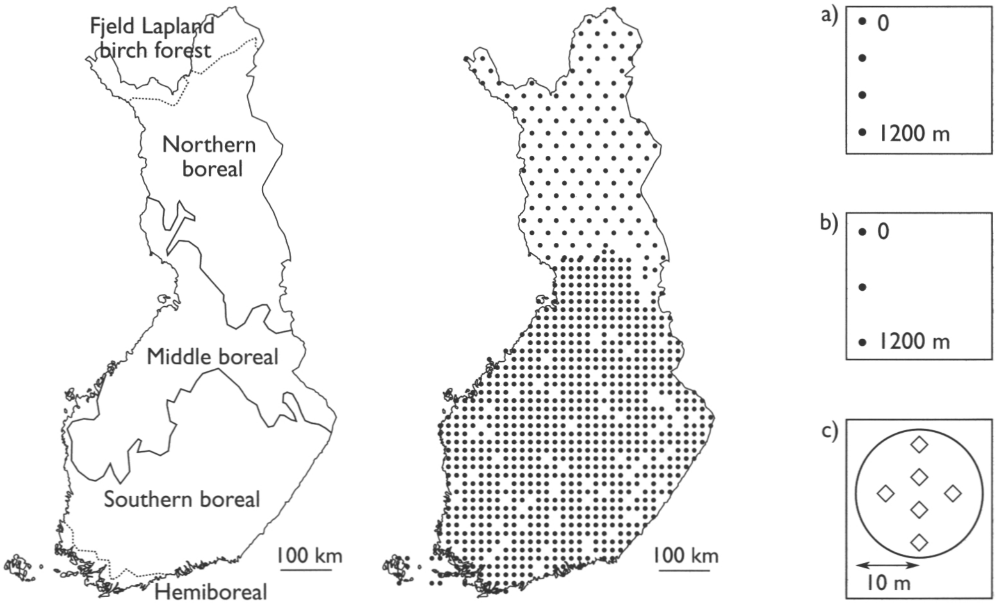


Fig. 4. The boreal vegetation zones in Finland and sampling frame-work with the tracts of the 8th (1985–1986) and 9th (1995) National Forest Inventory with permanent sample plots. a) = a sample tract with four permanent sample plots in southern and central Finland and b) = a sample tract with three permanent sample plots in northern Finland. c) = a sample plot with four to six 2 m^2 vegetation sample squares.

the undrained site types studied, was taken into account when selecting the drained sample plots. Application of these selection criteria resulted in a total of 245 sample plots. Additional selection criteria were: four vegetation sample quadrats on each plot, the tree stand had not been treated for at least ten years before inventory, and a tree stand age or forest succession coming within the range of young thinning stands to mature stands (forest development classes four to six, see e.g. Tomppo *et al.* 1997). In all, 156 plots satisfied all these criteria (III–IV). Of these, 82 were undrained and 74 had been drained (Fig. 4, Table 1). In the study of undrained, forested mire margin sites there were no limitations on the tree stand age and forest succession stage (92 sample plots I, II). The paludified mineral soil forest sample plots are included in the undrained plots.

2.1.3. Data collection in the field

The traditional 'Finnish forest-type approach of Cajander' (Cajander 1926, Frey 1973) was used to assign the sample plots into site classes. The paludified forest site types were classified according to Kalliola (1973). Mire site types were classified according to the principles presented by e.g. Eurola *et al.* (1984) using the nomenclature of Heikurainen and Pakarinen (1982). The wood (timber) production potential of the site types was estimated using the six-scale system of Huikari (1974), in which site fertility class I is the richest and VI the poorest (Table 1). The drainage phase of the sites was determined according to the system described by Sarasto (1961) and by Heikurainen and Pakarinen (1982, see also Paavilainen and Päivänen 1995). The species were classified into forest or mire plants, and allocated to forest site types presented in Kalliola (1973) and ecological groups according to Eurola *et al.* (1995a). The nomencalture for vascular plants follows that of the Hämet-Ahti *et al.* (1998) and for bryophytes Koponen *et al.* (1977).

Tree and ground layer vegetation data were collected on each plot. The field and ground layer vegetation (including tree and shrub plants shorter than 50 cm) were recorded by percentage cover of each species on four systematically located sample quadrats (2 m^2) on each plot. Percentage cover of each species was estimated as the sum of the cover projections of the leaves and stems according to the scale: 0.1 (< 0.125 %), 0.2 (0.126–0.375 %), 0.5, 1, 2, 3, 5, 7, 10, … with 5 % intervals…90, 93, 95, 97, 98, 99, 100.

The trees in the stand were divided into five canopy layers according to criteria based on the relative height and age of the trees and their position in relation to other trees in the stand (e.g. Kuusela and Salminen 1969, Tomppo *et al.* 1997). The percentage cover of each tree species, calculated from the sum of the crown projections (over 1.5 m high) in each canopy layer, and the percentage cover of each shrub and tree species (0.5–1.5 m high) in the shrub-layer (layer 6), were estimated visually.

The tree stand measurements on the sample plot were carried out according to the normal procedures of the Finnish National Forest Inventory (NFI) (Kuusela and Salminen 1969, Tomppo *et al.* 1997). The diameter at breast height (DBH) of all tally trees over 4.5 cm diameter was measured by species. In addition, DBH and height of the sample trees (= tally trees on a subplot with half the radius of the sample plot of all tally trees) were measured. The approximate stand age was obtained by taking an increment core from one representative sample tree of the dominant crown storey.

Table 1. Distribution of sample plots of **A) paludified mineral soil forests** and **B) forested mire margin spruce mires and thin peated pine mires** with their site types (Finnish abbreviations) in fertility level (I-II =meso-eutrophic, III = oligo-mesotrophic and IV = oligotrophic) and drainage phase (1 = paludified mineral soil forests, 2 = undrained forested mires, 3 and 4 = drained forested mires in phases 3 = recently drained and transforming phases and 4 = transformed phase) groups. Number of sample plots **(n)** and mean values of temperature sum (d.d.) and thickness of humus/peat layer are presented in each group.

Site types	Fertility levels	Drainage phases 1	2	3	4
			(n)		
A) Paludified mineral soil forests		**(n)**			
Herb rich forests Oxalis-Myrtillus type (sOMT)	**II**	**4**			
Mean temperature sum (d.d.)		1067.5			
Mean thickness of humus/peat layer (cm)		10.0			
Mesic forests Myrtillus type (sVMT,MT,sDeMT)	**III**	**26**			
Mean temperature sum (d.d.)		1058.1			
Mean thickness of humus/peat layer (cm)		8.6			
Sub-xeric forests Vaccinium type (sEVT,sVT)	**IV**	**13**			
Mean temperature sum (d.d.)		1032.3			
Mean thickness of humus/peat layer (cm)		7.7			
B) Forested mire margin spruce and pine mires					
Meso-eutrophic					
Eutrophic paludified hardwood-spruce forest (LhK)	**I**		2	-	1
Mesotrophic paludified spruce forest (RhKgK)	**II**		-	-	3
Herb rich hardwood-spruce swamp (RhK)	**II**		3	4	9
n			**5**	**4**	**13**
Mean temperature sum (d.d.)			1138.0	1230.0	1131.5
Mean thickness of peat layer (cm)			22.2	18.5	41.3
Oligo-mesotrophic					
Oligo-mesotrophic paludified spruce forest (KgK)	**III**		9	4	5
Oligo-mesotrophic spruce swamp(VK:MK, MkK)	**III**		13	13	7
n			**22**	**17**	**12**
Mean temperature sum (d.d.)			1101.4	1153.5	1091.7
Mean thickness of peat layer (cm)			29.7	55.0	56.3
Oligotrophic					
Paludified pine forests(KgR)	**IV**		5	5	1
Oligotrophic paludified spruce forest(KgK)	**IV**		1	-	-
Spruce-pine swamp(KR)	**IV**		5	10	4
Oligotrophic spruce swamp(VK:MrK)	**IV**		1	7	1
n			**12**	**22**	**6**
Mean temperature sum (d.d.)			1064.2	1052.3	1183.3
Mean thickness of peat layer (cm)			31.1	54.0	69.2
Sample plots total **156**		**43**	**39**	**43**	**31**

The dominant tree species was defined as that with the largest stand volume in the dominant layer (Tomppo *et al.* 1997).

The thickness of the humus (on paludified mineral soil forests) and the peat layer (on mire sites) was recorded as the mean of four measurements, one from each of the 2 m^2 vegetation quadrats.

2.2. Data analysis

Mean percentage cover for each understorey species was calculated from the four surveyed quadrats on each plot. The species present in only one or two plots, as well as the taxa not determined to the species level, were excluded from the numerical analyses, except for the species richness values and diversity indices. This left 88 plant species (out of a total of 135 species) on the 92 sample plots in the analysis of the undrained (pristine) sample plots (I, II), and a total of 124 plant species (out of a total of 226 species) in the analysis of the 156 plots including plots of both undrained sites and drained sites (III).

2.2.1. Species (alpha) and community level (beta) diversity analyses

The species level (alpha) diversity was understood as the species richness in the site (sample plot) and expressed using the species number and diversity indices (II, III, IV) Species richness, and diversity indices; Shannon diversity index H', (Shannon and Weaver 1949, Magurran 1988), Simpson heterogeneity index D (Magurran 1988) and Pielou's evenness index J (Pielou 1966, Magurran 1988), were calculated (II, III, IV).

The community level (beta) diversity was understood as the species diversity along ecological gradients and measured as the dissimilarity in species composition and the rate of change along a gradient. The community level variation in species composition was measured by using the multivariate ordination and classification methods most widely used in community ecological studies, although there has been some criticism, for example, of their gradient length estimates (e.g. Eilertsen *et al.* 1990). The average percentage value data of field and bottom layer species were also analysed by classification analysis (TWINSPAN, two-way-indicator-species-analysis, Hill 1979) in order to reveal the structure of the vegetation communities. Multivariate ordination was used in order to find the main gradients in the variation of species composition, and to interpret the gradients according to environmental variables. Multivariate ordination was also used to reveal community level diversity (I, II, III). The main compositional gradients in vegetation of the undrained forested mire margin sample plots were extracted by detrended correspondence analysis (DCA; Hill and Gauch 1980) using detrending by segments (ter Braak 1987b) in the CANOCO program (version 3.12) (I, II).

The global non-metric multidimensional (GNMDS) method of ordination, included in the DECODA program package version 2.04 (Minchin 1991), was used in analyzing the gradients in the vegetation composition of the undrained and drained sample plots (III). The Bray-Curtis (also called Czekanowski or Sørensen) dissimilarity index, robust to random variation or noise in the data (Faith *et al.* 1987) was used as a measure of dissimilarity between the sample plots. This matrix of dissimilarities between sample plots was calculated from the abundance values of the species. Standardization was not applied except for logarithmic transformation of the values for species percentage cover. One- to four-dimensional GNMDS solutions were carried out using ten randomly generated starting configurations. The minimum stress configurations were compared using Procrustean analysis (Schöneman and Carrol

1970). A Monte-Carlo approach (in DECODA) was used to test the significance of the maximum correlation for environmental variables through the correlation. To reveal ecological gradients in the data, variation by species composition and by environmental variables were also examined when the number of dimensions was determined. According to this procedure, a three-dimensional GNMDS-ordination solution was selected for further analysis by the lowest minimum stress value (0.1592), which was achieved with all ten starting configurations. The weighted averages of all the species included were derived from the sample plot ordination by calculating the means of the scores for the sample plots in which a species occurred, and then weighting them according to species abundance (III).

2.2.2. Analysis of structural diversity

In the analysis of understorey structural diversity, the mean percentage cover of species was summed according to their growth form groups on each sample plot. Mean covers (%) of field and ground layer vegetation in different growth-form groups in different phases of drainage and fertility levels were analyzed using two-way analysis of variance (ANOVA). Logarithmic transformation was used for the percentage values. The analysis was used to determine whether drainage, site fertility, or their interaction, had any impact on the structure of the field and bottom layer vegetation (IV).

In the overstorey structural diversity analyses, the basic variables were mean percentage cover for each tree species in each of five vertical canopy layers and the tree and shrub species in the shrub layer and field layer. Two-way analysis of variance (ANOVA) was used to examine whether drainage, site fertility, or their interaction, had any impact on the overstorey structure. Diameter distribution analysis for trees with a DBH of more than 45 mm was also used to describe the structure of the tree stand. Diameter distribution was expressed as stem number/ha divided into 8 diameter classes (40 mm intervals) for all tallied tree species by fertility level and drainage phase group (IV).

2.2.3. Environmental and ecological interpretation of the results

Biplot scores for explanatory ecological variables were obtained in the DCA-ordination analysis of the undrained sample plots (I, II). The relationship between the ordination pattern and the selected explanatory variables was obtained using a vector-fitting procedure in the GNMDS-ordination analysis (III).

Spearman correlation coefficients between DCA axes (plot scores) in the study of undrained sites (I, II), and between the three dimensions of GNMDS ordination in the study of undrained and drained sites (III) and explanatory variables, were calculated. One-way analysis of variance (ANOVA) was used to test TWINSPAN clusters for environmental differences (I, II, III).

The explanatory and ecological variables used in the analysis of the undrained sites were regional variables (temperature sum, latitude, longitude) and the site quality variables (peat thickness, tree cover, shrub cover) and tree stand variables (basal area, mean diameter at breast height, DBH, dominant height and stand age) (I and Table 2). Species richness, diversity indices; Shannon diversity index, H' and Pielou's evenness index J were used as explanatory variables in the diversity analysis of the undrained sites (II).

In the analysis of the effect of drainage (III, IV) besides the above mentioned regional, site quality and tree stand variables, drainage phase (III, IV) and sample plot level tree stand variables (basal area, basal area-weighted mean diameter at breast height, basal area-weighted mean height and stem number /ha) were used (IV and Table 2). The same, above mentioned, diversity describing variables were also used in the studies of the effect of drainage (III, IV).

Table 2. Mean values and standard deviations (S.D.) of the **a)** stand-wise and the **b)** plot-wise tree stand variables of the studied sites according to fertility levels, fl (I-II, meso-eutrophic, III oligo-mesotrophic and IV oligotrophic) and drainage phases, dp (1 paludified mineral soil forests, 2 undrained forested mires, phases 3 and 4 after drainage) used in the articles **I-IV** (note that only drainage phases 1 and 2 were included in article **I**).

Fertility levels (fl)	Drainage phases (dp) 1		2		3		4	
a) Stand age (years) **(I, III, IV)**								
I-II	82.5	(31.0)	90.2	(37.2)	76.3	(40.5)	62.3	(34.6)
III	107.9	(58.5)	102.3	(36.3)	90.3	(27.6)	76.7	(28.6)
IV	97.3	(43.0)	99.6	(52.3)	83.3	(25.4)	96.7	(27.2)
a) Forest development class (4-6) **(IV)**								
I-II	5.3	(0.5)	5.6	(0.6)	5.0	(1.2)	4.8	(0.7)
III	5.3	(0.8)	5.4	(0.8)	5.0	(0.6)	4.8	(0.7)
IV	5.0	(0.8)	5.1	(1.0)	4.5	(0.6)	5.5	(0.6)
a) Basal area (m^2/ha) **(I, III)**								
I-II	35.0	(4.4)	27.6	(9.0)	19.8	(9.5)	23.3	(6.5)
III	23.7	(9.4)	24.5	(7.1)	21.5	(5.6)	25.9	(5.1)
IV	15.9	(5.6)	17.3	(6.5)	18.3	(7.2)	24.0	(9.5)
a) Mean diameter (DBH) (cm) **(I, III)**								
I-II	16.0	(6.5)	19.0	(3.2)	16.8	(11.2)	14.2	(6.6)
III	14.7	(6.2)	13.4	(5.0)	13.4	(5.8)	11.2	(3.0)
IV	12.8	(4.4)	10.3	(4.9)	10.2	(3.2)	18.2	(6.1)
a) Dominant height (m) **(I, III)**								
I-II	21.4	(1.8)	20.2	(6.5)	21.5	0.1)	24.3	(6.1)
III	16.3	(5.9)	16.3	(4.7)	15.3	(6.3)	16.7	(4.3)
IV	13.5	(3.3)	11.9	(2.4)	11.9	(3.0)	17.5	(4.5)
b) Plot wise basal area (m^2/ha) **(IV)**								
I-II	22.0	(3.8)	19.3	(5.3)	14.7	(12.5)	15.4	(10.6)
III	18.7	(9.8)	16.2	(7.2)	14.8	(6.9)	17.6	(7.8)
IV	11.3	(4.0)	10.9	(5.5)	9.5	(5.1)	18.5	(7.3)
b) Basal area weighted mean diameter (mm) **(IV)**								
I-II	220.0	(59.5)	226.0	(53.4)	169.8	(85.9)	162.6	(58.7)
III	200.0	(60.0)	180.8	(52.9)	159.4	(51.6)	154.6	(40.0)
IV	159.4	(32.0)	157.2	(41.7)	128.3	(40.6)	201.3	(51.1)
b) Basal area weighted mean height (m) **(IV)**								
I-II	16.14	(4.39)	15.32	(2.12)	15.15	(6.21)	13.40	(5.65)
III	13.82	(4.10)	13.30	(3.46)	12.65	(3.83)	12.52	(2.50)
IV	11.17	(2.09)	10.61	(3.43)	9.64	(2.62)	15.90	(3.92)
b) Stem number/ha **(IV)**								
I-II	1750.0	(1762.5)	1080.0	(450.7)	2750.0	(1904.1)	1946.2	(1005.6)
III	1582.1	(901.2)	1575.8	(706.2)	2060.8	(1077.2)	2433.3	(842.3)
IV	1189.7	(390.5)	1511.1	(716.8)	2210.6	(1027.4)	1300.0	(440.7)

3. Results

3.1. The structure of vegetation and compositional gradients in undrained forested mire margin communities

In the DCA ordination of the 92 undrained forested mire margin sample plots and 88 plant species, the main gradient in the vegetation composition was interpreted, according to species ecology, as a fertility or trophic gradient from ombro-oligotrophy to meso-eutrophy. The secondary gradient was related to peat thickness, and was interpreted as a paludification succession gradient.

The species composition along the main gradient varied from the one end of the gradient of ombro-oligotrophic species, typical of bogs and xeric forests and the oligo- mesotrophic spruce mire species and mesic forest species, in the middle, to the other end of the gradient of herb rich forest and meso-eutrophic spruce mire species. Correspondingly, the site types varied from the bog and sub-xeric forest site types (KR, KgR and, sEVT, described in Table 1) to the mesic and herb-rich forest and spruce mire site types (LhK, RhK, MkK, KgK, MK, sMT, described in Table 1). The optimum for species typical of oligotrophic and meso-oligotrophic forest and species indicating paludification (*Carex globularis Polytrichum commune*) were located centrally on these two gradients. The site types from a variety of oligotrophic pine and spruce mires and paludified forest types were intermixed in the middle of the main gradient (I, II).

The main gradient was significantly correlated and relatively parallel with all the variables connected to tree stand productivity (basal area, dominant height, mean diameter) (I). The correlation with geographical variables also reflected inter-correlations with the forest production (fertility gradient) and climatic gradient (I).

The variation in species composition along the second (paludification) gradient was related to the peat thickness, varying from the average values of 30 cm for spruce-pine mires (KR) and *Vaccinium myrtillus* spruce mires (MK) to under 10 cm for the paludified sub-xeric and mesic forest site types (sEVT, sVMT, sMT, Table 1). Although only a two axis solution was presented in the DCA ordination of the undrained sample plots, the third gradient could be observed by inter-correlation of the stand age and geographical (climatic) variables, indicating a higher stand age in the more northern and eastern parts of the study area (I).

TWINSPAN classification of the undrained forested mire margin sites confirmed the main gradients found in the DCA-ordination analysis (I, II). The same ecological and environmental variables were most often the significant ones at the classification levels. The classification failed to separate paludified mineral soil forest sites and forested mire margin sites and, in general, the agreement between the TWINSPAN clusters and the site types determined in the field was relatively poor. In contrast, the TWINSPAN-vegetation clusters were separated well according to spruce and pine dominance and the proportions of deciduous trees (I).

3.2. The diversity of undrained forested mire margin communities at the species, community and structural levels

Alpha diversity was weakly correlated with site types. Only the most fertile site type (LhK) showed a higher species number and Shannon diversity index (H') between the undrained site types. According to species number and Pielou's evenness index, alpha diversity correlated better with the vegetational clusters formed by hierachic classification than with site types (II).

The ecological species groups (sub-xeric, mesic and herb-rich forest, bog, spruce swamp and poor fen species) were fairly well separated in the species ordination space of axes 1 and 2, except for marsh (surface water) and spring water species, which were evenly distributed in the ordination. Species richness was not clearly correlated with the site fertility gradient, but the evenness of the communities increased towards ombro-oligotrophic vegetation (II).

Slightly higher species richness (alpha diversity) and clearly longer gradients (beta diversity) were noted in the understorey diversity analyses of the undrained forested mire margin sites compared to the mineral soil forests (Tonteri *et al.* 1990) or genuine mires (sparsely treed and open mires) (II).

Structural diversity analysis of the overstorey of the undrained sites, using TWINSPAN classification for a total of 16 tree and shrub species in 5 canopy layers and in the shrub layer, produced six structurally different clusters. Differences in species composition and species distribution within the layers emerged between the clusters. The overstorey structure varied from the largest, richest in species, spruce-dominated cluster (n = 40 plots) to the most pine-dominated (n = 7), and lowest tree species number cluster. The parity with these overstorey structural clusters and site types or vegetation clusters was relatively poor.

3.3. Effect of drainage on the compositional variation and diversity of the understorey vegetation in forested mire margin communities

The main division of the TWINSPAN-classification analyses occurred according to trophic status (fertility level), between meso-eutrophy and ombro-oligotrophy, also when the drained and undrained sites were analysed together (n = 156) (III). On the main division level, the two cluster groups differed significantly in terms of their site fertility levels and tree stand variables, which indicate site productivity (III). The effect of drainage emerged as a more complex mixture of variation in species composition, and not until the fourth level of divisions could it be interpreted to have occurred according to moisture or post-drainage succession on the ombro-oligotrophic and oligo-mesotrophic part of the fertility gradient (III).

In the three-dimensional ordination space of the GNMDS ordination of the undrained and drained sample plots (III), too, the main gradient was interpreted to describe a fertility gradient. About 10 % of the species occurred at both ends of this gradient. Post-drainage succession emerged in the GNMDS ordination as a secondary gradient (III). Undrained and drained sites formed a continuum along these main gradients (III). An exception was the most herb-rich sample plots, which clearly differed from the other sample plots in both the ordination and classification analyses (III). These herb-rich, eutrophic drained sites also differed in having higher diversity indices in the last phase of drainage (transformed phase), which is most species-rich both in understorey and overstorey (III). The length of the second, post-drainage succession gradient was clearly shorter than the first one; about 40 % of the species occurred at both ends of this gradient (III).

The third gradient in the GNMDS ordination of undrained and drained sample plots (III) was as long as the second one, and it was related more to peat thickness or paludification and to the development of the tree stand (III). This gradient was a complex gradient related to moisture, peat-thickness and tree stand succession (III).

Understorey species richness, as well as the richness of tree and shrub species in the overstorey, correlated significantly with the direction of the main fertility gradient and with each other (III). Species diversity indices correlated best with the direction of the post-drainage succession (or drainage stage) gradient (III). The indices of species diversity were the highest in the drained sites, but there was no significant difference between drained and undrained communities (III).

The differences and changes in species ecological groups (guilds) fromundrained to different post-drainage successional phases were significant (III). In the field layer, a decrease in abundances or the disappearance of mire dwarf shrubs, *Vaccinium oxycoccos* and *Andromeda polifolia*, and a corresponding increase in forest dwarf shrubs, *Vaccinium vitis-idaea* and *Vaccinium myrtillus*, was observed (Table 3). Drainage also affected the increase of certain graminoid and forest herb species (Table 3 and 4). In the ground layer a decrease of *Sphagnum* species and an increase of certain forest bryophyte species (so-called carpet mosses; *Pleurozium schreberi*, *Hylocomium splendens*, *Dicranum* spp.) along post-drainage succession were obvious. (Table 3 and III).

Species richness and Shannon's diversity index (H') of the understorey were most clearly related to site fertility, but the effect of drainage was also significant (Table 4, and IV). Simpson heterogeneity (D) and Pielou's evenness (J) indices were more related to drainage (Table 4, and IV). The understorey species richness was greatest in meso-eutrophic sites in all drainage phases (IV).

3.4. Structural diversity of the forested mire margin communities and the effect of drainage

3.4.1. Effect of drainage on structural diversity of the understorey

Differences in the percentage covers of the different growth form groups in the field layer, such as dwarf shrubs and herbs (see Table 4 and IV), were strongly related to site fertility, although the effect of drainage was also significant (see Table 4 and IV). Mean percentage covers of dwarf shrubs on the oligotrophic mire sites and herbs and graminoids on the meso-eutrophic mire sites increased towards the last drainage

Table 3. The field and ground layer species, affected most by drainage as measured by the increased or decreased mean percentage covers, or not found at all in the last drainage phase (disappeared) in the studied site fertility and drainage phase groups of forested mire margin sites.

Increased	Decreased	Disappeared
Field layer		
Dwarf shrubs:		
Vaccinium vitis-idaea		*Vaccinium oxycoccos*
Calluna vulgaris		*Vaccinium microcarpum*
		Andromeda polifolia
		Chamaedaphne calyculata
Number of dwarf shrub species in undrained phase 11, in the last drainage phase 7.		
Graminoids and sedges:		
Calamagrostis purpurea	*Carex loliacea* (found only in middle phase)	*Carex echinata*
Deschampsia caespitosa	*Carex flava* (found only in middle phase)	*Carex digitata*
	Carex lasiocarpa (found only in middle phase)	*Carex pallescens*
	Carex vaginata (found only in middle phase)	*Melica nutans*
Number of graminoid and sedge species in undrained phase: 8 and 9, in the last drainage phase 12 and 7.		
Herbs:		
Dryopteris carthusiana	*Equisetum sylvaticum*	
Trientalis europaea	*Rubus chamaemorus*	
Epilobium angustifolium	*Oxalis acetosella*	
Maianthemum bifolium	*Thelyptheris palustirs*	
Viola palustris		
Dryopteris expansa		
Solidago virgaurea		
Number of species in undrained phase: 45, in the last drainage phase: 54.		
Ground layer		
Bryidae mosses:	*Sphagnum* species:	
Pleurozium schreberi	*Sphagnum angustifolium*	
Dicranum polysetum	*S. girgensohnii*	
D. scoparium	*S.magellanicum*	
Hylocomium splendens	*S.capillifolium*	
Brachytechium sp.	*S.centrale*	
	S.riparium	
Hepatics:	*S.wulfianum*	
Ptilidium ciliare		
Lichens:		
Cladina rangiferina		
Cladonia cornuta		
Number of species in undrained phase: *Sphagnum* 12, Bryidae 22, Hepatics 6, Lichens 5, in the last drainage phase: *Sphagnum* 11, Bryidae 35, Hepatics 5, Lichens 4.		

phases (Fig.5 and IV). The mean cover of herbs decreased on oligo-mesotrophic sites after drainage. The cover of cyperoids (sedge-like plants) decreased after drainage on meso-eutrophic and slightly also on oligo-mesotrophic sites (see Fig. 5 and IV).

The most drastic changes occurred in the mean cover values of growth form groups in the ground layer (Fig. 5 and IV). Drainage strongly affected the mean cover values

Table 4. Effect of fertility level and phase of drainage on the field and ground layer structure tested by two-way ANOVA. Values used are mean percentage covers of different growth form groups and number of species and diversity indices. Logarithmic transformations have been used for the values of variables with percentage covers.

	Fertility class		Drainage phase		Interaction	
	F	p	F	p	F	p
Total cover of field layer (%)	2.65	0.074	0.49	0.690	2.02	0.066
Dwarf shrubs (%)	18.12	0.000	3.75	0.012	1.46	0.195
Herbs (%)	21.49	0.000	6.06	0.001	1.33	0.246
Cyperoids (%)	0.33	0.784	3.12	0.146	0.66	0.685
Graminoids (%)	7.63	0.001	1.15	0.333	1.52	0.176
Total cover ground layer(%)	3.99	0.021	11.09	0.000	1.93	0.080
Mosses (%)	4.01	0.020	7.64	0.000	0.75	0.611
Sphagna (%)	0.21	0.815	13.76	0.000	1.48	0.189
Bryidae (%)	6.45	0.002	6.06	0.001	1.30	0.261
Forest (carpet) bryophytes (%)	4.23	0.016	6.15	0.001	1.45	0.201
Other Bryidae (%)	2.29	0.105	0.83	0.477	1.58	0.158
Hepatics (%)	1.12	0.329	2.33	0.077	1.59	0.154
Lichens (%)	3.99	0.021	1.75	0.160	0.65	0.692
Number of species	24.01	0.000	6.42	0.000	1.61	0.147
Simpson index D	1.20	0.303	4.92	0.003	0.55	0.768
Shannon index H'	7.37	0.001	5.46	0.001	0.90	0.494
Pielou's index J	0.84	0.433	6.72	0.000	0.71	0.644

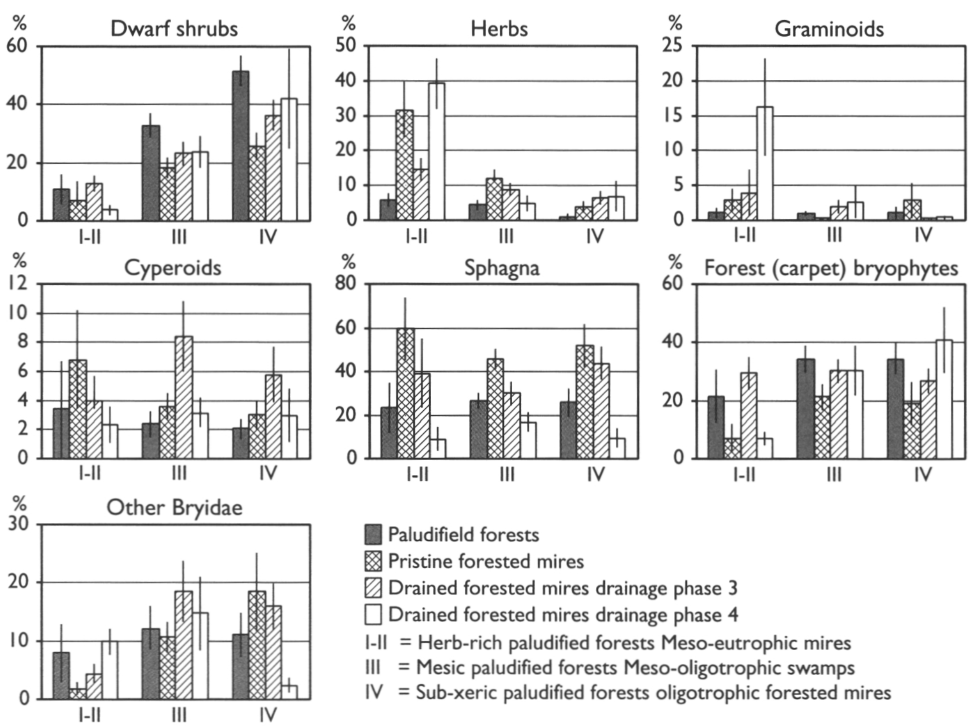


Fig. 5. Means and standard error of means (S.E.) of the percentage covers of the growth form groups of field (dwarf-shrubs, herbs, graminoids and cyperoids) and ground layer vegetation (Sphagna, forest carpet-bryophytes and other bryidae) according to four drainage phases and three fertility levels in forested mire margin communities.

of ground layer species (Table 4, Fig. 5, and IV). At all fertility levels, the percentage cover of the total ground layer was clearly smaller in the last drainage phase. The cover of bryophytes, and especially that of *Sphagnum* species, decreased after drainage on all the fertility levels (Fig. 5, Table 3, and IV). Drainage also had a statistically significant effect on the cover values of forest carpet mosses (e.g *Pleurozium schreberi*, *Hylocomium splendens*, *Dicranum* spp.), which increased after drainage on meso-oligotrophic and oligotrophic sites (Table 3, and IV). The increase in the cover values of forest bryophytes on the oligo-mesotrophic and oligotrophic sites of the last drainage phase reached the same level as on the paludified mineral soil forests (Fig. 5, and IV).

3.4.2. Effect of drainage on the structure of the overstorey

3.4.2.1. Canopy layer structure, species composition and diversity

The most apparent change in species composition in the different canopy layers was the increase of the cover of pubescent birch (*Betula pubescens*) in all tree layers on all fertility levels after drainage (Fig. 6, and IV). The increase of pubescent birch was clearest in the dominant (layer 2) and the intermediate (3) tree layers of the meso-eutrophic sites. There was also a clear increase of the cover of Scots pine (*Pinus sylvestris*) in the dominant tree layer on the oligotrophic sites in the last drainage phase (Fig. 6, and IV). The change in species assortment was the greatest on the drained meso-eutrophic sites, where the number of species also doubled even in the dominant tree layer and in the shrub layer because of the increase of deciduous tree species. The number of species on oligotrophic sites decreased clearly in the last drainage phase (Fig. 6, and IV).

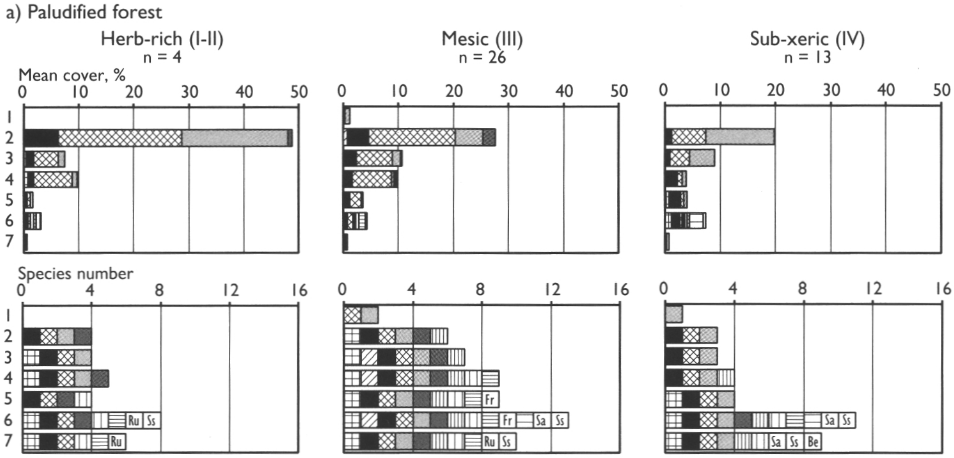


Fig. 6. The overstorey structure of undrained and drained forested mire margin sites. Mean percentage covers of species in 5 canopy layers (layers 1–5), in shrub (layer 6) and in field layer (layer 7) in fertility level (I–II, meso-eutrophic, III oligo-mesotrophic and IV oligotrophic) and drainage phase (1 paludified mineral soil forests, 2 undrained forested mires, phases 3 and 4 after drainage) groups. The species mean (%) cover and total number are expressed by different shadings in each layer.

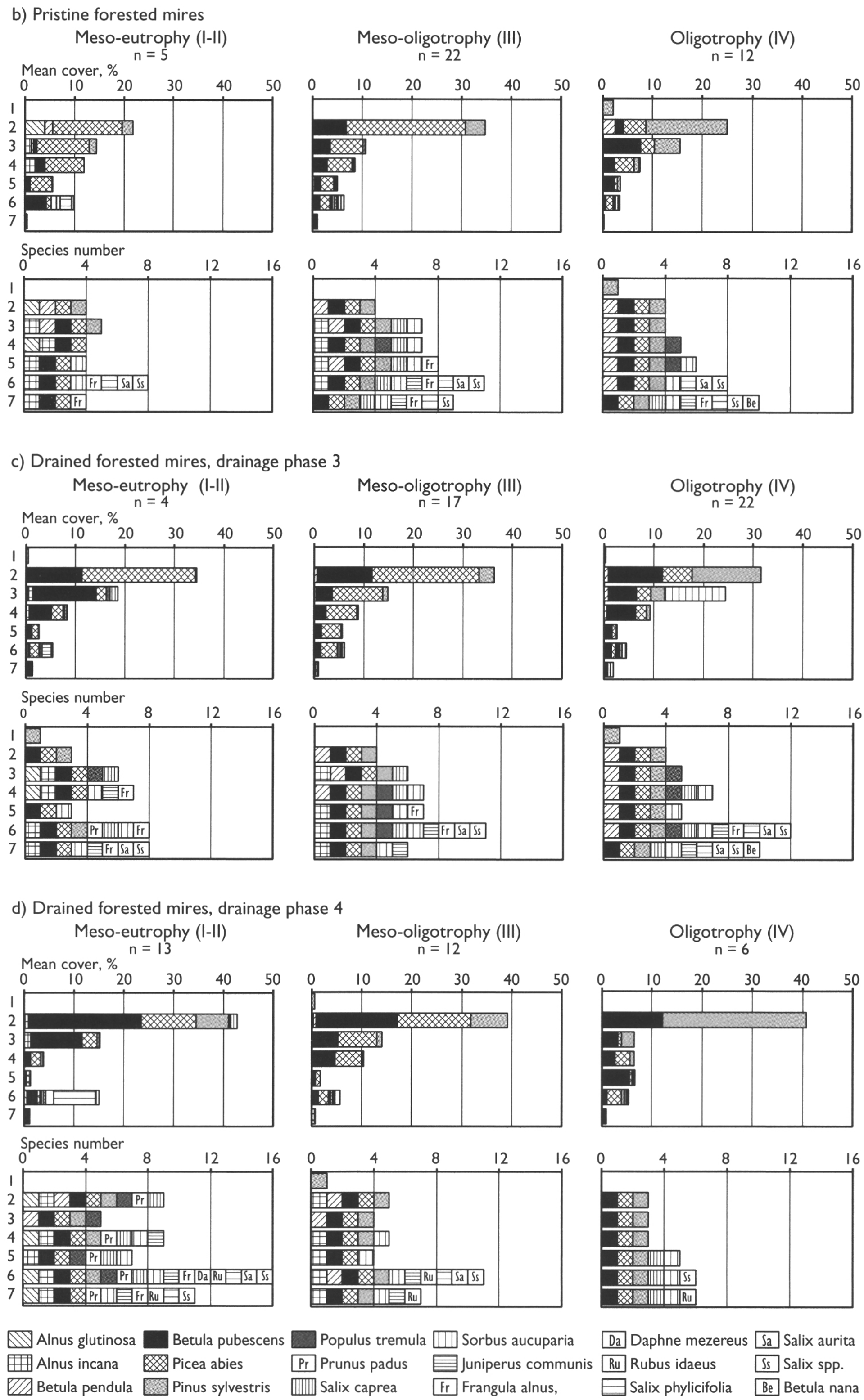


Fig. 6. Continued.

Table 5. Effect of drainage and site fertility level on **a) structural diversity**, expressed as percentage covers of canopy layers and **b) tree and shrub species diversity**, expressed with species number and diversity indices, in forested mire margin communities. Results of two-way Anova are presented. Logarithmic transformations have been used for the values of percentage covers.

	Fertility class		Drainage phase		Interaction	
	F	p	F	p	F	p
a) Structural diversity						
Number of canopy layers	1.73	0.181	0.71	0.545	0.99	0.437
Canopy layer 1. (%) (overtorey trees)	0.17	0.847	0.12	0.951	1.45	0.200
Canopy layer 2 (%) (dominant trees)	1.35	0.262	3.19	0.026	1.55	0.166
Canopy layer 3 (%) (intermediate trees)	1.08	0.344	3.12	0.028	1.41	0.215
Canopy layer 4 (%) (suppressed trees)	5.94	0.003	1.35	0.260	1.91	0.082
Canopy layer 5 (%) (understorey trees)	0.08	0.924	0.65	0.584	0.43	0.855
Shrub layer 6 (%)	0.24	0.351	1.10	0.789	1.06	0.390
Seedling layer 7 (%)	4.17	0.018	1.66	0.179	2.39	0.031
b) Species diversity						
Species number	6.80	0.002	0.25	0.863	0.09	0.373
Simpson index (D)	0.89	0.415	1.69	0.172	0.64	0.701
Shannon index (H)	0.12	0.886	0.90	0.443	0.57	0.751
Pielou's index (J)	3.44	0.035	1.34	0.262	0.63	0.705

There were no clear differences in the mean number of canopy layers between the fertility level and drainage phase groups (Table 5, and IV). The structural variables that were clearly affected by drainage were the mean cover of dominant trees (layer 2) and intermediate trees (layer 3) (Table 5, and IV). The mean percentage cover of the dominant trees was greatest in the last drainage phase on all fertility levels (Fig. 5, and IV). The difference was clearer ($p = 0.0165$, IV) when the paludified mineral soil forest sites were excluded.

The alpha diversity of the overstorey (tree and shrub species), measured on the basis of species richness, also differed significantly according to the fertility level (Table 5, and IV), but the diversity indices showed no clear differences in the overstorey among the fertility level and drainage phase groups (Table 5, and IV).

3.4.2.2. Stand structure

The variation in tree stand size structure, depicted as the variation in mean basal area and basal area weighted mean height, was related to site fertility (IV). However, the basal area weighted mean diameter (DBH) differed more through its interaction with the site fertility level and drainage phase. The effect of drainage also emerged as an increase in tree stand density, as depicted by stem number (IV).

In all drainage phases the mean values of all the tree size variables were larger on undrained meso-eutrophic and oligo-mesotrophic sites than on oligotrophic sites (IV). However, on oligotrophic sites they were the largest in the last drainage phase (IV). There was a correlation between the percentage cover of dominant trees (layer 2) and the basal area of the trees ($r = 0.327$, $p = 0.01$). The basal area weighted mean height also correlated best with the percentage cover of the dominant trees ($r = 0.216$, $p = 0.01$).

The shape of the diameter distributions on both undrained and drained forested mire margin sites showed great variation in size and age structure (IV). The shape of the diameter distributions resembled reversed J-shape distribution curves (IV). The differences between undrained mires and the last drainage phase of drained mires were greater in most nutrient- rich (meso-eutrophic) and nutrient-poorer (oligotrophic) site groups. The dominance of spruce in all diameter classes on undrained meso-eutrophic mire sites changed to a dominance of pubescent birch and other deciduous trees in the lower diameter classes, and the stem number in the larger diameter classes had also diminished (IV). As the proportion of pine and spruce had diminished in the smallest diameter class in the last drainage phase of the oligotrophic mire sites, the stem number of conifers had moved somewhat towards larger diameter classes and the shape of the diameter distribution curve of conifers started to resemble that of the sub-xeric paludified mineral soil forests (IV).

4. Discussion

4.1. Evaluation of the data and methods

4.1.1. NFI-data

The data used in this work were collected using systematic cluster sampling during the course of the Finnish NFI. Systematic sampling supports methods for reliable statistical analysis, although possible systematic variation in the data can effect the results. The data were collected using sampling in which all the areas have an equal probability of being sampled, and the sample size is equal, and therefore meet the criteria for objective results (Yee and Mitchell 1991). For inventories covering large areas, such as in the NFI, however, systematic cluster sampling is considered to be the most appropriate method owing to its relatively low costs and the fact that the results are accurate enough to provide reliable estimates (Päivinen 1987). The NFI data cover the whole forested area of Finland and, since the sample plots are located in clusters, the within-habitat and between-habitat variation is more accurately discovered. The size of the sample plot was also fixed and, in this respect, the data fulfilled the demands set for reliable data (Yee and Mitchell 1991).

The sample plots consisted of circular plots on which all the trees were measured. This kind of data, in which all the trees are of equal importance, is considered to be the most suitable for investigating the stand structure for biological diversity (e.g. Uuttera and Maltamo 1995). The NFI data also provide a unique opportunity for determining the structural diversity of the tree stands over large areas and determining the average structure of forests (Maltamo 2002). In the understorey vegetation survey, the size and number of the sample quadrats per plot were largely determined by practical considerations. As the total area of the 4×2 m^2 quadrats was the same on all the plots, this may not have been enough to include all the potential species and produce reliable mean coverage values (Trass and Malmer 1978, Pakarinen 1984, Økland 1990). The vegetation data were collected by 12 different people and the inter-observer difference in coverage values varied between 15–40 % depending on the plant species (Tonteri 1990). This range does, however, appear moderate compared to cover estimations in general (e.g. Bråkenhielm and Qinghong 1995). Jukola-Sulonen and Salemaa (1985) noted that high coverage values tend to be underestimated and low coverage values overestimated. The methods used in the study in hand provide data of sufficient quality to reveal the gradients (see chapter 4.1.2).

From the point of view of obtaining adequate data for pristine forested mire margin sites, systematic sampling may not be the best method since it represents the study material according to their frequency in Finland. This inevitably results in poor or inadequate representation of the variation in mire margin vegetation, because the most nutrient-rich sites, being ecologically and floristically distinct, are represented by only a few sample plots and the relationships between these site types and the rest of the data set are not adequately described (e.g. Økland 1990). It should also be kept in mind that these data represent a cross-section of the prevailing situation. Thus, the results obtained in this study can be used to support decision-making, but they more describe the quantitative trends than the qualitative pattern and processes required for for example in nature conservation purposes.

4.1.2. Statistical methods

4.1.2.1. Beta-diversity methods

The statistical methods used for describing ecological gradients (continuum) and structures and beta diversity, i.e. ordination and classification methods, have been found to be reliable and robust (Austin 1985, Kenkel and Orloci 1986, Økland 1986, Faith *et al.* 1987, Minchin 1987, Knox 1989, Podani 1989, Økland 1995, Austin 1999). Using a combination of ordination and classification techniques to determine the interactions between vegetation and environmental attributes has proved to be effective (Lindholm and Vasander 1987, Tonteri *et al.* 1990, Hotanen and Vasander 1992, Hotanen *et al.* 1999, Pitkänen 1997, 2000). The joint use of different ordination methods has also been recommended (Kenkel and Orloci 1986, Økland 1990). There has been considerable debate about which ordination method is most reliable in interpreting the ecological variation and gradients and the ecological dissimilarities and distances between and within communities according to the variation in species composition and abundances (e.g. Faith *et al.* 1987, Minchin 1987, ter Braak 1987a, Jongman *et al.* 1987, Peet *et al.* 1988, Oksanen 1988, Minchin 1989, Økland 1990, Eilertsen *et al.* 1990, Tausch *et al.* 1995, Oksanen and Minchin 1997, Økland 1999). The two paradigms, one using canonical correspondence analysis based methods (ter Braak 1986) and the other new forms of multidimensional scaling (Belbin 1991), continue to exist (Austin 1999). Both methods have been found to be very sensitive to ecological assumptions (Austin 1999). In this study, detrended correspondence analysis (DCA) and global non-metric multidimensional scaling (GNMDS) methods were used as they have been found to be effective and robust methods for finding ecological gradients (Gauch 1982, Faith *et al.* 1987, Minchin 1987, Økland 1990, Belbin 1991). The application of new regression techniques, i.e. Generalised Linear Models (GLM) (e.g. Austin *et al.*1994) and Generalised Additive Models (GAM) (Hastie and Tibshirani 1990, Yee and Mitchell 1991, Austin and Meyers 1996) especially with large data sets in vegetation analysis, has increased the ability to observe patterns of relationships between species and the environment (Austin 1999). This kind of statistical modelling has not been used in the study in hand because the most important environmental variables available in this study were classifying or indirect variables like fertility level and phase of drainage.

The hierarchical, polythetic, divisive, two-way indicator species technique TWINSPAN (Hill 1979, Gauch 1982) was used because it has proved to be successful in producing clear, easily interpreted classes in many plant ecological studies over the last twenty years (e.g. Kuusipalo 1985, Lindholm and Vasander 1987, Hotanen and Nousiainen 1990, Tonteri *et al.* 1990, Pitkänen 1997, 2000, Prieditis 1997). Since the results of ordination (DCA, GNMDS) methods and the TWINSPAN-classification method used in this study were similar, it was considered that the main ecologically meaningfull patterns of the vegetation composition and gradients were found.

4.1.2.2. Alpha-diversity methods

Species richness, their dominance and abundances, and diversity indices provided useful information both about within and between the obtained vegetation clusters and fertility level and drainage phase (structural) groups. The diversity indices used to describe alpha diversity were chosen from among the indices most commonly used. These indices are dependent on the species number and abundances (Peet 1974). The numerical values of diversity indices (as Shannon's diversity index H') increase as the number of species increases, and their occurrences become more even (Kouki 1994). Many researchers have pointed out the weaknesses of the underlying theory and the uncertain biological purpose of the indices of diversity (Whittaker 1972, Peet 1974, Alatalo 1981, van der Maarel 1988). However, they can be useful tools when interpreting results obtained by other analytical methods (i.e. when used as explanatory variables) as in this study (see also Korpela 1994).

4.1.2.3. Structural-diversity methods

Using the structural or physiognomic-structural vegetation classification (e.g. ground, field, shrub and tree layers) (Küchler 1967, Küchler and Zonneveld 1988) methods, which are specifically used in the large-scale mapping or primary mapping of regions with poorly known vegetation, gave new, useful information about the structural diversity of the studied sites. Although these methods are widely used throughout the world, they have not often been used in the Finnish vegetation classification (see e.g. Tuominen 1994). Since, the structure of tree stand determined in the form of species crown coverage's in different canopy layers as done in the NFI of permanent sample plots (1985–1986 and 1995), tree crown coverage has nowadays become the most important criterion for the world-wide definition of forests (Forest Resources… 2000).

4.2. The state of forested mire margin communities in relation to drainage in Finland

According to the statistics of the 8th National Forest Inventory (1986–1994), only 25 % of the peatland area of southern and central Finland is nowadays in an undrained state (Aapala *et al.* 1996, Hökkä *et al.* 2002). About 30 % of the undrained peatland area are spruce swamps, and 79 % of the spruce swamps have been drained for forestry (Eurola *et al.* 1991, Hökkä *et al.* 2002). Most of the drained peatland area is currently in the middle phase (transforming phase) of post-drainage succession (Tomppo 1999, Reinikainen *et al.* 2000, Hökkä *et al.* 2002). According to the data of this study, forested mire margin communities are almost equally distributed in the middle and last (transforming and transformed) phases of post-drainage succession. Most of the sites represented oligo-mesotrophy and oligotrophy (fertility levels III and IV) in undrained and in middle drainage phase, and the last drainage phase included more sample plots representing meso-eutrophic and meso-oligotrophic sites (levels I–II, III). There were only a few oligotrophic sites. Furthermore, according to this study the most nutrient-rich (meso-eutrophic) sites reached the last phase of post-drainage succession in a shorter time than the nutrient-poorer sites (see also Hotanen and Vasander 1992, Laine *et al.* 1995, Hotanen *et al.* 1999). This also reflects that the sites with the highest production potential have been drained first. It also should be noted that a part of the drained spruce mires, where the peat layer has almost completely disappeared and very little of the original peatland is left, are classified in the NFI as mineral soil forests (Hökkä *et al.* 2002).

The fact that the peat layer on the undrained mire margin sites is thinner than that on the drained sites might indicate that only the sites with the thinnest peat layer have been left undrained. As the study is based on cross-sectional data and the origin of the drained sites is often uncertain, the drained sites may also originally have been site types with a much thicker peat layer (the composite types) than is currently the situation. Also, the possible drawdown of the ground water level caused by drainage in the areas surrounding pristine sites may have affected the thickness of the peat layer on these undrained remnants of forested mire margins, which usually cover only small areas (Ohlsson *et al.* 1997, Aapala 2001). The fact that drainage has been more intensive in southern Finland is also reflected in the results of this study (see also Tomppo 1999, Reinikainen *et al.* 2000, Aapala 2001).

4.3. Importance of forested mire margin vegetation communities in maintaining the diversity of managed forests

4.3.1. Community and species level diversity

The fertility gradient that strongly dominates the pattern of boreal forest and mire vegetation in Finland (e.g. Eurola *et al.* 1984, Kuusipalo 1985, Lahti and Väisänen 1987, Tonteri *et al.* 1990) was clearly apparent in the analysis of mire margin influenced forested sites in both pristine and drained sites (I–IV).

Fertility, as indicated by the concentrations of nutrients in the soil, has been demonstrated to be the most important environmental factor increasing the diversity of vegetation in boreal forests and mires (e.g. Tuomikoski 1942, Pakarinen and Ruuhijärvi 1978, Pakarinen 1979, 1982, 1984, Kuusipalo 1985, Tonteri *et al.* 1990, Økland 1990, Jeglum 1991, Økland 1996). According to studies carried out in boreal forests, other important environmental gradients or variables affecting vegetation diversity are moisture (e.g. Lahti and Väisänen 1987, Økland 1996), altitude (e.g. Økland and Bendiksen 1985), tree species composition, basal area, crown cover, stand age (e.g. Kuusipalo 1985, Tonteri *et al.* 1990, Pitkänen 1998) and succession (Tonteri 1994), as well as the interaction between fertility, tree stand crown cover and age (Tonteri 1994, Pitkänen 1998). In other words, the conditions in the soil (nutrient concentrations, moisture etc.), amount of available light (crown cover, basal area) and stand age or succession have an effect on species diversity in boreal forests (see e.g. Pitkänen 1998).

In boreal mires the ecohydrological variation attributable to nutrient status (fertility), hydrology and mire margin/mire expanse gradients are the main factors that determine the diversity and variation in vegetation composition (e.g. Laine and Vasander 1996). As forested mire margin vegetation communities are typically situated in the transition zone between mineral soil forests and genuine mires, the forested mire sites and paludified mineral soil forest sites make up a continuum along the main (fertility) gradient (I–III).

Also the mire margin/mire expanse gradient (Lumiala 1937, Sjörs 1948, Eurola *et al.* 1984, Malmer 1985) was found to run parallel with the fertility gradient and to comprise a single complex gradient. As the indicators of margin influence in mire sites are mostly mesic forest species, while the indicators of mire expanse partly belong to the sub xeric forest species, it is difficult to separate these gradients (e.g. Eurola *et al.* 1995a). The significant correlations between tree stand productivity variables and species richness and the fertility gradient also accentuated the importance of this gradient.

The secondary gradient in the ordination of undrained (pristine) sample plots was interpreted as a moisture or paludification gradient (I–II). In Pakarinen's (1982) Bray-Curtis-ordination of South Finnish mire and forest types, the most dominant gradient was the paludification gradient. The moisture gradient on pristine forested mire margin sites is shorter than that on mires in general. The second gradient in the ordination analyses that included both undrained (pristine) and drained sites (III) represented the post-drainage succession and was found to describe the hydrological conditions better than peat thickness, because forested mire margin sites have a thin peat layer already when they are still undrained. The effect of drainage further shortened the second gradient and accentuated the importance of nutrient status (III). This illustrated the change towards mineral soil forest vegetation (III). The variation in species composition of the understorey along the post-drainage succession gradient also indicated changes in the availability of light (III). The increase in the diversity indices of the understorey vegetation along the post-drainage succession gradient in this study (III) can also be explained on the basis of increased number and cover of pioneer and colonist species, as according to Vasander (1987) and Vasander *et al.* (1997) three groups of plants has been found a number of years after drainage: original mire species, colonists and forests species.

Beta diversity of the understorey vegetation communities on forested mire margin sites in an undrained (pristine) state (I-II), as measured by the length of the gradients, seemed to be higher than that in forests in general (cf. Tonteri *et al.* 1990, Pitkänen 1997, 2000). In undrained (pristine) forested mire margin sites, the mixing of mire margin features, such as spring (ground water) and marsh (surface water) and spruce swamp, results in high floristic diversity owing to associations with the forest and bog species (I-II). After drainage, the species diversity still remained high when estimated on the basis of the species numbers and diversity indices only (III). This can be explained on the basis of the above-mentioned, increased number and cover of pioneer and colonist species (Vasander 1987, Vasander *et al.* 1997) (III). However, species number and diversity indices have not proved to be distinct enough to show differences between undrained and drained peatland sites (e.g. Vasander *et al.* 1997). When examined on the basis of the abundance of the species groups (guilds) indicative of ecological features, the drained forested mire margin communities change towards forest vegetation in which mesic and herb-rich forest species dominate and mire species are present as remnants (III). These changes indicate that the composition of the vegetation will resemble the corresponding forest sites at the same level of fertility (Reinikainen 1988, Laine 1989). The time required for the drained sites to develop to the last post-drainage succession phase has been found to vary between 15 and 50 years, mainly depending on the fertility, moisture conditions and tree stand of the original mire type (Laine *et al.* 1995).

Although there were no mire margin site types or vegetation clusters displaying species numbers higher than the forest sites of corresponding fertility (cf. e.g. Tonteri 1994), the species assortment seemed to be more diverse (II). The sources of species diversity were found in the analysis of the understorey vegetation communities (II). The effect of mire margin factors (spruce mire, surface water and spring factors) (Eurola *et al.* 1984) seemed to be weaker than expected, because the most abundant species belonged to either forest or bog guilds already in the undrained phase (II). Even so, out of a 'potential' number of ca. 200 species (Eurola *et al.* 1995a) for the site types studied, about 2/3 were found in NFI-plots. Consequently, the diversity value of these habitats was found to lie more on the community than on the species level (I–II). The post-drainage succession affected the alpha and beta components in different ways: species richness at the sample plot level decreased only slightly, and the ecological assortment of species became more monotonous due to the expansion of forest species (III).

4.3.2. Changes in structural diversity and species abundances of the understorey vegetation

The increase in the mean covers of the field layer was a consequence of the increase in forest herbs and grasses and forest dwarf shrubs (III, IV, see also Laine *et al.* 1995, Reinikainen *et al.* 2000), and even of forest graminoid species, which indicate a marsh and spring influence (III, IV, Reinikainen *et al.* 2000).

According to several studies (e.g. Sarasto 1961, Reinikainen 1965, Pienimäki 1982, Reinikainen 1984, Laine *et al.* 1995, Larmola 1997, Hotanen *et al.* 1999, Reinikainen *et al.* 2000), the cover of mesic forest herbs (e.g. *Dryopteris carthusiana* and *Trientalis europaea*) clearly increases with increasing drainage age; this was also apparent in the present study (III). Sedges and mire herbs disappear relatively soon after drainage (Laine *et al.* 1995). On the other hand, wetland herb species such as *Cirsium palustre* and *Viola palustris* may become even more abundant after drainage and also grow well on forested mire sites in the last phase of post-drainage succession (Aapala and Kokko 1988), as was also observed in this study (III). On nutrient-poor mire sites, the hummock species *Rubus chamaemorus* is almost the only herb species (Eurola *et al.* 1995a) and it has been found to benefit from the disappearance of competitors (Aapala and Kokko 1988). In this study on forested mire margin sites, this species was clearly the most abundant on undrained oligotrophic mire margin sites, and its abundance decreased towards drained and more nutrient rich forested mire sites (III). This is a typical phenomenon for drained spruce mire sites, where the tree stand cover has become more closed and the cover of competitors, herbs and grasses has increased (Sarasto 1961, Silfverberg 1991). Relatively soon after drainage mire dwarf shrubs like *Ledum palustre* might even gain dominance, as was found in the oligotrophic sites in this study (III). As the secondary succession proceeds, mire dwarf shrubs give space to *Vaccinium myrtillus* and *V. vitis-idaea* as the shading from the tree stand canopy increases (Laine *et al.* 1995), as was also found in this study in the oligotrophic sites especially (III).

Carex globularis, the indicator species of mire margin influence on oligotrophic sites, and which is also the most abundant *Carex* species on forested mire margin sites (Ruuhijärvi 1960, Eurola 1962), seemed to be indifferent to the effect of drainage (III).

However a decrease in its overall cover in Finland from the 1950s has been detected (Hotanen 2000). Most of the *Carex* species were found on undrained meso-eutrophic spruce mire sites (III). The intermediate and flark level tall sedges (e.g. *Carex lasiocarpa, C. chordorrhiza*) found as remnants on drained forested mires in the middle phase of post-drainage succession reflected the original tall-sedge dominated spruce mire sites (e.g. Laine *et al.* 1995). Tall sedges usually disappear during the post-drainage succession because of the increasing shading from trees and dwarf shrubs and the reduction in water flow (Aapala and Kokko 1988, Laine *et al.* 1995).

The increase of grasses, such as the most common forest graminoid species *Deschampsia flexuosa* after drainage on spruce mire sites, and the forest graminoid species that indicate surface water and spring influence, such as *Calamagrostis purpurea*, *C. canescens* and *Deschampsia cespitosa* on herb-rich sites in the last post-drainage succession phase, indicated that there was sufficient light, growth space and nitrogen available, and an influence of surface water on some species (Holmen 1964, Platonov 1976).

There was a clear decreasing trend in the cover of ground layer and bryophytes, especially the cover of *Sphagnum* (III, IV, Korpela and Reinikainen 1996b, Korpela 1998), and a simultaneous increase in the cover of forest bryophytes towards the last post-drainage succession phase (III, IV, e.g. Laine *et al.* 1995, Korpela and Reinikainen 1996b, Korpela 1998, Hotanen *et al.* 1999, Reinikainen *et al.* 2000). The decrease in the mean cover of the total ground layer was most drastic at the meso-eutrophic fertility level due to the increased cover of the field layer and also due to the increased growth of shrubs and trees (IV). Many forest bryophytes, including; *Pleurozium schreberi*, *Dicranum polysetum*, Hy*locomium splendens*, already occur on hummocks in undrained forested mires and, after drainage, they increase in abundance (Laine and Vanha-Majamaa 1992, Laine *et al.* 1995), as found in this study (III). *Sphagnum angustifolium* and *S. girgensohnii* clearly decreased on drained sites (III) compared to their abundances on undrained sites (I). Spring and surface water indicative of *Sphagnum riparium* and *S. squarrosum* were still found in the last phase of post-drainage succession (III). These species have been usually found near ditches, where the growing conditions are still optimal (Nousiainen, Hotanen, Vasander, pers. comm.).

As was the case in the studies on the species level diversity of the understorey vegetation (II, III), the investigation on the growth forms at the different fertility levels and in the different drainage phase groups confirmed that species richness was more related to site fertility (IV). Compared to the species number of the most nutrient-rich site groups on the undrained sample plots (II) and the most drained nutrient-rich site group in drained sample plots (III), the mean number of species decreased in the site group of the last drainage phase (II, III). Lower species numbers and also lower Shannon diversity indices (H') occurred in the groups of most of the spruce and hummock level vegetation dominated, oligo-mesotrophic, spruce mires and paludified mineral soil forests (II, III, IV). Otherwise, the effect of drainage on the differences in the diversity indices was greater than that of fertility (II, III, IV). This is explained with the earlier mentioned phenomen of original mire species, colonists and forest species a number of years after drainage (Vasander 1987, Vasander *et al.* 1997).

4.3.3. Temporal changes in the structure of understorey vegetation of forested mire margin sites

A preliminary comparison of the results for the growth-form groups of the understorey vegetation in three different National Forest Inventory surveys, i.e. at the beginning of the 1950's (NFI 3, 1951–1953), the middle of the 1980's (NFI 8, 1985–1986, the permanent sample plots of this study) and during the 1990's (NFI 9, 1995, the same permanent sample plots as in this study) shows the same kind of trends and direction of the development of the vegetation communities of forested mire margin sites as found this study (Fig. 7). The most striking feature in the 8th and 9th inventories compared to the 3rd inventory in the 1950's is, in addition to the small number of drained sample

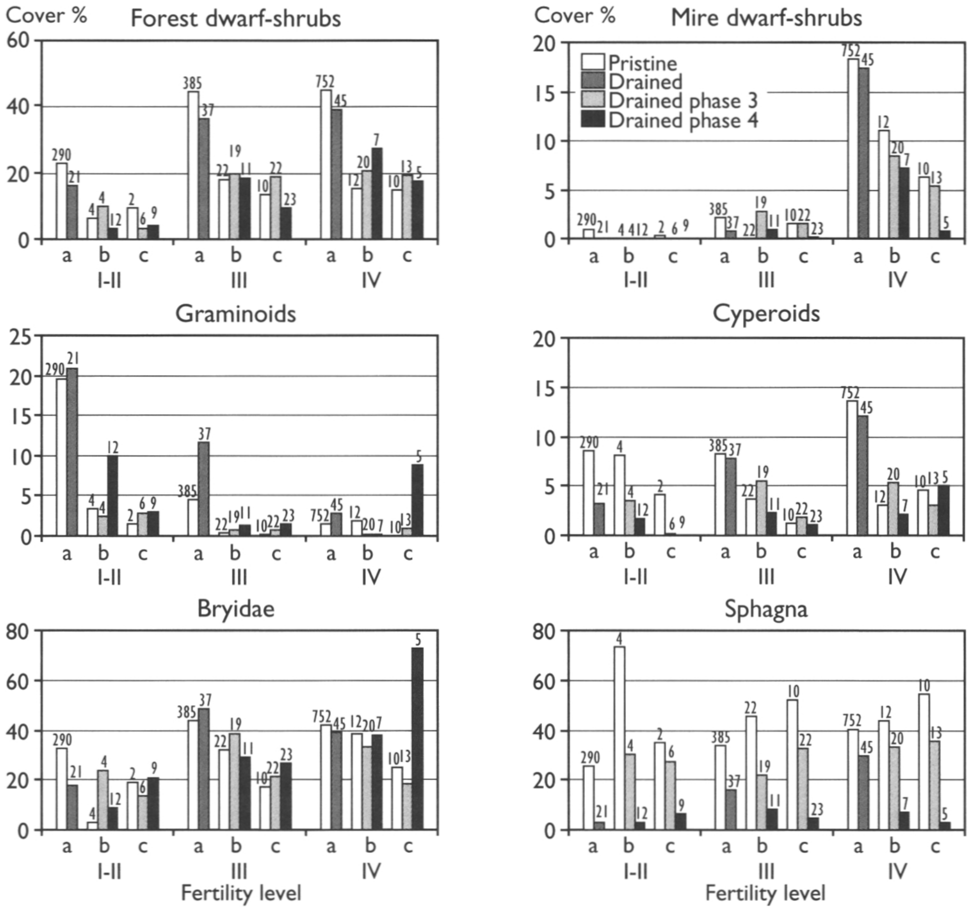


Fig. 7. The temporal changes according to mean percentage covers of some of the growth form groups of field (forest dwarf-shrubs, mire dwarf-shrubs, graminoids and cyperoids) and ground layer vegetation (sphagna and bryidae). The mean covers are expressed in three different fertility levels (**I–II**, meso-eutrophic, **III** oligo-mesotrophic and **IV** oligotrophic) and in pristine and drained phases according to the 3th National Forest Inventory (NFI) (1951–1953 = **a**) and in pristine and drained phases 3 and 4 according to the 8th NFI (1985–1986 = **b**) and the 9th NFI (1995 = **c**). The number of sample plots in each group is expressed above each bar.

plots, the large number of sample plots also in the undrained, most nutrient- and herb-rich, meso-eutrophic sites (Fig.7). The systematic, higher mean abundances in the 1950's survey are partly due to the different methods used in the assessment of the vegetation coverage (see Heikkinen and Reinikainen 2000).

The same kind of changes in the field layer vegetation as described earlier in this study, such as a slight increase of forest dwarf shrubs and a decrease of the mean covers of mire dwarf shrubs, in the drained oligo-mesotrophic and oligotrophic sites are most clearly evident in the surveys of the 8th and 9th NFI (Fig. 7). The comparison also shows that mire dwarf shrubs are most abundant in the oligotrophic sites according to all the inventories, and that the dwarf shrubs in the oligo-mesotrophic sites mainly comprise forest dwarf shrubs already in the pristine sites (Fig. 7). The changes between the undrained and drained sample plots of the 1950's survey are relatively small and are seen as decreased mean covers of all dwarf shrubs at all fertility levels (Fig.7). In the field layer, only the increased mean covers of graminoids and the decreased mean covers of sedge-like species after drainage are seen in all the inventories, as well as in in the data of the NFI in the 1950's (Fig. 7). These comparisons between different inventories further confirm that changes, such as the clear decrease of *Sphagnum* species and the increased mean cover of certain forest bryophytes, have taken place in the ground layer after drainage (Fig. 7, see also Mäkipää and Heikkinen 2003).

The changes that have taken place in the vegetation composition and abundances after the 1950's are considered to be mainly due to changes in land use and in forest management practices (see Vanha-Majamaa and Reinikainen 2000). The observed changes in the mean covers of the understorey vegetation between the 8th and 9th inventories are mainly caused by the post-drainage (secondary) succession and by changes in the density and cover of the tree canopy layers (see Hotanen *et al.* 2000).

4.4. Structural features of the overstorey of forested mire margins that contribute in maintaining the diversity of managed forests

4.4.1. Canopy layer structure, species diversity and composition

Generally, the variation in overstorey diversity could be explained on the basis of the same factors as the understorey diversity, namely fertility and site hydrology or post-drainage succession (IV). The number of tree and shrub species differed by site fertility in all drainage phases, which indicates that diversity in stand structure by type groups, as was found in this study, is more dependent on the fertility of the sites (e.g. Uuttera *et al.* 1997). There were no clear differences between the diversity indices of the tree and shrub species (IV), as was the case in the understorey vegetation (II–IV). There has been criticism that diversity indices are not, as such, entirely suitable for use in forestry because tree size and its variation, as well as many other important stand parameters, are not recorded (e.g. Lähde *et al.* 1999).

The effect of drainage was apparent as a change in the tree and shrub species composition and in the structural diversity expressed as percentage covers of the different canopy layers (IV). After drainage, the main change in the tree layer structure was the increased cover of the dominant trees at all fertility levels (IV). These changes can be explained on the basis of the competitive advantage obtained by the existing individual trees after drainage. The greater release growth of smaller compared to larger trees means that even the suppressed individual trees, especially birch and pine, benefit from the drawdown of the ground water level and subsequent improvement of the growth conditions (Hånell 1984, Hökkä and Laine 1988, Hökkä 1997, Uuttera *et al.* 1996, 1997, Sarkkola *et al.* 2003).

Minerotrophic mire sites, such as all the fertility levels in this study, have been found to develop into mixed stands of pubescent birch (*Betula pubescens*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) after drainage (Päivänen 1999). The more nutrient-poor sites will mainly support Scots pine (Keltikangas *et al.* 1986). On drained peatlands, pubescent birch is a typical pioneer tree species that can rapidly occupy sites that have free space as a result of ditching or cutting (Päivänen 1999). The increase of pubescent birch in this study was the clearest in the drained nutrient-rich sites (IV). The increase of deciduous trees, especially pubescent birch, has been found to be greatest in drained spruce swamps that were originally hardwood-spruce fens (so called nutrient-rich composite types) at the time of ditching (Keltikangas *et al.* 1986). According to the differences in the growth dynamics of spruce, pine and birch, spruce has lower growth rates, when small, than birch and pine, which grow fast when they are still small (e.g. Hökkä 1997). Spruce, on the other hand, may also grow fast when large (Mielikäinen 1985). The lower growth of small spruces on the most nutrient-rich sites after drainage might be also due to the fact that they grow in more densely stocked stands, on the average, already in the undrained phase and their growth might be also limited by competition from larger trees (e.g. Hökkä 1997), as well as from the pioneer tree species of birch (e.g. Päivänen 1999). The number of deciduous tree species and the presence of certain deciduous species (i.e. *Betula* sp., *Alnus* sp., and *Populus* tremula) and the cover of the shrub layer was still considerable in forested mire margin communities after drainage (see Norokorpi *et al.* 1997), but the abundances of species like *Alnus glutinosa* in the upper layers was clearly lower (cf. Aapala 2001).

4.4.2. Stand structure

The uneven-aged and uneven-sized structure, which is a typical feature of old-growth forests and also of pristine spruce mires (Heikurainen 1971, Gustavsen and Päivänen 1986, Segerström *et al.* 1994, Hörnberg *et al.* 1995, Segerström *et al.* 1996, Norokorpi *et al.* 1997), was the most evident feature on the undrained sites of this study (IV). The fact that drainage or site fertility had no effect on the number of canopy layers in the studied forested mire margin communities (IV) also indicates that the great variation in age and size was a relatively permanent phenomenon, because it has been found to continue during the first decades after drainage (e.g. Hökkä and Laine 1988, Uuttera *et al.* 1996, 1997, Päivänen 1999, Sarkkola *et al.* 2003). This was found in both the analyses of the diameter distribution and the canopy layer structure (IV).

The differences in the tree size distributions between undrained and drained forested mire margin sites of corresponding fertility levels were similar to the findings in other studies carried out on forest structure in undrained and drained forested peatlands (e.g. Hökkä and Laine 1988, Uuttera *et al.* 1996, 1997, Sarkkola *et al.* 2003). The reversed J-shape diameter distribution was clearly evident at all the fertility levels on the drained sites of this study. The most spruce-dominated, oligo-mesotrophic, spruce mire sites of this study had the most static reversed J-shaped diameter distribution in both the pristine and drained phases. The pristine phase differed in this respect from that of a case study carried out on pristine spruce mires in the middle boreal zone in Finland (Saaristo 1998), where the stem number distribution was found to be either only a slightly reversed J-shape or having two peaks, but the stand age was also higher than that of the spruce mires included in this study. In this study, in the most spruce-dominated group, the effect of drainage was most readily revealed by canopy layer structure analysis and by the change in tree species proportions than by the shape of the diameter distribution (see also Uuttera *et al.* 1996, 1997). Owing to a number of factors, such as the increase in stand density, caused by the improved growth conditions after drainage (Roy *et al.* 2000), the uneven-aged and uneven-sized structure may even be emphasized and continue for some decades after drainage (Hökkä and Laine 1988, Uuttera *et al.* 1996). This was clearly seen on the most nutrient-rich meso-eutrophic sites in the last drainage phase, and on the nutrient-poorer, oligotrophic sites in the middle phase of post-drainage succession (IV).

In this study the relatively small number of plots in the undrained phase, especially on the most nutrient-rich sites, made it difficult to compare the diameter distributions in each forest development class in each drainage phase and fertility level group (see Päivänen 1999). The uneven diameter distribution structure both in the undrained and drained phases of the forested mire margin sites of this study resembled that of the spruce and pine mire sites in the cross-sectional data of the whole 8th National Forest Inventory 1986–1994 (Hökkä *et al.* 2002), and differed from the more even diameter distribution structure of managed mineral soil forests (Hökkä *et al.* 2002).

4.4.3. Disturbance dynamics, restoration and management from the point of view of diversity

Instead of the earlier "balance-of-nature" paradigm, emphasizing stability, homogeneity, predictability of successional development and overemphasizing the role of succession and its assumed endpoint, the so called climax stage (Clements 1916, Cajander 1926), the role of disturbances has been found to be important in boreal forests (Kuuluvainen 2002). The earlier "balance-of-nature" paradigm, which was congruent with the optimality model of timber management, emphasizing maximum timber production through homogeneous stand and age-class structure, and avoiding losses due to natural disturbances, have been found to lead to a reduction in biodiversity and possibly the ability of ecosystems to adapt to environmental changes (Kouki 1994, Esseen *et al.* 1997, Linder and Östlund 1998, Siitonen 2001, Kuuluvainen 2002).

Since boreal forests are among the most disturbance-prone ecosystems (van der Maarel 1993), disturbance has a wide effect on the ecological conditions, vegetation and population dynamics in boreal forests (Zackrisson 1977, Kuuluvainen 1994). Natural disturbance, resulting from wildfires, tree uprooting, and animal activity, ranges from broad to fine scales (e.g. Zackrisson 1977, Kuuluvainen 1994, Linder *et al.* 1997, Rydgren *et al.* 1998). In many areas it has been found that small-scale disturbances that occur continuously can actually be more influential than infrequent catastrophic disturbances (Bergeron *et al.* 1999, Rouvinen *et al.* 2002).

In studies on old-growth *Picea abies* -swamp forests, Hörnberg *et al.* (1995) found that these sites are, in a short term perspective (< 300 years), characterized by an all-aged structure and a small-scale disturbance dynamics, in which individual trees reach senescence, die, and fall to the ground (Hörnberg *et al.* 1995). The tree layer and tree size distribution analyses, especially that of the undrained phase, gave hints of small-scale disturbance dynamics (see also Heikurainen 1971, Gustavsen and Päivänen 1986, Norokorpi *et al.* 1997), although information about the amount and quality of dead and decaying wood was not available and the highest stand age of the undrained spruce mire was not greater than about 200 years in this study.

An uneven-aged structure, indicating the continuity of natural regeneration (see Hörnberg *et al.* 1997), was also found in the tree layer structure analysis of this study, the lower undergrowth, shrub layer and tree and shrub seedlings (< 50 cm) being rather abundant at all fertility levels and in all drainage phases.

Disturbance dynamics on natural spruce mires and its effects on habitat and species diversity have not been studied in Finland (see Aapala 2001). According to recent palaeoecological studies carried out in Sweden (Segerström *et al.* 1994, Hörnberg *et al.* 1995, Segerström *et al.* 1996, Segertsröm 1997), spruce mires are not unchangeable refugees, but both natural and anthropogenic disturbances have occurred and resulted in changes in vegetation composition in long-term (> 300 years) dynamics (Segerström *et al.* 1994, Hörnberg *et al.* 1995, Segerström *et al.* 1996, Segerström 1997). On natural spruce mires, the fire frequency (often > 400 years) has been found to be generally much lower than that on mineral soil forests (50–180 years) (Zackrisson 1977, Hörnberg *et al.* 1998), which results in a longer continuation of undisturbed forest (see Aapala 2001). The effects of slash and burn cultivation, which continued up until the late 1800's in eastern Finland, might still be reflected in the tree stand structure and dynamics of spruce mires as a lack of old, large diameter trees or decaying wood (Aapala 2001).

Forest management is the main driving force affecting forest dynamics on drained forested mire margin sites but, as stated earlier in this study, there continues to be great variation in age and size during the first decades after drainage (e.g. Hökkä and Laine 1988, Uuttera *et al.* 1996, 1997, Päivänen 1999, Sarkkola *et al.* 2003). The drawdown of the water level and subsequent improvement of growth conditions have been found to even increase the regeneration and number and cover of seedlings reaching the measurable (DBH) height of 1.3 m in forest inventories (Hånell 1984, Hökkä and Laine 1988, Hökkä 1997, Uuttera *et al.* 1996, 1997, Sarkkola *et al.* 2003). This was also clearly seen in the different phases after drainage in this study. The diverse and uneven structure of drained spruce mires have been found to last for as much as 60 years after drainage, although there is a shift in the peaks of the DBH distributions towards larger diameters, and the stem number in smaller DBH classes decreases (Sarkkola *et al.* 2003). Some degree of self thinning (see e.g. Hynynen 1993), but almost more certainly the effects of forest management through removal of the "less valuable" and suppressed trees in order to allocate the growth resources to the more desired crop component to increase its production, results in the later phases of drained spruce mires becoming more unimodal or even-structured tree stands, and they start to resemble more the managed tree stands of mineral soil forests (see Sarkkola *et al.* 2003).

According to a recent study on the natural regeneration of spruce mires in central and northern Sweden (Hörnberg *et al.* 1997), small-scale disturbance dynamics was found. The seedlings of spruce have been found to survive the best on hummocks dominated by *Sphagnum girgensohnii* and/or *Polytrichum commune* and on decaying fallen trunks and stumps, and the poorest on microhabitats dominated by *Pleurozium schreberi* and *Hylocomium splendens* (Hörnberg *et al.* 1997). As was also observed in the study in hand, the cover of *Sphagnum girgensohnii* and *Polytrichum commune* decreased after drainage and that of the above mentioned forest mosses increased. This means that the regeneration of drained spruce and pine mires after commercial cuttings will be problematic (see Lukkala 1946, Hånell 1991, Hannerz and Hånell 1993). The sources of tree inequality on peatland sites during the first post-drainage tree generation are the original vertical structure of the stands, the mosaic of micro-sites, and their receptivity for regeneration (Saarinen 1997). The importance of these properties seems to decrease after regeneration (Saarinen 1997).

It was not until the 1990s, when the ecological sustainability of forest use became a significant issue in the marketing of forest products, that a major change took place in forestry practices as a result of international agreements to protect forest biodiversity (e.g. Kuuluvainen 2002). In Sweden and Finland, management guidelines based on site-specific consideration of natural disturbance (fire) dynamics have been influential in guiding many of the practical efforts to protect and restore forest biodiversity (Angelstam and Pettersson 1997, Angelstam 1998, Fries *et al.* 1998, Karvonen 1999). Guidelines for assessing and protecting the so-called key biotopes, usually small areas with high diversity value in managed forests such as e.g. the sites of herb-rich spruce mires, have also been produced (e.g. Meriluoto and Soininen 1998).

The restoration of drained spruce mires, especially in nature conservation areas, has become a very important issue in restoring the diversity in forested areas of Finland (Metsähallitus-Forest and Park Service 1999, Virkkala *et al.* 2000, Vasander *et al.* 2003). Some of the most urgent sites to be restored are densely wooded nutrient-rich peatlands (spruce mires), because they include both threatened peatland and forest species and often have a special landscape value (Metsähallitus-Forest and Park Service 1999, Virkkala *et al.* 2000). The total area of drained spruce mires in nature conservation areas in Finland that need to be restored is about 3 490 ha, which is about 17 % of all the peatland areas to be restored (Ennallistaminen… 2003).

Restoration of the uneven forest structure typical for old-growth forests and spruce mires, as described in this study, has been found to be problematic. In drained spruce mires, with a closed tree canopy, the dominant tree species is usually spruce, which is very sensitive to rapid changes in the ground water table level, that is caused by the normal restoration practices of filling and blocking the ditches (Heikkilä and Lindholm 1997, Ennallistaminen… 2003). New alternatives for restoring such areas, such as cutting some of the trees, have been suggested as one suitable approach, as this may raise the ground water table to a sufficient extent to start the recreation of a mosaic structure of hummocks and intermediate levels (Ennallistaminen… 2003). Generally, when restoring forest structure, alternative methods such as cutting small canopy openings, damaging some of the trees, and prescribed burning, have also been suggested (e.g. Tukia 2001). However, there is still a considerable need for research on alternative methods for restoring drained spruce mires.

5. Concluding remarks

This study (I–IV) supports the earlier conclusion that undrained mire margin forest communities conserve the different components of diversity.

The remnants of these biotopes, which represent less than 20 % of the undrained wetland area in Finland, deserve careful management of diversity at least (I–II).

According to the vegetation composition, the nutrient level of the forested mire sites in the last phase of post-drainage succession was generally higher than that in the remnants of the undrained sites. It was also evident that the effect of drainage further shortened the moisture gradient, which was already short in the pristine phase, and thus accentuated the importance of the nutrient status (III). Forest drainage has weakened their diveristy value (I–IV).

As stated e.g. by Tilman (1982), the enrichment of nutrients may cause an initial increase in diversity, but this can be only a transient phenomenon in the composition of the community. This conclusion was based on the groups of species (guilds) indicative of different ecological features (III). The drained forested mire margin communities change towards forest vegetation in which mesic and herb-rich forest species dominate and mire species are present as remnants (III).

The most drastic change after drainage took place in the ground layer of forested mire margin sites (III, IV). The decrease of *Sphagnum* species and their replacement by forest bryophyte species such as *Pleurozium schreberi* was clearly evident (III, IV). In the field layer, changes in different growth form groups were observed as an increase of the most common forest grasses and mesic forest herbs on meso-eutrophic drained sites, the increase of forests dwarf shrubs on oligotrophic sites, and the general decrease in sedges after drainage (IV). This reflected the change towards mineral soil forest vegetation in the understorey vegetation (III–IV).

According to this study, the effect of drainage on the tree stand was more evident as a change in tree and shrub species composition and abundance in different layers than in the tree size distributions (IV). This was most clearly seen as an increased percentage cover of the dominant trees and an increased percentage cover of deciduous trees, especially of pubescent birch (IV).

Further studies on the state of natural mire margin forests (spruce mires) are needed for developing silvicultural models that mimick natural forest dynamics and in restoring the drained spruce mires if they are to be successful in terms of ecosystem sustainability and biodiversity. Further studies are also needed on the regeneration of spruce mires under both undrained and drained conditions in Finland in order to find methods for preserving the diverse forest structure in later tree stand generations.

As the results from studies on natural forests are important as reference for the managed commercial forests (Hanski and Hammond 1995), and because there are nowadays so few remnants of natural forested mire margin sites in Finland, temporal studies on corresponding sites based on the NFI data stretching back to the 1950s would also be of utmost importance.

References

Aapala, K. 2001. Korpien ekologiset ominaispiirteet ja suojelutilanne (The protection status of spruce mires) In: Aapala, K. (ed.). Soidensuojelualueiden arviointi. (Summary: Assessment of the network of protected mires in Finland). Suomen ympäristö (the Finnish Environment) 490: 87-149. ISBN 952-11-0917-3.

Aapala, K. & Kokko, A. 1988. Changes in the ground vegetation of drained mires. (In Finnish with English Summary). Suo 39(3): 41-49.

Aapala, K., Heikkilä, R. & Lindholm, T. 1996. Protecting the diversity of Finnish mires. In: Vasander, H. (ed.). Peatlands in Finland. Finnish Peatland Society, Jyväskylä, Finland. pp. 45-57.

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968. Vegetation zones and their sections in northern Europe. Annales Botanici Fennici 5: 169-211.

Alatalo, R.V. 1981. Problems on measurement of evenness in ecology. Oikos 37: 199-204.

Anderson, L.S., Davies, C.E. & Moss, D. 1997. The UN Convention on Biological Diversity, Follow-up in EEA Member Countries 1996. European Environmental Agency. Topic Report 9/1997. Nature Conservation. Copenhagen. 40 p.

Angelstam, P. 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. Journal of Vegetation Science 9: 593-602.

Angelstam, P. & Pettersson, H. 1997. Principles of present Swedish forest biodiversity management. Ecological Bulletins 46: 191-203.

Annila, E. 2001. Monimuotoisuustutkimus. In: Siitonen, J. (ed.). Monimuotoinen metsä, Metsäluonnon monimuotoisuuden tutkimusohjelman loppuraportti. (In Finnish) Finnish Forest Research Institute. Research Papers 812: 5-8. ISBN 951-40-1787.

Austin, M.P. 1985. Continuum concept, ordination methods and niche theory. Annual Review of Ecology and Systematic 16: 39-61.

Austin, M.P. 1999. The potential contribution of vegetation ecology to biodiversity research. Ecography 22: 465-484.

Austin, M.P. & Meyers, J.A. 1996. Current approaches to modelling the environmental niche of eucalyptus: implications for management of forest biodiversity. Forest Ecology and Management 85: 95-106.

Austin, M.P., Nicholls, A.O., Doherty, M.D. & Meyers, J.A. 1994. Determining species response functions to an environmental gradient by means of a β-function. Journal of Vegetation Science 5: 215-228.

Attiwill, P.M. 1994. The disturbance dynamics of forest ecosystems: the ecological basis of conservative management. Forest Ecology and Management 147: 109-122.

Backman, A.L. 1919. Torvmarksundersökningar i mellersta Österbotten. Acta Forestalia Fennica 2 (3): 1-190.

Barbault, R. & Hochberg, M.E. 1992. Population and community level approaches to studying biodiversity in international research programs. Acta Oecologica 13(1): 137-146.

Belbin, L. 1991. Semi-strong hybrid scaling. A new ordination algorithm. Journal of Vegetation Science 2: 491-496.

Bergeron, Y., Engelmark, O., Harvey, B., Morin, H. & Sirois, L. (eds.). 1999. Key issues in disturbance dynamics in boreal forests. Journal of Vegetation Science 9: 463-610.

Bråkenhielm, S. & Qinghong, L. 1995. Comparison of field methods in vegetation monitoring. Water, Air and Soil Pollution 79: 75-87.

Cajander, A.K. 1926. The theory of forest types. Acta Forestalia Fennica 29(3): 1-108.

Clements, F.E. 1916. Plant succession: An analysis of the development of vegetation. Carnegie Institute Washington Publications 242. Washington, DC.

Di Castri, F. 1989. Global crises and the environment. In: Marini-Bettolo, G.B. (ed.). A modern approach to the protection of environment. Pontificiae Academiae Scientiarum Scritpa Varia 75, Vatican. pp. 7-39.

Di Castri, F. & Younes, T. 1990. Fonction de la diversité biologique au sein de l'écosystème. Acta Oecologica 11: 429-444.

Eilertsen, O., Økland, R.H., Økland, T. & Pedersen, O. 1990. Data manipulation and gradient lenght estimation in DCA ordination. Journal of Vegetation Science 1(2): 261-270.

Ennallistaminen suojelualueilla, Ennallistamistyöryhmän mietintö 2003. (Summary: Restoration in protected areas. Report by the working group on restoration). Suomen ympäristö (the Finnish Environment) 618: 1-220. ISBN 952-11-1376-6.
Esseen, P.A., Ehnström, B., Ericson, L. & Sjöberg, K. 1992. Boreal forests - The focal habitats of Fennoscandia. In: Hansson, L. (ed.). Ecological principles of nature conservation. Applications in temperate and boreal environments. Elsevier Applied Science. 430 p.
Esseen, P.A., Ehnström, B., Ericson, L. & Sjöberg, K. 1997. Boreal forests. Ecological Bulletins 46: 16-47.
Eurola, S. 1962. Über die regionale Einteilung der südfinnischen Moore. Annales Botanici Societatis Vanamo 33 (2): 1-243.
Eurola, S., Hicks, S. & Kaakinen, E. 1984. Key to Finnish mire types. In: Moore, P. D. (ed.). European mires: 11-117. Academic Press, London.
Eurola, S., Aapala, K., Kokko, A. & Nironen, M. 1991. Mire type statistics in the bog and southern aapa mire areas of Finland (60-66°N). Annales Botanici Fennici 28: 15-36.
Eurola, S., Huttunen, A. & Kukko-Oja, K. 1995a. Suokasvillisuusopas (A guide to mire vegetation, in Finnish). Oulanka Reports 14: 1-85.
Eurola, S., Laukkanen, A. & Moilanen, M. 1995b. The significance of the original mire site type in the classification of drained areas. An example from Muhos, Finland. Aquilo Series Botanica 35: 39-44.
Faith, D.P., Minchin, P.R. & Belbin, L. 1987. Compositional dissimilarity as a robust measure of ecological distances. Vegetatio 69: 57-68
Forest Resources of Europe 2000, CIS, North America, Australia, Japan and New Zealand. UN-ECE/FAO Contribution to the Global Forest Resources Assessment 2000. MAIN REPORT. Geneva Timber and Forest Study Papers, No. 17. UNITED NATIONS, New York and Geneva. 445 p.
Fries, C., Johansson, O., Pettersson, B., & Simonsson, P. 1997. Silvicultural models to maintain and restore natural stand structures in Swedish boreal forests. Forest Ecology and Management 94: 89-103.
Frey, T. E. A. 1973. The Finnish school and Forest-Site Types. In: Whittaker, R. H. (ed.). Ordination and classification of communities. The Hague. pp. 405-433.
Gauch, H.G. Jr. 1982. Multivariate analysis in community ecology. Cambridge Studies in Ecology. New York. 298 p.
Gustavsen, H. G. & Päivänen, J. 1986. Tree stands on virgin forested mires in the early 1950's. (In Finnish with English Summary). Folia Forestalia 673: 1-27.
Haila, Y. & Kouki. J. 1994. The phenomenon of biodiversity in conservation biology. Annales Zoologi Fennici 31: 5-18.
Hämet-Ahti, L., Suominen, J., Ulvinen, T., Uotila, P. & Vuokko, S. 1998. Retkeilykasvio (Field Flora of Finland), Ed. 4. Finnish Museum of Natural History, Botanical Museum. Helsinki. 656 p.
Hånell, B. 1984. Skogsdikningsboniteten hos Sveriges torvmarker. Sveriges lantbruksuniversitetet. Raporter i skogsekologi och skoglig marklära 50: 1-125.
Hånell, B. 1988. Post-drainage forest productivity of peatlands in Sweden. Canadian Journal of Forest Research 18: 1443-1456.
Hånell, B. 1991. Förnyelse av gransumpskog på bördiga torvmarker genom naturlig föryngrig under högskärm. Shelterwood regeneration of spruce forests on productive peatlands. Swedish University of Agricultural Sciences, Department of Silviculture. Report 32: 1-35 p.
Hannerz, M. & Hånell, B. 1993. Changes in the vascular plant vegetation after different cutting regimes on a productive peatland site in Central Sweden. Scandinavian Journal of Forest Research 8: 193–203.
Hanski, I. & Giplin, M. 1991. Metapopulation dynamics: brief history and conseptual domain. Biological Journal Linnean Society 42: 3-16.
Hanski, I. & Hammond, P. 1995. Biodiversity on boreal forests. Trends in Ecolocy and Evolution 10: 5-6.
Harper, J.L. 1977. Population Biology of Plants. Academic Press, London.
Hastie, T. & Tibshirani, R. 1990. Generalised additive models. Chapman and Hall.
Havas, P. 1961. Vegetation und Ökologie der ostfinnischen Hangmoore. Annales Botanici Societatis Vanamo 31(2): 1-188.

Heikkilä, R. 1994a. Mire conservation in Finland. (In Finnish with English Summary). Terra 106 (3): 226-231.
Heikkilä, R. 1994b. Threatened types of peatland. In: Forestry Environment Guide. Finnish Forest and Park Service, Helsinki. Appendix 3.
Heikkilä, H. & Lindholm, T. 1997. Soiden ennallistamistutkimus 1987-1996. (English Summary: The mire restoration study from 1987 to 1996, Finnish Forest and Park Service, Nature Protection) Metsähallituksen luonnonsuojelujulkaisuja Sarja A 81: 75 p. ISBN 952-446-036-X.
Heikkilä, R. & Lindholm, T. 2000. Conservation of the biodiversity of mires in Finland. In: Rochefort, L. & Daigle, J-Y (eds.). Sustaining Our Peatlands, Proceedings of Quebec 2000, the 11th International Peat Congress August 6-12, 2000, Quebec-City, Canada, Volume II. CSPP, IPS. pp. 1038-1043.
Heikkinen, J. & Reinikainen, A. 2000. Inventointiaineisto ja tulosten laskenta. In: Reinikainen, A., Mäkipää, R., Vanha-Majamaa, I. & Hotanen, J.-P. (eds.). Kasvit muuttuvassa metsäluonnossa. (English Summary: Changes in the frequency and abundance of forest and mire plants in Finland since 1950). Tammi, Helsinki. pp. 44-56.
Heikurainen, L. 1954. Korpisuus ruskorämeillä. Luonnon Tutkija 58: 42-48.
Heikurainen, L. 1957. Die kiefernbewachsenen eutrophen Moore Norrfinnlands. Annales Botanici Societatis Vanamo 26(2): 1-189.
Heikurainen, L. 1971. Virgin peatland forests in Finland. Acta Agraria Fennica 123: 11-26.
Heikurainen, L. 1979. Peatland classification in Finland and its utilization for forestry. In: Kivinen, E., Heikurainen, L. & Pakarinen, P. (eds.). Classification of peat and peatlands. IPS, Helsinki. pp. 135-146.
Heikurainen, L. & Pakarinen, P. 1982. Mire vegetation and site types. In: Laine, J. (ed.). Peatlands and their utilization in Finland. Finnish Peatland Society. Helsinki. pp. 14-23
Heino, R. & Hellsten, E. 1983. Climatological statistics in Finland 1961-1980. Supplement to the Meteorological Yearbook of Finland 80 (1a): 1-560.
Hill, M.O. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54 (2): 427-432.
Hill, M.O. 1979. TWINSPAN- a fortran program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. Cornell University, Itacha, NY. 90 p.
Hill, M.O. & Gauch, H.G. 1980. Detrended correspondence analysis, an improved ordination technique. Vegetatio 42: 47-58.
Hökkä, H. 1997. Models predicting growth and yield in drained peatlands in Finland. Academic dissertation of the Faculty of Agriculture and Forestry of the University of Helsinki. The Finnish Forest Research Institute, Research Papers 651: 1-178.
Hökkä, H. & Laine, J. 1988. Post-drainage development of structural characteristics in peatland forest stands. (In Finnish with English Summary). Silva Fennica 22(1): 45-65.
Hökkä, H., Kaunisto, S., Korhonen, K.T., Päivänen, J., Reinikainen, A. & Tomppo, E. 2002. Suomen suometsät 1951-1994. Metsätieteen aikakauskirja 2B: 201-357 (In Finnish). Finnish Forest Research Institute, Finnish Society of Forest Science. ISSN 1455-2515.
Holmen, H. 1964. Forest ecological studies on drained peat land in the province of Uppland, Sweden. Parts I-III. Studia Forestalia Suecica 16: 1-236.
Hörnberg, G.1995. Boreal old-growth Picea abies swamp-forests in Sweden. – disturbance history, structure and regeneration pattern. Doctoral dissertation, Department of Forest Vegetation Ecology, Swedish University of Agricultural Sciences, Umeå, Sweden.
Hörnberg, G., Ohlsson, M. & Zackrisson, O. 1995. Stand dynamics, regeneration patterns and long-term continuity in boreal old-growth Picea abies swamp forests. Journal of Vegetation Science 6: 291-298.
Hörnberg, G., Ohlson, M. & Zackrisson, O. 1997. Influence of bryophytes and microrelief conditions on Picea abies seed regeneration patterns in boreal old-growth swamp forests. Canadian Journal of Forest Research 27: 1015-1023.
Hörnberg, G., Zackrisson, O., Segerström, U., Svensson, B.W., Ohlson, M. & Bradshaw R. 1998. Boreal swamp forests. Biodiversity "hotspots" in an impoverished forest landscape. Bioscience 48: 795-802.
Hotanen, J-P. 2000. Carex globularis In: Reinikainen, A., Hotanen, J-P., Mäkipää, R., Vanha-Majamaa, I. 2000 (eds.). Kasvit muuttuvassa metsäluonnossa. (Summary: Changes in the frequency and abundance of forest and mire plants in Finland since 1950). Tammi, Helsinki. pp. 164-165.

Hotanen, J-P. & Nousiainen, H. 1990. The parity between numerical units and site types of forest and mire vegetation. (In Finnish with English Summary). Folia Forestalia 763: 54 p.
Hotanen, J-P. & Vasander, H. 1992. Post-drainage development of vegetation in southern Finnish peatlands studied by numerical analysis. (In Finnish with English Summary). Suo - Mires and Peat 43(1): 1-10.
Hotanen, J-P., Nousiainen, H. & Paalamo, P. 1999. Vegetation succession and diversity on Teuravuoma experimental drainage area in northern Finland. Suo - Mires and Peat 50 (2): 55-82.
Hotanen, J-P., Korpela, L., Mikkola, K., Mäkipää, R., Nousiainen, H., Reinikainen, A., Salemaa, M., Silfverberg, K., Tamminen, M., Tonteri, T. & Vanha-Majamaa, I. 2000. Metsä- ja suokasvien yleisyys ja runsaus 1951-95. In: Reinikainen, A., Hotanen, J-P., Mäkipää, R., Vanha-Majamaa, I. 2000 (eds.). Kasvit muuttuvassa metsäluonnossa. (Summary: Changes in the frequency and abundance of forest and mire plants in Finland since 1950). Tammi, Helsinki. pp. 84-282.
Huikari, O. 1974. Site quality estimation on forest land. In: Heikurainen, L. (ed.). Proceedings of the International Symposium on Forest Drainage, 2nd-6th September, 1974. Jyväskylä-Oulu, Finland, IPS. pp. 15-24.
Hunter, M.L. 1999 (ed.). Maintaining biodiversity in forest ecosystems. Cambridge University Press. United Kingdom 698 p.
Huston, M.A. 1994. Biological Diversity. The Coexistence of Species on Changing Landscapes. Cambridge, Cambridge University Press, 681 p.
Hynynen, J. 1993. Self-thinning models for even-aged stands of Pinus sylvestris, Picea abies and Betula pendula. Scandinavian Journal of Forest Research 8: 326-336.
Ilvessalo, Y. 1956. The forests of Finland from 1921-24 to 1951-53. A survey based on three national forest inventories. (In Finnish with English Summary). Communicationes Instuti Forestalis Fenniae 47 (1): 1-227.
Ilvessalo, Y. 1957. The mires of Finland. A survey based on the 3 rd National Forest Inventory. (In Finnish with English Summary). Suo 8: 51-61.
Interim Report on the Follow-up of the Second Ministerial Conference Ministry of Agriculture and Forestry. Helsinki 1995.
Jeglum, J. K. 1991. Definition of trophic classes in wooded peatlands by means of vegetation types and plant indicators. Annales Botanici Fennici 28: 175-192.
Jongman, R.G.H., ter Braak, C.J.F. & van Tongeren, O.F. 1987. Data analysis in community and landscape ecology. Pudoc, Wageningen.
Jukola-Sulonen, E-L. & Salemaa, M. 1985. A comparison of different sampling methods of quantitative vegetation analysis. Silva Fennica 19 (3): 325-337.
Kalela, A. 1961. Waldvegetationszonen Finnlands und ihre klimatischen paralleltypen. Archivum Societatis Zoologicae Botanicae Fennicae 'Vanamo' 16 (Suppl.): 65-83.
Kalliola, R. 1973. Suomen yleisimpien metsätyyppien floristinen rakenne. (The floristic composition of the most common forest site types in Finland). Suomen kasvimaantiede (Plant geography of Finland, in Finnish). Helsinki. pp. 260-267.
Kangas, P., Jäppinen, J-P., von Weissenberg, M. & Karjalainen, H. (eds.). 1997. Suomen biologista monimuotoisuutta koskeva kansallinen toimintaohjelma 1997-2005. Suomen ympäristö, Luonto ja luonnonvarat 137. Ympäristöministeriö Helsinki. 189 p.
Karvonen, L. 1999. Alue-ekologisen suunnittelun ohje (Guide to landscape ecological planning). (In Finnish). Metsähallitus (Finnish Forest and Park Service). 23 p.
Kaunisto, S. & Paavilainen, E. 1988. Nutrient stores in old drainage areas and growth of stands. Communicationes Instituti Forestalis Fenniae 145: 39 p.
Keltikangas, M., Laine, J., Puttonen, P., & Seppälä, K. 1986. Vuosina 1930-1978 metsäojitetut suot: Ojitusalueiden inventoinnin tuloksia. (Summary: Peatlands drained for forestry during 1930- 1978. Results from field surveys of drained areas). Acta Forestalia Fennica 193: 1-94.
Kempton, R.A. & Taylor, L.R. 1976. Models and statistics for species diversity. Nature 262: 818-820.
Kenkel, N.C. & Orloci, L. 1986. Applying metric and nonmetric multidimensional scaling to ecological studies: some new results. Ecology 67 (4): 919-928.
Knox, R.G. 1989. Effects of detrending and rescaling on correspondence analysis: solution stability and accuracy. Vegetatio 83: 129-136.
Koponen, T., Isoviita, P. & Lammes, T. 1977. The bryophytes of Finland: An annotated checklist. Flora Fennica 6: 1-77.

Korpela, L. 1994. Do the diversity indices specify classification and the interpretation of ordinations? In: Reinikainen. A. & Lehtinen, K-M. (eds.). Workshop of forest site classification, Vantaa, Finland, October 27, 1994. (in Finnish with English Summary). The Finnish Forest Research Institute. Research Papers 531: 45-50. ISBN 951-40-1401-4.
Korpela, L. 1998. Reunavaikutteisen suokasvillisuuden merkitys metsien monimuotoisuudelle. In: Annila, E. (ed.). Monimuotoinen metsä. Metsäluonnon monimuotoisuuden tutkimusohjelman väliraportti. (In Finnish). The Finnish Forest Research Institute. Research Papers 705: 163-177. ISBN 951-40-1647-5.
Korpela, L. 2004. Structural and species diversity of boreal forested mire margin communities in South and Central Finland– effect of drainage. Silva Fennica (submitted manuscript).
Korpela, L. & Reinikainen, A. 1996a. Patterns of diversity in boreal mire margin vegetation. Suo - Mires and Peat 47(1): 17-28.
Korpela, L. & Reinikainen, A. 1996b. Sphagnum communities before and during the post-drainage succession of boreal forested mire margin sites. Proceedings of the Second International Symposium on the Biology of Sphagnum (IAB), Université Laval, Québec-City, Canada, July 12th-13th 1996. Faculté des sciences de l'agriculture et de l'alimentation Université Laval, Canada. pp. 38.
Kouki, J. (ed.) 1994. Biodiversity in the Fennoscandian boreal forests: Natural variation and its management. Annales Zoologi Fennici 31: 3-4.
Kotiranta, H. & Niemelä, T. 1996. Uhanalaiset käävät Suomessa. Ympäristöopas 10: 1-184. Suomen Ympäristökeskus, Helsinki.
Küchler, A.W. 1967. Vegetation mapping. Ronald Press. New York, N.Y. 462 p.
Küchler, A.W. & Zonnevelt, I. S. (eds.) 1988. Vegetation mapping. Handbook of vegetation science 10. Kluwer Academic Publishers, Dorcdrecht Boston London. 635 p.
Kutnar, L. & Martinčič, A. 2003. Ecological relationships between vegetation and soil-related variables along the mire margin-mire expanse gradient in the eastern Julian Alps, Slovenia. Annales Botanici Fennici 40: 177-189.
Kuuluvainen, T. 1994. Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland, a review. Annales Zoologici Fennici 31: 35-51.
Kuuluvainen, T. 2002. Natural variability of forests as reference for restoring and managing biological diversity in boreal Fennoscandia. In: Korpilahti, E & Kuuluvainen, T. (eds.). Disturbance Dynamics in Boreal Forests: Defining the Ecological Basis of Restoration and Management of Biodiversity. Silva Fennica 36(1): 97-125.
Kuusela, K. & Salminen, S. 1969. The 5th National Forest Inventory in Finland. General design, instructions for field work and data processing. Communicationes Instituti Forestalis Fenniae 69 (4): 1-72.
Kuusinen, M. 1996. Importance of spruce swamp-forests for epiphyte diversity and flora on Picea abies in southern and middle boreal Finland. Ecography 19: 41-45.
Kuusipalo, J. 1985. An ecological study of upland forest site classification in southern Finland. Acta Forestalia Fennica 192: 1-77.
Laaka, S. 1992. The threatened epixylic bryophytes in old primeval forests in Finland. Biological Conservation 59: 151-154.
Lähde, E., Laiho, O., Norokorpi, Y. & Saksa, T. 1999. Stand structure as the basis of diversity index. Forest Ecology and Management 115: 213-220.
Lahti, T. & Väisänen, R. A. 1987. Ecological gradients of boreal forests in South Finland: an ordination test of Cajander's forest site type theory. Vegetatio 68: 145-156.
Laiho, R., Vasander, H., Penttilä, T. & Laine, J. 2003. Dynamics of plant -mediated organic matter and nutrient cycling following water-level drawdown in boreal peatlands. Global Biogeochemical Cycles 17 (2): 1053, 22-1 - 22-11.
Laine, J. 1989. Classification of peatlands drained for forestry. (In Finnish with English Summary). Suo - Mires and Peat 40: 37-51.
Laine, J. & Vanha-Majamaa, I. 1992. Vegetation ecology along a trophic gradient on drained pine mires in southern Finland. Annales Botanici Fennici 29: 213-233.
Laine, J. & Vasander, H. 1996. Ecology and vegetation gradients of peatlands. In: Vasander, H. (ed.). 1996. Peatlands in Finland. Finnish Peatland Society, Helsinki. 168 p.
Laine, J., Vasander, H. & Laiho, R. 1995. Long-term effects of water level draw down on the vegetation of drained pine mires in Southern Finland. Journal of Applied Ecology 32: 785-802.

Laine, J., Komulainen, V.-M., Laiho, R., Minkkinen, K., Rastinmäki, A., Sallantaus, T., Sarkkola, S., Silvan, N., Tolonen, K., Tuittila, E.-V., Vasander, H. & Päivänen, J. 2004. Lakkasuo – a guide to mire ecosystem. University of Helsinki Department of Forest Ecology Publications 31: 123 p.
Larmola, T. 1997. Kasvillisuuden muutokset ojituksen jälkeen Oriveden Lakkasuolla ja Vilppulan Jaakkoinsuolla. Pro gradu, Helsingin yliopisto, Ekologian ja systematiikan laitos, Systemaattisen biologian osasto. 56 p.
Larsen, J.B. 1995. Ecological stability of forests and sustainable silviculture. Forest Ecology and Management 73: 85-96.
Leppäniemi, P., Hallikainen, V., Mikkola, K., Puoskari, J. & Sepponen, P. 1998. Forest structure classes in Central Finnish Lapland. Scandinavian Journal of Forest Research 13: 442-450.
Linder, P., Elfving, B. & Zackrisson, O. 1997. Stand structure and successional trends in virgin boreal forest reserves in Sweden. Forest Ecology and Management 98: 17-33.
Linder, P. & Östlund, L. 1998. Structural changes in three mid-boreal Swedish forest landscapes 1885-1996. Biological Conservation 85: 9-19.
Lindholm, T. & Vasander, H. 1987. Vegetation and stand development of mesic forest after prescribed burning. Silva Fennica 21 (3): 259-278.
Lindholm, T & Tuominen, S. 1989. Vanhojen luonnonmetsien rakennetyypit eräillä eteläboreaalisilla luonnonsuojelualueilla. Summary: The structure classes of southern boreal natural forests in some Finnish nature protection areas. In: Poikajärvi, H., Sepponen, P., Varmola, M. (eds.). Research activities on the nature conservation areas. Folia Forestalia 736 (7): 46-52.
Lukkala, O.J. 1929. Über die Dicke der Torfschicht und die Neigungsverhältnisse der Mooroberfläche auf verschiedenen Moortypen. Acta Forestalia Fennica 34 (16): 1-16.
Lukkala, O. J. 1946. Korpimetsien luontainen uudistaminen. Referat: Die naturliche Verjungung der Bruchwälder. Communicationes Instituti Forestalis Fenniae 34(3): 1–150.
Lumiala, O.V. 1937. Über die Standortsfaktoren bei den Wasser-und Moorplflanzen sowie deren Untersuchung. Ann. Acad. Sci. Fennicae (IV Biol.) 6: 1-47.
MacArthur, R. H. 1965. Pattern in species diversity. Biological Review 40: 510-533.
MacArthur, R.H. & MacArthur J.W. 1961. On bird species diversity. Ecology 42: 594-598.
Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Great Britain. 179 p.
Mäkipää, R. & Heikkinen, J. 2003. Large-scale changes in abundance of terricolous bryophytes and macrolichens in Finland. Journal of Vegetation Science 14 (4): 497-508.
Malmer, N. 1985. Remarks to the classification of mires and mire vegetation - Scandinavian arguments. Aquilo Ser. Botanica 21: 9-17.
Malmström, C. 1928. Våra torvmarker ur skogsdiknings synpunkt. (Summary: Our peat areas from the point of forest-draining). Meddelanden från statens skogsforskningsinstitut 24: 251-372.
Maltamo, M. 2002. Puuston rakennetunnusten analysointi, vertailu ja ennustaminen. In: Kangas, J., Kokko, A., Jokimäki, J. & Store, R. (eds.). Tutkimuksia ekologisen informaation liittämisestä metsäsuunnitteluun. The Finnish Forest Research Institute, Research Papers 858: 45-57.
Mattila, E. & Penttilä, T. 1987. Peatland forests of Lappi and Koillis-Suomi forestry board districts, North Finland, 1952-1984. (In Finnish with English Summary). Folia Forestalia 703: 1-49.
Meriluoto, M. & Soininen, T. 1998. Metsäluonnon arvokkaat elinympäristöt. (In Finnish). Metsälehti Kustannus, Metsätalouden kehittämiskeskus Tapio. 192 p. ISBN 952-5118-12-6.
Metsähallitus, Forest and Park Service (Natural Heritage Services) 1999. The Principles of Protected Area Management in Finland 1999. Guidelines on the Aims, Function and Management of State-owned Protected Areas. Nature Protection Publications of the Finnish Forest and Park Service, Series B No 54. Helsinki, Finland.
Mielikäinen, K. 1985. Koivusekoituksen vaikutus kuusikon rakenteeseen ja kehitykseen. (Summary: Effect of an admixture of birch on the structure and development of Norway spruce stands). Communicationes Instituti Forestalis Fenniae 133. 79 p.
Minchin, P.R. 1987. An evaluation of the relative robustness of techniques of ecological ordination. Vegetatio 69: 89-107.
Minchin, P.R. 1989. Montane vegetation of the Mt. Field Massif, Tasmania: a test of some hypotheses about properties of community patterns. Vegetatio 83: 97-110.
Minchin, P.R. 1991. DECODA. Database for ecological community data. Vers. 2.04. Australian National University, Canberra.
Molinari, J. 1989. A calibrated index for the measurement of evenness. Oikos 56: 319-326.

Moss, D. 1978. Diversity of woodland song-bird populations. J Anim. Ecol. 47: 521-527.
Norokorpi, Y., Lähde, E., Laiho, O. & Saksa, T. 1997. Stand Structure, Dynamics, and Diversity of Virgin Forests on Northern Peatlands. In: Trettin, C., Jurgensen, M. F., Grigal, D. F., Gale, M. R., & Jeglum, J. (eds.). Northern Forested Wetlands, Ecology and Management. pp. 73-87. Lewis Publishers, Florida.
Nurminen, K. 1964. Suomen korpikasvillisuuden ekologisesta ryhmittymisestä. Pro gradu-tutkielma, Helsingin yliopisto, Kasvitieteen laitos. Helsinki. 88 p.
Ohlson, M. 1990. Dikning av näringsrik sumpskog - ett hot mot våra mest artrika skogsekosystem. Skogsfakta Flora, fauna, miljö, 14. (In Swedish, issued by the Swedish University of Agricultural Sciences, Uppsala).
Ohlson, M., Söderström, L., Hörnberg, G., Zackrisson, O. & Hermansson, J. 1997. Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. Biological Conservation 81: 221-231.
Ohlson, M. & Tyrterud, E. 1999. Long-term spruce forest continuity – a challenge for a sustainable Scandinavian forestry. Forest Ecology and Management 124: 27-34.
Økland, R.H. 1986. Rescaling of ecological gradients. Calculation of ecological distance between vegetation stands by means of their floristic composition. Nordic Journal of Botany 6: 651-660.
Økland, R.H. 1989. A phytoecological study of the mire Northern Kisselbergmosen, SE Norway. I. Introduction, flora, vegetation and ecological conditions. Sommerfeltia 8: 1-172.
Økland, R.H. 1990. Vegetation ecology: theory, methods and applications with reference to Fennoscandia. Sommerfeltia Supplement 1: 1-233.
Økland, R.H. 1995. Persistance of vascular plants in Norwegian boreal coniferous forests. Ecography 18: 3-14.
Økland, R.H. 1999. On the variation explained by ordination and constrained ordination axes. Journal of Vegetation Science 10: 131-136.
Økland, R. H. & Bendiksen, E. 1985. The vegetation of the forest-alpine transition in the Gunningsdalen area, Telemark, S.Norway. Sommerfeltia 2: 1-224.
Økland, T. 1996. Vegetation-environment relationships of boreal spruce forests in ten monitoring reference areas in Norway. Sommerfeltia 22: 1- 349.
Oksanen, J. 1988. A note on the occasional instability of detrending in correspondence analysis. Vegetatio 74: 29-32.
Oksanen, J. & Minchin, P. R. 1997. Instability of ordination results under changes input data order: explanations and remedies. Journal of Vegetation Science 8: 447-454.
Paavilainen, E. & Tiihonen, P. 1988. Peatland forests in Finland in 1951-1984. (In Finnish with English Summary). Folia Forestalia 714. 29 p.
Paavilainen, E. & Päivänen, J. 1995. Peatland Forestry. Ecology and Principles. Ecological Studies 111. Springer-Verlag, Berlin-Heidelberg. 248 p.
Päivänen, J. 1999. Tree stand structure on pristine peatlands and changes after forest drainage. International Peat Journal 9: 66-72.
Päivinen, R. 1987. Metsän inventoinnin suunnittelumalli. (Summary: A planning model for forest inventory). Joensuun yliopiston luonnontieteellisiä julkaisuja, University of Joensuu. Publications in Science, No.11. 179 p.
Pakarinen, P. 1979. Ecological indicators and species groups of bryophytes in boreal peatlands. In: Kivinen, E., Heikurainen, L. & Pakarinen, P. (eds.). Classification of peat and peatlands. International Peat Society. pp. 121-134.
Pakarinen, P. 1982. Etelä-Suomen suo- ja metsätyyppien numeerisesta luokittelusta. (Summary: Numerical classification of south Finnish mire and forest types.) Suo 33: 97-103.
Pakarinen, P. 1984. Cover estimation and sampling of boreal vegetation in Northern Europe. In: Knapp, R. (ed.). Sampling methods and taxon analysis in vegetation science. Handbook of Vegetation Science, part 4. Dr. W. Junk Publishers, The Hague. pp. 35-44.
Pakarinen, P. & Ruuhijärvi, R. 1978. Ordination of northern Finnish peatland vegetation with factor analysis and reciprocal averaging. Annales Botanici Fennici 15: 147-157.
Parviainen, J. 1996. Tasks of Forest Biodiversity Management and Monitoring Deriving from International Agreements. Silva Fennica 30(2-3): 373-377.
Peet, R.K. 1974. The measurement of species diversity. Annual Review of Ecology and Systematics 5: 285-307.

Peet, R. K., Knox, R.G., Case, J.S. & Allen, R.B. 1988. Putting things in order: the advantages of detrended correspondence analysis. American Naturalist 131: 924-934.

Peltola, A. (ed.) 2003. Finnish Statistical Yearbook of Forestry 2003. SVT Agriculture, forestry and fishery 2003: 45. Finnish Forest Research Institute, Helsinki. 388 p.

Persson, Å. 1961a. Mire and spring vegetation in an area north of the Lake Torneträsk, Torne Lappmark, Sweden. I Description of the vegetation. Opera botanica 6 (1): 1-187.

Persson, Å. 1961b. Mire and spring vegetation in an area north of the Lake Torneträsk, Torne Lappmark, Sweden. II Habitat conditions. Opera botanica 6 (3): 1-100.

Pickett, S.T.A., Ostfeld, R.S., Shachak, M. & Likens, G.E. 1997. The ecological basis of conservation: heterogeneity, ecosystems, and biodiversity. Chapman & Hall, New York.

Pielou, E.C. 1966. The measurement of diversity in different types of biological collections. Journal of Theoretical Biology 13: 131-144.

Pienimäki, T. 1982. Kasvillisuuden ojituksen jälkeinen kehitys eräillä suotyypeillä Pohjois-Pohjanmaalla. (Summary: Development of vegetation on some drained mire site types in North-Ostrobotnia). Suo 33(4-5): 113-123.

Pitkänen, S. 1997. Correlation between stand structure and ground vegetation: an analytical approach. Plant Ecology 131: 109-126.

Pitkänen, S. 1998. Diversity of ground vegetation in managed boreal forests in relation to the properties of tree stand and site. Doctoral dissertation. The Faculty of Forestry, University of Joensuu, Finland. 35 p.

Pitkänen, S. 2000. Classification of vegetational diversity in managed boreal forests in Eastern Finland. Plant Ecology 146: 11-28.

Platonov, G.M. 1976. The Shift of Bog Vegetation Under the Influence of Drying. In: P'yvachenko, N. (ed.). Interrelation of Forest and Bog - Results of Station Research. New Delhi. pp. 129-140.

Podani, J. 1989. Comparison of ordinations and classifications of vegetation data. Vegetatio 83: 111-126.

Prieditis, N. 1997. Vegetation of wetland forests in Latvia: A synopsis. Annales Botanici Fennici 34: 91-108.

Prieditis, N. 1999. Status of wetland forests and their structural richness in Latvia. Environmental Conservation 26 (4): 332-346.

Rautiainen, V-P., Ryttäri, T., Kurtto, A. & Väre, H. (eds.). 2002. Putkilokasvien uhanalaisuuden arviointi - lajikohtaiset perustelut. Suomen ympäristö. Luonto ja luonnonvarat. Suomen ympäristökeskuksen julkaisuja 593. ISBN 952-11-1283-0 (PDF).

Recher, H.F. 1969. Bird species diversity and habitat diversity in Australia and North America. American Naturalist 103: 75-80.

Reinikainen, A. 1965. Vegetationsuntersuchungen auf dem Walddüngsungs-Versuchsfeld des Moores Kivisuo, Kirchsp. Leivonmäki, Mittelfinnland. Communicationes Instituti Forestalis Fenniae 59.5: 62 p.

Reinikainen, A. 1984. Suotyypit ja ojituksen vaikutus pintakasvillisuuteen. In: Paarlahti, K. (ed.). Jaakkoinsuon koeojitusalue 75 vuotta. Finnish Forest Research Institute. Research Papers 156: 7-21.

Reinikainen, A. 1988. Metsäojitettujen soiden kasvupaikkaluokituksen suunnanhakua (Summary: The need of improving the site classification of mires drained for forestry). Suo 39: 61-71.

Reinikainen, A. 1990. Ecological monitoring as part of the Finnish National Forest Inventory. In: Proceedings of the seminar on ecological statistics. Rome, 28 March - 1 April 1988. Annali di Statistica 119 (IX): 8.

Reinikainen, A., Lindholm, T. & Vasander, H. 1984. Ecological variation of mire site types in the small kettle-hole mire Heinisuo, southern Finland. Annales Botanici Fennici 21: 79-101.

Reinikainen, A., Hotanen, J-P., Mäkipää, R. & Vanha-Majamaa, I. 2000 (eds.). Kasvit muuttuvassa metsäluonnossa. (Summary: Changes in the frequency and abundance of forest and mire plants in Finland since 1950). Tammi, Helsinki. 384 p.

Rescia, A.J., Schmitz, M.F., Martin de Agar, P., de Pablo, C.L., Atauri, J.A. & Pineda, F.D. 1994. Influence of landscape complexity and land management on woody plant diversity in northern Spain. Journal of Vegetation Science 5: 505-516.

Roy, V., Ruel, J-C. & Plamondon, A.P. 2000. Establishment, growth and survival of natural regeneration after clearcutting and drainage on forested wetlands. Forest Ecology and Management 129: 253-267.

Rouvinen, S., Kuuluvainen, T. & Siitonen, J. 2002. Tree mortality in a Pinus sylvestris dominated boreal forest landscape in Vienansalo wilderness, eastern Fennoscandia. Silva Fennica 36(1): 127-145.
Ruhling, Å., Rasmussen, L., Pilegaard, K., Mäkinen, A. & Steinnes, E. 1987. Survey of atmospheric heavy metal deposition in the Nordic countries in 1985. Nord 1987:21. The Nordic Council of Ministers. 44 p.
Ruuhijärvi, R. 1960. Über die regionale Einteilung der nordfinnischen Moore. Annales Botanici Societatis Vanamo 31 (1): 1-360.
Ruuhijärvi, R. 1981. Suotyypit. In: Nurminen, M. (ed.). Otavan Iso Ensyklopedia 9: 6707-6713.
Ruuhijärvi, R. 1982. Mire complex types in Finland. In: Laine, J. (ed.). Peatlands and their utilization in Finland. Finnish Peatland Society, Helsinki. pp. 24-28.
Rydgren, K., Økland, R.H. & Økland, T. 1998. Population biology of the clonal moss Hylocomium splendens in Norwegian boreal spruce forests. 4. Effects of experimental fine-scale disturbance. Oikos 82: 5-19.
Saarinen, M. 1997. Effect of site factors on restocking of old drainage areas. A literature review. (In Finnish with English Summary) Suo- Mires and Peat 48(3): 61-70.
Saaristo, L. 1998. Korpikolvan elinympäristövaatimukset ja populaatiorakenne. Pro-gradu tutkielma. Ekologian ja systematiikan laitos, Populaatiobiologian osasto. Helsingin yliopisto. 51 p.
Salemaa, M., Jukola-Sulonen, E-L. & Lindgren, M. 1991. Forest condition in Finland, 1986-1990. Silva Fennica 25 (3): 147-175.
Sarasto, J. 1957. Metsän kasvattamiseksi ojitettujen soiden aluskasvillisuuden rakenteesta ja kehityksestä Suomen eteläpuoliskossa (Referat: Über Struktur und Entwicklung der Bodenvegetation auf für Walderziehung entwässerten Mooren in der Südlichen Hälfte Finnlands). Acta Forestalia Fennica 65(7): 1-108.
Sarasto, J. 1961. Über die Klassifierung der für Walderziehung entwässerten Moore. Acta Forestalia Fennica 74(5): 1-57.
Sarkkola, S., Alenius, V., Hökkä, H., Laiho, R., Päivänen, J. & Penttilä, T. 2003. Changes in structural inequality in Norway spruce stands on peatlands sites after water-level drawdown. Canadian Journal of Forest Research 33: 222-231.
Schönemann, P. H. & Carroll, R. M. 1970. Fitting one matrix to another under choice of central dilation and a rigid motion. Psychometrika 35: 245-255.
Segerström, U. 1997. Long-term dynamics of vegetation and disturbance of a southern boreal spruce swamp forest. Journal of Vegetation Science 8: 295-306.
Segerström, U., Bradshaw, R., Hörnberg, G. & Bohlin, E. 1994. Disturbance history of swamp forest refuge in northern Sweden. Biological Conservation 68: 189-196.
Segerström, U., Hörnberg, G. & Bradshaw, R. 1996. The 9000 year history of vegetation development and distrubance patterns of a swamp-forest in Dalarna, northern Sweden. The Holocene 6(1): 37-48.
Shannon, C.E. & Weaver, W. 1949. The mathematical theory of communication. Univeristy of Illionois Press, Urbana. 117 p.
Siitonen, J. 1998. Lahopuun merkitys metsäluonnon monimuotoisuudelle - kirjallisuuskatsaus. Julkaisussa: Annila, E. (ed.). Monimuotoinen metsä. Metsäluonnon monimuotoisuuden tutkimusohjelman väliraportti. Finnish Forest Research Institute. Research Papers 705: 131-163.
Siitonen, J. & Saaristo, L. 2000. Habitat requirements and conservation of Phyto kolwenis, a beetle species of old-growth boreal forest. Biological Conservation 94: 211-220.
Siitonen, J. 2001. Forest management, coarse wood debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49: 11-41.
Silfverberg, U. 1991. Eteläsuomalaisten korpikoealojen ojituksen jälkeinen kehitys. Pro gradu-tutkielma. Helsingin yliopisto, Suometsätieteen laitos. 75 p.
Sjöberg, K. & Ericson, L. 1992. Forested and open wetland complexes. In: Hansson, L. (ed.). Ecological principals of nature conservation. Application in temperate and boreal environments. Conservation Ecology Series. Elsevier Science Publications. London. pp. 326-351.
Sjöberg, K. & Ericson, L. 1997. Mosaic boreal landscapes with open and forested wetlands. Ecological Bulletins 46: 48-60.
Sjörs, H. 1948. Myrvegetation i Bergslagen. Acta Phytogeographica Suecica 21: 1-299.
Sjörs, H. 1983. Mires of Sweden. In: Gore, A. J. P. (ed.). Mires: swamp, bog, fen and moor: 69-94. Ecosystems of the World. 4B, Regional studies, Elsevier, Amsterdam.

Solbrig, O.T. 1991. Biodiversity. Scientific issues and collaborative research proposals. MAB Digest 9. Paris, UNESCO.
Southwood, T.R.E., Brown, V.K. & Reader, P.M. 1979. The relationship of plant and insect diversities in succession. Biol. J. Linn. Soc. 12: 327-48.
Tahvanainen, T., Sallantaus, T. & Heikkilä, R. 2003. Seasonal variation of water chemical gradients in three boreal fens. Annales Botanici Fennici 40: 345-355.
Tausch, R.J., Charlet, D.A., Weixelman, D.A. & Zamudio, D.C. 1995. Patterns of ordination and classification instability resulting from changes in input data order. Journal of Vegetation Science 6: 897-902.
ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167-1179.
ter Braak, C.J.F. 1987a. The analysis of vegetation environment relationships by canonical correspondence analysis. Vegetatio 69: 69-77.
ter Braak, C.J.F. 1987b. CANOCO- A FORTRAN program for canonial community ordination by partial detrended correspondence analysis, principal components analysis and redundancy analysis. TNO Inst. Applied Computer Science, Wageningen,The Netherlands. 95 p.
Tilman, D. 1982. Resource competition and community structure. Monographs in population biology 17. Princeton, New Jersey. Princeton University Press. 296 p.
Tilman, D. 1997. Mechanisms of plant competition. In: Crawley, M.J. (ed.). Plant Ecology. Second Edition. Blackwell Science, Oxford. 717 p.
Tilman, D. 1999. The ecological consequences of changes in biodiversity: A research for general principals. Ecology 80(5): 1455-1474.
Tolvanen, P. 1994. Suon ja kangasmetsän välisen kasvillisuusvyöhykkeen rakenne ja leveys. Pro-gradu tutkielma. Systemaattis-ekologinen kasvitiede. Kasvitieteen laitos, Helsingin yliopisto. 48 p.
Tomppo, E. 1999. Forest Resources of Finnish Peatlands in 1951-1994. International Peat Journal 9: 38-44.
Tomppo, E., Varjo, J., Korhonen, K., Ahola, A., Ihalainen, A., Heikkinen, J., Hirvelä, H., Mikkelä, H., Mikkola, E., Salminen, S. & Tuomainen, T. 1997. Country report for Finland. In: Study on European Forestry Information and Communication Systems. Reports on forestry inventory and survey systems. Vol. 1. European Commission. pp. 145-226.
Tonteri, T. 1990. Inter-observer variation in forest vegetation cover assessments. Silva Fennica 24 (2): 189-196.
Tonteri, T. 1994. Species richness of boreal understorey forest vegetation in relation to site type and successional factors. Annales Zoologici Fennici 31: 53-60.
Tonteri, T., Mikkola, K. & Lahti, T. 1990. Compositional gradients in the forest vegetation of Finland. Journal of Vegetation Science 1: 691-698.
Trass, H. & Malmer, N. 1978. North European Approaches to Classification. In: Whittaker, R. H. (ed.). Classification of Plant Communities. The Hague. pp. 201-246.
Tuhkanen, S. 1980. Climatic parameters and indices in plant geography. Acta Phytogeographica Suecica 67: 1-105.
Tukia, H. 2001. Metsien ennallistamisen ekologiaa. Metsähallituksen luonnonsuojelujulkaisuja Sarja A, 124: 1-68. ISBN 952-446-250-8.
Tuomikoski, R. 1942. Untersuchungen über die Untervegetation der Bruchmoore in Ostfinnland. I. Zur Methodik der pflanzensoziologischen Systematik. Annales Botanici Societatis Vanamo 7(1): 1-203.
Tuominen, S. 1994. Structural classification of forests. In: Reinikainen. A. & Lehtinen, K-M. (eds.). Workshop of forest site classification, Vantaa, Finland, October 27,1994. (In Finnish with English Summary). The Finnish Forest Research Institute. Research Papers 531: 97-99. ISBN 951-40-1401-4
Ulvinen, T., Syrjänen, K. & Anttila, S. (eds.) 2002. Suomen sammalet - levinneisyys, ekologia, uhanalaisuus. (Summary: Bryophytes of Finland: distribution, ecology and red list status). Suomen ympäristö (The Finnsih Environment) 560. 354 p. ISBN952-11-1152-6.
Uuttera, J. & Maltamo, M. 1995. Impact of regeneration method on stand structure prior to first thinning. Comparative study North Karelia, Finland vs. Republic of Karelia, Russian Federation. Silva Fennica 29(4): 267-285.

Uuttera, J., Maltamo, M. & Hotanen, J-P. 1996. Stand structure of undrained peatland forests in central Finland. Suo-Mires and Peat 47(4): 125-135.
Uuttera, J., Maltamo, M. & Hotanen, J-P. 1997. The structure of forest stands in virgin and managed peatlands: a comparison between Finnish and Russian Karelia. Forest Ecology and Management 96: 125-138.
Väisänen, R. & Jäppinen, J.-P. 1994. A Research Agenda for Global Change in Finland: Research Priorities for Conservation and Sustainable Use of Biodiversity. In: Boyle, T.J.B. & Boyle, C.E.B. (eds.). Biodiversity. Temperate Ecosystems and Global Change. NATO ASI Series 1(20): 371-387.
Valmari, A. 1956. Über die edaphische Bonität von Mooren Nordfinnlands. Acta Agralia Fennica 88(1): 1-126.
van der Maarel, E. 1988. Species diversity in plant communities in relation to structure and dynamics. In: During, H. J., Werger, M.J.A. & Willems, H.J. (eds.). Diversity and pattern in plant communities. SPB Academic Publishing, The Hague. pp. 1-14.
van der Maarel, E. 1993. Some remarks on disturbance and its relations to diversity and stability. Journal of Vegetation Science 4: 733-736.
Vanha-Majamaa, I. & Reinikainen, A. 2000. Muuttuvan maankäytön vaikutus kasvillisuuteen. In: Reinikainen, A., Hotanen, J-P., Mäkipää, R. & Vanha-Majamaa, I. 2000 (eds.). Kasvit muuttuvassa metsäluonnossa. (Summary: Changes in the frequency and abundance of forest and mire plants in Finland since 1950). Tammi, Helsinki. pp. 318- 326.
Vasander, H. 1987. Diversity of understorey biomass in virgin and drained and fertilized southern boreal mires in Eastern Fennoscandia. Annales Botanici Fennici 24(2): 137-153.
Vasander, H., Laiho, R. & Laine, J. 1997. Changes in species diversity in peatlands drained for forestry. In: Trettin, C. C., Jürgensen, M., Grigal, D., Gale, M. & Jeglum, J. (eds.). Northern forested wetlands: Ecology and management. Lewis Publishers. pp. 109-119.
Vasander, H., Tuittila, E.-S., Lode, E., Lundin, L., Ilomets, T., Sallantaus, T., Heikkilä, R., Pitkänen, M.-L. & Laine, J. 2003. Status and restoration of peatlands in northern Europe. Wetlands Ecology and Management 11: 51-63.
Virkkala,R., Korhonen, K.T., Haapanen, R. & Aapala, K. 2000. Metsien ja soiden suojelutuilanne metsä- ja suokasvillisuusvyöhykkeittäin valtakunnan metsien 8. inventoinnin perusteella. (Summary: Protected forests and mires in forest and mire vegetation zones in Finland based on the 8th National Forest Inventory.) Suomen Ympäristö (The Finnsih Environment) 395: 1-49.
Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30: 279-338.
Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon 21 (2/3): 213-251.
Whittaker, R.H. 1977. Evolution of species diversity in land communities. In: Hecht, M.K., Steere, W.C. & Wallace, B. (eds.). Evolutionary Biology 10: 1-67.
Wilson, M.F. 1974. Avian community organization and habitat structure. Ecology 55: 1017-1029.
Wilson, E.O. (ed.). 1988. Biodiversity. National Academy Press, Washington D.C. 521 p.
Wilson, E.O. 1989. Threats to biodiversity. Scientific American 261: 108-116.
Wilson, M.V. & Shmida, A. 1984. Measuring beta diversity with presence-absence data. Journal of Ecology 72: 1055-1064.
Yee, T. & Mitchell, N.D. 1991. Generalised additive models in plant ecology. Journal of Vegetation Science 2: 587-602.
Zackrisson, O. 1977. Influence of forest fires on the North Swedish boreal forests. Oikos 29: 22-32.

Paper I

I

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A numerical analysis of mire margin forest vegetation in South and Central Finland

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The ecological structure of boreal mire margin vegetation (paludified forests, mire margin forests and forested pine and spruce mires) in South and Central Finland was examined using ordination (DCA) and classification (TWINSPAN) techniques on the vegetation data of 92 sample plots from the 8th National Forest Inventory (1985–86). The first DCA axis was interpreted as respond to a complex-gradient of nutrient availability on the basis of site classification, species composition and correlation with all measured tree stand variables. According to the distribution of species ecological groups along DCA1 axis the mire margin/mire expanse gradient was one of the main factors determining this nutrient availability. The second axis was interpreted in terms of paludification on the basis of species composition, site classification and its correlation with peat depth. Seven clusters resulted from a TWINSPAN classification of the vegetation data. These could be arranged into a sequence along the nutrient availability gradient by their species composition: three clusters represented ombro-oligotrophic, three clusters meso-oligotrophic and one cluster mesotrophic vegetation. The clusters corresponded only weakly to the traditional Finnish forest and mire site types as determined in the field.

Key words: boreal forest, boreal mire, ecological gradient, forest site types, mire site types

INTRODUCTION

Classification of boreal mires in Finland has traditionally followed the ecological site type principle proposed by Cajander (1913). As species distributions are determined by environmental factors, units ('types') at all hierachical levels, i.e., mire complex types (e.g. Ruuhijärvi 1982, Påhlsson 1994), site type groups (bogs, fens and swamps, see Heikurainen & Pakarinen 1982), site types (Eurola *et al.* 1984), and subtypes characterised by Eurola and Kaakinen (1979) and Eurola *et al.* (1994) can be placed in an environmental space defined by physical and chemical environmental factors.

Knowledge of the ecological indicator value of species has accumulated by autecological studies (e.g. Kotilainen 1927, Pankakoski 1939), studies of site quality (e.g. Lumiala 1945, Reinikainen *et al.* 1984) and description of vegetation types (e.g. Paasio 1933, 1941, Tuomikoski 1942, Ruuhijärvi 1960, Havas 1961, Eurola 1962). More recently, species, site types or mire complex types have been related to environmental factors by use of numerical classification and ordination techniques (e.g. Pakarinen & Ruuhijärvi 1978, Pakarinen 1979, 1982, Økland 1990ab, Jeglum 1991).

A distinction between mire expanse and mire margin vegetation was made already in early mire vegetation studies (Lumiala 1937, Sjörs 1948). Later on, the mire expanse and mire margin gradient has been confirmed as one of the main ecological gradients in mire vegetation in the Nordic countries (Eurola & Holappa 1985, Malmer 1985). In this study the Finnish definition (Eurola & Kaakinen 1979) of the mire margin concept is used. There is a difference to the Scandinavian interpretation (Sjörs 1983, Økland 1989, 1990c) according to which also marginal pine forests of bogs despite being ombrotrophic are included in mire margin sites. According to Finnish environmental characterisations mire margin vegetation occurs often on sites with a thin peat layer (Ilvessalo 1956, Ruuhijärvi 1960, Eurola 1962) that receive a supplementary input of mineral nutrients from surrounding mineral soil (Heikurainen 1954, Eurola & Holappa 1985). The importance of this external nutrient flow is strongly related to topography and slope (Backman 1919, Lukkala 1929) and the inflow of oxygen-rich surface or spring water (e.g. Havas 1961, Persson 1961, Eurola & Kaakinen 1979). Mire expanse vegetation, in contrast, is often characterised by thick peat, by high and slowly moving watertable and by lacking external nutrient flow (Eurola & Kaakinen 1979).

Mire margin vegetation typically occurs in a zone between proper upland vegetation and mire expanse vegetation. The sites include 1) paludified forests (= paludified mineral soil forests), 2) mire margin forests and 3) forested pine and spruce mires (Lumiala 1937, Tuomikoski 1942). Descriptions of the flora and vegetation of forested mire margins have appeared in several regional studies (e.g. Cajander 1913, 1926, Kujala 1921, Auer 1922, Aario 1932, Paasio 1933, Ruuhijärvi 1960, Eurola 1962, Tolonen 1967). Rather few special studies, however, have been made on the community structure, ecology and classification of mire margin forest and forested pine and spruce mire sites and vegetation (Lumiala 1937, Tuomikoski 1942, Heikurainen 1954, Nurminen 1964, Hotanen 1989, Hotanen & Nousiainen 1990, Tolvanen 1994). Paludified forests have typically remained without detailed vegetation studies or classification supported by investigations, they have merely been mentioned in early typological studies (e.g. Cajander 1909, 1913, 1926, Kujala 1921, Kalela 1962).

Because of their potential productivity, the mire margin forests and forested pine and spruce mires have been drained to a large extent (Heikurainen 1971, Gustavsen & Päivänen 1986). The area of these undrained mire margin sites in 1985–86 according to the data of permanent sample plots of the 8th National Forest Inventory (8th NFI) was half of what it was in the early 1950's according to data from the 3rd NFI (Ilvessalo 1956, 1957).

Our study was motivated by the lack of coherence between different descriptions of forested mire margin vegetation and by the assumed relative importance of these communities as sources of biodiversity. The aims were (1) to explore the structure of the vegetation of forested mire margins located in South and Central Finland, using systematically sampled data and ordination and classification techniques, and (2) to compare the traditional Finnish site type classification and the results of the numerical analyses.

MATERIAL AND METHODS

Sample plots and study area

We used the vegetation and tree stand data of the permanent plots collected during the eighth National Forest Inventory (8th NFI). In 1985–86, 3 009 permanent plots covering the entire forestry land (forests and mires, see Aarne 1995) area of Finland (Reinikainen 1990) were established for monitoring tree vitality (Jukola-Sulonen *et al.* 1990), ground vegetation (Tonteri *et al.* 1990), and deposition (Ruhling *et al.* 1987). Circular plots were placed systematically: four circular plots in one cluster (a sample plot tract) in each 16 × 16 km grid square in Southern and Central Finland (S of 66°N; 2 618 plots) (see Salemaa *et al.* 1991). On each of the circular plots (300 m^2) there were three to six vegetation sample quadrates (2 m^2).

In this study, only plots that satisfied the following criteria were included: 1) location S of the 66th latitude, 2) classified as paludified forest site types, mire margin forest site types, or forested pine and spruce mire site types, 3) each plot classified to one site type, 4) four vegetation sample quadrates on the plot, 5) site not drained, 6) tree stand untreated at least two years before inventory. Altogether, 92 plots fulfilled all criteria.

Biogeographically, the area (Fig. 1) investigated extends from the northernmost border of the hemiboreal zone to the southern parts of the northern subzone of the boreal zone (according to Ahti *et al.* 1968). The study area comprise three subzones of forest vegetation (coast-Finland, South-Finland and West-Central-East-Finland, Kalela 1961) and the border between the zones of raised bogs and aapafens runs through the area (Ruuhijärvi 1982).

The mean annual temperature (for the period 1961–80) within the study area ranges from +1 to +5°C; the temperature sum (threshold +5°C) from 850 to 1 350 degree days (Heino & Hellsten 1983); the mean annual precipitation from 500 to 600 mm; the duration of the growing season from 135 to 180 days; Conrad's continentality index from 24 to 34; and Thornthwaite's index of humidity from 20 to 50 (Tuhkanen 1980).

The traditional Finnish forest type approach of Cajander (Cajander 1926, Frey 1973) was used in classification of the 92 plots on site type classes. Paludified forest site types are classified in accordance with Kalela (1973). Mire site types are classified in accordance with Heikurainen and Pakarinen (1982). For each site type, fertility classes I (richest)–VI (poorest) according to the six-scale system of Huikari (1974) describe the forest production potential of site types (Table 1).

Field work and vegetation survey

The vegetation survey of the plots was carried out by a biologist member of each inventory crew. The data were collected in 1985–86 by 12 crews.

Four 2 m^2 sample quadrates placed systematically along a line passing through the centre of the plot in a S–N direction were used for description of the field and bottom layer vegetation. Percentage cover was estimated for vascular plants (tree and shrub specimens lower than 50 cm included), bryophytes and terricolous lichens. The nomenclature follows Hämet-Ahti *et al.* (1986) for vascular plants, Koponen *et al.* (1977) for bryophytes and Santesson (1993) for lichens. Vascular plants were determined to species. Mosses were identified to species except for the genera *Brachythecium, Plagiothecium* and the family *Mniaceae*, in which only the genera *Plagiomnium* and *Rhizomnium* were separated. Hepatics were treated collectively. *Sphagna* and lichens (*Cladonia*) were identified to species level in the field without subsequent microscopic checking. The 12 biologists who carried out the survey attended a training course before the field work began and the inter-observer variation in species cover estimation was determined in a study afterwards (see Tonteri 1990). Inter-observer variation in ability to recognise taxa was not checked.

The canopy cover of trees (> 1.5 m high) and shrubs (0.5–1.5 m high) was recorded for all species in 300 m^2 sample plot. Total basal area was estimated using three telascope observations. Determination of the mean diameter was based on a tree tally. By coring of one representative dominant canopy tree, stand age and dominant height (site index H_{100} = height of dominant trees at 100 year age) were approximated. The dominant tree species was defined as the one with largest volume in the dominant canopy layer. Peat depth was recorded as the mean of four measurements in each of the 2 m^2 vegetation.

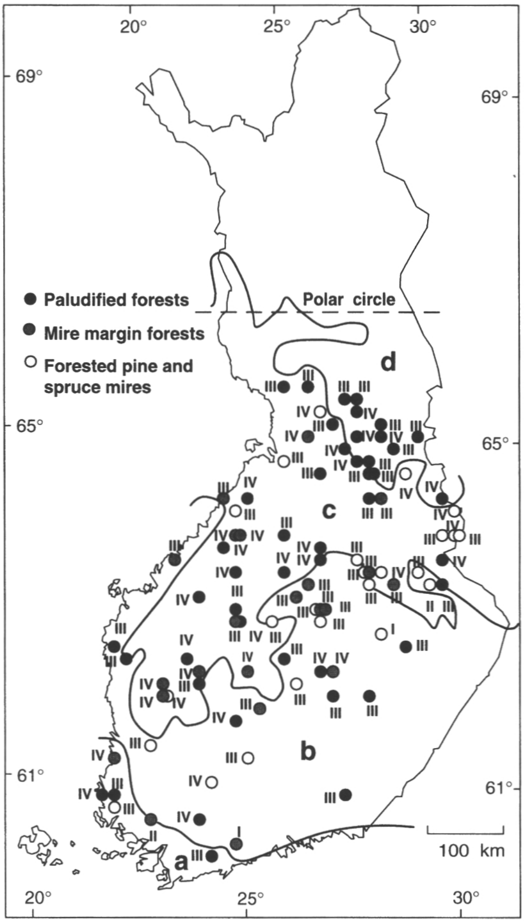

Fig. 1. Distribution of the 92 sample plots. The vegetation zones are: a = hemiboreal zone and b = southern, c = middle, and d = northern boreal subzones of boreal zone (Ahti *et al.* 1968). The fertility classes (I–IV) (Huikari 1974) of the sites are indicated.

Data analysis and ecological interpretation

The mean percentage cover for each species was calculated from the four surveyed quadrates on each plot. Species present in only one or two plots as well as the taxa not determined to species level were excluded from numerical analyses, leaving 88 plant species (from the total of 135 species, see Appendix) in 92 sample plots.

The main compositional gradients in vegetation were extracted by detrended correspondence analysis (DCA; Hill & Gauch 1980). DCA was carried out with the CANOCO program, using detrending by segments (Ter Braak 1987). After testing first the default option the use of 15 segments gave the most interpretable configuration of ordination for 92 sample plots. No rescaling of the axes and no transformation options except that the down-weighting option for rare species was used (see Økland 1990c). Biplot scores for regional variables (temperature sum, latitude, longitude) and the measured site variables (peat depth, tree cover, shrub cover) and tree stand variables (basal area, mean diameter at breast height (= DBH), dominant height and stand age) were obtained.

The vegetation data was classified numerically by TWINSPAN (two-way indicator species analysis; Hill 1979). TWINSPAN was applied using default options for minimum group size (5), maximum number of indicator species (7), and pseudo-species cut levels (0, 2, 5, 10, 20 cover %). Three levels of division were used.

Spearman correlation coefficients between DCA axes (plot scores) and explanatory variables were calculated (cf. Sokal & Rohlf 1981). Analysis of variance (ANOVA) was used to test TWINSPAN clusters for environmental differences.

In the ecological interpretation of the results the indicator values of forest and mire plants were used, according to several earlier Finnish studies and mainly synthesised by Eurola *et al.* (1984, 1994) for mires and by Kalela (1973) for forests, respectively. The grouping of species into different ecological groups (see Fig. 2) was carried out on the basis of the same lists.

RESULTS

DCA ordination and ecological interpretation

In the DCA ordination of 92 sample plots and 88 species, the eigenvalue of the first axis was 0.49, and the eigenvalues of axes two to four were distinctly lower (0.22, 0.20, 0.14). The gradient length along the DCA axis 1 was 4.2 *S.D.*-units and the gradient lengths along axis two to four were 3.2, 3.3 and 2.5 *S.D.*-units, respectively. For the two-axis solution axes 1 and 2 was chosen on the basis of interpretation (Figs. 2 and 3).

In the species ordination space (Fig. 2), ombro-oligotrophic species typical of bogs (e.g. *Vaccinium uliginosum, Ledum palustre, Betula nana, Eriophorum vaginatum, Vaccinium microcarpum, Sphagnum russowii, S. angustifolium, S. nemoreum*) and also xeric forest species (e.g. *Cladonia* spp., *Empetrum nigrum, Calluna vulgaris*) obtained high DCA1 scores and the more mesotrophic spruce mire species (e.g. *Equisetum sylvaticum, Sphagnum girgensohnii, S. squarrosum*) and herb rich forest species (e.g. *Athyrium filix-femina, Oxalis acetosella, Maianthemum bifolium*) obtained low scores along

Table 1. The studied site types and their Finnish abbreviations within 1) paludified upland forests according to Kalela (1973), 2) mire margin forests and (3) forested pine and spruce mires according to Heikurainen and Pakarinen (1982) and fertility classes of the site types according to Huikari (1974).

Site types	Abbrev.	Fertility classes
1. Paludified forests		
Paludified *Empetrum–Vaccinium* type	sEVT	IV
Paludified *Vaccinium* type	sVT	IV
Paludified *Vaccinium–Myrtillus* type	sVMT	III,IV
Paludified *Myrtillus* type	sMT	III,IV
Paludified *Deschampsia–Myrtillus* type	sDeMT	III
2. Mire margin forests		
Paludified pine forest	KgR	IV
Oligo-mesotrophic paludified spruce forest	KgK	II,III
Eutrophic paludified hardwood-spruce forest	LhK	I
3. Forested pine and spruce mires		
Rubus chamaemorus-spruce swamp (mire)	MrK	IV
Spruce-pine swamp (mire)	KR	III,IV
Vaccinium myrtillus-spruce swamp (mire)	MK	III
Equisetum sylvaticum-spruce swamp (mire)	MkK	III
Herbrich hardwood-spruce swamp (mire)	RhK	II

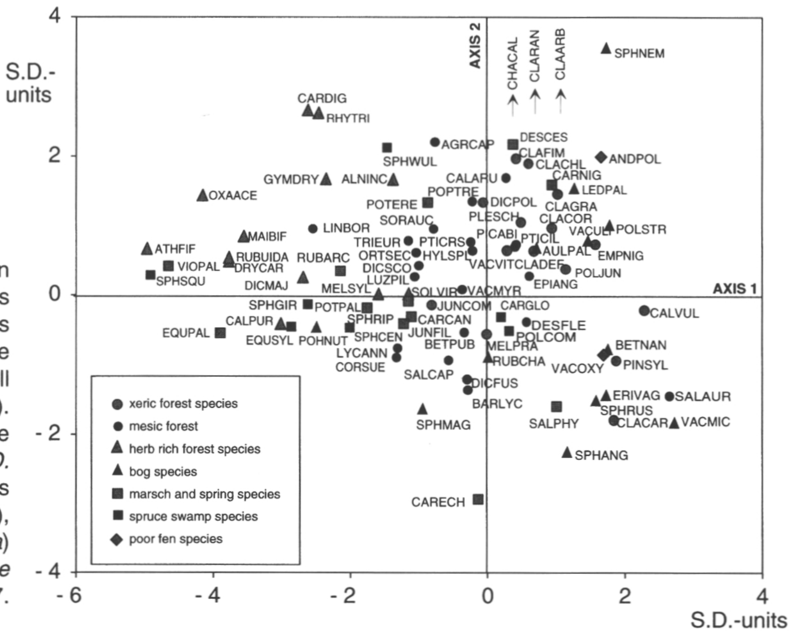

Fig. 2. DCA species ordination for axes 1 and 2. Species names are the first three letters of the genus and the first three letters of the species (for full species names see Appendix). Species ecological groups are presented. On axis 2 the *S.D.* values of the outlying species CLAARB (*Cladonia arbuscula*), CLARAN (*Cladonia rangiferina*) and CHACAL (*Chamaedaphne calyculata)* are 6.8, 5.5 and 4.7.

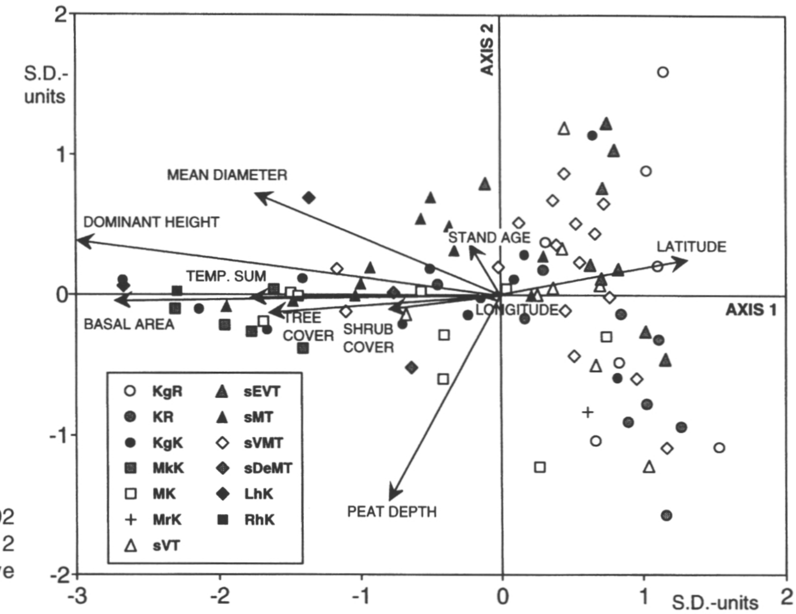

Fig. 3. DCA ordination of the 92 sample plots for axes 1 and 2 with the vectors of passive explanatory variables.

DCA1. The optima of constant species typical of oligotrophic and meso-oligotrophic forests (*Vaccinium vitis-idaea, V. myrtillus Pleurozium schreberi, Dicranum polysetum, Hylocomium splendens*) were in the centrum of the ordination space. *Carex globularis* and *Polytrichum commune*, the constant species for paludification, were also centrally placed. In the sample plot ordination space (Fig. 3), the bog and xeric forest site types (KR, KgR and sEVT, see Table 1) obtained correspondingly high DCA1 scores and the mesic and herb-rich forested spruce mire and forest site types (LhK, RhK, MkK, KgK, MK, sMT, see Table 1) obtained low scores along DCA1. Along the mid-point of DCA1, plots from a wide variety of oligotrophic pine and spruce mire types and paludified forest types occurred intermixed.

The first DCA axis was significantly correlated and rather parallel with all the measured variables connected with tree stand productivity (basal area, dominant height, mean diameter, see Fig. 3 and Table 2). The significant negative correlation of DCA1 with temperature sum and the significant positive correlation with latitude is likely to reflect intercorrelations with the tree stand variables indicating forest production (fertility gradient) and geographical variables (climatic gradient). Significant correlations occurred between dominant height and temperature sum and between dominant height and latitude (Table 3). Most fertile site types (LhK and RhK, fertility classes I and II) were absent from the northern third of the study area. Most commonly recorded fertility classes, III and IV, were equally frequent in each of the northern, middle and southern third of the study area (see Fig. 1).

Variation in vegetation along the second axis was related only to the peat depth variable (Table 2). Most of the mire expanse species (bogs and poor fens species like, *Sphagnum russowii, S. angustifolium, S. magellanicum, Vaccinium oxycoccus,* in Fig. 2) and also the spruce mire species had low scores along this axis while most of the xeric (e.g. *Cladonia* species) and mesic forest species (e.g. *Oxalis acetosella, Rhytidiadelphus triquetrus, Carex digitata*) obtained high scores. In the sample plot ordination space (Fig. 3) mires like spruce-pine mires (KR) and *Vaccinium myrtillus*-spruce mires (MK) had low scores along this axis and paludified xeric and mesic forests (sEVT, sVMT, sMT, see Table 1 for abbreviations) obtained high scores correspondingly. Less fertile site types and bog species had wide amplitudes along this axis. Variation along DCA1 was lower in plots with low DCA1 scores. The significant negative correlation between stand age and the third axis and between temperature sum and the third axis revealed significant intercorrelation with these variables (– 0.39***, Table 3).

The ecological species groups (xeric, mesic and herb-rich forest, bog, spruce swamp and poor fen species) were fairly well separated in the species ordination, axes 1 and 2, except marsh and spring water species, which were evenly distributed on the ordination space Fig. 2.

TWINSPAN classification

The TWINSPAN classification of the 92 sample plots separated one cluster with six plots (cluster G) from the remaining 86 plots at the first dichotomy. *Dryopteris carthusiana* and *Oxalis acetosella* were indicator species for cluster G. Several mesotrophic herbs otherwise rare in the data with few species in common with the other clusters, occurred in this cluster (see Fig. 4, Table 4 and Appendix).

The first division of the remaining 86 plots separated ombro-oligotrophic pine mire type (KR and KgR) and xeric forest type (sEVT and most of the sVMT) plots (left, $n = 44$) from the oligo-mesotrophic spruce mire (MK, MkK and KgK) and mesic forest type (sMT and the remaining sVMT and sVT) plots (right, $n = 42$). The ombro-oligotrophic group had bog species and xeric forest species as preferentials

Table 2. Spearman rank correlations between DCA scores and 1) tree stand, 2) site quality and 3) geographical variables. *** = $P \leq 0.001$, ** = $0.001 < P \leq 0.010$, * = $0.010 < P \leq 0.050$.

DCA axis	1	2	3	4
1. Basal area	– 0.46***	– 0.13	0.05	– 0.01
1. Dominant height	– 0.57***	0.01	0.08	0.05
1. Mean DBH	– 0.26**	0.04	0.06	0.15
1. Stand age	0.09	– 0.05	0.40***	– 0.01
2. Tree cover	– 0.30**	– 0.15	– 0.07	0.03
2. Shrub cover	– 0.09	0.02	– 0.11	0.16
2. Peat depth	– 0.04	– 0.50***	– 0.01	– 0.20
3. Temperature sum	– 0.35**	– 0.05	– 0.40***	– 0.03
3. Latitude	0.27**	0.08	0.30**	0.09
3. Longitude	– 0.04	– 0.03	0.35**	0.01

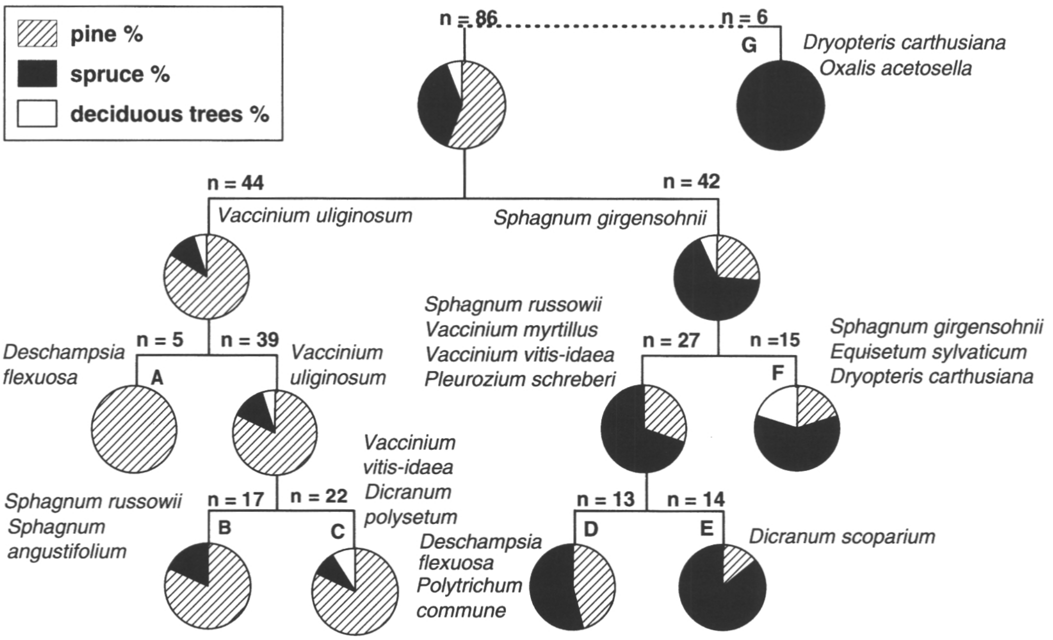

Fig. 4. TWINSPAN- clustering dendrogram for the 92 sample plots. Indicator species for each division level and each final vegetation cluster are included. Pies describe the percentage of sample plots with different tree species domination on each division level and in each final vegetation cluster.

and *Vaccinium uliginosum* as indicator, the oligo-mesotrophic group was indicated by the presence of *Sphagnum girgensohnii,* and had meso-oligotrophic mire margin species and constant species of mesic forests as preferentials. Thus the first division of the 86 plots appeared to represent a division between ombro-oligotrophy and meso-oligotrophy.

The second division of the ombro-oligotrophic group (on the left, $n = 44$) resulted in the separation of a final cluster A, which contained paludified xeric forest (sVT, sEVT) and mire margin forest (KgR) plots, indicated by *Deschampsia flexuosa* and characterized by several pioneer species (Fig. 4, Table 4 and Appendix). The rest of the plots ($n = 39$) which, according to their preferential species, had a more boggy character, were further divided to form clusters B ($n = 17$) and C ($n = 22$). Cluster B was indicated by *Sphagnum russowii* and *S. angustifolium,*

Table 3. Correlations between 1) tree stand, 2) site quality and 3) geographical variables.*** = $P \leq 0.001$, ** = $0.001 < P \leq 0.010$, * = $0.010 < P \leq 0.050$.

	1	2	3	4	5	6	7	8	9
1. Basal area (1)									
2. Dominant height (1)	0.65***								
3. Mean DBH (1)	0.46***	0.61***							
4. Stand age (1)	0.35***	0.39***	0.46***						
5. Tree cover (2)	0.36***	0.12	0.02	−0.02					
6. Shrub cover (2)	−0.29**	−0.12	−0.28**	−0.22*	0.09				
7. Peat depth (2)	−0.02	−0.15	−0.21*	−0.03	0.05	−0.04			
8. Temperature sum (3)	0.12	0.26*	0.07	−0.39***	0.16	0.07	0.08		
9. Latitude (3)	−0.21*	−0.29**	−0.08	0.29**	−0.17	−0.01	−0.09	−0.91***	
10. Longitude (3)	0.11	0.07	0.04	0.33**	−0.06	0.15	0.07	−0.56***	0.54***

and had many bog species as preferentials and consisted mainly of plots representing mire site types. Cluster C was indicated by *Vaccinium vitis-idaea* and *Dicranum polysetum* and contained most of the northern paludified forest site type (sEVT and sVMT) plots (Fig. 4, Table 4 and Appendix).

The second division of the meso-oligotrophic group (on the right, $n = 42$) resulted in a separation of a final cluster F ($n = 15$). Cluster F was indicated by the slightly mesotrophic species *Sphagnum girgensohnii, Equisetum sylvaticum* and *Dryopteris carthusiana* and preferred by other meso-oligotrophic mire margin species as well. This cluster mainly consisted of plots assumed to be the most fertile among the remaining 86 plots not in G; the ordinary spruce-hardwood mire site types (MK, MkK and KgK) and mesic paludified forest site types (sMT, sDeMT). The remaining set of plots ($n = 27$), indicated by *Sphagnum russowii, Vaccinium myrtillus, Vaccinium vitis-idaea* and *Pleurozium schreberi* were divided once more to form final clusters D ($n = 13$) and E ($n = 4$). Cluster D had *Deschampsia flexuosa* and *Polytrichum commune* as indicators. Cluster E was indicated by *Dicranum scoparium* with some oligotrophic mire margin species as preferentials. Cluster E was dominated by mire type plots while cluster D with forest type plots (Fig. 4, Table 4 and Appendix).

Table 4. Distribution of 1) paludified forest, 2) mire margin forest and 3) forested pine and spruce mire site types within 7 TWINSPAN vegetation clusters (A–G). The amount of each site type in each cluster and total (*n*) are presented.

Site types	Fertility classes	TWINSPAN-clusters A	B	C	D	E	F	G	*n*
1. sEVT	IV	1	2	6					9
1. sVT	IV	3	1	1	3				8
1. sVMT	III,IV		3	9	2	2			16
1. sMT	III,IV				3	3	5		11
1. sDeMT	III				1		1		2
2. KgR	IV	1	5	3					9
2. KgK	II,III				2	5	3	1	11
2. LhK	I							2	2
3. MrK	IV		1						1
3. KR	III,IV		5	2	1				8
3. MK	III			1	1	4	3		9
3. MkK	III						3	2	5
3. RhK	II							1	1
n		5	17	22	13	14	15	6	92

Ecological interpretation of TWINSPAN clusters

The dominant tree species on each division level and in each final vegetation cluster is included in Fig. 4. The main division between ombro-oligotrophic and meso-oligotrophic groups separated the Scots pine-dominated stands (group $n = 44$) from the Norway spruce-dominated stands (group $n = 42$). Tree species composition also clearly differed between clusters at lower TWINSPAN division levels. The tree cover was significantly higher in the Norway spruce-dominated meso-oligotrophic group (clusters D, E, F and G) than in the Scots pine-dominated ombro-oligotrophic group (clusters A, B and C). The oligotrophic boggy cluster B differed significantly from the meso-oligotrophic mire margin clusters E and F (see Table 5).

The stand productivity variables, basal area and dominant height, differed strongly between clusters (Table 5). In the ombro-oligotrophic group the values for these variables were lower than in the meso-oligotrophic group. The basal area was significantly higher in the most spruce dominated clusters E and G. The oligotrophic cluster A differed clearly from all the other clusters with lower values for the tree stand variables, i.e. including the stands with the lowest tree stand age.

Clusters A, C and D which included most of the paludified forests had the lowest mean peat depths while cluster B with higher prominence of bog species and the spruce mire cluster G had the highest.

There was a significant difference in temperature sum between the clusters, reflecting distributional differences along the S–N-gradient. Clusters B and C, which contained most of the northern forest (sEVT and sVMT) plots, and clusters F and G, made up extremes with respect to temperature sums.

Parity of TWINSPAN clusters and conventional site classification

All final TWINSPAN clusters with more than 10 sample plots (clusters B–F) included plots classified into four or more site types. Plots classified as mire and forest site types were included in all clusters A–F, while cluster G contained mire sites only. All plots of the KgR (oligotrophic mire) and sEVT (xeric forest) types were classified to the ombro-oligotrophic main group (clusters A–C) and all plots of the KgK (oligo-mesotrophic mire) and sMT (mesic forest) types were classified to the meso-(oligo)trophic main group (clusters D–G). Most of the paludified forest types were divided into several clusters, sVT and sVMT were both distributed on all clusters A–E. The mire types KgK and MK had the widest distribution between clusters D and G and between clusters C and F. KR plots concentrated in cluster B but were also found in clusters C and D.

DISCUSSION

Results of ordination and clustering

The fertility gradient that strongly dominates the pattern of boreal forest and mire vegetation in Finland (e.g. Eurola *et al.* 1984, Kuusipalo 1985, Lahti & Väisänen 1987, Tonteri *et al.* 1990) was also apparent in this analysis of mire margin influenced forested sites. The mire sites and paludified forest sites seemingly make up a continuum along the main ordination axes. The assumed gradient mire margin/mire expanse was parallel with the fertility gradient, apparently making up one complex gradient. The analysis failed to separate these two gradients because the indicators of margin influence in mire sites are mesotrophic forest and wetland species. The indicators of mire expanse, on the other hand, partly belong to the xeric forest species (e.g. Eurola *et al.* 1994). The secondary gradient (second axis) was interpreted as a paludification gradient. In Pakarinen's (1982) Bray-Curtis-ordination of South Finnish mire and forest types the most dominant gradient was the paludification gradient, which was shortened in our study by not including unpaludified forest sites.

A distinct regional variation was evident, but the site type distribution in our material was too uneven for a thorough analysis in this respect due to a relatively low number of plots. The forest types have parallel regional variants in the vegetation (climatic)

Table 5. Mean values (± *S.E.*) of 1) tree stand 2) site quality and 3)geographical variables in the final TWINSPAN-vegetation clusters (A–G). For each variable TWINSPAN-clusters with different letters are significantly different ($P < 0.05$).

Variables	TWINSPAN-clusters A	B	C	D	E	F	G	*F*-values
1. Basal area (m²/ha)	5.4 b (1.4)	11.4 a (2.2)	16.9 a (1.7)	20 a (1.8)	27.6 abc (2.2)	21.8 ab (2.2)	28.7 abc (2.6)	9.88 ***
1. Dominant height (m)	5.9 (10.3)	9.2 (12.3)	13.3 a (6.3)	14.5 ab (10.5)	16.3 ab (9.5)	17.9 abc (10.8)	19.8 ab (15.7)	13.0 ***
1. Mean DBH (cm)	9.0 (1.0)	10.6 (1.4)	12.8 (1.3)	13.5 (1.8)	15.2 (1.8)	13.3 (1.3)	18.2 ab (1.4)	1.7
1. Stand age (years)	21.8 b (2.2)	82.1 a (16.0)	105.5 a (11.0)	88.7 a (14.0)	125.7 a (16.7)	82.3 a (7.7)	90.0 a (10.0)	3.1 **
2. Tree cover (%)	38.3 (5.1)	28.8 (5.1)	36.6 (4.4)	40.3 (5.7)	51.7 b (5.1)	48.7 b (3.9)	52.1 (8.3	2.8 *
2. Shrub cover (%)	8.8 (1.9)	5.6 (1.5)	7.6 (2.0)	5.8 (1.1)	2.6 (0.5)	9.5 (3.0)	6.2 (1.9)	1.2
2. Peat depth (dm)	0.5 b (0.2)	2.7 a (0.6)	1.3 (0.3)	1.4 (0.3)	2.6 (0.7)	1.7 (0.4)	3.2 (1.6)	2.1*
3. Temp. sum (dd)	1142 (5.3)	1022 (2.6)	1016 (1.6)	1093 (3.2)	1056 (2.9)	1185 bc (3.1)	1145 (4.0)	5.6 ***
Number of plots	5	17	22	13	14	15	6	

subzones (Kalela 1960). No analogous system exist for mire site types or paludified forest site types.

The rather poor agreement between the TWINSPAN clusters and the site types determined in the field was not surprising (see Hotanen & Nousiainen 1990). There may be at least three different reasons for this: 1) the relatively high floristic similarity between different site types in the Finnish classification system, e.g., between forested mires and paludified forests, 2) continuity of the vegetation along the main gradient and, in particular, effects of the other subsidiary complex gradients on the cluster formation in TWINSPAN, and 3) errors in the field determination of site types (see Hotanen 1989, Hotanen & Nousiainen 1990).

Data quality and sources of error

The number of mire margin plots included in this study was relatively small. Due to systematic sampling the types are represented in the material according to their frequency in Finland. This inevitably causes poor or inadequate representation of the variation in mire margin vegetation; ecologically and floristically distinct types are represented by few sample plots and the relationships between these types and the rest of the data set is not adequately described (e.g. Økland 1990c). This is one reason why the few most fertile plots separated at the first division level in TWINSPAN.

The size and number of sample squares per plot was largely decided upon by practical considerations. The total area of 4×2 m^2 squares was the same on all plots but this may not have been enough to include all the potential species and produce reliable mean coverage values (Trass & Malmer 1978, Pakarinen 1984, Økland 1990c).

The vegetation data was collected by 12 different persons and the inter-observer difference in coverage values varied between 15–40% depending on the plant species (Tonteri 1990). This range does, however, appear moderate when considering cover estimations in general (e.g. Bråkenhielm & Qinghong 1995). Jukola-Sulonen and Salemaa (1985) noted that high coverage values tended to be underestimated and the low coverage values overestimated. With the methods used, the quality of the data was sufficient for revealing the gradients (see also Hotanen 1990).

CONCLUSIONS

In this first, as far as we know, simultaneous ordination of mire and paludified forest types, the similarity in the vegetation of mire and paludified upland forest habitats was clearly revealed by the numerical analysis. The difficulties in the field determination of site types studied are well-known (Hotanen 1989). In practice, characteristics of the site such as peat depth and peat morphology are used in addition to vegetation and tree stand structure when site types are determinated. Thus, there seems to be a discrepancy between usage and the site-type principle (Eurola *et al.* 1984) in establishment of typology in the studied forest and mire sites. Instead of a revision of the classification we first suggest more extensive use of gradient analyses and non-classifying methods (Lahti 1994ab).

This study demonstrates the high floristic diversity of mire margin vegetation. High species richness results from the mixing of mire and forest species and the occurrence of special mire margin features, such as spring, flooding and marsh, whereby species richness is added through associations with the forest and bog species groups. These sites represent an ecological edge effect (Tolvanen 1994). In Finland where the mire margin sites have decreased after intensive forest drainage also this kind of — still pristine — rather trivial mire margin sites should be studied in more detail. Being still more common than the boreal mire margin types with the highest alpha diversity, i.e. the most fertile hardwood-spruce mire site types, for instance, (Eurola *et al.* 1991, Forestry Environment Guide 1993, Heikkilä 1994) the recent remnants of forested mire margin types in southern Finland should be protected against further amelioration activities.

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REFERENCES

Aario, L. 1932: Pflanzengeographische und paläogeographische Untersuchungen in N-Satakunta. — Comm. Inst. For. Fenniae 17: 1–189.

Aarne, M. (ed.) 1995: Statistical yearbook of forestry. — The

Finnish Forest Research Institute 1995, SVT; Agriculture and forestry 1995: 5.
Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in northwestern Europe. — Ann. Bot. Fennici 5: 169–211.
Auer, V. 1922: Moorforschungen in den Vaaragebieten von Kuusamo und Kuolajärvi. — Comm. Inst. For. Fenniae 6: 1–368. (In Finnish with German summary.)
Backman, A. L. 1919: Torvmarksundersökningar i mellersta Österbotten. — Acta For. Fennica 2: 1–190.
Bråkenhielm, S. & Qinghong, L. 1995: Comparison of field methods in vegetation monitoring. — Water, Air and Soil Pollution 79: 75–87.
Cajander, A. K. 1909: Über Waldtypen. — Acta For. Fennica 1: 1–175.
Cajander, A. K. 1913: Studien über die Moore Finnlands. — Acta For. Fennica 2: 1–208.
Cajander, A. K. 1926: The theory of forest types. — Acta For. Fennica 29: 1–108.
Eurola, S. 1962: Über die regionale Einteilung der südfinnischen Moore. — Ann. Bot. Soc. Vanamo 33: 1–243.
Eurola, S. & Holappa, K. 1985: The Finnish mire type system. — Aquilo Ser. Bot. 21: 101–110.
Eurola, S. & Kaakinen, E. 1979: Ecological criteria of peatland zonation and the Finnish mire type system. — In: Kivinen, E., Heikurainen, L. & Pakarinen, P. (eds.), Classification of Peat and Peatlands. Proc. Int. Symp. held in Hyytiälä, Finland, Sept. 17–21, 1979: 20–32. Int. Peat Soc., Helsinki.
Eurola, S., Hicks, S. & Kaakinen, E. 1984: Key to Finnish mire types. — In: Moore, P. D. (ed.), European mires: 11–117. Acad. Press, London.
Eurola, S., Aapala, K., Kokko, A. & Nironen, M. 1991: Mire type statistics in the bog and southern aapa mire areas of Finland (60–66°N). — Ann. Bot. Fennici 28: 15–36.
Eurola, S., Huttunen, A. & Kukko-oja, K. 1994: Suokasvillisuusopas. — Oulanka Reports 13: 1–81. Univ. Oulu.
Forestry Environment Guide 1993. — Finnish Forest and Park Service. 112 pp.
Frey, T. E. A. 1973: The Finnish school and forest-site types. — In: Whittaker, R. H. (ed.), Ordination and classification of communities: 405–433. 'Publisher' The Hague.
Gustavsen, H. G. & Päivänen, J. 1986: (Tree stands on virgin forested mires in the early 1950's. — Folia Forestalia 673: 1–27. (In Finnish with English summary.)
Hämet-Ahti, L., Suominen, J., Ulvinen, T., Uotila, P. & Vuokko, S. (eds.) 1986: Retkeilykasvio. — Suomen Luonnonsuojelun Tuki, Helsinki. 598 pp.
Havas, P. 1961: Vegetation und Ökologie der ostfinnischen Hangmoore. — Ann. Bot. Soc. Vanamo 31: 1–188.
Heikkilä, R. 1994: Soidensuojelu Suomessa. — Terra 106: 226–231.
Heikurainen, L. 1954: Korpisuus ruskorämeillä. — Luonnon Tutkija 58: 42–48.
Heikurainen, L. 1971: Virgin peatland forests in Finland. — Acta Agr. Fennica 123: 11–26.
Heikurainen, L. & Pakarinen, P. 1982: Mire vegetation and site types. — In: Laine, J. (ed.), Peatlands and their utilization in Finland: 14–23. Finnish Peatland Soc., Helsinki.
Heino, R. & Hellsten, E. 1983: Climatological statistics in Finland 1961–1980. — Supplement to the Meteorological Yearbook of Finland 80(1a): 1–560.
Hill, M. O. 1979: TWINSPAN – a fortran program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. — Cornell Univ., Ithaca, NY. 90 pp.
Hill, M. O. & Gauch, H. G. 1980: Detrended correspondence analysis, an improved ordination technique. — Vegetatio 42: 47–58.
Hotanen, J.-P. 1989: The place of spruce-pine mires and oligotrophic spruce mires in Finnish peatland site type classifications. — Suo 40: 21–30. (In Finnish with English summary.)
Hotanen, J.-P. 1990: The effect of pseudospecies cut level settings on the results of TWINSPAN classification. — Suo 41: 43–53. (In Finnish with English summary.)
Hotanen, J.-P. & Nousiainen, H. 1990: The parity between numerical units and site types of forest and mire vegetation. — Folia Forestalia 763: 1–54. (In Finnish with English summary.)
Huikari, O. 1974: Site quality estimation on forest land. — In: Heikurainen, L. (ed.), Proc. Int. Symp. Forest Drainage, 2–6 September, 1974: 15–24. Jyväskylä-Oulu, Finland.
Ilvessalo, Y. 1956: The forests of Finland from 1921–24 to 1951–53. A survey based on three national forest inventories. — Comm. Inst. For. Fenniae 47: 1–227. (In Finnish with English summary.)
Ilvessalo, Y. 1957: The mires of Finland. A survey based on the 3rd National Forest Inventory. — Suo 8: 51–61. (In Finnish with English summary.)
Jeglum, J. K. 1991: Definition of trophic classes in wooded peatlands by means of vegetation types and plant indicators. — Ann. Bot. Fennici 28: 175–192.
Jukola-Sulonen, E.-L. & Salemaa, M. 1985: A comparison of different sampling methods of quantitative vegetation analysis. — Silva Fennica 19: 325–337.
Jukola-Sulonen, E.-L., Mikkola, K. & Salemaa, M. 1990: The vitality of conifers in Finland. — In: Kauppi, P., Anttila, P. & Kenttämies, K. (eds.), Acidification in Finland: 523–566. Springer Verlag, Berlin, Heidelberg, New York.
Kalela, A. 1960: Classification of the vegetation, especially of the forests, with particular reference to regional problems. — Silva Fennica 105: 40–49.
Kalela, A. 1961: Waldvegetationszonen Finlands und ihre klimatischen Paralleltypen. — Arch. Soc. Vanamo 16 (Suppl.): 65—83.
Kalela, A. 1962: Notes on the forest and peatland vegetation in the Canadian clay belt region and adjacent areas I and II. — Comm. Inst. For. Fenniae 55(32): 1–11 and 5(5): 1–19.
Kalela, A. 1973: Suomen yleisimpien metsätyyppien floristinen rakenne. — In: Kalliola, R. (ed.), Suomen kasvimaantiede: 260–267. WSOY, Helsinki.
Kotilainen, M. 1927: Untersuchungen über die Beziehungen

zwischen der Pflanzendecke der Moore und der Beschaffenheit, besonders der Reaktion des Torfbodens. Eine pflanzenökologische Studie mit Rücksicht auf die pracktische Bewertung der Ergebnisse. — Wiss. Veröff. Finnlands Moorkulturver. 7: 1–219.
Koponen, T., Isoviita, P. & Lammes, T. 1977: The bryophytes of Finland: An annotated checklist. — Flora Fennica. 6: 1–77.
Kujala, V. 1921: Beobachtungen über die Wald- und Moortypen von Kuusamo und der südlich von dort gelegenen Fichtenwaldgebiete. — Acta For. Fennica 18(5): 1–68. (In Finnish with German summary.)
Kuusipalo, J. 1985: An ecological study of upland forest site classification in southern Finland. — Acta For. Fennica 192: 1–77.
Lahti, T. 1994a: Understorey vegetation as an indicator of forest site potential in Southern Finland. — Acta For. Fennica 246: 1–68.
Lahti, T. 1994b: Do we need forest site types? — In: Reinikainen, A. & Lehtinen, K.-M. (eds.), Workshop of forest site classification, held in Vantaa, Finland, October 27, 1994. The Finnish Forest Research Institute. Research Papers 531: 5–7.
Lahti, T. & Väisänen, R. A. 1987: Ecological gradients of boreal forests in South Finland: an ordination test of Cajander's forest site type theory. — Vegetatio 68: 145–156.
Lukkala, O. J. 1929: Über die Dicke der Torfschicht und die Neigungsverhältnisse der Mooroberfläche auf verschiedenen Moortypen. — Acta For. Fennica 34: 1–16.
Lumiala, O. V. 1937: Pflanzengeographische und oberflächenmorphologische Mooruntersuchungen im nordwestlichen Karelien. — Ann. Bot. Soc. Vanamo 10: 1–115. (In Finnish with German summary.)
Lumiala, O. V. 1945: Über die Standortsfaktoren bei den Wasser-und Moorplflanzen sowie deren Untersuchung. — Ann. Acad. Sci. Fennicae (IV Biol.) 6: 1–47.
Malmer, N. 1985: Remarks to the classification of mires and mire vegetation – Scandinavian arguments. — Aquilo Ser. Bot. 21: 9–17.
Nurminen, K. 1964: (On the ecological grouping of spruce-hardwood swamp vegetation in Finland.) — M.Sc.-thesis, Univ. Helsinki, Bot. Inst., 87 pp. (In Finnish.)
Økland, R. H. 1989: A phytoecological study of the mire Northern Kisselbergmosen, SE-Norway. I. Introduction, flora, vegetation and ecological conditions. — Sommerfeltia 8: 1–172.
Økland, R. H. 1990a: A phytoecological study of the mire Northern Kisselbergmosen, Rødenes, SE-Norway. II. Identification of gradients by detrended (canonical) correspondence analysis. — Nordic J. Bot. 10: 79–108.
Økland, R. H. 1990b: A phytoecological study of the mire Northern Kisselbergmosen, SE-Norway. III. Diversity and habitat niche relationships. — Nordic J. Bot. 10: 191–220.
Økland, R. H. 1990c: Vegetation ecology: theory, methods and applications with reference to Fennoscandia. — Sommerfeltia Suppl. 1: 1–233.
Paasio, I. 1933: Über die Vegetation der Hochmoore Finnlands. — Acta For. Fennica 39: 1–210.
Paasio, I. 1941: Zur pflanzensoziologischen Grundlage der Weissmoortypen. — Acta For. Fennica 49: 1–84.
Påhlsson, L. (ed.) 1994: Vegetationstyper i Norden. — Tema Nord 1994: 665. Nordiska Ministerrådet, Köpenhamn. 630 pp.
Pakarinen, P. 1979: Ecological indicators and species groups of bryophytes in boreal peatlands. — In: Kivinen, E., Heikurainen, L. & Pakarinen, P. (eds.), Classification of peat and peatlands: 121–134. Int. Peat Soc., Helsinki.
Pakarinen, P. 1982: (Numerical classification of south Finnish mire and forest types.) — Suo 33: 97–103. (In Finnish with English summary.)
Pakarinen, P. 1984: Cover estimation and sampling of boreal vegetation in Northern Europe. — In: Knapp, R. (ed.), Sampling methods and taxon analysis in vegetation science. Handbook of Vegetation Science, 4: 35–44. Dr. W. Junk Publishers, The Hague.
Pakarinen, P. & Ruuhijärvi, R. 1978: Ordination of northern Finnish peatland vegetation with factor analysis and reciprocal averaging. — Ann. Bot. Fennici 15: 147–157.
Pankakoski, A. 1939: (Ökologisch-floristische Untersuchungen in Naturpark von Hiisijärvi in Südostfinnland.) — Ann. Bot. Soc. Vanamo 10: 1–154. (In Finnish with German summary.)
Persson, Å. 1961: Mire and spring vegetation in an area north of the Lake Torneträsk, Torne Lappmark, Sweden. I Description of the vegetation. — Opera Botanica 6: 1–187; II Habitat conditions. — Ibid. 6: 1–100.
Persson, Å. 1961: Mire and spring vegetation in an area north of the Lake Torneträsk, Torne Lappmark, Sweden. II Habitat conditions. — Opera Botanica 6: 1–100.
Reinikainen, A. 1990: Ecological monitoring as a part of the Finnish National Forest Inventory. — In: Proc. of the seminar on ecological statistics. Rome, 28 March – 1 April 1988. Annali di Statistica 119 (IX): 8.
Reinikainen, A., Lindholm, T. & Vasander, H. 1984: Ecological variation of mire site types in the small kettle-hole mire Heinisuo, southern Fnland. — Ann. Bot. Fennici 21: 79–101.
Ruhling, Å., Rasmussen, L., Pilegaard, K., Mäkinen, A. & Steinnes, E. 1987: Survey of atmospheric heavy metal deposition in the Nordic countries in 1985. — Nord 1987:21. The Nordic Council of Ministers. 44 pp.
Ruuhijärvi, R. 1960: Über die regionale Einteilung der nordfinnischen Moore. — Ann. Bot. Soc. Vanamo 31: 1–360.
Ruuhijärvi, R. 1982: Mire complex types in Finland. — In: Laine, J. (ed.), Peatlands and their utilization in Finland: 24–28. Finnish Peatland Soc., Helsinki.
Salemaa, M., Jukola-Sulonen, E.-L. & Lindgren, M. 1991: Forest condition in Finland, 1986–1990. — Silva Fennica 25: 147–175.
Santesson, R. 1993: Lichens and lichenicolous fungi of Sweden and Norway. — SBT-förlaget, Lund. 240 pp.
Sjörs, H. 1948: Myrvegetation i Bergslagen. — Acta Phytogeogr. Suecica 21: 1–299.
Sjörs, H. 1983: Mires of Sweden. — In: Gore, A. J. P. (ed.), Mires: swamp, bog, fen and moor. Ecosystems of the

world. 4B., Regional studies: 69–94. Elsevier, Amsterdam.

Sokal, R. R. & Rohlf, F. J. 1981: Biometry. — Freeman, San Fransisco.

Ter Braak, C. J. F. 1987: CANOCO – A FORTRAN program for canonical community ordination by partial detrended canonical correspondence analysis, principal components analysis and redundancy analysis. — TNO Inst. Applied Computer Science. Wageningen, The Netherlands. 95 pp.

Tolonen, K. 1967: Über die Entwicklung der Moore im finnischen Nordkarelien. — Ann. Bot. Fennici 4: 219–416.

Tolvanen, P. 1994: Structure and width of the vegetational margin zone between mire and upland forest. — M.Sc.-thesis, Univ. Helsinki, Bot. Inst., 48 pp.

Tonteri, T. 1990: Inter-observer variation in forest vegetation cover assesments. — Silva Fennica 24: 189–196.

Tonteri, T., Mikkola, K. & Lahti, T. 1990: Compositional gradients in the forest vegetation of Finland. — J. Veg. Sci. 1: 691–698.

Trass, H. & Malmer, N. 1978: North European approaches to classification. — In: Whittaker, R. H. (ed.), Classification of plant communities: 201–246. The Hague.

Tuhkanen, S. 1980: Climatic parameters and indices in plant geography. — Acta Phytogeogr. Suecica 67: 1–105.

Tuomikoski, R. 1942: Untersuchungen über die Untervegetation der Bruchmoore in Ostfinnland. I. Zur Methodik der pflanzensoziologischen Systematik. — Ann. Bot. Soc. Vanamo 7: 1–203.

APPENDIX

Field and ground layer vegetation in seven TWINSPAN-clusters (A–G). Mean cover percentage value of each species in each cluster (+ < 0.1%) are presented. Total number of species was 135. The amount of sample plots in each cluster = (*n*).

	TWINSPAN-clusters						
	A (*n* = 5)	B (*n* = 17)	C (*n* = 22)	D (*n* = 13)	E (*n* = 14)	F (*n* = 15)	G (*n* = 6)
Field layer							
Trees and shrubs:							
Salix aurita	0.1	1.3	+	–	–	–	–
Salix phylicifolia	–	–	+	–	–	–	–
Pinus sylvestris	+	0.1	+	0.1	–	+	–
Betula pubescens	0.1	0.1	0.1	0.1	+	0.2	+
Picea abies	0.5	0.2	0.1	0.2	0.1	0.1	0.1
Sorbus aucuparia	0.4	+	0.1	0.1	+	+	0.2
Salix caprea	–	0.1	0.2	–	+	0.1	0.1
Juniperus communis	–	+	+	0.1	–	+	–
Populus tremula	0.1	–	–	+	–	+	–
Alnus incana	–	–	+	–	–	+	+
Rubus idaeus	–	–	–	–	–	+	+
Dwarf-shrubs:							
Betula nana	–	0.8	–	–	–	–	–
Vaccinium microcarpum	–	+	+	–	–	–	–
Arctostaphylos uva–ursi	–	–	+	–	–	–	–
Andromeda polifolia	–	0.3	0.1	–	–	–	–
Vaccinium oxycoccus	–	0.1	+	+	–	–	–
Chamaedaphne calyculata	–	0.3	+	–	0.1	–	–
Empetrum nigrum	4.0	4.1	5.4	0.9	0.3	–	–
Calluna vulgaris	2.9	6.9	0.9	+	–	0.1	–
Ledum palustre	–	2.3	8.9	+	–	0.1	–
Vaccinium uliginosom	0.3	7.8	10.1	+	–	0.4	–
Vaccinium vitis-idaea	6.5	2.5	11.7	10.7	4.4	2.6	3.3
Vaccinium myrtillus	2.0	7.0	11.3	16.5	28.0	10.4	3.0
Graminoids:							
Calamagrostis epigejos	1.4	–	–	–	–	–	–
Festuca ovina	0.1	–	–	–	–	–	–
Eriophorum vaginatum	–	0.3	–	–	–	–	–
Eriophorum angustifolium	–	–	+	–	–	–	–
Carex nigra	–	+	0.1	+	–	–	–
Carex globularis	2.0	3.6	2.7	2.6	5.0	2.0	1.0
Deschampsia flexuosa	13.1	0.2	1.0	5.8	0.1	0.4	0.1
Luzula pilosa	0.2	–	+	0.1	+	0.1	0.1
Calamagrostis arundinacea	0.1	+	0.1	+	+	0.1	+
Carex echinata	–	–	+	+	–	–	–
Juncus filiformis	–	–	+	0.2	–	–	–
Agrostis capillaris	–	–	+	+	–	+	–

(continues)

	TWINSPAN-clusters						
	A (*n* = 5)	**B** (*n* = 17)	**C** (*n* = 22)	**D** (*n* = 13)	**E** (*n* = 14)	**F** (*n* = 15)	**G** (*n* = 6)
Carex canescens	–	–	+	+	–	–	+
Deschampsia cespitosa	–	–	0.3	+	–	+	0.1
Calamagrostis purpurea	–	–	0.1	–	–	1.6	0.3
Calamagrostis canescens	–	–	–	–	–	+	–
Carex digitata	–	–	–	–	–	+	0.1
Melica nutans	–	–	–	–	–	–	0.1
Carex lasiocarpa	–	–	–	–	–	–	+
Carex rostrata	–	–	–	–	–	–	+
Herbs:							
Potentilla erecta	0.1	–	–	–	–	+	–
Melampyrum pratense	0.1	+	+	0.1	0.1	+	–
Epilobium angustifolium	0.2	–	0.2	0.1	–	+	0.1
Solidago virgaurea	0.3	+	–	0.1	–	0.4	0.1
Rubus chamaemorus	–	1.5	1.4	+	4.3	+	0.6
Equisetum sylvaticum	–	+	0.8	0.2	1.8	6.1	9.1
Trientalis europea	+	+	0.4	0.7	+	0.3	0.7
Linnaea borealis	0.1	+	–	0.3	+	0.1	1.7
Cornus suecica	–	+	0.1	0.3	–	0.4	–
Goodyera repens	–	–	+	–	–	–	–
Epilobium palustre	–	–	–	+	–	–	–
Lycopodium annotinum	–	–	+	+	+	+	–
Melampyrum sylvaticum	–	–	–	–	+	0.1	–
Listera cordata	–	–	–	+	–	+	–
Orthilia secunda	0.1	+	0.3	0.2	+	0.1	0.7
Rubus arcticus	–	–	0.1	+	–	0.1	0.1
Gymnocarpium dryopteris	–	–	+	–	+	1.3	2.7
Dryopteris carthusiana	–	–	–	–	0.4	0.3	4.5
Oxalis acetosella	–	–	–	+	–	0.1	4.0
Maianthemum bifolium	–	–	+	0.1	0.1	0.5	3.8
Equisetum palustre	–	–	+	–	–	–	0.9
Dryopteris expansa	–	–	–	1.1	–	–	0.2
Potentilla palustris	–	–	–	0.2	–	–	0.1
Thelypteris phegopteris	–	–	–	0.2	–	–	–
Lysimachia vulgaris	–	–	–	–	–	+	–
Viola palustris	–	–	–	–	–	–	0.6
Athyrium filix-femina	–	–	–	–	–	–	1.8
Rubus saxatilis	–	–	–	–	–	–	0.4
Anemone nemorosa	–	–	–	–	–	–	0.3
Cirsium helenioides	–	–	–	–	–	–	0.1
Equisetum arvense	–	–	–	–	–	–	+
Equisetum pratense	–	–	–	–	–	–	+
Geranium sylvaticum	–	–	–	–	–	–	+
Geum rivale	–	–	–	–	–	–	+
Ranunculus repens	–	–	–	–	–	–	+
Stellaria palustris	–	–	–	–	–	–	+
Ground layer							
Sphagnum mosses:							
Sphagnum nemoreum	5.0	4.4	3.5	–	0.1	+	–
Sphagnum russowii	–	25.1	5.0	5.7	5.4	+	–
Sphagnum magellanicum	–	0.1	+	–	1.0	+	–
Sphagnum angustifolium	7.4	34.0	8.0	8.0	8.1	3.1	1.5
Sphagnum girgensohnii	0.2	+	4.0	15.8	24.5	42.1	48.5
Sphagnum compactum	–	0.1	–	0.3	–	–	–
Sphagnum centrale	–	–	–	0.5	0.4	–	1.7
Sphagnum wulfianum	–	–	+	–	–	–	+
Sphagnum fallax	–	–	–	1.2	–	–	–
Sphagnum riparium	–	–	–	0.7	–	–	–
Sphagnum squarrosum	–	–	–	–	–	0.1	1.0
Sphagnum teres	–	–	–	–	–	+	–
Other mosses:							
Polytrichum strictum	2.0	0.7	0.1	+	+	–	–
Polytrichum juniperinum	3.4	+	0.1	0.1	+	–	–
Dicranum drummondii	–	+	–	–	–	–	–
Ptilidium pulcherrimum	–	0.1	–	–	–	–	–
Dicranum fuscescens	–	–	+	–	+	+	–
Aulacomnium palustre	1.1	0.8	0.2	0.3	0.1	0.2	0.3
Pleurozium schreberi	31.8	15.7	29.0	23.0	22.7	8.6	2.9
Polytrichum commune	24.2	10.4	6.9	20.7	3.8	7.7	0.4
Hylocomium splendens	1.7	0.6	5.0	3.3	9.1	3.0	2.4
Dicranum polysetum	3.3	0.2	1.1	0.5	1.5	1.6	0.3
Dicranum scoparium	0.5	+	0.2	0.2	2.0	0.4	0.2
Hepaticae spp.	–	0.1	+	+	0.1	+	0.1

(continues)

	TWINSPAN-clusters						
	A (*n* = 5)	B (*n* = 17)	C (*n* = 22)	D (*n* = 13)	E (*n* = 14)	F (*n* = 15)	G (*n* = 6)
Barbilophozia lycopodioides	–	0.1	–	–	–	+	0.1
Pohlia nutans	+	+	+	+	+	+	0.4
Ptilidium ciliare	+	–	+	+	+	–	–
Ptilium crista-castrensis	–	–	+	+	1.0	0.2	–
Mnium spp.	–	–	+	–	–	+	0.2
Calliergon stramineum	–	–	+	0.1	–	–	–
Barbilophozia barbata	–	–	–	–	+	–	–
Atrichum undulatum	–	–	–	–	–	+	–
Blepharostoma trichophyllum	–	–	–	–	–	+	–
Rhodobryum roseum	–	–	–	–	–	+	–
Brachythecium spp.	–	–	+	+	+	0.2	3.0
Dicranum majus	–	–	+	0.1	1.6	0.5	2.6
Rhizomnium spp.	–	–	+	–	–	–	+
Plagiomnium spp.	–	–	–	+	–	–	+
Rhytidiadelphus triquetrus	–	–	–	–	+	+	0.2
Plagiochila asplenioides	–	–	–	–	–	–	+
Lichens:							
Cladonia botrytes	+	–	–	–	–	–	–
Cladonia crispata	+	–	–	–	–	–	–
Cladonia gracilis	0.1	–	+	–	–	–	–
Cladonia stellaris	0.1	–	0.2	–	–	–	–
Cladonia cariosa	+	+	+	–	–	–	–
Cladonia cornuta	2.0	+	–	–	–	+	–
Cladonia arbuscula	0.1	1.1	0.3	–	+	–	–
Cladonia rangiferina	0.3	1.1	0.6	0.1	0.1	+	–
Cladonia fimbriata	+	+	–	–	–	+	–
Cladonia deformis	+	+	+	–	–	+	–
Cladonia chlorophaea	+	–	+	–	–	+	–
Cladonia furcata	–	–	–	–	–	+	–
Peltigera aphthosa	–	+	–	–	–	–	–

Paper II

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II

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Patterns of diversity in boreal mire margin vegetation

Boreaalisen reunavaikutteisen suokasvillisuuden monimuotoisuuden analyysia

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Mire margin communities are mosaics of forest and mire vegetation which consist of several ecological guilds (forest, spruce mire, marsh and spring vegetation). Diversity patterns of undrained forested mire margin communities were examined by using numerical classification (TWINSPAN) and ordination (DCA) techniques. The understorey vegetation was tested for both alfa (species richness, Shannon H' and Pielou J diversity indices) and beta diversity (DCA dimensions). The structural diversity of the overstorey was examined by producing structural (TWINSPAN) clusters based on the percentage cover of tree and shrub species in six canopy layers and in one shrub layer. The study was based on the systematic sample plot data collected from permanent plots of the 8th Finnish National Forest Inventory (1985–86). The material consisted of 92 plots of undrained forested mire margin sites in south and central Finland (60°–66°N). The alfa diversities between the seven site clusters differed more clearly than those between the site types. A considerable variety of species of different ecological guilds were found that represented the ecological sources of high beta diversity. Structural diversity varied between clusters formed from overstorey data.

Key words: boreal forest, peatland, structural diversity, vegetation diversity,

INTRODUCTION

The vegetation gradient between mire margin and mire expanse communities is important in the ecology and classification of boreal mires in Finland (Heikurainen & Pakarinen 1982, Ruuhijärvi 1983). The position of plant species and vegetation site types along this gradient has been studied in several investigations (e.g.Tuomikoski 1942, Sjörs 1948, Pakarinen 1982, Reinikainen et al. 1984, Eurola & Holappa 1985, Malmer 1985, Hotanen 1989, Hotanen & Nousiainen 1990, Jeglum 1991). In Finland 422 plant taxa (415 species), including vascular plants, *Bryidae*, *Sphagnum* mosses and ground lichens occur frequently on mire sites (Eurola et al. 1994). About 70% of these species favour mire margin influenced sites (Fig. 1), which have thin peat layer (Ilvessalo 1956, Ruuhijärvi 1960, Eurola 1962) and receive supplementary input of mineral nutrients from surrounding mineral soil (Heikurainen 1954, Eurola & Holappa 1985). This group can be divided into two main components, namely forest species and wetland species. In the latter group the

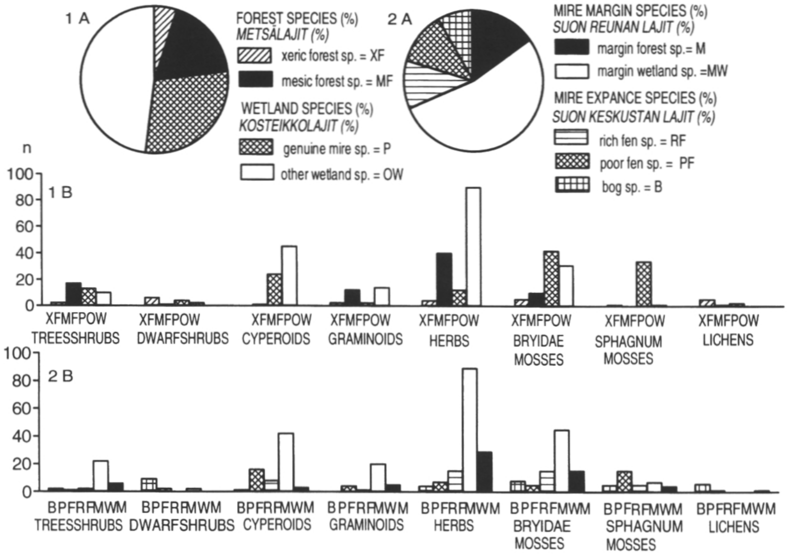


Fig. 1. Distribution of the Finnish mire flora (422 taxa) between different ecological guilds (1A, 1B) and the number of species of the ecological guilds in different life forms (2A, 2B). Drawn according to Eurola et al. (1994).

Kuva 1. Suomen suokasvilajiston (422 taksonia) jakautuminen ekologisiin ryhmiin (1A, 2A) ja ekologisten ryhmien lajimäärät elomuodoittain (1B, 2B). 1 A) Metsälajit: kuivien = XF ja tuoreiden = MF kankaiden lajit, Kosteikkojen lajit: aidot suolajit = P ja muut kosteikkolajit = OW. 2A) Reunavaikutteiset lajit: metsä- = M ja kosteikkolajit = MW. Keskustavaikutteiset lajit: meso-eutrofiset nevalajit = RF, oligotrofiset nevalajit = PF ja rämelajit = B. Piirretty Eurolan ym. (1994) mukaan.

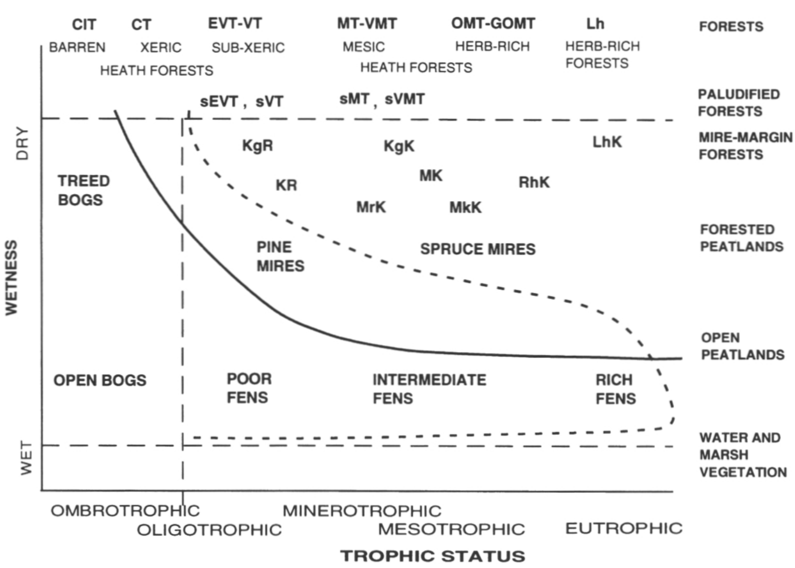


Fig. 2. An idealized two-dimensional ordination of boreal forest and wetland sites with location of the studied types. Site types with Finnish symbols (see Table 1 and Appendix 2). Dotted line = border between mire margin and mire expanse influenced site types. Solid line = border between types suitable and not suitable for forest drainage.

Kuva 2. Idealisoitu kaksisuuntainen ordinaatio Suomen metsä- ja suotyyppien esiintymisestä trofian ja vesitalouden mukaan. Katkoviivakäyrä = raja reuna- ja keskustavaikutteisten tyyppien välillä, yhtenäinen käyrä = raja metsäojituskelpoisten ja -kelvottomien suotyyppien välillä.

species other than genuine mire plants (= plants which grow on peat) are more frequent. The majority of genuine mire plants seem to prefer mire expanse influenced bog and fen sites (Fig. 1).

With respect to diversity, site types situated on the border zones of different ecological influences are of special interest (Fig. 2). It can be assumed that due to the ecological multi-source origin of the flora and to the location of the sites on topographic gradients (e.g. Lumiala 1937) the mire margin communities could show high species richness. In order to test that simple hypothesis the species and structural diversity on sites typically situated on the transition zone between forest and mire was examined.

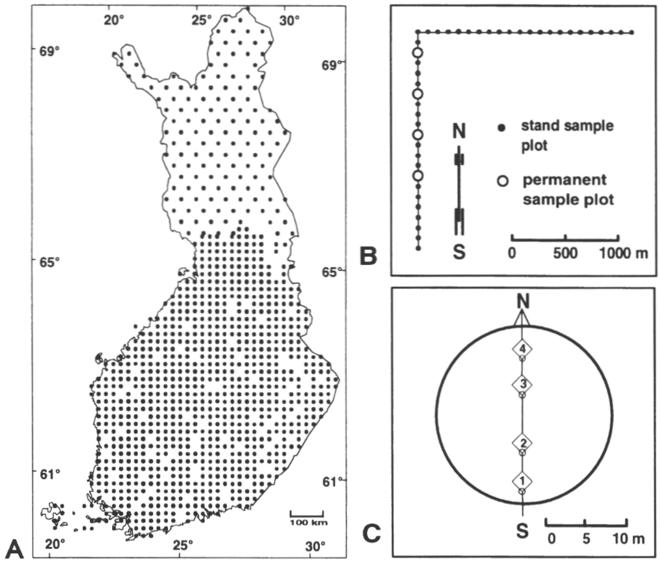


Fig. 3. Sampling frame-work. A) = tracts of the National Forest Inventory with permanent sample plots, B) = a sample tract with four permanent sample plots, C) = a sample plot with four 2 m² vegetation sample squares.

Kuva 3. A) = Valtakunnan metsien inventoinnin pysyvien koealojen lohkot, B) = inventoinnin lohko, jolla neljä pysyvää koealaa, C) = pysyvä koeala, jolla neljä 2 m² kasvillisuusruutua.

MATERIAL AND METHODS

The vegetation data of this study were derived from permanent sample plots of the 8th National Forest Inventory (NFI) 1985–86 (Reinikainen & Nousiainen 1985, Reinikainen 1990) (Fig. 3). Sample plots were chosen according to the following criteria: (1) appropriate site type inside the categories paludified forests (= paludified mineral soil forests), mire margin forests and forested pine and spruce mires, (2) plot homogenous for the type; (3) at least four vegetation sample squares on the plot; (4) site not drained; (5) tree stand untreated at least for two years before inventory. Altogether, 92 plots fulfilling these criteria were found (Table 1, Figs. 2 and 4).

The field data were collected by 12 biologists of the NFI crews during late may-september 1985–86. The field and bottom layer vegetation was recorded by estimating the percentage cover of species on four 2 m² sample squares on each plot. The overstorey cover of tree and shrub species was estimated on the whole 300 m² sample plot (Fig. 3).

In the data processing the basic variables were mean cover percentage values for the field and bottom layer species and the cover percentages of tree species in six vertical canopy layers (according to the instructions of NFI, see e.g. Yli-Kojola 1995) and tree and shrub species in one shrub layer for the overstorey species. The data were analyzed with TWINSPAN classification (Hill 1979) by default options and with DCA ordination by using CANOCO program with detrending by segments and downweighting of rare species (ter Braak 1987). Average species richness, diversity indices (Shannon H', Shannon & Weaver 1949) and evenness indices (Pielou J, Pielou 1966) were calculated. The species were arranged into ecological guilds according to Eurola et al. (1994).

The site types and their Finnish symbols are according to Kalela (1961) for paludified forests and according to Heikurainen & Pakarinen (1982) for mires (Fig. 2, Table 1, Appendix 2). The nomenclature follows Hämet-Ahti et al. (1986) for vascular plants, Koponen et al. (1977) for bryophytes and Santesson (1993) for lichens.

RESULTS

The species diversity of understorey communities

In TWINSPAN analysis a group of six sample plots was first separated to form cluster G. From the rest 86 sample plots clusters A–F were generated on the second and third levels of division (Fig. 5). The size of TWINSPAN clusters and their parity with site types are presented in Table 1.

The species richness did not vary much between site types. Only the most fertile site type LhK (eutrophic paludified hardwood-spruce forest) showed higher species number than the other site types. The site type variation had a nearly significant effect on the H' and the J values but the cluster division had much clearer effect on species richness and the J value (Table 1). The variation of H' values between clusters was smaller than between site types. There were correlations of H' ($r = 0.46$) and J ($r = -0.89$*) for the species number in clusters ($n = 7$) but not in site types ($n = 13$, $r = 0.30$ and $r = -0.01$).

Composition of gradient diversity

Long axes (1st axis 7.7 and 2nd axis 9.7 S.D.-units) of species ordination (Fig. 6) and sample plot ordination (1st axis 4.2 and 2nd axis 3.2 S.D.-units) (Fig. 7) displayed the dissimilarity of the ecological origin in the floristic composition. From a potential species number of about 200 for the sites and study area (according to the list of Eurola et al. 1994) a total of 135 species was found of which 88 had a frequency of > 2 /92. In the two-dimensional species ordination (Fig. 6) islets

Table 1. Distribution of studied paludified forest (1., according to Kalela 1961), mire margin forest and forested pine and spruce mire site types (2. and 3., according to Heikurainen & Pakarinen 1982) within TWINSPAN vegetation clusters. The mean species richness, Shannon (H') diversity and Pielou (J) evenness indices for types and clusters are presented. All 135 species of 92 plots are included (cf. Fig. 6). The full English site type names for the Finnish site type symbols are presented in Appendix 2.

Taulukko 1. Aineiston soistuneiden kangasmetsätyyppien (1., Kalelan 1961 mukaan) ja metsäisten, reunavaikutteisten suotyyppien (2. ja 3., Heikuraisen & Pakarisen 1982 mukaan) esiintyminen TWINSPAN-kasvillisuusryhmissä. Keskimääräiset lajimäärät, Shannon diversiteetti- (H') ja Pieloun (J) tasaisuusindeksit on ilmaistu tyypeittäin ja ryhmittäin (indeksit on laskettu 135 lajia/92koealaa mukaan).

Site types	Trophic status	TWINSPAN clusters A	B	C	D	E	F	G	n	Species n (mean)	H' (mean)	J (mean)
1. sEVT	oligo	1	2	6					9	18.4	2.09	0.74
1. sVT	oligo	3	1	1	3				8	21.8	1.90	0.62
1. sVMT	oligo-meso		3	9	2	2			16	17.9	1.87	0.66
1. sMT	oligo-meso				3	3	5		11	18.7	1.73	0.60
1. sDeMT	oligo-meso				1		1		2	21.5	2.23	0.73
2. KgR	oligo	1	5	3					9	17.6	1.93	0.68
2. KgK	oligo-meso				2	5	3	1	11	17.8	1.83	0.64
2. LhK	eutrophic							2	2	33.0	2.59	0.74
3. MrK	(oligo)-meso		1						1	22.0	2.08	0.67
3. KR	oligo-(meso)		5	2	1				8	18.7	1.88	0.65
3. MK	oligo-meso			1	1	4	3		9	19.1	1.85	0.63
3. MkK	oligo-meso						3	2	5	21.4	1.52	0.50
3. RhK	meso-eu							1	1	20.0	1.61	0.54
Sample plots n		5	17	22	13	14	15	6	92	F=1.63	F=2.15*	F=2.37*
Species n (mean)		25.2	18.7	18.3	19.2	15.3	19.9	26.8		F=5.43***		
Shannon H' (mean)		2.03	1.91	1.95	1.90	1.87	1.67	2.00		F=1.32		
Pielou J (mean)		0.63	0.66	0.68	0.65	0.69	0.56	0.60		F=3.11**		

corresponding to different ecological guilds could be distinguished. Mire margin species seem to associate with fertile forest species and mire expanse species with xeric forest species. As the mire margin species occur sporadically they only slightly increase the average species richness per site or plot. The vector of increasing species number was not parallel with any of the ordination axes and increased slightly towards the mesic forest and herb-rich spruce mire sites. The evenness of communities (according to H' and J) seemed to increase along the 1st axis towards the bog and xeric forest vegetation communities (Fig. 7).

Overstorey diversity

For the structural TWINSPAN classification from the actual 16 tree and shrub species, occurring in six canopy layers and in one shrub layer, a total of 91 'layer species' was generated. On the third division level TWINSPAN produced six structurally different clusters when one outlier plot was eliminated on the second division level (Fig. 8).

There emerged clear differences between the clusters in species composition, canopy structure and species distribution. The first division between clusters 1–2 and 3–6 was determined by dominant species of the stand (spruce/pine), regularity of canopy structure (regular/more irregular), and species number (13 woody species against 9–11 species). Among the final clusters cl 1 was spruce-dominated and rich in species, cl 2 differed from cl 1 only by the dominance of pine in upper canopy, cl 3 and 4 were pine-dominated but having different distribution of species into layers, cl 5 was the only with birch (*Betula pubescens*) dominated upper canopy and cl 6 was characterized by purest pine dominance and lowest tree species number.

The parity between the described structural clusters and site types or vegetational clusters was rather poor. The majority of mesic forest types and mesotrophic mire types and the corresponding vegetation clusters D, E, F and G belonged to the structural clusters cl 1 and cl 2. Respectively, the bulk of xeric forest types and oligotrophic mire types fell into structural clusters cl 4 and cl 6.

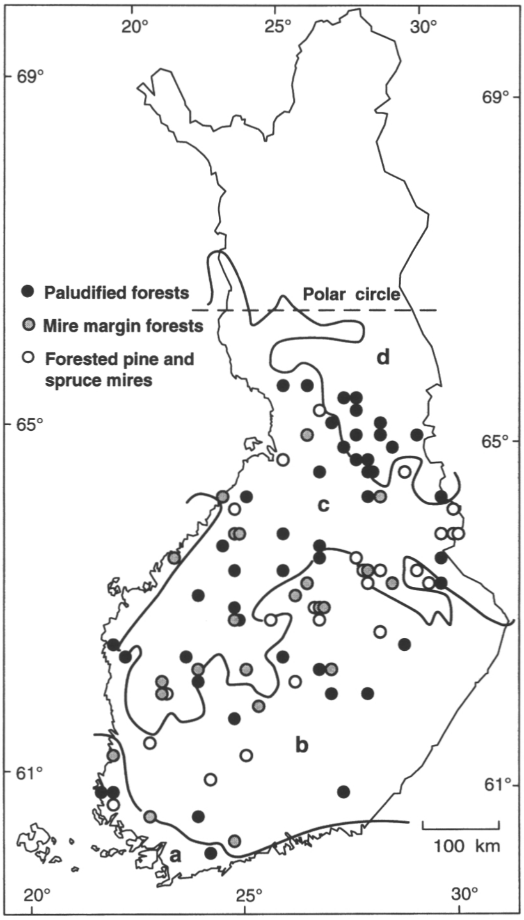
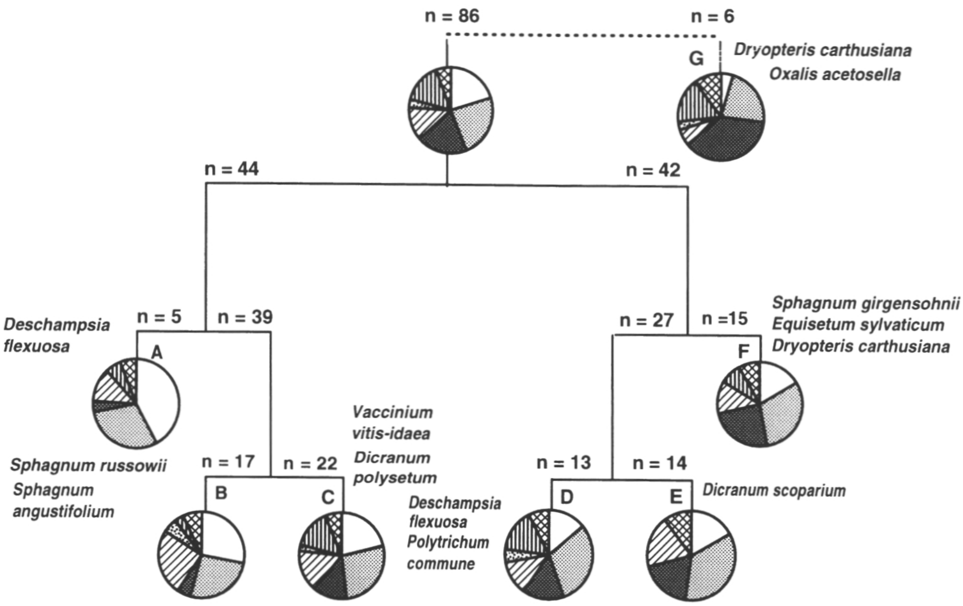


Fig. 4. Distribution of sample plots within a = hemiboreal, b = southern boreal, c = middle boreal and d = northern boreal subzones. The boreal subzones are drawn according to Ahti et al. (1968).

Kuva 4. Koealojen esiintyminen a = hemi-, b = etelä-, c = keski- ja d = pohjoisboreaalisella kasvillisuusvyöhykkeellä. Kasvillisuusvyöhykkeet Ahti ym. (1968) mukaan.

DISCUSSION AND CONCLUSIONS

As far as we know rather few studies among the extensive literature on vegetation of boreal mires and forests have particularly concentrated on the diversity of communities (e. g. Helliwell 1978, Kuusipalo 1984, Vasander 1984, Oksanen 1986, Vasander 1987a,b, Tonteri et al. 1990, Økland 1990, Tonteri 1994, Vasander et al. 1996). Site



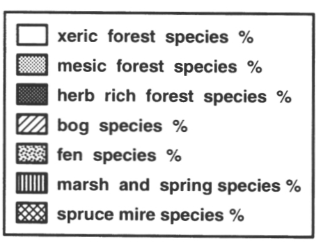


Fig. 5. Ecological 'spectra' of the floral composition of TWINSPAN understorey clusters with the most important indicator species.

Kuva 5. Aluskasvillisuuden 'ekologinen kirjo' TWINSPAN- kasvillisuusryhmissä pääindikaattorilajeineen.

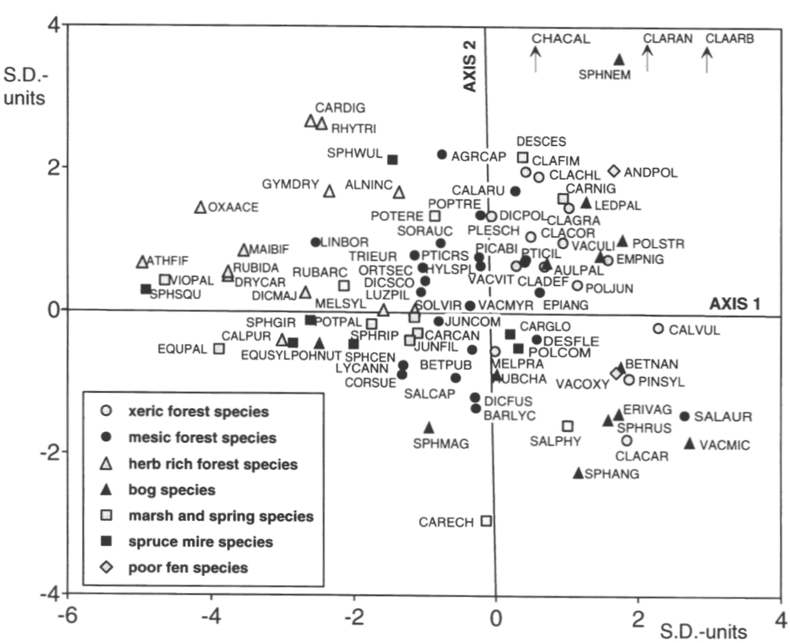


Fig. 6. DCA ordination for the understorey species with more than two occurrences (88 species). For full species names in each ecological guild, see Appendix 1.

Kuva 6. DCA-ordinaatio aluskasvillisuuden lajeille, jotka esiintyvät useammalla kuin kahdella koealalla (88 lajia). Lajinimet ja ekologinen ryhmittely on esitetty Liitteessä 1.

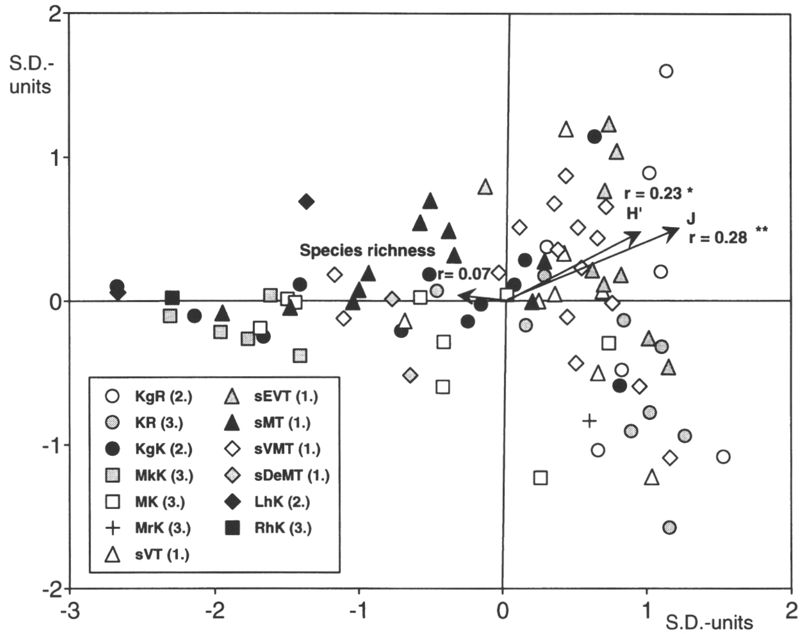


Fig. 7. Sample plot DCA ordination. The vectors of passive variables: species richness, H' and J indices with their correlations against DCA axis 1. For full English site type names see Appendix 2.

Fig. 7. Koealojen DCA ordinaatio. Nuolet kuvaavat passiivisia ympäristömuuttujia, lajimäärää, H'-ja J-indeksiä, ja niiden korrelaatioita DCA 1 akseliin.

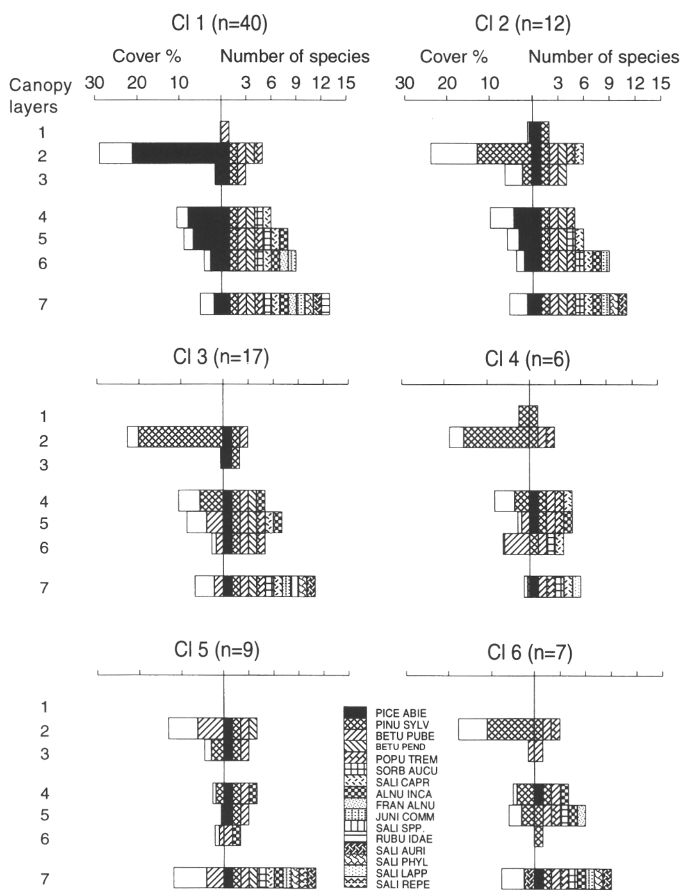


Fig. 8. The overstorey structure in TWINSPAN clusters obtained from the 'layer species' matrix. For each cluster the left side of the diagram presents the total cover (white) of the canopy layer and the cover of the dominant species (shaded) and the right side of the diagram describes the number and the names of the species on each layer.

Kuva 8. 'Latvuskerroslajeista' TWINSPAN-luokittelulla saadut rakenteelliset ryhmät. Vasemman puolen pylväät kuvaavat puu- tai pensaslajin kokonaispeittävyyttä (valkoinen alue) ja vallitsevan lajin osuutta (varjostettu) ja oikean puolen pylväät kuvaavat lajimäärää ja lajeja latvuskerroksittain.

classification, for instance, commonly operates with species numbers and distribution but rarely uses these criteria in the determination of site types. Only the extreme types (by trophic status) of boreal forests and mires are described to be especially rich or poor in species (e.g. Kalliola 1973). In the present analysis the parameters of diversity seemed to be significant characteristics of numerical vegetation clusters.

Although there were no mire margin site types or clusters displaying higher species number than the forest sites of corresponding fertility (see e.g. Tonteri 1994) the species assortment seemed to be more versatile (Figs. 5 and 6). The assumed sources of species diversity were found in the analysis of the understorey communities. The effect of mire margin factors (spruce mire, marsh and spring factors) (Eurola et al. 1984) seemed to be relatively weak. Most of the abundant species belonged to either forest or bog guilds. From a 'potential' of ca. 200 species (Eurola et al. 1994) for the studied site types about 2/3 were found. Most species of mire margin guilds seem to be rather rare on these sites. Consequently, the diversity value of these habitats is more on the community than on the species level.

Beta diversity of understorey as measured by gradient lengths seemed to be higher in the sites in this study than in forests in general (cf. Tonteri et al. 1990) despite the fact that in our data the variation caused by site fertility and stand age (age succession) was reduced when compared to the main sources of beta diversity described by Tonteri et al. (1990) and Tonteri (1994). This difference was due both to the occurrence of wetland mire margin guilds and bog and fen guilds in our data.

A new approach for describing and analysing the layer structure of forest communities was introduced (cf. Lindholm & Tuominen 1989). We succeeded in separating interpretable groups, 'structural types' which should be later ecologically explained. More in general, the importance of mire margin forests for biotope and landscape diversity should be further analyzed by comparing their structure to other forested communities using different approaches (e.g. Lähde et al. 1991, Kuuluvainen, T., Penttinen, A., Leinonen, K. & Nygren, M. 1996, unpublished data). Our hypothesis for further studies is that stands growing on undrained wetland sites are under slight silvicultural treatment and thus relatively pristine, so they probably increase the diversity of local forest habitats.

Mire margin forest communities seem to conserve different components of diversity rather efficiently (see e.g. Ruuhijärvi 1983, Eurola & Holappa 1985). On the basis on this systematic but too small sample it remains unclear what is the ability of these biotopes to conserve species and mire type rareness and maintain threatened species. Having been popular and successful objects of forest drainage the remnants of these biotopes which represent less than 20% of the undrained wetland area in Finland (according to the permanent sample plot data of 8th National Forest Inventory 1985–86), now deserve at least management of diversity.

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REFERENCES

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. Annales Botanici Fennici 5: 169–211.

Eurola, S. 1962. Über die regionale Einteilung der südfinnischen Moore. Annales Botanici Societatis Zoologicae Botanicae Fennicae 'Vanamo' 33 (2): 1–243.

Eurola, S. & Holappa, K. 1985. The Finnish mire type system. Aquilo Ser. Botanica 21: 101–110.

Eurola, S., Hicks, S. & Kaakinen, E. 1984. Key to Finnish Mire Types. In: Moore, P. (ed.), European Mires. pp. 11–117. Academic Press, London.

Eurola, S., Huttunen, A. & Kukko-Oja, K. 1994. Suokasvillisuusopas. Oulanka Reports 13. University of Oulu. 81pp.

Hämet-Ahti, L., Suominen, J., Ulvinen, T., Uotila, P. & Vuokko, S. (eds.) 1986. Retkeilykasvio. Suomen Luonnonsuojelun Tuki, Helsinki. 598 pp.

Heikurainen, L. 1954. Korpisuus ruskorämeillä. Luonnon Tutkija 58: 42–48.

Heikurainen, L. & Pakarinen, P. 1982. Mire vegetation and site types. In: Laine, J., (ed.). Peatlands and their utili-

zation in Finland, pp. 14–23. Finnish Peatland Society, Helsinki.
Helliwell, D. R. 1978. Floristic diversity in some central Swedish forests. Forestry 51: 151–161.
Hill, M.O. 1979. TWINSPAN – A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. Cornell University, Ithaca, NY. 90 pp.
Hotanen, J-P. 1989. Korpirämeet ja korvet suomalaisessa suoluokitusjärjestelmässä (Summary: The place of spruce-pine mires and oligotrophic spruce mires in Finnish peatland site type classifications). Suo 40: 21–30.
Hotanen, J-P. & Nousiainen, H. 1990. Metsä- ja suokasvillisuuden numeerisen ryhmittelyn ja kasvupaikkatyyppien rinnastettavuus (Summary: The parity between numerical units and site types of forest and mire vegetation). Folia Forestalia 763: 1–54.
Ilvessalo, Y. 1956. Suomen metsät vuosista 1921-24 vuosiin 1951–53. Kolmeen valtakunnan metsien inventointiin perustuva kuvaus (Summary: The forests of Finland from 1921–24 to 1951–53. A survey based on three national forest inventories). Communicationes Instituti Forestalis Fenniae 47(1): 1–227.
Jeglum, J. K. 1991. Definition of trophic classes in wooded peatlands by means of vegetation types and plant indicators. Annales Botanici Fennici 28: 175–192.
Kalela, A. 1961. Waldvegetationszonen Finnlands und ihre klimatischen Paralleltypen. Archium Societatis Vanamo 16 (Suppl.): 65–83.
Kalliola, R. 1973. Suomen kasvimaantiede. WSOY, Porvoo - Helsinki. 308 pp.
Koponen, T., Isoviita, P. & Lammes, T. 1977. The bryophytes of Finland: An annotated cheklist. Flora Fennica 6:1–77.
Kuusipalo, J. 1984. Diversity pattern of the forest understorey vegetation in relation to some site characteristis. Silva Fennica 18: 121–131.
Lähde, E. , Laiho, O. , Norokorpi, Y. & Saksa, T. 1991. The structure of advanced virgin forests in Finland. Scandinavian Journal of Forest Research 6: 527–537.
Lindholm, T. & Tuominen, S. 1989. Vanhojen luonnonmetsien rakennetyypit eräillä eteläboreaalisilla luonnonsuojelualueilla (Summary: The structure classes of southern boreal natural forests in some Finnish nature protection areas). Folia Forestalia 736: 46–52.
Lumiala, O. 1937. Kasvimaantieteellisiä ja pintamorfologisia suotutkimuksia Luoteis-Karjalasssa (Referat: Pflanzengeographische und obermorfologische Mooruntersuchungen im nordwestlichen Karelien). Annales Botanici Societatis Zoologicae Botanicae Fennicae Vanamo 10(1): 1–115.
Malmer, N. 1985. Remarks to the classification of mire vegetation – Scandinavian arguments. Aquilo Ser. Botanica 21: 9–17.
Økland, R. H. 1990. A phytogeographical study of the Northern Kisselbergsmosen, SE Norway. III Diversity and habitat niche relationships. Nordic Journal of Botany 10: 191–220.
Oksanen, J. 1986. Succesion, dominance and diversity in lichen-rich pine forest vegetation in Finland. Holarctic Ecology 9: 261–266.
Pakarinen, P. 1982. Etelä-Suomen suo- ja metsätyyppien numeerisesta luokittelusta. (Summary: Numerical classification of south Finnish mire and forest types). Suo 33: 97–103.
Pielou, E.C. 1966. Shannon's Formula as a measure of specific diversity: Its use and misuse. American Nature 100: 463–465.
Reinikainen, A. 1990. Ecological monitoring as a part of the Finnish National Forest Inventory. In: Proc. of the seminar on ecological statistics. Rome, 28 March–1 April 1988. Annali di Statistica 119 (IX):8, pp. 258–271.
Reinikainen, A. & Nousiainen, H. 1985. Biologien työohjeet VMI 8:n pysyviä koealoja varten. The Finnish Forest Research Institute, Vantaa. Moniste/Mimeographed 42 pp.
Reinikainen, A., Lindholm, T. & Vasander, H. 1984. Ecological variation of mire site types in the small kettlehole mire Heinisuo, southern Finland. Annales Botanici Fennici 21: 79–101.
Ruuhijärvi, R. 1960. Über die regionale Einteilung der nordfinnische Moore. Annales Botanici Societatis Zoologicae Botanicae Fennicae 'Vanamo' 31 (1): 1–360.
Ruuhijärvi, R. 1983. The Finnish mire types and their distribution. In:Gore, A.J.P. (ed.), Mires: swamps, bog, fen and moor. Regional studies. Ecosystems of the World. 4 B, pp. 47–67. Elsevier, Amsterdam.
Santesson, R. 1993. Lichens and lichenicolous fungi of Sweden and Norway. SBT-förlaget, Lund. 240 pp.
Shannon, C.E. & Weaver, W. 1949. The mathematical theory of communication. University of Illinois Press, Urbana. 117 pp.
Sjörs, H. 1948. Myrvegetation i Bergslagen. Acta Phytogeographica Suecica 21: 1–299.
Ter Braak, C.J.F. 1987. CANOCO – A FORTRAN program for canonical community ordination by partial detrended canonical correspondence analysis, principal components analysis and redundancy analysis. TNO Institute of Applied Computer Science, Wageningen, The Netherlands.
Tonteri, T. 1994. Species richness of boreal understorey forest vegetation in relation to site type and successional factors. Annales Zoologici Fennici 31: 53–60.
Tonteri, T., Mikkola, K. & Lahti, T. 1990. Compositional gradients in the forest vegetation of Finland. Journal of Vegetation Science 1: 691–698.
Tuomikoski, R. 1942. Untersuchungen über die Untervegetation der Bruchmoore in Ostfinnland. I. Zur Methodik der pflanzensoziologischen Systematik. Annales Botanici Societatis Vanamo 7(1): 1–203.
Vasander, H. 1984. Effect of forest amelioration on diversity in an ombrotrohic bog. Annales Botanici Fennici 21:7–15.
Vasander, H. 1987a. The effect of forest amelioration on the understorey biomass, species richness and diver-

sity of southern boreal Finnish mires. Symposia Biologica Hungarica 35 (1987): 685–698

Vasander, H. 1987b. Diversity of understorey biomass in virgin and drained and fertilized southern boreal mires in eastern Fennoscandia. Annales Botanici Fennici 24: 137–153.

Vasander, H., Laiho, R. & Laine J. 1996. Changes in species diversity in peatlands drained for forestry. In: Trettin, C. et al. (eds.), Ecology and Management: Forested Wetlands. Lewis Publishers (In press).

Yli-Kojola, H. (ed.) 1995. Pysyvien koealojen 3. mittaus 1995. Maastotyön ohjeet. The Finnish Forest Research Institute, Helsinki. Moniste/Mimeographed. 104 pp.

TIIVISTELMÄ:

Boreaalisen reunavaikutteisen metsä- ja suokasvillisuuden monimuotoisuuden analyysia

Eurolan ym. (1994) luetteloimasta Suomessa soilla kasvavasta lajistosta (maksasammalet poisluettuna) n. 70% on kasvupaikan reunavaikutteisuutta suosivia. Tämä lajisto voidaan jakaa ekologian perusteella kahteen pääryhmään: mineraalimaan metsien kasveihin ja reunavesi- ja lisäravinnevaikutuksesta riippuvaisiin kosteikkokasveihin. Ehdottomat suokasvit näyttävät suosivan keskustavaikutteisuutta ja niitä on reunafloorassa niukasti (Kuva 1).

Esitetään oletus, että metsäisten reunavaikutteisten kasvupaikkojen lajistollinen ja rakenteellinen monimuotoisuus voi olla merkittävä. Oletusta testataan VMI:n pysyvien koealojen systemaattisesta koealaverkosta erotetun otoksen avulla (Kuva 3).

Otokseen kelpuutettiin 92 koealaa, jotka täyttivät seuraavat kriteerit: (1) metsä- ja suotyyppi (Taulukko1), (2) koeala oli tyypin suhteen homogeeninen, (3) koealalla oli vähintään neljä kasvillisuusnäyteruutua (Kuva 3), (4) koealakuvio oli ojittamaton, (5) kuviolla ei esiintynyt tuoreita harvennushakkuita (1–2 v.).

Kasvillisuusaineisto (lajien keskipeittävyydet koealalla) ja rakenneaineisto (puuston latvuskerrosten ja pensaskerroksen latvuspeittävyydet koealalla) käsiteltiin luokittelu- (TWINSPAN) ja ordinaatio- (DCA, CANOCO) menetelmin. Lisäksi operoitiin koealojen lajirunsauksilla ja Shannon diversiteetti-indekseillä (H') ja Pieloun tasaisuus-indeksillä (J).

Tutkittujen soistuneiden kankaiden ja metsäisten reunavaikutteisten suotyyppien alfadiversiteetti (inventaariodiversiteetti) oli lajimäärän, H'-indeksin ja J-indeksin perusteella samaa luokkaa kuin vastaavan viljavuustason kangasmetsissä, mutta lajivalikoima oli laajempi. Vain rehevimmät tyypit erottuivat muita lajirikkaampina. Kasvillisuusklusterit erottuivat selvästi lajimäärän ja J-indeksin perusteella. H'-indeksin vaihtelu klustereiden välillä oli vähäisempää kuin tyyppien välillä.

N. 200 lajiksi arvioidusta tutkittujen tyyppien potentiaalisesta kokonaislajimäärästä aineistoon sattui 135 lajia. DCA-ordinaatiot lajeille ja koealoille (Kuvat 6 ja 7) osoittivat korkeata betadiversiteettiä tutkitussa osassa ekologista vaihteluavaruutta (Kuva 2). Lajiordinaatio (Kuva 6) paljasti myös odotetusti monimuotoisuuden ekologiset lähteet: metsälajistoytimeen liittyvät yhtäällä hydrologista lisäravinnevaikutusta vaativat lajit ja toisaalla keskustavaikutteista rämeisyyttä ilmaisevat lajit. Lajimäärän vaihtelu ei korreloinut kumpaankaan vahvimmista ordinaatioakseleista. Yhteisöjen tasaisuus (H'- ja J-indeksi) kasvoi lähes 1. akselin suunnassa karuuden ja rämeisyyden lisääntyessä (Kuva 7).

Puiden ja pensaiden nk. kerroslajeilla suoritettu TWINSPAN-luokitus antoi lupaavan tuloksen. Muodostui luokkia, jotka pohjautuivat eroihin lajimäärässä, latvuskerrosjakaumassa ja lajien suhteessa siihen.

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Appendix 1. List of understorey species in each ecological guild. The numbers indicate the order in which they occur on the first DCA axis (according to the species scores) from left to right (see Fig. 6).

Liite 1. Aluskasvillisuuden ekologisten ryhmien lajilista. Numero ilmoittaa missä järjestyksessä laji esiintyy ensimmäisellä DCA-akselilla (pistearvon mukaan) vasemmalta oikealle (ks. Kuva 6).

Species

Xeric forest species

49 Melampyrum pratense
53 Vaccinium vitis-idaea
57 Cladonia fimbriata
59 Pleurozium schreberi
61 Cladonia chlorophaea
63 Cladonia deformis
65 Cladonia cornuta
68 Cladonia gracilis
69 Polytrichum juniperinum
73 Empetrum nigrum
82 Cladonia rangiferina
83 Cladonia cariosa
84 Pinus sylvestris
85 Cladonia arbuscula
86 Calluna vulgaris

Mesic forest species

14 Linnea borealis
24 Cornus suecica
25 Lycopodium annotinum
28 Trientalis europea
31 Luzula pilosa
32 Orthilia secunda
33 Dicranum scoparium
36 Juniperus communis
37 Sorbus aucuparia
38 Agrostis capillaris
39 Salix caprea
40 Vaccinium myrtillus
41 Betula pubescens
42 Dicranum fuscescens
43 Barbilophozia lycopodioides
44 Ptilium crista-castrensis
45 Populus tremula
46 Hylocomium splendens
52 Calamagrostis arundinacea
56 Picea abies
58 Ptilidium ciliare
60 Deschampsia flexuosa
62 Epilobium angustifolium
87 Salix aurita

Herb rich species

1 Athyrium filix-femina
4 Oxalis acetosella
7 Rubus idaeus
6 Dryopteris carthusiana
8 Maianthemum bifolium
11 Dicranum majus
13 Carex digitata
16 Rhytidiadelphus triquetrus
17 Gymnocarpium dryopteris
21 Melampyrum sylvaticum
23 Alnus incana
29 Solidago virgaurea

Bog species

15 Pohlia nutans
34 Sphagnum magellanicum
50 Rubus chamaemorus
64 Aulacomnium palustre
70 Sphagnum angustifolium
71 Ledum palustre
72 Vaccinium uliginosum
74 Sphagnum russowii
75 Chamaedaphne calyculata
78 Sphagnum nemoreum
79 Eriophorum vaginatum
80 Betula nana
81 Polytrichum strictum
88 Vaccinium microcarpum

Marsh and spring water species

3 Viola palustris
5 Equisetum palustre
9 Calamagrostis purpurea
18 Rubus arcticus
20 Potentilla palustris
26 Juncus filiformis
27 Sphagnum riparium
30 Carex canescens
35 Potentilla erecta
47 Carex echinata
55 Deschampsia cespitosa
66 Carex nigra
67 Salix phylicifolia

Spruce mire species

2 Sphagnum squarrosum
10 Equisetum sylvaticum
12 Sphagnum girgensohnii
19 Sphagnum centrale
22 Sphagnum wulfianum
51 Carex globularis
54 Polytrichum commune

Poor fen species

76 Andromeda polifolia
77 Vaccinium oxycoccus

Appendix 2. The Finnish site type symbols of paludified forests (1., Kalela 1961), mire margin forests and forested pine and spruce mires (2. and 3., Heikurainen & Pakarinen 1982) and their English names.

Liite 2. Soistuneiden kangasmetsätyyppien (1, Kalela 1961) ja metsäisten, reunavaikutteisten suotyyppien (2. ja 3., Heikurainen & Pakarinen 1982) suomalaisten tyyppilyhenteiden vastaavat englanninkieliset nimet

1. Paludified forest site types

sEVT	Paludified Empetrum Vaccinium - type
sVT	Paludified Vaccinium - type
sVMT	Paludified Vaccinium Myrtillus - type
sMT	Paludified Myrtillus - type
sDeMT	Paludified Deschampsia Myrtillus - type

2. Mire margin forest site types

KgR	Paludified pine forest
KgK	Paludified spruce forest
LhK	Eutrophic paludified hardwood-spruce forest

3. Pine and spruce mire site types

MrK	Rubus chamaemorus spruce swamp
KR	Spruce-pine swamp
MK	Vaccinium myrtillus spruce swamp
MkK	Equisetum sylvaticum spruce swamp
RhK	Herbrich hardwood-spruce swamp

Paper III

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III

DIVERSITY OF VEGETATION IN PRISTINE AND DRAINED FORESTED MIRE MARGIN COMMUNITIES IN FINLAND

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SUMMARY

Within the Scandinavian boreal landscape, forested mire margin communities (e.g. swamp forests) are natural centres of biodiversity. The change in diversity of vegetation, caused by drainage, of forested mire margin communities (paludified forests, mire margin forests and forested pine and spruce mires) in south and central Finland was examined. Data for the sample plots of the 8th National Forest Inventory (1985-86) were used in this study. The diversity of the vegetation was analysed at community level (b-diversity) with multivariate methods of ordination (NMDS) and classification (TWINSPAN). The diversity at species level (a-diversity) was also analysed by species richness and diversity indices. The main compositional gradient in the NMDS-ordination of the pristine and drained sites was site fertility or trophic gradient, from ombro-oligotrophy to meso-eutrophy. The drainage state of the sites determined the secondary gradient. The third interpretable gradient was related to tree stand succession and peat thickness. In general, the results showed that species diversity was relatively high in mire margin forests. When estimated only by numbers of species, the species diversity remains high after drainage, but the species composition of these communities changes towards forest vegetation dominated by mesic and herb-rich forest species with mire species present only as relicts.

Keywords: forest vegetation, mire vegetation, forested peatland, vegetation diversity, forest drainage.

INTRODUCTION

Forested mire margin communities, in the boreal region, are mosaics that include both upland forest and peatland vegetation (spruce swamp, bog, marsh and spring) (Eurola, 1962; Ruuhijärvi, 1960) that show high species richness and diversity (Korpela & Reinikainen, 1996a,b). Within the boreal landscape in Scandinavia, swamp forests are natural centres of biodiversity (e.g. Ohlsson *et al.*, 1997). In Finland these biotopes have, to a large extent, been drained owing to their potential for wood production (Gustavsen & Päivänen, 1986) and in Sweden they have also been exploited extensively (Ohlsson *et al.,* 1997). According to the data of permanent sample plots of the 8th National Forest Inventory (8th NFI), the area of undrained mire margin sites in 1985-86 was half of what it had been in the early 1950s compared to data from the 3rd NFI (Ilvessalo, 1956, 1957).

In their undrained condition these wetland habitats have remained relatively pristine in their stand structure and ground vegetation, although they have been often subjected to some silvicultural management. Thus on the community and species level they are assumed to be important for local and regional diversity.

Mire margin forests and forested pine and spruce mires are included in so-called genuine forested mire sites, which are characterized by hummock and intermediate level vegetation resembling forest vegetation, especially at the more nutrient-rich end of the vegetation continuum. These sites have often developed from the paludification of forest land. The more nutrient-rich types are called spruce mires, with vegetation characterized by shade-tolerant herbs and dwarf shrubs. The sites with lower nutrient levels are called pine mires with characteristic hummock dwarf shrub vegetation (Vasander, 1996). The vegetation gradient between mire margin and mire expanse communities is one of the main ecological gradients, in addition to the gradients of nutrient availability (trophic status) and hydrology, in the ecology and classification of boreal mires in Finland and Sweden (Heikurainen & Pakarinen, 1982, Eurola *et al.,* 1984, Malmer, 1985). A distinction between mire expanse and mire margin vegetation was made in early mire vegetation studies (Sjörs, 1948). According to Finnish environmental characterisation mire margin vegetation occurs often on sites with a thin peat layer that receive a supplementary input of mineral nutrients from surrounding mineral soil and are thus minerotrophic (Eurola *et al.,* 1984). This differs from the Scandinavian interpretation (Sjörs, 1983, Økland, 1989, 1990), according to which marginal pine forests of bogs are included in mire margin sites despite being ombrotrophic. In this study the Finnish definition (Eurola *et al.,* 1984) of the mire margin concept is used. Mire margin vegetation occurs typically in a zone between proper upland vegetation and mire expanse vegetation. The sites include (1) paludified forests (= paludified mineral soil forests), (2) mire margin forests and (3) forested pine and spruce mires (Lumiala, 1937; Tuomikoski, 1942).

There has been a demand for a practical site classification of all drained peatlands in Finland (about 6 million hectares during the years 1950-1990 (Sevola, 1997)), which undergo different stages of post-drainage succession. The system for this classification is based on the gradual decrease of mire plants along the succession following drainage. The criteria for distinguishing the four different drainage phases are: (1) *pristine mire* vegetation, (2) *recently drained phases* with unchanged vegetation, (3) *transforming phase* with a 25-75% proportion of mire species of the original community, and (4) *transformed phase* with less than 25% of mire species left (Sarasto, 1961; Heikurainen & Pakarinen, 1982; Paavilainen & Päivänen, 1995).

According to Cajander (1913), after drainage a mire community will change until it finally resembles a mineral-soil forest community of the corresponding fertility level. This assumption has generally proved to be correct, but present experience shows that special characteristics of the original mire and peat substrate remain (Laine, 1989; Reinikainen, 1990). The time required for this development varies between 15 and 50 years, depending mainly on the fertility, moisture and tree stand of the original mire type (Laine *et al.*, 1995).

Previous studies of the effect of forest drainage on vegetation have concentrated either on sparsely forested or treed pine mires (treed pine bogs) (Laine & Vanha-Majamaa, 1992; Laine *et al.*, 1995) or on a broader scale of all peatland sites, also including treeless mires (Sarasto, 1961; Reinikainen, 1988; Hotanen & Vasander, 1992). After drainage, with the subsequent changes in the growth substrate and tree layer, the composition of the lower layers of vegetation also change drastically. Plant species adapted to wet habitats are the first to disappear, while hummock-dwelling species (e.g. dwarf shrubs) may benefit from drainage (Sarasto, 1961; Eurola *et al.*, 1984; Laine *et al.*, 1995). Only a few studies have concentrated solely on the influence of mire margin on drained sites (Eurola *et al.*, 1995).

The objectives of this study were to describe and analyse changes in the diversity of the vegetation of forested mire margin communities. The vegetation diversity was analysed at both species and community levels on pristine and drained sites.

MATERIALS AND METHODS

Sample Plots and Study Area

The material in this study consists of data collected from the permanent sample plots of the 8th National Forest Inventory (1985-86) in southern and central Finland (S of 66° N, 2618 plots). The following criteria had to be fulfilled: (1) location S of the 66th latitude, (2) site type either undrained paludified forest, mire margin forest, forested pine mire or spruce swamp, or (3) drained mire margin forest, drained forested pine mire or spruce swamp, (4) the whole plot classified as a single site type, (5) vegetation sampled from four (2 m^2) vegetation sample quadrats on the plot, (6) tree stand untreated for at least ten years before the inventory and (7) forest development class from 4 (young thinning stands) to 6 (mature stands). A total of 156 plots met all these criteria: 82 undrained and 74 drained for forestry (Fig. 1, Table 1). On each of the circular plots (300 m^2) on four 2 m^2 sample quadrats percentage cover of the understorey vegetation (including tree and shrub species lower than 50 cm) was estimated visually. The canopy cover of tree (>1.5 m high) and shrub (0.5-1.5 m high) species was estimated for the whole plot. The study area, field work and vegetation surveys are described in more detail in previous articles (Korpela & Reinikainen, 1996a, b).

The traditional "Finnish-forest-type approach of Cajander" (Cajander, 1926; Frey, 1973) was used to separate the sample plots into site classes. The paludified forest site types were classified according to Kalela (1973). The mire site types were classified using the site types of Heikurainen and Pakarinen (1982). The wood production potential of the site types was estimated using the six-scale system of Huikari (1974) in which site fertility class I is the

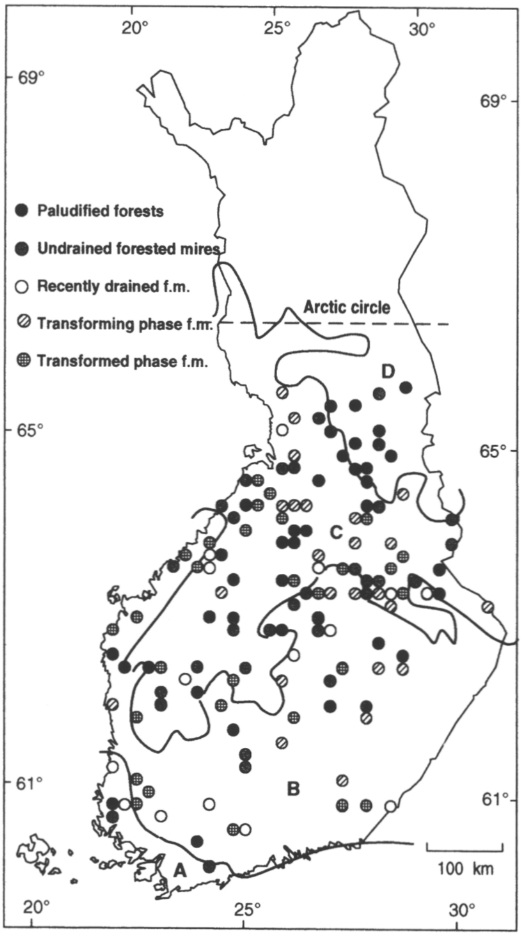

Fig. 1: Distribution of sample plots within A = hemiboreal, B = southern boreal, C = middle boreal and D = northern boreal subzones (Ahti et al., *1968). The drainage phase of the sample plots is also presented according to Heikurainen & Pakarinen (1982).*

richest and VI the poorest (Table 1). The drainage phase of the sites was determined according to the system described by Sarasto (1961) and by Heikurainen & Pakarinen (1982). The species were classified into forest or mire plants and placed into ecological groups according to Kalela (1973) and Eurola *et al.* (1994).

The nomenclature for vascular plants follows that of Hämet-Ahti *et al.* (1998), for bryophytes Koponen *et al.* (1977) and for lichens Vitikainen *et al.* (1997).

Data Analyses

Mean percentage cover for each understorey species was calculated from the four surveyed quadrats on each plot. If a species was present in only one or two plots, it was excluded from the numerical analyses, except for the species richness values and diversity indices. This left a total of 124 plant species (from a total of 226 species, see Appendix 1) on the 156 sample plots. The data were analysed using multivariate ordination and classification methods. The classification analysis was used to reveal the structure of the vegetation communities. The TWINSPAN (two-way indicator species analysis) method of classification (Hill 1979) was applied using default options for minimum group size (5); maximum number of indicator species (7) and pseudo-species cut levels (0, 2, 5, 10, 20 cover %). Four levels of division were used.

The data were analysed by multivariate ordination in order to find the main gradients in the variation of species composition and to interpret the gradients according to environmental variables. Multivariate ordination was also used to reveal community level diversity. In simulation tests, non-metric multidimensional scaling has been found to be the most efficient method of ordination (Prentice, 1980; Minchin, 1987) for showing the floristic relationships between sample plots. The Bray-Curtis (Czekanowski or Sørensen) dissimilarity index, which is robust to random variation or noise in the data (Faith *et al.* 1987) was used as a measure of dissimilarity between the sample plots. A global non-metric multidimensional (GNMDS) method of ordination, which is included in the DECODA program package version 2.04 (Minchin, 1991), was used. This matrix of dissimilarities between sample plots was calculated from abundance values of species. Standardization was not applied except for logarithmic transformation of the values for species percentage cover. One- to four-dimensional GNMDS solutions were carried out using ten randomly generated starting configurations. The minimum stress configurations were compared by the Procrustean analysis (Schöneman & Carrol 1970). A Monte-Carlo approach (in DECODA) was used to test the significance of the maximum correlation for environmental variables through the correlation. To reveal ecological gradients in the data, variation by species composition and environmental variables was also examined when the number of dimensions was determined. According to this procedure, a three-dimensional GNMDS-ordination solution was selected for further analysis by the lowest minimum

Table 1: Site types studied and their Finnish abbreviations within 1) paludified upland forests according to Kalela (1973), 2) mire margin forests and 3) forested mires according to Heikurainen & Pakarinen (1982). Fertility class of the site types are according to Huikari (1974) and drainage phase groups (1 = undrained, 2 = recently drained, 3 = transforming phase, 4 = transformed phase) according to Paavilainen & Päivänen (1995).

Site types	Abbrev.	Fert. class	Drainage phase groups (n) 1	2	3	4
1. Paludified forests						
Empetrum-Vaccinium type	sEVT	IV	9			
Vaccinium type	sVT	IV	4			
Vaccinium-Myrtillus type	sVMT	III	10			
Myrtillus type	sMT	III	14			
Deschampsia-Myrtillus type	sDeMT	III	2			
Oxalis-Myrtillus type	sOMT	II	4			
2. Mire margin forests						
Paludified pine forests	KgR	IV	5	2	3	1
Oligo-mesotrophic paludified spruce forest	KgK	II,III	10	4	-	8
Eutrophic paludified hardwood-spruce forest	LhK	I	2	-	-	1
3. Forested pine and spruce mires						
Spruce-pine swamp	KR	IV	5	2	9	3
Spruce swamp	VK	III,IV	14	5	14	9
Herb rich hardwood-spruce swamp	RhK	II	3	2	2	9
Sample plots total 156			82	15	28	31

stress value (0.1592), which was achieved with all ten starting configurations. The weighted averages of all the species included were derived from the sample plot ordination by calculating the means of the scores for the sample plots in which a species occurred and then weighting them according to species abundance.

The relationship between the ordination pattern and the selected explanatory variables was obtained using a vector-fitting procedure. This option calculates a vector for each variable through the ordination configuration, along which the scores of the sample plots have maximum linear (Pearson) correlation with the variable in question (Kantvilas & Minchin, 1989; Minchin, 1991).

The environmental and other explanatory variables used to explain the results of the ordination and classification were site variables (temperature sum, fertility class, drainage phase and peat thickness), tree stand variables (basal area, mean diameter, dominant height, stand age and stand development class) and species diversity variables (species richness, diversity indices; Shannon diversity index, H', Simpson heterogeneity index D, and Pielou's evenness index J, according to Magurran (1988)). Spearman correlation coefficients between the three dimensions of GNMDS ordination and explanatory variables were calculated. One-way analysis of variance (ANOVA) was used to test the TWINSPAN clusters for environmental differences.

RESULTS

TWINSPAN Classification and Its Ecological Interpretation

The analysis by TWINSPAN classification resulted in eight vegetation clusters that could be interpreted as ecologically distinct. On the first division level, a cluster of ten (cluster H) sample plots was separated from the rest of the 156 sample plots. These plots were drained, were in the transformed phase and had herb-rich or mesic forest species vegetation (Fig. 2, Table 2, Appendix 1). The indicator species were *Dryopteris carthusiana* (the most dominant species in this cluster), *Trientalis europaea* and the genus *Brachythecium* (the most abundant moss taxon in this cluster). Marsh and spring species (e.g. *Filipendula ulmaria, Viola palustris, Cirsium palustre, Calamagrostis purpurea, Deschampsia cespitosa* and *Sphagnum riparium*) were most abundant in this cluster, while xeric forest species such as dwarf shrubs and lichens were rare. Only 14% of the species occurred in the rest of the sample plots (Fig. 2, Appendix 1). The drainage phase and the site fertility class of these plots were the variables that best explained the early separation from the rest of the plots. The age of the tree stands on these sample plots was also clearly lower than those of other plots (Table 3).

In the second division the remaining 146 plots were divided into two main cluster groups containing 85 and 61 plots. This main division was made according to trophic status, between meso-eutrophy and ombro-oligotrophy. The group of 85 sample plots (E-G, Fig. 2, Table 2) clearly represented meso-eutrophic spruce mire types (KgK, VK, RhK, LhK) and paludified southern mesic forest types (sMT) and herb rich forest types (sOMT). The most important indicator species of these meso-eutrophic plots was *Sphagnum girgensohnii,* which is typical of spruce mires.

The group of 61 sample plots (clusters A-D) were separated into xeric paludified forest types (sEVT, sVT), northern paludified mesic forest types (sVMT) and ombro-oligotrophic pine mire types (KgR, KR), including some of the oligotrophic spruce mire types. These ombro-oligotrophic plots had bog indicator species (e.g. *Vaccinium uliginosum, Ledum palustre, Empetrum nigrum, Sphagnum angustifolium* and *S. russowii*) (Fig. 2, Table 2).

On the meso-eutrophic side of the second division level (n = 85), the eutrophic cluster G (n = 22) was separated on the third division level by the indicator species *Trientalis europaea* (mesic forest species) and *Viola palustris* (marsh and spring species). The most abundant species in this cluster, however, were the spruce mire species *Sphagnum girgensohnii*

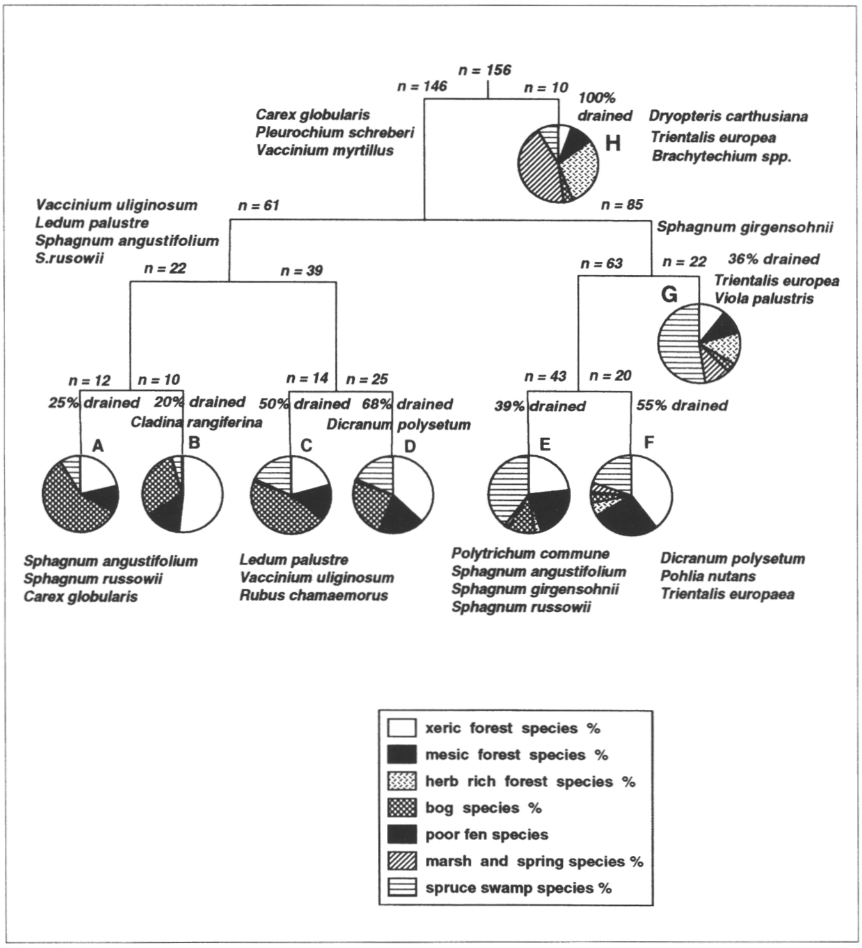

Fig. 2: Division of the TWINSPAN vegetation clusters and distribution of the ecological groups in each cluster with their indicator species.

Table 2. Distribution of site types of paludified forests (1.) and site types and phases of drainage of mire margin forests (2.) and forested mires (3.) in different TWINSPAN-clusters. The numbers of undrained sample plots are marked on the same row as the abbreviations of site types (see Table 1) and corresponding trophic status.

Site types/ Drainage phase	Trophic status	TWINSPAN-clusters A	B	C	D	E	F	G	H	n
1. sEVT	oligo	4	4				1			9
1. sVT	oligo		2		1	1				4
1. sVMT	meso-oligo	1	1	2	3	3				10
1. sMT	meso-oligo			1	1	6	4	2		14
1. sDeMT	meso-oligo					2				2
1. sOMT	meso						3	1		4
2. KgR	oligo	4	1							5
recently dr.		2								2
transforming					2	1				3
transformed			1							1
2. KgK	meso-oligo				2	6		1	1	10
recently dr.						2	2			4
transforming										-
transformed					1	2	1	2	2	8
2. LhK	eutrophic							2		2
recently dr.										-
transforming										-
transformed									1	1
3. KR	oligo			3			1	1		5
recently dr.					1					1
transforming		1		3	4	1				9
transformed					2			1		3
3. VK	meso-oligo			1	1	8		4		14
recently dr.				1	1	3	1			6
transforming			1	2	5	3	2	1		14
transformed				1	1	4	2		1	9
3. RhK	meso							3		3
recently dr.								2		2
transforming						1	1			2
transformed							2	2	5	9
Number of plots		12	10	14	25	43	20	22	10	156

and *Equisetum sylvaticum*. This cluster included the undrained sites of eutrophic paludified hardwood-spruce forest and herb rich and mesotrophic spruce mires. Most of the drained sample plots (36%) in this cluster were herb-rich spruce mires in the transformed phase (Fig. 2, Table 2). A total of 52 herb species, 21 graminoid species and 11 *Sphagnum* species occurred and altogether 136 species were present in this cluster (Appendix 1). The richness of tree and shrub species differed significantly from clusters A-B and clusters E-F and species richness differed from clusters A-B (Table 3).

Divisions at the fourth level occurred most obviously according to moisture gradient. The mesotrophic plots (n = 63) were divided on the fourth division level into clusters E (n = 43) and F (n=20).

Table 3: The mean values (± S.E.) of 1) site quality, 2)tree stand and 3)species diversity variables in the eight final TWINSPAN-vegetation groups (A-H). For each variable TWINSPAN groups with different letters are significantly different (P < 0.05).

	A	B	C	D	E	F	G	H	F-values
Site quality									
1. Temperature sum (dd)	1033.3 (9.8)	1034.0 (8.8)	1015.0 (8.8)	1081.6 (7.03)	1089.3 (11.2)	1155.5**c** (9.81)	1153.2 (11.63)	1117.0 (9.63)	4.74***
1. Site fertility class	3.8 (0.4)	3.9 (0.3)	3.7 (0.6)	3.6 (0.5)	3.1**a-d** (0.3)	3.1**ab** (0.6)	2.5**a-d** (0.8)	2.0**a-df** (0.5)	22.19***
1. Drainage phase class	1.9 (1.0)	1.8 (1.5)	2.8 (1.4)	3.2**a** (1.4)	2.5 (1.4)	2.8 (1.7)	2.7 (1.5)	4.7**a-g** (0.9)	4.56***
1. Peat thickness (dm)	23.6 (26.2)	18.6 (29.9)	43.6 (31.6)	47.6 (36.0)	29.8 (27.0)	31.0 (32.3)	32.5 (31.9)	43.5 (35.3)	1.71
Tree stand									
2. Basal area (m^2/ha)	15.3 (6.3)	16.4 (6.3)	16.6 (6.7)	20.9 (6.0)	24.9**abc** (7.7)	24.7**a** (9.5)	25.1**abc** (7.1)	23.1 (6.6)	5.43***
2. Mean DBH (cm)	12.8 (4.6)	12.5 (4.6)	9.7 (4.6)	10.8 (3.1)	14.3 (6.5)	14.7 (6.1)	15.3**d** (5.6)	14.4 (6.2)	2.53*
2. Dominant height (m)	11.5 (3.7)	12.6 (2.7)	12.6 (3.1)	12.8 (4.0)	16.2 (5.1)	20.2**a-d** (3.2)	20.9**a-e** (5.2)	24.2 (5.50)	12.94***
2. Development class	5.0 (1.0)	5.4 (0.79	4.7 (0.9)	4.9 (0.7)	5.1 (0.8)	5.0 (0.7)	5.1 (0.8)	4.9 (0.7)	0.93
2. Stand age (years)	108.3 (47.4)	113.0 (32.3)	95.1 (48.9)	94.6 (27.6)	101.6 (48.1)	77.5 (31.1)	75.1 (32.3)	58.0**bde** (20.4)	3.19**
Species diversity									
3. Tree and shrub species richness	4.2 (1.0)	4.1 (0.9)	4.2 (1.3)	5.3 (1.8)	4.6 (1.6)	5.3 (1.6)	6.1**a-ce** (1.8)	7.0 (3.3)	5.06***
3. Species richness	15.3 (1.9)	16.5 (4.2)	18.4 (4.1)	18.6**a** (4.4)	16.0 (4.3)	19.9 (6.6)	22.4**ae** (8.6)	22.9**ae** (5.6)	4.93***
3. D - index	0.82 (0.069	0.75 (0.11)	0.81 (0.08)	0.81 (0.07)	0.76 (0.11)	0.80 (0.09)	0.72 (0.16)	0.84**e** (0.06)	2.90**
3. H'- index	2.02 (0.23)	1.83 (0.33)	2.03 (0.32)	2.02 (0.34)	1.82 (0.36)	2.03 (0.41)	1.92 (0.57)	2.32**be** (0.30)	2.53*
3. J - index	0.75 (0.09)	0.66 (0.10)	0.70 (0.10)	0.70 (0.10)	0.67 (0.12)	0.69 (0.09)	0.63 (0.17)	0.75 (0.07)	2.15*
Number of sample plots	12	10	14	25	43	20	22	10	

The sample plots of cluster E included most of the paludified forests and spruce mires. The paludified forests accounted for 30% and the spruce mires for 70% of the sample plots of cluster E; of these spruce mire plots 60% were undrained and 40% drained. The sample plots of cluster F (n = 20) were drained spruce mires and paludified mesic and herb-rich forests (Fig. 2, Table 2).

In cluster E the indicator species were the oligo-mesotrophic *Sphagnum* mosses *S. angustifolium* and *S. russowii*, although *Polytrichum commune* was most abundant in this cluster. The typical spruce mire species *S. girgensohnii* was almost as abundant here as in the meso-eutrophic cluster G. Furthermore, the typical spruce mire herb species *Equisetum sylvaticum* was almost as abundant as in cluster G.

The species composition in cluster F was more forest-like. The indicator and also the most abundant species in this cluster was the forest carpet moss *Dicranum polysetum,* which is typical of xeric forests. Other xeric forest species (e.g. *Calluna vulgaris, Vaccinium vitis-idaea, Deschampsia flexuosa, Pleurozium schreberi, Polytrichum juniperinum* and *Cladonia* spp.) were also more abundant than in cluster E. In addition, the number of herb species was higher than in cluster E. The mesic forest species *Trientalis europaea* was an indicator and other typical mesic forest herbs (e.g. *Lycopodium annotinum, Orthilia secunda, Rubus saxatilis*) and herb rich forest species (e.g. *Oxalis acetosella, Maianthemum bifolium*) and marsh and spring species (e.g. *Caltha palustris, Potentilla erecta*) also occurred in this cluster. Other graminoids, in addition to *Deschampsia flexuosa,* were slightly more abundant here as well. The cover of *Sphagnum* species was clearly less than in cluster E.

In the fourth level division sample plots of the ombro-oligotrophic group (n= 61) were divided into clusters A (n=12), B (n = 10), C (n = 14) and D (n=25). Clusters A and B consisted mainly of undrained paludified xeric forest types and forested pine mire types. Clusters C and D included most of the drained ombro-oligotrophic pine mire types, which mainly were in the transforming phase (Fig. 2, Table 2). There were clear differences in the phase of drainage and in the peat thickness between cluster groups A-B and C-D (Table 3).

The composition of species in cluster A was dominated by bog species; the most abundant species were the indicator species *Sphagnum russowii* and *S. angustifolium.* In cluster B xeric forest species dominated, with indicator species *Cladina rangiferina* being the most abundant of the reindeer lichens. In cluster C both undrained and drained spruce-pine mire types were found. The indicator species here were dwarf shrubs typical of bogs (*Ledum palustre, Vaccinium uliginosum*) and the herb *Rubus chamaemorus,* which was most abundant in this cluster. Other bog species (e.g. *Eriophorum vaginatum, Sphagnum angustifolium*) were also abundant in this cluster. Cluster D contained most of the drained spruce-pine mires and some of the drained spruce mires; the few undrained sites in this cluster were paludified xeric and mesic forests. The indicator species was the xeric forest moss *Dicranum polysetum* which, as well as other forest carpet mosses, was more abundant here than in cluster C. The xeric forest dwarf shrub *Vaccinium vitis-idaea* was also more abundant in cluster D.

On the main division level, the cluster group A-D differed significantly from cluster group E-H in terms of their site fertility classes (F-value 39.6, p = 0.0000) and those tree stand variables that indicate site productivity, such as dominant height (F-value 19.6, p = 0.0000) and basal area (F-value 8.7, p = 0.0000). There was also a significant difference in temperature sums (F-value 5.5, p = 0.0003) between cluster groups A-D and E-H. This main division happened also according to pine and spruce dominance in the canopy layer (see Appendix 1).

Ordination of Plant Communities and the Main Ecological Gradients

In the ordination space of the three dimensions, the sample plots separated well according to their site trophic level. This main gradient was interpreted to describe a fertility gradient. The oligotrophic mire sites and paludified xeric forest sites were situated at one end and the meso-eutrophic and herb rich sites at the opposite end of this gradient in the ordination space (Fig. 3a). Site-fertility class and tree-stand variables such as dominant height had the strongest correlations with this direction in the ordination space (Fig. 3a, Table 4). Inter-correlation between tree stand variables: dominant height, basal area and mean diameter, was also strong (0.494 ***, 0.435 ***) and the correlation between them and site fertility class was significant (-0.494 ***, -0.410 ***, -0.277 ***).

The second gradient was interpreted to describe the post-drainage succession. Most of the undrained forested mire sites were situated at one end and most of the drained forested mire sites, in the transformed phase, were situated at the opposite end of this gradient in the ordination space (Fig. 3a). The

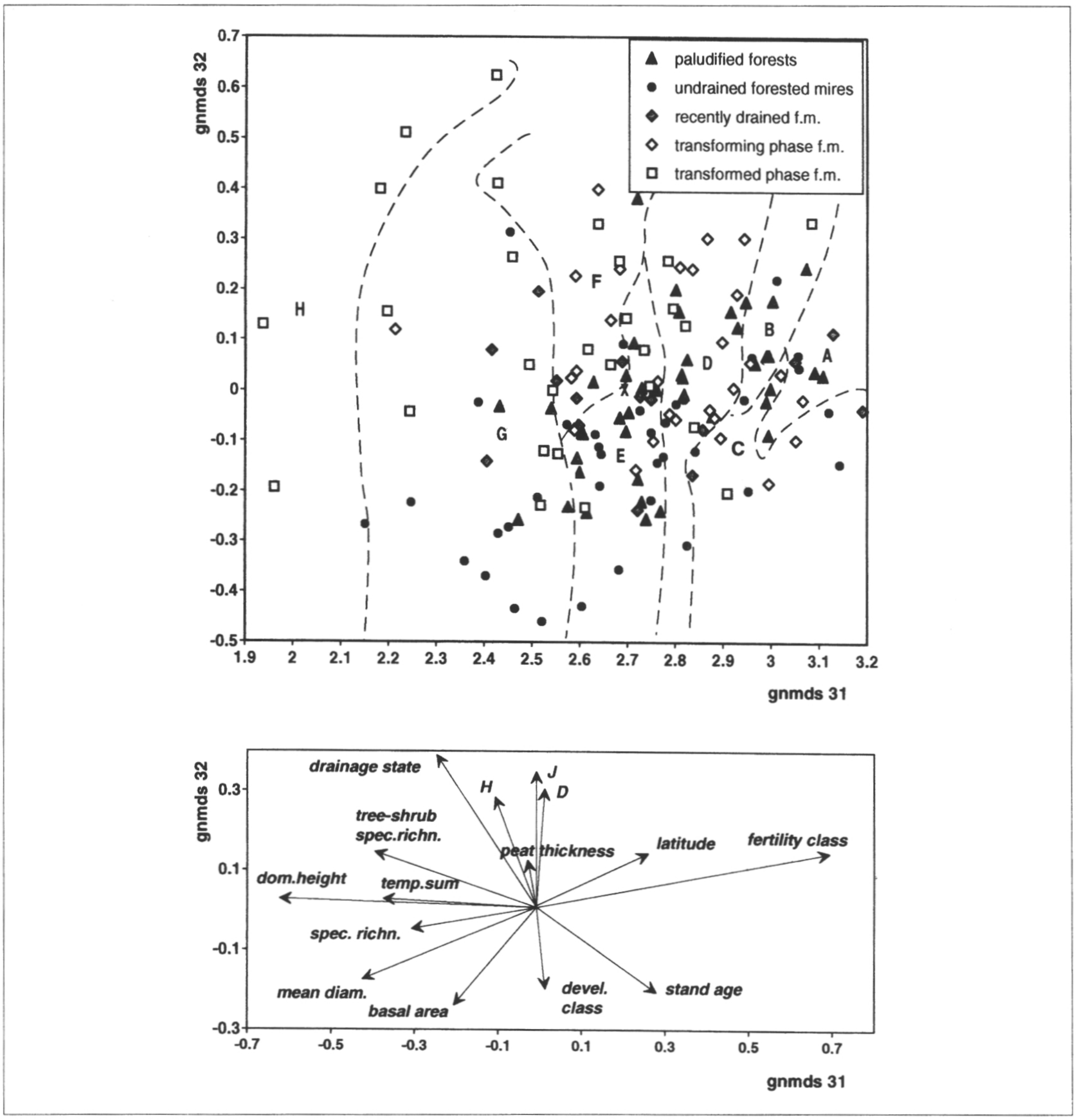

Fig. 3a: GNMDS ordination with the first and second dimensions of the three dimensions. The sample plot symbols relate to drainage phases. Sample plots are divided by dotted lines into TWINSPAN vegetation groups indicated by corresponding letters, which are placed in the centers of the groups. The directions of the maximum correlations of the environmental variables are indicated with arrows. The length of the arrow describes the strength of the correlation (the midpoint of the arrows = x in the upper figure).

paludified forests were situated between these two groups. State of drainage was best correlated with the first and the second directions in the ordination space (Fig. 3a, Table 4). Species richness as well as richness of tree and shrub species correlated significantly with the direction of the fertility gradient and with each other. Species diversity indices correlated best with the direction of drainage-state gradient (Fig. 3a, Table 4). Inter-correlation between state of drainage and peat thickness was strong (0.640 ***). State of drainage correlated significantly also with Shannon (H') diversity-index (0.289 ***) and with Simpson (D) heterogeneity-index and Pielou's (J) evenness-index (0.214 **, 0.240 **).

A gradient appeared to be related to peat thickness, although the maximum correlation of peat thickness was not significant in the three-dimensional ordination (Fig. 3b, Table 4). On this gradient peat

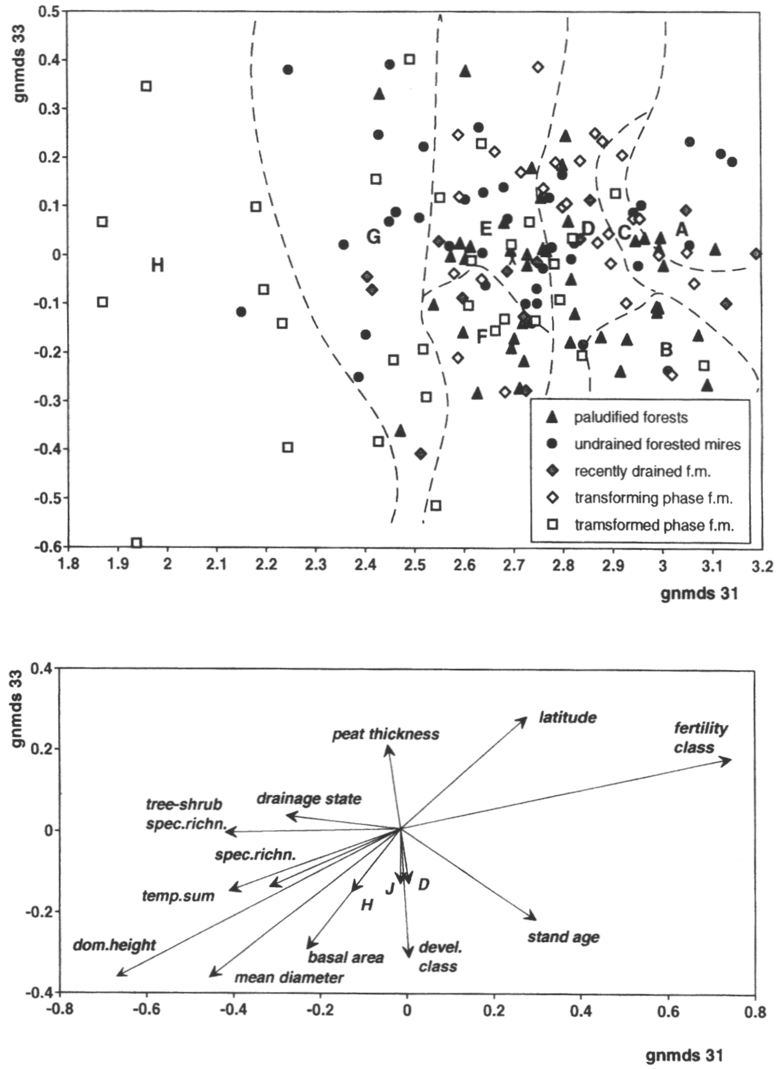

Fig. 3b: GNMDS-ordination with the first and third dimensions of the three dimensions. The sample plot symbols relate to drainage phases. Sample plots are divided by dotted lines into TWINSPAN vegetation groups indicated by corresponding letters, which are placed in the centers of the groups. The directions of the maximum correlations of the environmental variables are indicated with arrows. The length of the arrow describes the strength of the correlation (the midpoint of the arrows = x in the upper figure).

thickness increased towards most of the undrained and some of the drained forested mires in the transforming and transformed phase. The tree-stand variables (development class, basal area, mean diameter) also had significant negative correlations with this gradient (Fig. 3b, Table 4). Peat thickness had significant negative correlation with stand development class, mean diameter and dominant height (-0.272 ***, -0.273 ***, -0.227 **).

Species Indicating the Main Gradients

The weighted averages for species in the GNMDS ordination of the sample plots also showed that the main gradient was related to site fertility. Species common for xeric forests and ombro-oligotrophic bogs (e.g. *Calluna vulgaris, Vaccinium vitis-idaea, Empetrum nigrum, Ledum palustre, Vaccinium uliginosum, V. microcarpum, Eriophorum vaginatum, Sphagnum nemoreum,*

*Table 4: Spearman rank correlations between the explanatory variables and the dimensions of the three-dimensional GNMDS ordination (p = * < 0.05, ** < 0.01, *** < 0.001).*

Variables	Dimension 1		Dimension 2		Dimension 3		
	r	p	r	p	r	p	N
Latitude	0.35	***	0.04		0.14		156
Temperature sum	-0.44	***	-0.05		-0.05		156
Peat thickness	0.06		-0.04		0.12	-	156
Site fertility class	0.73	***	0.29	***	0.10		156
Drainage state	-0.14	*	0.17	*	0.01		156
Basal area	-0.48	***	-0.27	**	-0.31	***	156
Mean diameter	-0.37	***	-0.05		-0.32	***	156
Dominant height	-0.65	***	-0.12	-	-0.30	***	132
Development class	-0.12	-	-0.12	-	-0.29	***	156
Stand age	0.24	**	-0.05		-0.19	*	156
Tree-shrub species richness	-0.29	***	0.074		0.14	*	156
Species richness	-0.15	*	-0.11		0.03		156
H'-index	-0.01		0.21	**	0.01		156
D-index	0.11	-	0.28	***	-0.01		156
J-index	0.10		0.31	***	-0.02		156

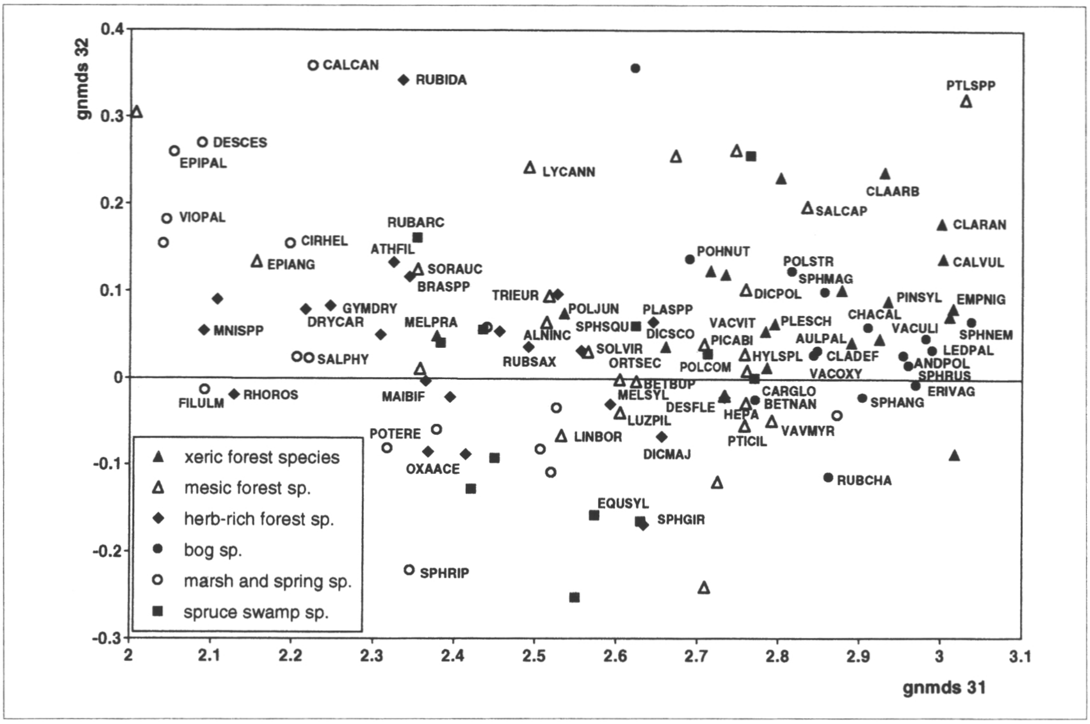

Fig. 4a: Optima of the species investigated in the ordination space of the first and the second dimensions of three dimensional GNMDS-ordination. The species are in ecological groups according to Eurola et al. (1994). Species names are the first three letters of the genus and the first three letters of the species (only the species which occur at least on ten sample plots are marked by letters, for full species names see Appendix 1).

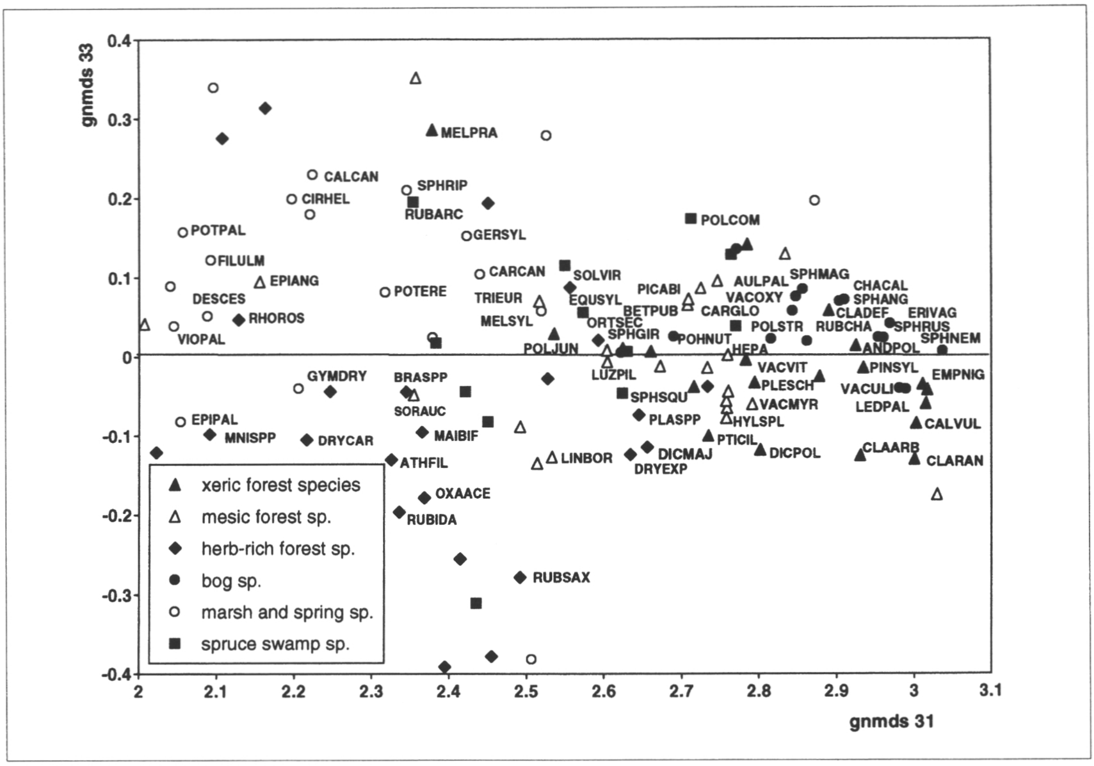

Figure 4 b: Optima of the species investigated in the ordination space of the first and the third dimensions of three dimensional GNMDS-ordination. Species are in ecological groups according to Eurola et al. *(1994). Species names are the first three letters of the genus and the first three letters of the species (only the species which occur at least on ten sample plots are marked by letters, for full species names see Appendix 1).*

S. russowii, S. angustifolium, Cladonia spp.) were situated towards one end of the fertility gradient and herb-rich forest species (e.g. *Oxalis acetosella, Maianthemum bifolium, Athyrium filix-femina, Dryopteris carthusiana, Rhodobryum roseum, Mniaceae* spp.) and mesotrophic and eutrophic marsh and spring species (e.g. *Viola palustris, Potentilla palustris, Epilobium palustris, Deschampsia cespitosa, Cirsium helenioides, Calamagrostis canescens, Sphagnum riparium*) at the opposite end of this gradient. Most of the constant species, for example, mesic forest plants (e.g. *Vaccinium myrtillus, Hylocomium splendens, Linnaea borealis, Trientalis europaea*) and mesotrophic spruce swamp species (e.g. *Sphagnum girgensohnii, Equisetum sylvaticum, Polytrichum commune*), had their optima in the centre of the gradient (Fig. 4a and 4b). The third gradient, indicating moisture or peat-thickness separated forest and mire species better than the second gradient. Most of the xeric, mesic and herb-rich forest species were situated at one end and most of the bog, spruce swamp as well as marsh and spring species at the opposite end of this third gradient. (Fig. 4b).

DISCUSSION

Changes in Diversity on the Community Level (β-diversity)

In the analysis of the main compositional gradients, the multivariate ordination (GNMDS) method revealed that the main gradient was a fertility gradient. This is a gradient that strongly dominates the patterns of boreal forest and mire vegetation (Eurola *et al.*, 1984; Kuusipalo, 1985; Lahti & Väisänen, 1987; Tonteri *et al.*, 1990; Korpela & Reinikainen, 1996a & b). The sample plots at the opposite ends of this gradient still had about 10% of the species in common (see Appendix 1). It is important to notice that when forested site types with mire margin (supplementary nutrients) influence are concerned, all the trophic levels from oligotrophy to eutrophy are minerotrophic and that these usually are richer in nutrients than sites with mire expanse (mire inherent) influence (Eurola *et al.*, 1995).

Compared to the ordination of undrained sites in an earlier study (Korpela & Reinikainen, 1996a), the variation in species composition along the site fertility gradient was not affected by drainage. In addition, the gradient between mire margin and mire expanse, which is one of the main gradients in Scandinavian mire vegetation (Sjörs, 1983; Eurola *et al.*, 1984; Malmer, 1985), was parallel to the site fertility gradient. Together these two gradients illustrate the mixture caused partly by indicators of mire margin influence, which are mesotrophic forest and wetland species, and partly by mire expanse indicators, some of which are xeric forest species. Generally it is difficult to separate these gradients (e.g. Eurola *et al.*, 1994; Eurola *et al.*, 1995).

After drainage, correlation between the variables that describe tree-stand productivity and the fertility gradient, remained equally high or increased compared to the same variables on the undrained sites (Korpela & Reinikainen, 1996a). When compared to studies of mires with sparse tree stands before drainage (e.g. Laine *et al.*, 1995), the importance of the tree stand becomes more dominating after drainage. In this study of forested mire margin sites it is equally dominating on undrained and drained sites. Age of the tree stand was, in general, lower on drained sites both at the ombro-oligotrophic and the meso-eutrophic ends of the fertility gradient.

Temperature sum and latitude also correlated with the fertility gradient, reflecting the differences in distribution of the site types along the S-N gradient. This is because most of the paludified xeric forest sites, at the lower nutrient level end of the fertility gradient, belong to northern forest site types where bog dwarf shrubs are typical (Kalela, 1973) while most of the herb-rich, drained sites of the transformed phase, at the higher nutrient level end, are located in the south.

The undrained and drained sites were in a continuum along these main gradients, except for the ten herb-rich sites in cluster H, which clearly differed from the rest of the sites in both the ordination and classification analyses. In general, the trophic status (nutrient level) of the forested mire sites in the transformed phase was higher (see Table 1). One of the reasons for this is that usually the most productive sites have been drained first. On the other hand, the change in species composition has been fastest on the more nutrient-rich site types (Sarasto, 1961; Pienimäki, 1982; Hotanen *et al.* 1999). In addition, these sites reach the final transformed phase in a shorter time (Hotanen & Vasander, 1992; Laine *et al.*, 1995). In the early works of Fenno-Scandinavian forest scientists (Tanttu, 1915; Melin, 1917; Cajander, 1926; Lukkala, 1929) it was evident even then that after drainage the effect of moisture diminishes while that of nutrient status increases. On pristine forested mire margin sites the moisture gradient is shorter than on mires in general. The effect of drainage further shortens this gradient and accentuates the importance of the nutrient status according this study.

The length of the second gradient, which describes post-drainage succession, is shorter than the first one; about 40% of the species occur at both ends of this gradient. Most of the undrained oligo-mesotrophic and meso-eutrophic spruce mires were situated at one end of this gradient and the drained spruce mires, mostly in the transformed phase, at the other. The paludified mesic and herb-rich forests were situated in the middle of the gradient, together with mesotrophic drained spruce mires in the transforming and transformed phase. The situation of these sample plots in different drainage phases in the ordination space showed the degree of change from mire vegetation to forest vegetation along the post-drainage succession.

The third gradient was as long as the second and related more to peat thickness or paludification and to development of the tree stand. In this study of mire margin forested sites, however, peat thickness was not a statistically significant variable. The clearest difference in peat thickness was at the ombro-oligotrophic end of the fertility gradient between paludified xeric forests and undrained forested pine mires.

Changes in the Diversity of Species (α-diversity)

Diversity of species is expressed as numbers of species (species richness) and is related to the fertility gradient. At the ombro-oligotrophic end of the fertility gradient the mean richness of species was highest in cluster (D) that had the most sample plots in the transforming phase. At the meso-eutrophic end of the gradient the lowest mean richness of species was in cluster (E) with undrained mesotrophic spruce mire sites. According to Vasander (1987) and Vasander *et al.* (1997) the number of plant species is highest some years after drainage, at which time three groups of plants are found on the sites: original mire species, colonists and forest species. These groups of species were most evenly distributed in cluster D. The opposite situation prevails in cluster (E) with the least species richness and the lowest indices of diversity, e.g. the group of undrained mesotrophic spruce mires, where typical, constant spruce mire species dominated. For example, clusters E and F had the same number of ecological groups of species (Fig. 2). In cluster E the spruce swamp species were dominant, followed by xeric and mesic forest and bog species whilst herb-rich forest and marsh and spring species had much lower abundance. The drained mesotrophic sites in cluster F had a more evenly distributed abundance of xeric and mesic forest species, spruce swamp species and, on a smaller scale, an even distribution of herb-rich forest, bog, and spring and marsh species. Cluster E had the highest number of mire species.

The highest mean species richness was in the eutrophic end of the fertility gradient where the herb-rich forest species and spring and marsh species were most abundant. In the drained, herb-rich sites in the transformed phase (cluster H) the marsh and spring species were most abundant and dominated together with herb-rich forest species. In the undrained eutrophic and herb-rich sites (cluster G) spruce mire species were most dominant. The indices of diversity of species were the highest in the drained sites but there was no significant difference between drained and undrained communities. Only the Shannon-index (H'), which weights rare species (Hill, 1973), differed significantly between the most herb-rich, transformed phase sites of cluster H, the most paludified xeric forest sites in cluster B and the undrained mesotrophic spruce mire sites in cluster E (Table 3). The diversity indices have not proven to be distinct enough to show differences between undrained and drained peatland sites (Vasander *et al.*, 1997). Many scientists have pointed out the weaknesses of the theory behind and the uncertain biological purpose of the indices of diversity (Whittaker, 1972; Peet, 1974; Alatalo, 1981; van der Maarel, 1988). In this study the ordination methods used in analysing the beta-diversity proved to be more relevant in revealing the differences between pristine and drained mire margin sites.

Changes in the Composition of Species

A list of species coverage by clusters is presented in Appendix 1.

Along the sample plots groups of oligotrophic mire sites (from undrained to different successional phases of drainage) there was an apparent decrease in mire dwarf shrubs such as *Vaccinium uliginosum* and a corresponding increase in forest dwarf shrubs, for example, *Vaccinium vitis-idaea*. The abundance of *Vaccinium myrtillus*, a dwarf shrub of mesic forests, were quite even throughout the main gradients; only on the most eutrophic sites was abundance very low compared to an earlier study of undrained forested mire margin sites (Korpela & Reinikainen, 1996a).

Carex species usually disappear during the post-drainage succession because of increasing shading from trees and dwarf shrubs and the lack of nutrients (Aapala & Kokko, 1988; Laine *et al.*, 1995). The most abundant *Carex* species on forested mire margin sites with a thin peat layer is *Carex globularis* (Eurola, 1962; Ruuhijärvi, 1960). This species seemed to be indifferent to the effect of drainage. It was most abundant on drained, oligotrophic forested mires in the transforming phase but occurred sparsely even on the most nutrient-rich forested mires in the transformed phase. Most of the *Carex* species were found on undrained meso-eutrophic spruce mire sites, but the intermediate and flark level tall sedges (e.g. *Carex lasiocarpa, C. chordorriza*) were found as relicts on drained forested mires in the transforming phase. The hummock level species *Eriophorum vaginatum* was most abundant on undrained oligotrophic forested mire sites and was found in small numbers on drained sites in the transforming phase, although it is quite resistant to or even benefits from disturbance (Chapin *et al.*, 1979).

The most common xeric forest graminoid species was *Deschampsia flexuosa* and it was most abundant on xeric and mesic paludified forest sites and drained spruce mire sites in different drainage phases. The forest graminoid species that indicate marsh and spring influence, such as *Calamagrostis purpurea, C. canescens* and *Deschampsia cespitosa,* were more abundant on herb-rich sites in the transformed phase. The increase of grasses is an indication that sufficient light, growth space and mineral nitrogen is available, as well as influnce of surface water for some species (Holmen 1964; Platonov 1976).

The herbs were clearly related to the meso-eutrophic side of the fertility gradient. The only herbs present throughout the main gradients were *Rubus chamaemorus* and, very sparsely, *Melampyrum pratense. Rubus chamaemorus* is a hummock species of nutrient-poor mire sites (Eurola *et al.*, 1994) and it benefits from the disappearance of competitors (Aapala & Kokko, 1988). In this study, this species was clearly most abundant on undrained oligotrophic forested mire sites, and its abundance decreased towards drained and more nutrient rich forested mire sites, but was still found on herb-rich sites in the transformed phase. *Epilobium angustifolium* had clearly benefitted from drainage and was most abundant on herb-rich forested mires in transformed phase. *Equisetum sylvaticum* was most abundant on undrained meso-eutrophic spruce mires. Of the forest herbs *Maianthemum bifolium* was most abundant on undrained, eutrophic paludified hardwood-spruce forests and *Oxalis acetosella* on herb-rich forested mires in the transformed phase. According to Laine *et al.* (1995), the cover of mesic forest herbs (e.g. *Dryopteris carthusiana* and *Trientalis europaea*) clearly increased with increasing drainage-age; this was also apparent in the present study. On the other hand, wetland herbs such as *Cirsium palustre* and *Viola palustre* may even become more abundant after drainage and also grow well on forested mire sites in the transformed phase (Aapala & Kokko, 1988).

In this study the decrease of *Sphagnum* species along post-drainage succession was clear. Many forest mosses including *Pleurozium schreberi* and *Hylocomium splendens* already occur on hummocks in undrained forested mires and, after drainage, they increase in abundance (Laine *et al.*, 1995). The forest carpet moss *Dicranum polysetum* also becomes more abundant. In this study it was found in all clusters, but not so abundantly as *Pleurozium schreberi*. An increase in the abundance of *Brachythecium* species on the meso-eutrophic side of the fertility gradient was also apparent. *Sphagnum riparium* and *S. squarrosum,* which indicate spring and marsh influence, were most abundant on sites in the transformed phase. Usually they are found in or near ditches, where optimal growth conditions still prevail. *Sphagnum angustifolium* was still found in all clusters and *S. girgensohnii* also occurred sparsely on the drained eutrophic sites of the transformed phase, although greatly decreased compared to its abundance on undrained herb-rich and eutrophic sites (Korpela & Reinikainen, 1996a).

CONCLUSIONS

The main gradients on undrained mires are nutrient level and hydrological condition. After drainage hydrological conditions become more uniform and, consequently, the influence of the tree stand, which depends on the nutrient level, gradually becomes more dominating. Along the post-drainage succession, mire species (e.g. *Sphagnum* spp.) are gradually replaced by forest species, which already dominate in the surrounding forests (Laine *et al.*, 1995). In this study, site fertility determined the main gradient on both undrained and drained sites. Nutrient availability was not restricted even on the undrained mire margin sites. This main gradient correlated with site productivity and with stand variables such as dominant height.

The second gradient representing the drainage state described the hydrological conditions better than peat thickness, because already when undrained, forested mire margin sites have a thin peat layer. The drainage phase is determined according to the proportions of mire and forest species. The effect of drainage was stronger on the meso-eutrophic forested mire margin sites than on more oligotrophic sites. Similar results have been obtained in other studies where pristine and drained mire sites have been investigated (Hotanen & Vasander 1992; Laine *et al.* 1995; Hotanen *et al.* 1999). On undrained forested mire margin sites the influence of tree stands is dominating. It was not even possible to determine whether drainage increased the effect of tree stand on the vegetation.

The mixing of mire margin features, such as spring and marsh and spruce swamp, results in high floristic diversity by associations with the forest and bog species. After drainage, the diversity of species still remains high when only species numbers are examined. Structurally, the communities change towards forest vegetation where mesic and herb-rich forest species dominate, with mire species present as relicts. These changes indicate that the composition of the vegetation will resemble corresponding forest sites at the same or higher level of fertility. It remains to be seen whether the tree stand structure of the drained sites also will become more forest like.

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References

Aapala, K, and Kokko, A. (1988) Ojituksen vaikutuksesta soiden kenttäkerroksen kasvilajeihin. (Summary: Changes in the ground vegetation of drained mires). *Suo,* **39**(3): 41-49.

Ahti, T., Hämet-Ahti, L. and Jalas, J. (1968) Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici,* **5**: 169-211.

Alatalo, R. V. (1981) Problems in the measurement of eveness in ecology. *Oikos,* **37**: 199-204.

Cajander, A. K. (1913) Studien über die Moore Finnlands. *Acta Forestalia Fennica,* **2** (3): 1-208.

Cajander, A. K. (1926) The theory of forest types. *Acta Forestalia Fennica,* **29** (3): 1-108.

Chapin, F.S. III, van Cleve, K. and Chapin, M. C. (1979) Soil temperature and nutrient cycling in tussock growth form of *Eriophorum vaginatum. Journal of Ecology,* **67**: 169-189.

Eurola, S. (1962) Über die regionale Einteilung der südfinnischen Moore. *Annales Botanici Societatis Vanamo,* **33** (2): 1-243.

Eurola, S., Hicks, S. and Kaakinen E. (1984) Key to Finnish mire types. In: Moore, P. D. (ed.): *European mires*: 11-117. Academic Press, London.

Eurola, S., Huttunen, A. and Kukko-Oja, K. (1994) Suokasvillisuusopas. 'A guide for mire vegetation' *Oulanka Reports* **13**. University of Oulu. 81 pp.

Eurola, S, Laukkanen, A. and Moilanen, M. (1995) The significance of the original mire site type in the classification of old drainage areas. An example from Muhos, Finland (6449'N,26E). *Aquilo Ser. Botanica,* **35**: 39-44.

Faith, D.P., Minchin, P.R. and Belbin, L. (1987) Compositional dissimilarity as a robust measure of ecological distances. *Vegetatio,* **69**: 57-68.

Frey, T. E. A. (1973) The Finnish school and Forest-Site Types. In: Whittaker, R. H. (ed.): *Ordination and classification of communities*: 405-433. The Hague.

Gustavsen, H. and Päivänen, J. (1986) Luonnontilaisten soiden puustot kasvullisella metsämaalla 1950-luvun alussa. (Summary: Tree stands on virgin forested mires in the early 1950's). *Folia Forestalia,* **673**: 1-27.

Heikurainen, L. and Pakarinen, P. (1982) Mire vegetation and site types. In: Laine, J., (ed.): *Peatlands and their utilization in Finland.* Finnish Peatland Society. Helsinki

Hill, M.O. (1973) Diversity and evenness. A unifing notation and its consequences. *Ecology,* **54**: 427-432.

Hill, M. O. (1979) *TWINSPAN - a fortran program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes.* Cornell University, Ithaca, NY. 90 pp.

Holmen, H. (1964) Forest ecological studies on drained peatland in the Province of Uppland, Sweden. Parts I-III. *Studia Forestalia Suecica* **16**: 1-236.

Hotanen, J-P. and Vasander, H. (1992) Eteläsuomalaisten metsäojitettujen turvemaiden kasvillisuuden numeerinen ryhmittely. (Summary: Post-drainage development of vegetation in southern Finnish peatlands studied by numerical analysis). *Suo,* **43**(1): 1-10.

Hotanen, J-P., Nousiainen, H. and Paalamo, P. (1999) Vegetation succession and diversity on Teuravuoma experimental drainage area in northern Finland. *Suo,* **50**(2): 1-55.

Huikari, O. (1974) Site quality estimation on forest land. In: Heikurainen, L. (ed.): *Proceedings of the International Symposium on Forest Drainage,* 2nd-6th September, 1974: pp. 15-24. Jyväskylä-Oulu, Finland. 416 pp.

Hämet-Ahti, L., Suominen, J., Ulvinen, T., Uotila, P. and Vuokko, S. (1998) *Retkeilykasvio (Field Flora of Finland),* Ed. 4. 656 pp. Finnish Museum of Natural History, Botanical Museum. Helsinki.

Ilvessalo, Y. (1956) Suomen metsät vuosista 1921-24 vuosiin 1951-53. Kolmeen valtakunnan metsien inventointiin perustuva kuvaus. (Summary: The forests of Finland from 1921-24 to 1951-53. A survey based on three national forest inventories). *Communicationes Insttituti Forestalis Fenniae,* **47** (1): 1-227.

Ilvessalo, Y. (1957) Suomen suot. Valtakunnan metsien inventointiin perustuva kuvaus. (Summary: The mires of Finland. A survey based on the 3rd National Forest Inventory). *Suo,* **8**: 51-61.

Kalela, A. (1973) Suomen yleisimpien metsätyyppien floristinen rakenne. 'The floristic composition of the most common forest site types in Finland'. In: Kalliola, R. (ed.):*Suomen kasvimaantiede 'Plant geography of Finland'*, (in Finnish). Helsinki. 308 pp.

Kantvilas, S.G. and Minchin, P.R. (1989) An analysis of epiphytic lichen communities in Tasmanian cool temperature rainforest. *Vegetatio,* **84**: 99-112.

Koponen, T., Isoviita, P. and Lammes, T. (1977) The bryophytes of Finland: An annotated checklist. *Flora Fennica,* **6**: 1-77.

Korpela, L. and Reinikainen, A. (1996a) A numerical analysis of mire margin forest vegetation in South and Central Finland. *Annales Botanici Fennici,* **33**: 183-197.

Korpela, L. and Reinikainen, A. (1996b) Patterns of diversity in boreal mire margin vegetation. *Suo,* **47** (1): 17-28.

Kuusipalo, J. (1985) An ecological study of upland forest site classification in southern Finland. *Acta Forestalia Fennica,* **192**: 1-77.

Lahti, T. and Väisänen, R. A. (1987) Ecological gradients of boreal forests in South Finland: an ordination test of Cajander's forest site type theory. *Vegetatio,* **68**: 145-156.

Laine, J. (1989) Metsäojitettujen soiden luokittelu. English summary: Classification of peatlands drained for forestry. *Suo,* **40**: 37-51.

Laine, J. and Vanha-Majamaa, I. (1992) Vegetation ecology along a trophic gradient on drained pine mires in southern Finland. *Annales Botanici Fennici,* **29**: 213-233.

Laine, J., Vasander, H. and Laiho, R. (1995) Long-term effects of water level drawdown on the vegetation of drained pine mires in Southern Finland. *Journal of Applied Ecology,* **32**: 785-802.

Lukkala, O. J. (1929) Über die Dicke der Torfschicht und die Neigungsverhältnisse der Mooroberfläche auf verschiedenen Moortypen. *Acta Forestalia Fennica,* **34** (16): 1-16.

Lumiala, O. (1937) Kasvimaantieteellisiä pintamorfologisia suotutkimuksia Luoteis-Karjalassa. (Referat: Pflanzengeographische und obermorfologische Mooruntersuchungen im nordwestlichen Karelien). *Annales Botanici Societatis Zoologicae Botanicae Fennicae Vanamo,* **10** (1): 1-115.

Magurran, A.E. (1988) *Ecological diversity and its measurement.* Princeton University Press, 179 pp. Great Britain.

Malmer, N. (1985) Remarks to the classification of mires and mire vegetation - Scandinavian arguments. *Aquilo Ser. Botanica,* **21**: 9-17.

Melin, E. (1917) Studier över de norrländska myrmarkernas vegetation med särskild hänsyn till deras skogsvegetation efter torrläggning. *Norrländskt Handbibliotek,* **7**: 1-426.

Minchin, P. R. (1987) An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio,* **69**: 89-107.

Minchin, P. R. (1991) *DECODA. Database for ecological community data.* Vers. 2.04. Australian National University, Canberra.

Ohlsson, M., Söderström, L., Hörnberg, G., Zackirsson, O. and Hermansson, J. (1997) Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. *Biological Conservation,* **81**: 221-231.

Økland, R. H. (1989) A phytoecological study of the mire Northern Kisselbergmosen, SE Norway. I. Introduction, flora, vegetation and ecological conditions. *Sommerfeltia,* **8**: 1-172.

Økland, R. H. (1990) Vegetation ecology: theory, methods and applications with reference to Fennoscandia. *Sommerfeltia Supplement,* **1**: 1-233.

Paavilainen, E. and Päivänen, J (1995) *Peatland Forestry. Ecology and Principles.* Ecological Studies, Vol. **111**. Springer - Verlag, Berlin-Heidelberg. 248 pp.

Peet, R.K. (1974) The measurement of species diversity. *Annual Review of Ecology and Systematics,* **5**: 285-307.

Pienimäki, T. (1982) Kasvillisuuden ojituksen jälkeinen kehitys eräillä suotyypeillä Pohjois-Pohjanmaalla. (Summary: Development of vegetation on some drained mire site types in North-Ostrobotnia). *Suo,* **33**(4-5): 113-123.

Platonov, G. M. (1976) The Shift of Bog Vegetation Under the Influence of Drying. In: P'yvachenko, N. (ed.): *Interrelation of Forest and Bog* - Results of Station Research, pp. 129-140. New Delhi.

Prentice, I.C. (1980) Vegetation analysis and order invariant gradient models. *Vegetatio,* **42**: 27-34.

Reinikainen, A. (1988) Metsäojitettujen soiden kasvupaikkaluokituksen suunnanhakua (Summary: The need of improving the site classification of mires drained for forestry). *Suo,* **39**: 61-71.

Reinikainen, A. (1990) The peatland ecosystem in change. In: Hånell, B.(ed.) *Biomass production and element fluxes in forested peatland ecosystems.* Swedish University of Agricultural Science, Umeå, Dep-artment of Forest Site Research, pp 167-175.

Ruuhijärvi, R. (1960) Über die regionale Einteilung der nordfinnischen Moore. *Annales Botanici Societatis Vanamo,* **31** (1): 1-360.

Sarasto, J. (1961) Über die Klassifierung der für Walderziehung entwässerten Moore. *Acta Forestalia Fennica,* **74**(5): 1-57.

Schönemann, P. H. and Carroll, R. M. (1970) Fitting one matrix to another under choice of central dilation and a rigid motion. *Psychometrika* **35**: 245-255.

Sevola, Y. (ed.) (1997) *Finnish Statistical Yearbook of Forestry 1997.* Finnish Forest Research Institute, Gummerus Kirjapaino Oy, Jyväskylä. 347 pp.

Sjörs, H. (1948) Myrvegetation in Bergslagen. *Acta Phytogeographica Suecica,* **21**: 1-299.

Sjörs, H. (1983) Mires of Sweden. In: Gore, A. J. P. (ed.): *Mires: swamp, bog, fen and moor. Ecosystems of the world.* **4B**., *Regional studies*, pp. 69-94. Elsevier, Amsterdam.

Tanttu, A. (1915) Tutkimuksia ojitettujen soiden metsittymisestä. (Summary: Studien über die Aufforstungsfähigkeit der entwässerten Moore). *Acta Forestalia Fennica,* **5**(2):1-211.

Tonteri, T., Mikkola, K. and Lahti, T. (1990) Compositional gradients in the forest vegetation of Finland. *Journal of Vegetation Science,* **1**: 691-698.

Tuomikoski, R. (1942) Untersuchungen ber die Untervegetation der Bruchmoore in Ostfinnland. I Zur Methodik der Pflanzensoziologischen Systematik. *Annales Botanici Societatis Vanamo,* **7** (1): 1-203.

van der Maarel, E. (1988) Species diversity in plant communities in relation to structure and dynamics. In: During, H. J., Werger, M.J.A. & Willems, H.J. (eds.): *Diversity and pattern in plant communities: 1 - 14.* SPB Academic Publishing, The Hague.

Vasander, H. (1987) Diversity of understorey biomass in virgin and drained and fertilized southern boreal mires in Eastern Fennoscandia. *Annales Botanici Fennici,* **24**(2): 137-153.

Vasander, H. (ed.) (1996) *Peatlands in Finland.* Finnish Peatland Society, Helsinki, 168 pp.

Vasander, H., Laiho, R. and Laine, J. (1997) Changes in species diversity in peatlands drained for forestry. In: Trettin, C. C., Jürgensen, M., Grigal, D., Gale, M. & Jeglum, J. (eds.): *Northern forested wetlands: Ecology and management: 109 - 119.* Lewis Publishers, 486 pp.

Vitikainen, O., Ahti, T., Kuusinen, M., Lommi, S. and Ulvinen, T. (1997) Checklist of Lichens and allied Fungi of Finland. *Norrlinia,* **6**, Botanical Museum, Finnish Museum of Natural History, Helsinki University Press, Helsinki, 123 pp.

Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon,* **21**(2-3): 213-251.

Appendix 1.

Tree and shrub layer and field and ground layer vegetation in the eight TWINSPAN-clusters (A-H). Mean percentage cover is presented for each species in each cluster. Total number of field and ground layer species included was 226. Total number of species present in each cluster by growth-form groups are also presented. The number of sample plots in each cluster = (n).

	TWINSPAN-clusters							
	A	B	C	D	E	F	G	H
	(n = 12)	(n = 10)	(n = 14)	(n =25)	(n = 43)	(n = 20)	(n = 22)	(n = 10)
Tree and shrub layer								
Alnus glutinosa	-	-	-	-	-	-	1.00	0.8
Alnus incana	-	-	0.04	0.5	0.4	1.95	1.88	3.38
Betula pendula	-	-	0.47	0.05	1.49	2.90	1.36	0.60
Betula pubescens	7.92	6.00	23.32	20.26	14.88	15.84	25.05	34.19
Daphne mezereum	-	-	-	-	-	-	-	0.02
Frangula alnus	-	-	-	0.02	0.02	-	0.31	0.05
Juniperus communis	-	-	0.29	1.02	0.58	0.66	0.20	0.70
Picea abies	13.55	6.88	13.93	18.51	38.18	38.89	26.20	16.38
Pinus sylvestris	21.31	22.12	14.46	18.18	7.43	6.99	9.26	6.75
Populus tremula	0.01	0.15	2.86	0.160.	0.20	0.05	1.26	0.66
Prunus padus	-	-	-	-	-	-	0.01	0.31
Salix caprea	0.01	0.07	0.04	0.29	0.21	0.15	0.44	2.22
Rubus idaeus	-	-	-	-	0.02	0.23	-	2.00
Sorbus aucuparia	-	0.16	0.37	0.34	0.56	1.10	0.84	1.16
Salix spp.	2.98	1.13	1.17	1.38	0.89	0.41	1.61	11.59
Total number of species	6	7	10	11	12	11	13	15
Field layer								
Trees and shrubs:								
Alnus incana	-	-	-	-	0.02	0.11	0.08	-
Betula pubescens	-	0.01	0.50	0.09	0.16	0.10	0.43	0.22
Frangula alnus	-	-	-	-	-	-	0.13	0.02
Juniperus communis	-	-	-	0.17	0.10	-	0.03	0.10
Picea abies	-	0.08	0.11	1.01	0.41	0.20	0.21	0.24
Pinus sylvestris	0.01	0.11	0.06	0.15	0.02	0.01	-	-
Populus tremula	-	-	-	-	-	-	0.01	-
Prunus padus	-	-	-	-	-	-	-	0.05
Rubus idaeus	-	-	-	-	-	0.11	0.01	0.28
Salix aurita	0.01	-	0.07	0.82	-	0.01	0.05	-
Salix caprea	-	-	-	0.35	0.01	0.03	0.02	-
Salix phylicifolia	-	-	-	0.03	0.04	-	0.10	0.60
Salix repens	-	-	-	0.02	-	0.01	-	-
Salix rosmarinifolia	0.33	-	-	-	-	-	-	-
Salix spp.	-	-	-	-	0.07	-	-	1.55
Sorbus aucuparia	-	0.03	0.09	0.05	0.10	0.14	0.09	0.89
Total number of species	3	4	5	10	9	9	11	9
Dwarf-shrubs:								
Andromeda polifolia	0.12	0.05	0.28	0.02	0.01	-	0	-
Arctostaphylos uva-ursi	-	-	-	-	-	0.01	-	-

	TWINSPAN-clusters							
	A	B	C	D	E	F	G	H
	(n = 12)	(n = 10)	(n = 14)	(n =25)	(n = 43)	(n = 20)	(n = 22)	(n = 10)
Betula nana	0.06	-	0.01	0.26	0.44	-	-	-
Calluna vulgaris	2.14	3.79	0.01	0.01	-	0.63	-	-
Chamadaphne calyculata	-	-	0.33	0.55	0.02	-	-	-
Empetrum hermaphroditum	-	-	1.24	2.07	-	-	-	-
Empetrum nigrum	6.67	7.27	1.74	0.65	0.01	0.08	0.00	-
Ledum palustre	8.66	11.52	10.43	0.91	0.05	0.34	-	-
Vaccinium microcarpum	0.02	-	-	-	-	-	-	-
V. myrtillus	11.26	14.11	14.59	13.55	16.62	13.42	3.56	0.94
V. oxycoccus	0.04	0.00	0.09	0.07	0.02	0.02	-	-
V. uliginosum	10.28	7.79	8.47	2.23	0.09	0.46	0.05	0.20
V. vitis-idaea	6.57	10.82	6.42	11.83	6.30	7.27	3.42	0.59
Total number of species	10	8	11	11	9	8	6	3
Graminoids:								
Agrostis canina	-	-	-	-	-	-	-	1.5
A. capillaris	-	-	-	-	0.01	0.02	0.14	1.95
A. tenuis	-	-	-	-	0.010	0.04	-	-
Calamagrostis arundinacea	-	-	0.14	-	0.01	0.20	0.01	0.01
C. canescens	-	-	-	-	0.01	0.21	0.50	2.10
C. purpurea	-	-	0.01	0.01	0.08	0.29	0.98	5.68
Carex brunnescens	-	-	-	0.01	0.01	0.03	-	0.08
C. canescens	-	-	0.22	-	0.20	-	0.63	0.02
C. chordorriza	-	-	-	0.01	-	-	-	-
C. digitalis	-	-	-	-	0.01	-	0.03	-
C. echinata	-	-	-	0.01	-	-	-	-
C. flava	-	-	-	-	-	-	0.02	-
C. globularis	3.10	0.42	2.68	6.45	3.36	3.62	1.36	0.01
C. lasiocarpa	-	-	-	0.12	-	-	-	-
C. loliacea	-	-	-	-	-	-	0.01	-
C. nigra	-	-	-	0.24	-	0.08	0.70	0.02
C. ovalis	-	-	-	-	-	0.01	-	-
C. pallescens	-	-	-	-	-	-	0.57	-
C. spp.	-	-	-	-	0.01	0.10	0.13	0.80
C. vaginata	-	-	-	-	-	0.03	-	-
Deschampsia cespitosa	-	-	-	-	0.12	0.53	0.18	8.60
Deschampsi flexuosa	0.01	0.10	1.91	0.34	0.28	2.25	0.21	0.45
Eriophorum vaginatum	0.01	-	2.59	0.25	0.02	-	0.05	-
Festuca spp.	-	-	-	-	-	-	0.05	-
Juncus filiformis	-	-	0.01	0.12	0.04	-	-	0.72
Luzula pilosa	-	-	0.18	-	0.07	0.12	0.09	0.07
Melica nutans	-	-	-	-	-	-	0.02	-
Molinia caerulea	-	-	-	-	-	-	0.03	-
Phragmites australis	-	-	-	-	0.07	-	-	-
Poa nemoralis	-	-	-	-	-	-	0.19	-
P. pratensis	-	-	-	-	-	-	-	0.10
P. spp.	-	-	-	-	-	0.06	0.05	-
Total number of species	3	2	8	10	16	16	21	15

	TWINSPAN-clusters							
	A (n = 12)	**B** (n = 10)	**C** (n = 14)	**D** (n =25)	**E** (n = 43)	**F** (n = 20)	**G** (n = 22)	**H** (n = 10)
Herbs:								
Aegopodium podagraria	-	-	-	-	-	-	-	0.08
Anemone nemorosa	-	-	-	-	-	-	0.05	-
Angelica sylvestris	-	-	-	-	-	-	-	0.31
Athyrium filix-femina	-	-	-	-	-	-	0.27	0.50
Calla palustris	-	-	-	-	-	-	0.01	-
Caltha palustris	-	-	-	-	-	0.05	0.02	0.80
Campanula rotundifolia	-	-	-	-	-	0.01	-	-
Cardamine pratensis	-	-	-	-	-	-	-	0.01
Centaurea jacea	-	-	-	-	-	-	-	0.05
Cirsium helenoides	-	-	-	-	-	-	0.03	0.55
C. palustre	-	-	-	-	-	-	0.01	0.27
Cornus suecica	-	-	0.11	-	0.22	-	-	-
Crepis paludosa	-	-	-	-	-	-	0.11	0.01
Dactylis maculata	-	-	-	-	0.01	0.01	-	-
Dryopteris expansa	-	-	-	-	0.48	0.55	0.06	-
D. carthusiana	-	-	-	0.41	0.38	0.25	2.58	10.6
Epilobium angustifolium	-	-	-	0.11	0.03	0.29	0.14	2.85
E. palustre	-	-	-	-	-	0	0.01	0.07
E. spp.	-	-	-	-	-	-	0.03	-
Equisetum arvense	-	-	-	-	-	0.09	0.27	-
Equisetum palustre	-	-	0.04	0.05	-	0.05	0.23	0.11
E. pratense	-	-	-	-	-	-	0.01	-
E. sylvaticum	0.02	-	0.31	0.96	2.53	0.66	3.63	1.44
Filipendula ulmaria	-	-	-	-	-	-	0.61	3.18
Fragaria vesca	-	-	-	-	-	-	0.01	0.06
Galium boreale	-	-	-	-	-	-	0.08	-
Galium palustre	-	-	-	-	-	-	0.02	0.08
G. spp.	-	-	-	-	-	-	0.01	-
Geranium sylvaticum	-	-	-	-	-	-	0.03	1.70
Geum rivale	-	-	-	-	-	-	0.07	0.06
Goodyera repens	-	0.01	-	-	-	0.05	-	-
Gymnocarpium dryopteris	-	-	-	-	0.29	0.75	0.83	4.36
Huperzia selago	-	-	-	-	-	-	-	0.01
Linnaea borealis	-	0.02	0.10	0.02	0.15	0.72	0.46	0.14
Listera cordata	-	-	-	-	0.01	-	-	-
Lychnis viscaria	-	-	-	-	-	-	-	0.29
Lycopodium annotinum	-	-	0.11	0.01	0.03	0.56	0.03	0.58
Lysimachia vulgaris	-	-	-	-	-	-	0.09	-
Maianthemum bifolium	-	-	0.06	0.05	0.17	0.52	2.45	0.25
Melampyrum pratense	0.01	0.02	0.08	0.09	0.07	0.10	0.49	0.30
M. sylvaticum	-	-	-	0.01	0.03	0.03	0.02	0.02
Menyanthes trifoliata	-	-	-	0.01	-	0.05	-	-
Orthilia secunda	-	-	0.02	0.27	0.20	0.57	0.21	0.07
Oxalis acetosella	-	-	-	-	0.13	0.22	0.74	0.96
Polygonum viviparum	-	-	-	-	-	-	0.01	-
Potentilla erecta	-	-	-	-	-	0.03	0.10	0.07
P. palustris	-	-	-	-	0.06	-	0.36	1.17

	TWINSPAN-clusters							
	A (n = 12)	B (n = 10)	C (n = 14)	D (n =25)	E (n = 43)	F (n = 20)	G (n = 22)	H (n = 10)
Prunella vulgaris	-	-	-	-	-	-	0.01	-
Pyrola chlorantha	-	-	-	-	-	0.01	-	-
P. minor	-	-	-	-	-	-	0.03	-
P. rotundifolia	-	-	-	0.02	-	-	0.09	0.55
Ranunculus acris	-	-	-	-	-	-	0.01	1.26
R. auricomus	-	-	-	-	-	-	0.01	-
R. repens	-	-	-	-	-	0.75	-	0.05
R. spp.	-	-	-	-	-	-	-	0.05
Rubus arcticus	-	-	-	0.02	0.09	0.11	0.65	1.58
R. chamaemorus	1.39	0.48	8.86	1.67	1.75	0.36	0.98	0.05
R. saxatilis	-	-	-	-	-	0.35	0.3	0.13
Rumex acetosa	-	-	-	-	-	-	-	0.01
Solidago virgaurea	-	-	0.14	0.01	0.15	0.01	0.17	0.55
Stellaria graminea	-	-	-	-	-	-	-	0.01
S. longifolia	-	-	-	-	-	-	-	0.07
S. uliginosa	-	-	-	-	-	0.01	-	-
S. palustris	-	-	-	-	-	-	0.01	-
Thelypteris paludosa	-	-	-	-	-	0.15	0.51	-
Veronica serpyllifolia	-	-	-	-	-	-	0.02	-
Viola canina	-	-	-	-	-	-	0.01	-
V. epipsila	-	-	-	-	-	-	-	1.90
V. palustris	-	-	-	-	-	-	0.42	4.06
V. riviniana	-	-	-	-	-	-	0.02	-
Thelypteris phegopteris	-	-	-	-	0.06	-	0.05	0.20
Trientalis europaea	-	-	0.96	0.06	0.17	0.83	1.60	1.86
Urtica dioica	-	-	-	-	-	-	-	0.40
Total number of species	3	4	11	16	21	30	52	47
Ground layer								
Sphagnum mosses:								
Sphagnum angustifolium	31.35	1.85	20.77	11.89	6.56	0.87	1.62	2.23
S. centrale	-	-	-	-	0.27	-	1.28	0.10
S. compactum	-	-	-	0.04	-	-	-	-
S. fallax	-	-	-	-	0.35	-	-	-
S. fuscum	-	1.00	-		-	-	-	
S. girgensohnii	-	4.50	12.49	2.78	24.11	14.35	28.56	2.38
S. magellanicum	0.04	-	1.50	1.88	0.29	0.08	0.01	-
S. nemoreum	11.31	4.95	0.20	1.20	0.04	-	0.17	-
S. papillosum	-	-	0.01	-	-	0.75	0.09	-
S. riparium	-	-	1.07	-	0.21	-	2.73	5.01
S. rubellum	-	0.20	-		-	-	-	-
S. russowii	20.23	9.13	9.52	8.54	2.98	-	0.15	-
S. spp.	-	-	-	-	-	0.01	-	0.02
S. squarrosum	-	-	-	-	1.16	0.25	0.24	0.45
S. subsecundum	-	-	-	-	-	-	-	0.02
S. teres	-	-	-	-	-	0.25	0.07	-
S. wulfianum	-	0.01	-	-	0.05	-	1.23	-
Total number of species	4	7	7	6	10	7	11	7

	TWINSPAN-clusters							
	A (n = 12)	B (n = 10)	C (n = 14)	D (n =25)	E (n = 43)	F (n = 20)	G (n = 22)	H (n = 10)
Carpet mosses:								
Dicranum fuscescens	0.01	-	-	0.01	0.01	0.10	0.02	-
D. majus	-	0.06	0.07	0.15	0.97	0.38	0.61	0.02
D. polysetum	0.23	2.01	0.19	3.54	1.43	5.54	0.38	0.70
D. scoparium	0.02	0.46	0.56	0.93	1.87	1.42	0.9	0.31
D. spp.	-	-	-	-	-	-	0.05	-
Hylocomium splendens	5.29	2.88	1.57	6.06	7.08	7.20	1.34	0.36
Pleurozium schreberi	15.99	39.16	18.11	26.63	16.33	22.83	4.08	2.83
Ptilium crista-castrensis	0.02	0.05	-	0.01	0.32	0.14	-	-
P. spp.	-	-	-	0.01	-	-	-	-
Rhytidiadelphus triquetrus	-	-	-	-	-	0.06	0.16	0.05
Total number of species	6	6	5	8	7	8	8	6
Other Bryidae:								
Atrichum undulatum	-	-	-	0.06	-	-	0.01	0.05
Aulacomium palustre	0.87	1.42	0.22	0.58	0.13	0.22	0.24	0.27
Brachythecium albicans	-	-	-	-	-	0.10	-	-
B. curtum	-	-	-	-	0.01	-	-	-
B. oedipodium	-	-	-	0.02	-	0.05	-	-
B. spp.	-	0.03	0.03	0.08	0.31	1.36	0.62	6.08
Calliergon cordifolium	-	-	-	-	-	-	-	0.90
C. cuspidatum	-	-	-	-	-	-	-	0.01
C. spp.	-	-	-	-	-	-	0.01	-
C. stramineum	-	-	-	-	-	-	-	0.10
Campylium spp.	-	-	-	-	-	-	0.01	-
Ceratodon purpureus	-	-	-	-	-	0.01	-	-
Climacium dendroides	-	-	-	-	-	-	0.51	0.01
Gymnodontium strumiferum	-	-	-	-	-	0.01	-	-
Mnium spp.	-	-	-	-	0.01	0.15	0.10	0.54
Musci spp.	-	-	-	-	-	-	0.01	-
Paraleucobryum longifolium		-	-	-	-	0.01	-	-
Plagiochila asplenioides	-	-	-	-	-	0.10	0.03	0.20
Plagiomnium affine	-	-	-	-	-	0.01	-	-
P. ellipticum	-	-	-	-	-	0.01	-	-
Plagiomnium spp.	-	-	-	-	0.02	0.09	0.01	0.06
Plagiothecium spp.	-	-	-	0.14	0.07	0.09	0.07	0.10
Pogonatum spp.	-	-	-	-	-	0.01	-	-
Pohlia cruda	-	-	-	0.01	-	0.01	-	-
P. nutans	-	0.01	0.13	0.28	0.02	0.64	0.10	0.24
Polytrichastrum formosum	-	-	-	-	-	-	0.01	0.01
P. spp.	-	-	-	-	-	-	0.14	-
Polytrichum commune	10.05	0.58	10.09	13.11	16.23	1.27	9.52	0.45
P. juniperum	0.01	0.13	0.09	0.15	0.99	1.50	-	0.35
P. longisetum	-	-	-	-	0.02	-	-	-
P. strictum	0.91	0.22	0.32	0.66	0.02	0.68	0.01	0.50
Pseudobryum cinclidioides	-	-	-	-	-	0.75	-	-
Rhodobrym roseum	-	-	-	-	-	-	0.01	0.04
Rhizomnium spp.	-	-	-	0.01	-	-	0.01	0.05

	TWINSPAN-clusters							
	A	B	C	D	E	F	G	H
	(n = 12)	(n = 10)	(n = 14)	(n =25)	(n = 43)	(n = 20)	(n = 22)	(n = 10)
Tetraphis pellucida	-	-	-	0.02	-	-	0.02	-
Warnstofia fluitans	-	-	-	-	0.02	-	-	-
Total number of species	4	6	6	12	13	19	19	18
Hepatics:								
Barbilophozia barbata	-	-	-	-	0.01	-	-	-
B. lycopodioides	-	-	0.09	-	0.01	-	0.03	-
B. spp.	-	-	-	0.04	-	-	0.11	-
Blepharostoma trichopyllum	-	-	-	-	-	0.01	-	-
Hepaticae	0.07	0.01	0.10	0.24	0.10	0.01	0.17	0.02
Mylia anomala	-	-	0.01	-	-	-	-	-
Pellia spp.	-	-	-	-	-	0.25	-	-
Ptilidium ciliare	-	-	0.07	0.09	0.03	-	0.04	-
P. spp.	-	1.50	-	0.04	0.02	0.03	0.01	-
Total number of species	1	2	4	4	6	3	5	1
Lichens:								
Cladina arbuscula	-	0.72	0.01	0.05	0.01	0.15	-	-
C. rangiferina	0.01	0.13	0.52	0.03	0.01	-	-	-
C. stellaris	-	0.38	-	-	-	-	-	-
Cladonia cariosa	-	-	0.01	0.04	-	-	-	-
C. chlorophaea	-	-	0.01	-	-	0.01	-	-
C. cornuta	-	0.16	-	0.01	0.01	0.06	-	-
C. deformis	0.01	0.01	0.08	0.04	0.01	0.01	-	-
C. fimbriata	-	0.01	-	0.01	-	-	0.01	-
C. furcata	-	-	-	-	-	-	0.01	-
C. gracilis	-	0.01	0.11	-	-	0.01	-	-
C. spp.	-	-	-	0.05	0.01	0.12	0.01	0.01
C. sulphurina	-	-	-	0.1	-	0.01	-	-
Peltigera aphtosa	-	0.20	0.16	-	-	-	-	-
Total number of species	2	8	7	8	5	8	3	1
Total number of species present	36	45	64	85	96	108	136	107

Paper IV

Korpela, L. 2004. Structural and species diversity of boreal forested mire margin communities in South and Central Finland– effect of drainage. Silva Fennica (submitted manuscript).

IV

Structural and species diversity of boreal forested mire margin communities in Finland - effect of drainage

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Abstract

In Finland forested mire margin communities have, to a large extent, been drained owing to their potential for wood production. In this study the effect of forest drainage on structural diversity of forested mire margin communities was studied by analyzing the percentage covers of tree and shrub species in all vegetation layers and the proportions of different growth forms in the field and ground layers in connection with stem diameter distribution changes after drainage. Drained sites were compared to corresponding undrained sites. The interpretation factors used were: species number and abundance, size distribution of the tree stand, species diversity, and layer structure. The succession stages from a diverse mixture of mire and forest vegetation towards a more homogenous structure of forest vegetation was indicated by differences in growth form groups of the field and ground layer vegetation between undrained and drained forested mire margin communities. Site fertility was the most important factor in the changes in species richness of both the overstorey and understorey. There was a clear relationship between overstorey and understorey diversity. Even on the drained sites the tree stands were uneven-aged and uneven-sized. Analysis of species percentage covers in the different canopy layers revealed that there was an evident effect of drainage on structural diversity of the overstorey. The mean cover of dominant trees and pubescent birch was clearly increased after drainage. The clearest effect of drainage on the tree stand size distribution was in the most nutrient-rich and nutrient-poor sites.

Keywords: biodiversity, boreal forest, spruce mires, structural diversity, forest structure

1. Introduction

In forest ecosystems the vegetation that forms the structure of the habitat is by definition composed of tree species, but shrub and field vegetation layers can also be included. A diverse growing stock is the basis of the diversity of the entire forest ecosystem (MacArthur 1965, Wilson 1974, Franzreb 1978, Rice *et al.* 1984). Wide variation in the structure of the vegetation is considered necessary for an increase in the potential biodiversity of a forest habitat (Camp 1994, Siitonen *et al.* 1995).

In the boreal landscape of Fennoscandia and the hemiboreal landscape of northeastern Europe swamp forests and wetland forest communities are sites with high biodiversity (e.g. Ohlsson *et al.* 1997, Prieditis 1999). Even at the southern border of the Sphagnum-mire distribution in Europe the *Picea abies* dominated mire-margin communities show high species diversity (Kutnar and Martinčič 2003). In boreal vegetation zone special attention has been focused on nutrient-rich and herb-dominated swamp forests (Ohlsson *et al.* 1997), rich in vascular plant species (e.g. Ohlsson 1990) and with high forest productivity after drainage (Malmström 1928, Holmen 1964, Hånell 1988, Hökkä *et al.* 2002). In Finland these biotopes have, to a large extent, been drained (Eurola *et al.* 1991, Hökkä *et al.* 2002). Compared to the early 1950s only one half, and in southern Finland, only a fourth of the area of forested mire margin sites remain undrained (Ilvessalo 1957, Hökkä *et al.* 2002). In Sweden they have also been extensively exploited (Ohlsson *et al.* 1997). In Finland the most nutrient-rich sites

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are nowadays considered threatened (Heikkilä 1994a, b, Heikkilä and Lindholm 2000).

In Finnish mire site type classification (i. e. Heikurainen and Pakarinen 1982, Laine and Vasander 1996) swamp forests are included in genuine forested mire site types, and belong to the so called forested mire margin communities that typically are situated in the transition zone between upland mineral soil forests and open peatlands. The sites are thus minerotrophic, trophic gradient reaching from oligotrophy to meso-eutrophy. The vegetation consists of both upland forest and peatland species. In recent studies, results of the vegetation statistics of these sites have indicated high species richness and diversity (Korpela and Reinikainen 1996a, b, Korpela 1999). In general, very little timber harvesting has been carried out on undrained forested mires in Finland (Päivänen 1999). Thus, the stand structure and ground vegetation of the undrained sites have remained relatively pristine and are assumed to be important for local and regional habitat diversity.

In Finland, the structure of peatland forests, both drained and undrained, has been studied extensively. According to tree stand size distributions the structure of undrained peatland forests is uneven-aged with a great range in tree diameter (Heikurainen 1971, Gustavsen and Päivänen 1986). In uneven-aged stands, most of the trees are concentrated to small diameter classes and the shape of the diameter distribution is usually shaped as a reversed J. Regardless of partial cuttings, which are usually applied in the connection of drainage (Paavilainen and Päivänen 1995) the shape of the diameter distribution remains negatively skewed up to 30–50 years after drainage (Keltikangas *et al.* 1986, Hökkä and Laine 1988). This has been explained by the post-drainage ingrowth of new seedlings and by the greater release growth of smaller compared to larger trees as a response to the drawdown of the water level and subsequent improvement of growth conditions (Hånell 1984, Hökkä and Laine 1988).

However, when examining the stand structure using other characteristics than the tree stand distribution, such as the proportions of tree species, the effect of drainage and cuttings can be clearly seen in the structure and dynamics of peatland forests (Uuttera *et al.* 1996, 1997). In the analysis of structural diversity of pristine forested mire margin communities different structural groups were obtained according to mean percentage covers of different tree species in different canopy layers (Korpela and Reinikainen 1996b). In classification of old growth forests the differentiation of canopy layers has also been used (Lindholm and Tuominen 1989, Leppäniemi *et al.* 1998).

The aims of this study were 1) to describe and analyze the structural diversity of forested mire margin communities by taking all structural layers of vegetation into account, 2) to detect the structural changes of forested mire margin communities caused by water level draw-dawn (drainage) and, 3) to test the hypothesis that forested mire margin sites become more uniform both in the understorey vegetation and in the forest structure after drainage.

2. Material and Methdos

2.1. Material

The vegetation and tree stand data of this study were derived from permanent sample plots of the 8th National Forest Inventory (NFI 8th) performed in 1985–86. This material consists of data from 3009 systematically placed permanent sample plots (each 300 m^2 in area) covering the entire forested area of Finland (see Tomppo *et al.* 1997). The data collection in the field is described in more detail by Korpela and Reinikainen (1996a,b). In this study, the sample plots that fulfilled the following criteria, where included: 1) location south of the 66° N latitude (2618 sample plots), 2) each plot consisting of only one site type, 3) each plot classified as forested mire margin sites (paludified mineral soil forest, thin-peated paludified mire margin forest or forested pine and spruce mire sites) as described in introduction (245 sample plots), 4) four vegetation sample quadrates on each plot, 5) tree stand untreated for at least ten years before inventory and, 6) tree stand age or forest succession matching the range from young thinning stands to mature stands (forest development classes four to six, see e.g. Tomppo *et al.* 1997). In all, 156 plots satisfied all these criteria. Of these 82 were undrained and 74 had been drained (Table 1).

2.2 Study area

Biogeographically, the sampled area extends from the northernmost border of the hemiboreal zone to the southern parts of the northern subzone of the boreal zone (Ahti *et al.* 1968). The study area comprises three forest vegetation subzones: the coastal area of Finland, southern Finland, and the western, central and eastern parts of Finland (Kalela 1961). The border between the zones of raised bogs and aapa-fens runs through the area (Ruuhijärvi 1982). The mean annual temperature (for the period 1961–1980) within the study area ranges from +1 to +5°C; the effective temperature sum (threshold +5°C) from 850 to 1 350 degree days, d.d. (Heino and Hellsten 1983); the mean annual precipitation from 500 to 600 mm; the duration of the growing season from 135 to 180 days; Conrad's continentality index from 24 to 34; and Thornthwaite's index of humidity from 20 to 50 (Tuhkanen 1980).

2.3. Data collection

The field data were collected by 12 NFI crews during the late May - September 1985–1986. On each plot (circular 300 m^2) tree stand and

Table 1. Distribution of sample plots of A) paludified mineral soil forests and B) forested mire margin spruce and pine mires with their site types (Finnish abbreviations) in fertility level (I-II, III, IV) and drainage phase (1 = paludified mineral soil forests, 2 = undrained forested mires, 3 = drained forested mires in phase 3 after drainage, 4 = drained forested mires in phase 4 after drainage) groups.

Site types	Fertility levels	Drainage phases 1	2	3	4
			(n)		
A) Paludified mineral soil forests		**(n)**			
Herb rich forests Oxalis-Myrtillus type (sOMT)	**II**	**4**			
Mesic forests Myrtillus type (sVMT,MT,sDeMT)	**III**	**26**			
Sub-xeric forests Vaccinium type (sEVT,sVT)	**IV**	**13**			
B) Forested mire margin spruce and pine mires					
Meso-eutrophic					
Eutrophic paludified hardwood-spruce forest (LhK)	**I**		2	-	1
Mesotrophic paludified spruce forest (RhKgK)	**II**		-	-	3
Herb rich hardwood-spruce swamp (RhK)	**II**		3	4	9
n			**5**	**4**	**13**
Oligo-mesotrophic					
Oligo-mesotrophic paludified spruce forest (KgK)	**III**		9	4	5
Oligo-mesotrophic spruce swamp(VK:MK, MkK)	**III**		13	13	7
n			**22**	**17**	**12**
Oligotrophic					
Paludified pine forests(KgR)	**IV**		5	5	1
Oligotrophic paludified spruce forest(KgK)	**IV**		1	-	-
Spruce-pine swamp(KR)	**IV**		5	10	4
Oligotrophic spruce swamp(VK:MrK)	**IV**		1	7	1
n			**12**	**22**	**6**
Sample plots total **156**		**43**	**39**	**43**	**31**

ground vegetation data were collected. The field and bottom layer vegetation (including tree and shrub plants lower than 50 cm) was recorded by estimating the percentage cover of each species on four systematically placed sample quadrates (2 m^2) on each plot.

The trees of the stand were divided into five canopy layers according to criteria based on the relative height of the trees and their position in relation to other trees in the forest stand (e.g. Kuusela and Salminen 1969, Tomppo *et al.* 1997). The canopy layers are as follows: dominant trees (canopy layer 2 in this study) of the dominating tree layer (trees which are always taken into account considering forest management treatments), intermediate trees (canopy layer 3), suppressed trees (canopy layer 4), undergrowth trees (canopy layer 5, clearly shorter), overstorey trees (canopy layer 1, the trees clearly taller, < 2 m, or clearly older, < 40 years, trees than the dominant trees) (e.g. Kuusela and Salminen 1969, Tomppo *et al.* 1997). On the plot (300 m^2) the percentage covers of each tree species, as the sum of crown projections (> 1.5 m high) in each canopy layer and the percentage cover of each shrub and tree species in the shrub-layer (0.5–1.5 m high, layer 6) were estimated. The mean cover of tree and shrub species in the field layer (< 50 cm, assessed from the four 2 m^2 sample quadrates) formed the lowest layer (layer 7).

The tree stand measurements on the sample plot were carried out according to regular routines of the NFI (Kuusela and Salminen 1969, Tomppo *et al.* 1997). The diameter at breast height (DBH) of all tally trees was measured by species. In addition, DBH and height of sample trees were measured on a small subplot with half the radius of the sample plot of tally trees. The approximate stand age was obtained by coring one representative sample tree of the dominant crown storey. The dominant tree species was defined as the one with the largest stand volume in the dominant layer (Tomppo *et al.* 1997).

In the site type classification the traditional Finnish forest type approach of Cajander (Cajander 1926, Frey 1973) was used. Paludified mineral soil forest site types were classified according to Kalliola (1973). Mire site types were classified according to the principles presented by e.g. Eurola *et al.* (1984) using the nomenclature of Heikurainen and Pakarinen (1982). Each site type was assigned a fertility (or nutrient) level according to the six-scale system of Huikari (1974) used in NFI, that estimates the forest production potential of the site. In this study, all the chosen sites belonged to the four following levels: I, herb-rich forests and eutrophic swamps; II, herb-rich mineral soil forests and mesotrophic herb-rich hardwood-spruce swamps; III, mesic mineral soil forests and oligo-mesotrophic spruce swamps and; IV, sub-xeric mineral soil forests and oligotrophic spruce swamps and spruce-pine swamps (Huikari 1974, see also Paavilainen and Päivänen 1995). Because only a few plots of the most nutrient-rich site types were recorded, the fertility levels I and II were combined to one fertility level in the data analyses.

The drainage phase assigned to each site describes the state of change and development of the site regarding forest drainage and the proportions of mire and forest plants. Mineral soil forests are considered to be paludified and in the first phase of paludification succession when the proportion of mire plants is about 50 % of the total vegetation cover and no continuous peat layer (> 30 cm) is found (Lehto 1978). In this study they are included in the first group (43 plots, Table 1). The different drainage phases of the sites were distinguished in the field according to the criteria by Sarasto (1961), Heikurainen and Pakarinen (1982), Paavilainen and Päivänen (1995). The criteria and drainage phases were: (group 2) pristine mire vegetation in undrained sites (39 plots, Table 1), (group 3) the recently drained sites with unchanged vegetation and forest growth and the transforming phase sites with 25–75 % proportion of mire species of the original community (altogether 43 plots, Table 1) and (group 4) the transformed phase sites, with less than 25 % of mire species left (31 plots, Table 1).

The thickness of the humus (on paludified mineral soil forests) and the peat layer (on mire sites) was recorded as the mean of four measurements, one from each of the $2m^2$ vegetation quadrates.

2.4. Data analysis

The mean percentage covers of each understorey species in the field and bottom layer was calculated from the four surveyed quadrates on each plot. The mean percentage cover of species was summed according to their growth form on each sample plot. Field layer species were divided into four growth-form groups (dwarf shrubs, herbs, graminoids and cyperoids including also *Juncaceae*-species). Bottom layer species were first divided into bryophytes and lichens, and then bryophytes were further divided into Sphagna, Bryidae, and Hepatics. Bryidae-species were divided to carpet mosses (*Dicranum* spp., *Pleurozium schreberi, Polytrichum* spp. *Hylocomium splendens, Rhytidiadelphus triquetrus, Ptilium crista-castrensis*) and other Bryidae. Mean cover (%) of field and bottom layer vegetation in different growth-form groups in different phases of drainage and fertility levels were analysed using two-way analysis of variance (ANOVA). Logarithmic transformation was used for the percentage values. The analysis was used to determine if drainage phase, site fertility, or their interaction had any impact on the structure of the field and bottom layer vegetation.

In the overstorey canopy layer analyses, the basic variables were mean percentage cover for each tree species in each of five vertical canopy layers and the tree and shrub species in the shrub layer and field layer. Two-way ANOVA was used to examine whether drainage, site fertility, or their interaction had any impact on the overstorey structure. Also the diameter distribution analysis was used for trees more than 45 mm DBH. Stem number/ha was divided into 8 diameter classes (1. 45–90 mm, 2. 90–130 mm, 3. 130–170 mm, 4. 170–210 mm, 5. 210–250 mm, 6. 250–290 mm, 7. 290–330 mm and 8. 330 mm>) for all tallied tree species by fertility level and drainage phase groups.

According to the differences between drainage phases in mean temperature sums (d.d.) the most of the sites of paludified mineral soil forests are situated in the northern part of the study area and most of the drained sites more south (Table 2). Mean thickness of peat/humus layer being lowest in the paludifed mineral soil forests as espected but in mire sites it was higher in drained than in undrained sites (Table 2). Tree stand variables (Table 2); stand age (years), forest development class (from 4 = young thinning stands to 6 =mature stands); basal area (m^2/ha), basal area-weighted mean diameter at breast height (cm), basal area-weighted mean height (m) and stem number/ha were used to describe the differences between drainage phase and fertility level groups. Diversity variables as understorey species number and diversity indices, tree and shrub species number and diversity indices: Simpson's heterogeneity index D, Shannon's diversity index H', and Pielou's evenness index J (Peet 1974, Magurran 1988) were used to estimate differences in species diversity between the fertility level and drainage phase groups. Variables like number of canopy layers of tree stand and total mean cover (%) of tree and shrub species in the different canopy layers were used to measure differences in structural diversity between the fertility level and drainage phase groups.

3. Results

3.1. Variation in species diversity

In the understorey vegetation species richness and Shannon's diversity index (H') differed significantly according to fertility level (Table 3) and also according to drainage phase (Table 3). Species richness was greatest in meso-eutrophic sites in all drainage phases. The drained sites differed more in diversity according to Shannon's diversity index (H') than the undrained sites (Table 3). Also the Pielou's evenness (J) and Simpson's heterogeneity (D) indices differed according to drainage phase (Table 3).

In the overstorey tree and shrub species richness differed significantly according to fertility level (Table 3). Species richness was

Table 2. Mean values and standard deviations (S.D.) of a) the environmental variables of the sites and of b) the tree stand age and structure variables of the sites in fertility level (I-II, meso-eutrophic, III oligo-mesotrophic and IV oligotrophic) and drainage phase (1 paludified mineral soil forests, 2 undrained forested mires, phases 3 and 4 after drainage) groups.

Fertility levels (fl)	Drainage phases (dp) 1	2	3	4
a) Temperature sum (dd)				
I-II	1067.5 (22.2)	1138.0 (186.9)	1230.0 (35.6)	1131.5 (102.0)
IIII	1058.1 (158.0)	1101.4 (81.8)	1153.5 (94.9)	1091.7 (61.0)
IV	1032.3 (68.0)	1064.2 (75.1)	1052.3 (55.1)	1183.3 (106.0)
a) Depth of humus/peat layer (cm)				
I-II	10.0 (7.5)	22.2 (15.0)	18.5 (15.6)	41.3 (33.6)
III	8.6 (6.0)	29.7 (26.8)	55.0 (34.6)	56.3 (31.1)
IV	7.7 (4.7)	31.1 (24.2)	54.0 (31.9)	69.2 (29.7)
b) Stand age (years)				
I-II	82.5 (31.0)	90.2 (37.19)	76.3 (40.5)	62.3 (34.6)
III	107.9 (58.5)	102.3 (36.3)	90.3 (27.6)	76.7 (28.6)
IV	97.3 (43.0)	99.6 (52.3)	83.3 (25.4)	96.7 (27.2)
b) Forest development class (4-6)				
I-II	5.3 (0.5)	5.6 (0.6)	5.0 (1.2)	4.8 (0.7)
III	5.3 (0.8)	5.4 (0.79)	5.0 (0.6)	4.8 (0.7)
IV	5.0 (0.8)	5.1 (1.0)	4.5 (0.6)	5.5 (0.6)
b) Basal area (m^2/ha)				
I-II	22.0 (3.8)	19.3 (5.3)	14.7 (12.5)	15.4 (10.6)
III	18.7 (9.8)	16.2 (7.2)	14.8 (6.9)	17.6 (7.8)
IV	11.3 (4.0)	10.9 (5.5)	9.5 (5.1)	18.5 (7.3)
b) Basal area weighted mean diameter (mm)				
I-II	220.0 (59.5)	226.0 (53.4)	169.8 (85.9)	162.6 (58.7)
III	200.0 (60.0)	180.8 (52.9)	159.4 (51.6)	154.6 (40.0)
IV	159.4 (32.0)	157.2 (41.7)	128.3 (40.6)	201.3 (51.1)
b) Basal area weighted mean height (m)				
I-II	16.14 (4.39)	15.32 (2.12)	15.15 (6.21)	13.40 (5.65)
III	13.82 (4.10)	13.30 (3.46)	12.65 (3.83)	12.52 (2.50)
IV	11.17 (2.09)	10.61 (3.43)	9.64 (2.62)	15.90 (3.92)
b) Stem number/ha				
I-II	1750.0 (1762.5)	1080.0 (450.7)	2750.0 (1904.1)	1946.2 (1005.6)
III	1582.1 (901.2)	1575.8 (706.2)	2060.8 (1077.2)	2433.3 (842.3)
IV	1189.7 (390.5)	1511.1 (716.8)	2210.6 (1027.4)	1300.0 (440.7)

greatest in meso-eutrophic sites in all drainage phases. Pielou's evenness index (J) was greatest in oligotrophic sites in all phases of drainage (Table 3). The Shannon's (H') diversity and Simpson's heterogeneity indices showed no clear differences among the groups (Table 3).

3.2. Structure of understorey vegetation

The differences in the percentage cover of the different growth form groups in the field layer as dwarf shrubs and herbs (Fig. 1) were strongly related to site fertility ($p<0.0001$) but the effect of the drainage phase was also significant ($p=0.0124$, $p=0.0006$). The cover of dwarf shrubs was greatest in the oligotrophic sites of all drainage phases (Fig. 1). As expected, it was especially high in paludified sub-xeric forests but the cover was also great high in the post-drainage succession phases of oligotrophic mire sites (Fig. 1). The cover of herbs was greatest on the meso-eutrophic sites and increased towards the last drainage phases, while on oligo-mesotrophic sites it decreased after drainage ($p=0.0006$). The fertility level also had an effect on the percentage cover of graminoids ($p=0.0007$) (Fig. 1), which

Table 3. Mean values and standard deviations (S.D.) of **understorey** and **overstorey** species number and diversity indices of the studied sites according to fertility levels (I-II, meso-eutrophic, III oligo-mesotrophic and IV oligotrophic) and drainage phases (1 paludified mineral soil forests, 2 undrained forested mires, and phases 3 and 4 after drainage). The significances of differences (F, p<0.001 denoted as 0.000), determined by two-way ANOVA, between the fertility level and drainage phase groups, are presented.

Fertility	Drainage phases				Fertility level		Drainage phase		Interaction	
levels	1	2	3	4	F	p	F	p	F	p
Understorey										
Species number					24.0	0.002	6.42	0.000	1.61	0.147
I-II	18.8 (5.1)	29.8 (8.5)	29.0 (7.1)	23.2 (6.8)						
III	16.3 (4.5)	17.4 (4.9)	18.7 (5.5)	15.9 (4.4)						
IV	16.5 (3.4)	16.6 (3.0)	19.2 (4.8)	15.0 (1.1)						
Shannon index (H')					7.37	0.001	5.46	0.001	0.90	0.494
I-II	1.9 (0.6)	2.2 (0.5)	2.5 (0.3)	2.4 (0.3)						
III	1.7 (0.4)	1.8 (0.4)	2.0 (0.3)	2.0 (0.3)						
IV	2.0 (0.3)	1.8 (0.4)	2.1 (0.3)	2.0 (0.2)						
Simpson index (D)					1.20	0.303	4.92	0.003	0.55	0.768
I-II	0.8 (0.2)	0.8 (0.1)	0.9 (0.1)	0.9 (0.1)						
III	0.7 (0.1)	0.7 (0.1)	0.8 (0.1)	0.8 (0.1)						
IV	0.8 (0.1))	0.7 (0.1)	0.8 (0.1)	0.8 (0.1)						
Pielou's index (J)					0.84	0.433	6.72	0.000	0.71	0.644
I-II	0.6 (0.2)	0.6 (0.1)	0.7 (0.1)	0.8 (0.1)						
III	0.6 (0.1)	0.6 (0.1)	0.7 (0.1)	0.7 (0.1)						
IV	0.7 (0.1)	0.6 (0.1)	0.7 (0.1)	0.7 (0.1)						
Overstorey										
Species number					6.80	0.002	0.25	0.863	0.09	0.373
I-II	5.0 (1.4)	6.0 (1.4)	6.5 (2.7)	6.8 (3.0)						
III	5.2 (1.9)	5.2 (1.8)	4.8 (1.8)	5.0 (1.7)						
IV	4.8 (1.3)	3.9 (0.9)	4.8 (1.5)	3.9 (0.7)						
Shannon index (H')					0.12	0.888	0.90	0.443	0.57	0.751
I-II	0.9 (0.3)	1.0 (0.5)	0.7 (0.5)	1.1 (0.4)						
III	0.9 (0.5)	0.9 (0.3)	0.8 (0.3)	0.9 (0.4)						
IV	0.9 (0.3)	0.9 (0.3)	0.9 (0.3)	0.9 (0.2)						
Simpson index (D)					0.89	0.415	1.69	0.172	0.64	0.701
I-II	0.5 (0.1)	0.5 (0.2)	0.3 (0.2)	0.5 (0.2)						
III	0.5 (0.2)	0.5 (0.2))	0.4 (0.2)	0.5 (0.2)						
IV	0.5 (0.2)	0.5 (0.2)	0.5 (0.2)	0.5 (0.1)						
Pielou's index (J)					3.44	0.035	1.34	0.262	0.67	0.705
I-II	0.6 (0.2)	0.6 (0.2)	0.4 (0.2)	0.6 (0.2)						
III	0.5 (0.3)	0.5 (0.2)	0.5 0.2)	0.6 (0.2)						
IV	0.6 (0.2)	0.7 (0.2)	0.6 (0.2)	0.7 (0.1)						

increased towards the last drainage phases on meso-eutrophic sites. The cover of cyperoids decreased after drainage on meso-eutrophic sites (Fig.1, p=0.1461).

Post-drainage succession affected the mean cover of ground layer species (Fig. 1, dp p<0.0001, fl p=0.0205). On all fertility levels, the percentage cover of all the ground layer species was clearly smaller in the last drainage phase. The cover of bryophytes, and especially the cover of *Sphagnum* mosses, decreased after drainage on all fertility levels (dp p<0.0001, fl p=0.8145). The difference in the cover of Bryidae was as significant between fertility levels (p=0.0021) as between drainage phases (p=0.0006). The increase in the covers of Bryidae on oligo-mesotrophic and oligotrophic sites of the last drainage phase reached the same level as on paludified mineral soil forests, where the vegetation had not been subject to changes by water level drawdown (Fig. 1). The drainage phase had more significant effect on the covers of forest carpet mosses (dp p=0.0000) than the fertility level (fl p=0.0164). On meso-eutrophic

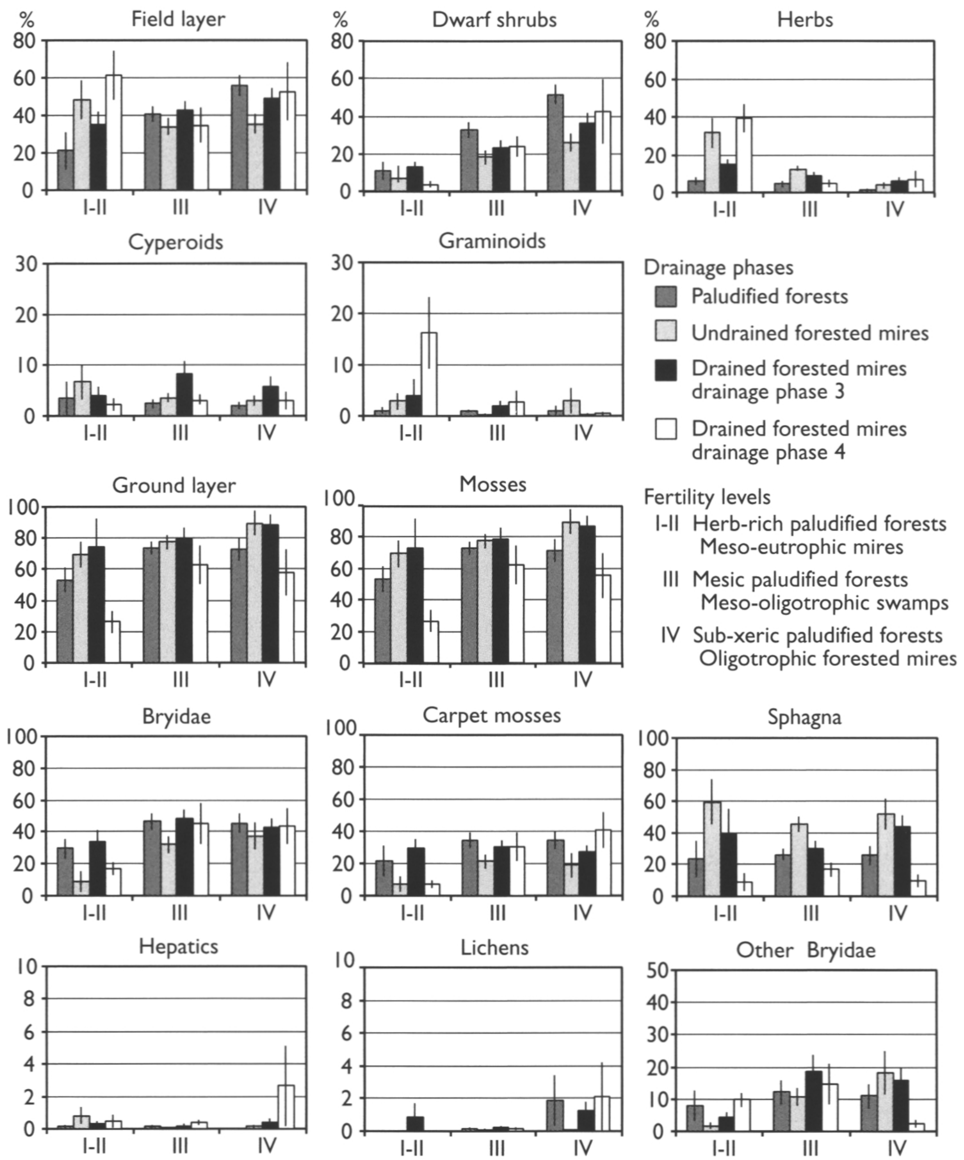

Fig. 1. Means and standard error of means (S.E.M.) of the percentage covers of the growth form groups of field and ground layer vegetation according to four drainage phases and three fertility levels in forested mire margin communities.

sites of third drainage phase the cover of carpet mosses as all Bryidae increased after drainage but decreased again in the fourth drainage phase (Fig 1). The increase of the cover of forest carpet mosses towards the last drainage phase was most obvious on oligotrophic mire sites (Fig 1). The fertility level had a greater effect on the changes of the cover of lichens than the drainage phase (fl $p=0.0206$, dp $p=0.1599$). As expected, the cover of lichens was high on the sub-xeric paludified mineral soil forest sites and increased on oligotrophic mire sites after drainage (Fig.1). The increase of the mean cover of hepatics in the last drainage phase of oligotrophic mire sites was affected by drainage (Fig. 1, $p=0.0773$,).

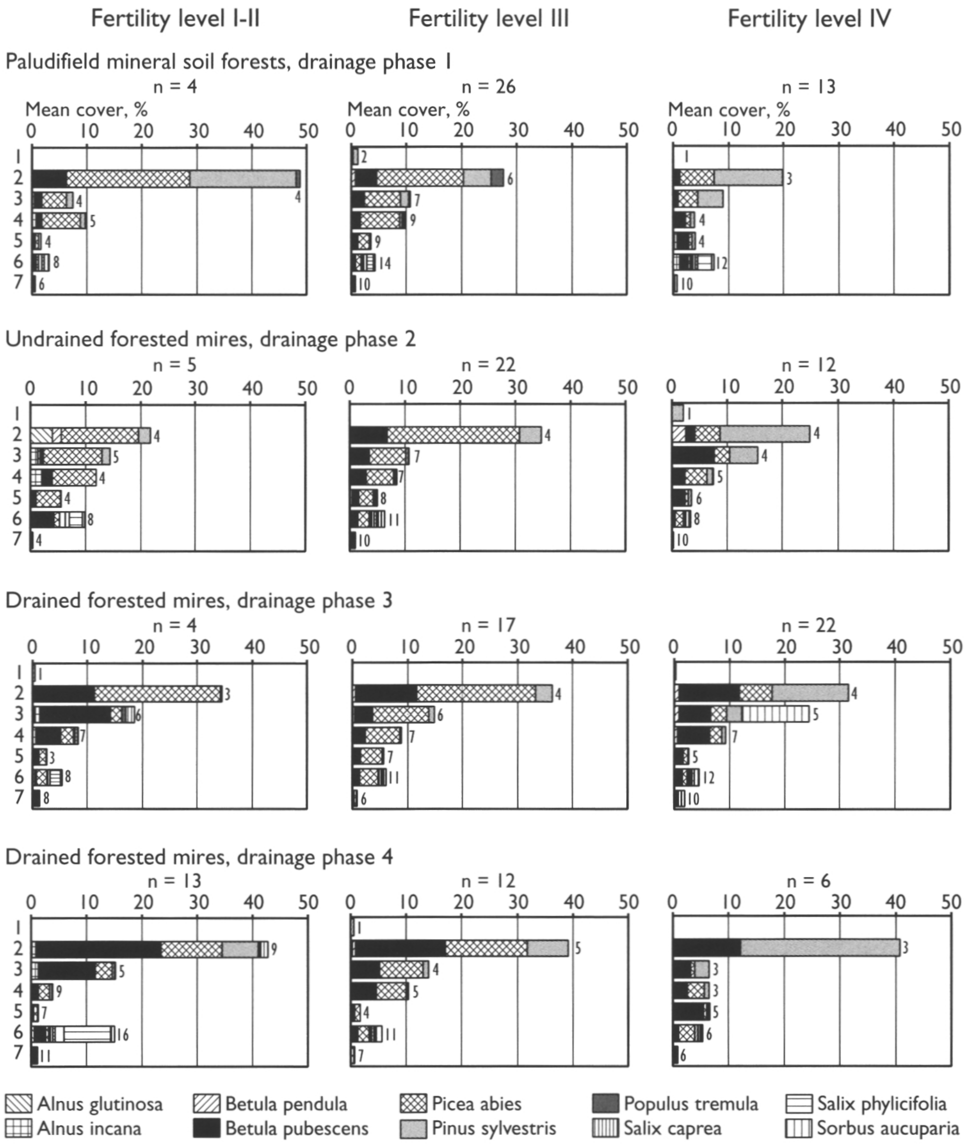

Fig.2. The overstorey structure of undrained and drained forested mire margin sites. Mean percentage covers of species in 5 canopy layers (layers 1-5), in shrub (layer 6) and in field layer (layer 7) in three fertility level (I-II, meso-eutrophic, III oligo-mesotrophic and IV oligotrophic) and four drainage phase groups. The most abundant species are expressed by different shadings in each layer. The total number of tree and shrub species in each layer is expressed by numbers beside the mean cover bars.

3.3. Species composition in the overstorey

The proportions of different tree and shrub species in the different layers changed after drainage. The most apparent change was the increase of the cover of pubescent birch (*Betula pubescens*) in all tree layers on all fertility levels after drainage (Fig. 2). The increase of pubescent birch was clearest in the dominant (layer 2) and the intermediate (3) tree layers of the meso-eutrophic sites. There also was a clear increase of the cover of Scots pine (*Pinus sylvestris*) in the dominant tree layer on the oligotrophic sites of the fourth drainage phase (Fig. 2). The change in species assortment was greatest on the drained meso-eutrophic sites, where also the number of species doubled even in the dominant tree layer as well as in the shrub layer because of an increase of deciduous tree species. On oligo-mesotrophic sites the proportion of spruce decreased and the proportion of pubescent birch increased, otherwise the change in species composition was small. On oligotrophic sites the number of species decreased clearly in the fourth drainage phase (Fig. 2).

3.4. Structure of the overstorey

The structural variables that clearly were affected by drainage were the mean cover of dominant trees (layer 2, $p = 0.0257$) and intermediate trees (layer 3, $p = 0.0280$, Fig 2). The mean percentage cover of the dominant trees was greatest in the fourth drainage phase on all fertility levels (Fig. 2). When the paludified mineral soil forest sites were excluded the difference was clearer ($p = 0.0165$, Fig. 2).

The mean values of all tree size variables were larger on undrained meso-eutrophic and oligo-mesotrophic sites than on oligotrophic sites (Table 2). However, on oligotrophic sites they were largest in the fourth drainage phase (Table 2). The site fertility effected significantly on the tree size variables as basal area and basal area weighted mean height (Table 4). On the other hand, tree stand density described as stem number/ha increased after drainage in all fertility levels (Table 2) and was clearly affected by drainage (Table 4). The largest stem number occurred in the third drainage phase of meso-eutrophic sites (Table 2).

There was a correlation between the percentage cover of dominant trees (layer 2) and the basal area of trees ($r = 0.327$, $p = 0.01$). The basal area weighted mean height also correlated best with the percentage cover of the dominant trees ($r = 0.216$, $p = 0.01$).

This was most prominent in oligotrophic sites, where the mean percentage cover of the dominant trees and the basal area weighted mean height of the trees clearly increased after drainage (Table 2, Fig. 2). There was an increase of the percentage cover of dominant conifer trees on the oligotrophic sites with larger diameter after drainage (Table 2, Fig. 2). In meso-eutrophic and oligo-mesotrophic sites those tree size variables were higher in undrained sites (Table 2), as also mean stand age and forest development class were higher in undrained phases of those sites (Table 2). The increased mean percentage cover of the dominant tree layer after drainage in meso-eutrophic and oligo-mesotrophic sites was more due by the increased stem number (Table 2, Fig. 2).

The shape of the diameter distributions of forested mire sites resembled reversed J-shape distribution curves (Fig. 3). This was

Table 4. The effect of drainage on forested mire margin communities described by the significances of differences (F, $p < 0.001$ denoted as 0.000) in site a) environmental and b) tree stand age and structure variables between fertility level (I-II, meso-eutrophic, III oligo-mesotrophic and IV oligotrophic) and drainage phase (1 paludified mineral soil forests, 2 undrained forested mires, phases 3 and 4 after drainage) groups determined by two-way ANOVA.

	Fertility level (fl)		Drainage phase (dp)		Interaction (fl x dp)	
	F	p	F	p	F	p
a) Temperature sum (dd)	2.38	0.0966	4.37	0.0056	2.34	0.0346
a) Depth of humus/peat layer (cm)	3.44	0.0347	16.10	0.0000	0.90	0.4968
b) Stand age (years)	1.47	0.2343	1.43	0.2355	0.34	0.1959
b) Forest development class (4-6)	0.29	0.7521	2.63	0.0525	1.99	0.0710
b) Basal area (m^2/ha)	5.42	0.0054	1.81	0.1478	1.24	0.2877
b) Basal area weighted mean diameter (mm)	2.97	0.0546	3.30	0.0221	2.20	0.0465
b) Basal area weighted mean height (m)	5.25	0.0063	0.83	0.4806	2.33	0.0354
b) Stem number/ha	2.18	0.1169	5.70	0.0010	1.51	0.1800

most obvious on the oligo-mesotrophic spruce dominated sites in all drainage phases (Fig. 3). The most visible difference on the oligo-mesotrophic level (III) compared to undrained spruce mires and the fourth drainage phase was the increased proportion of pubescent birch in small diameter classes (Fig 3). The differences between undrained mires and the fourth drainage phase were greater in the meso-eutrophic and oligotrophic levels (I-II, IV). On meso-eutrophic sites the number of stems was increased greatly and pubescent birch and other deciduous trees had become clearly dominant in the lower diameter classes

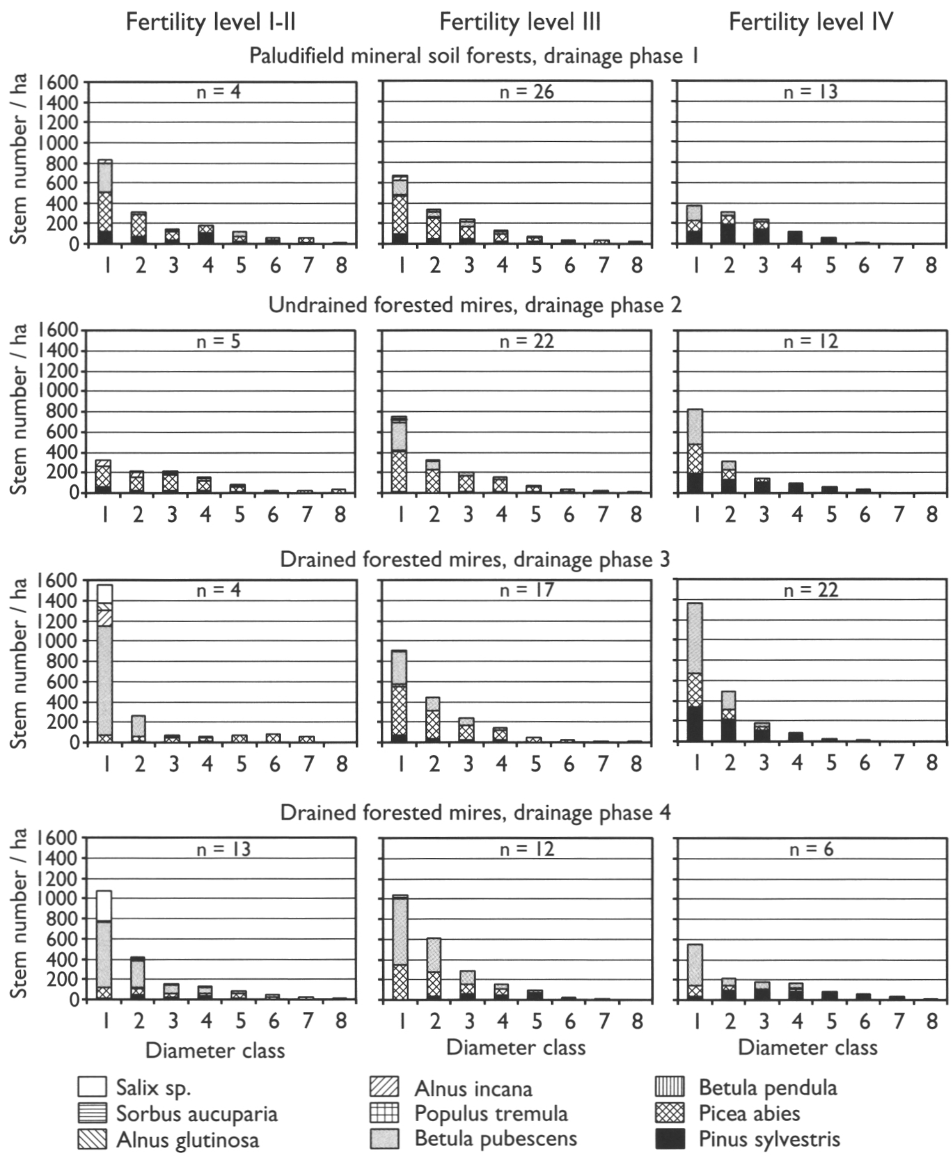

Fig. 3. The diameter distribution of tree species of forested mire margin communities in three fertility level (I–II, meso-eutrophic, III oligo-mesotrophic and IV oligotrophic) and four drainage phase groups. Stem number/ha of trees with more than 45 mm diameter at breast height (DBH) are included. Diameter classes are 1) 45–90 mm, 2) 90–130 mm, 3) 130–170 mm, 4) 170–210 mm, 5) 210–250 mm, 6) 250–290 mm, 7) 90–330 mm and 8) 330 mm>.

and the clear dominance of spruce in all diameter classes was diminished in the fourth drainage phase (Fig. 3). On oligotrophic sites the stem number of conifer trees in the smallest diameter classes had moved somewhat towards larger classes in the fourth drainage phase and the shape of the diameter distribution curve of conifer trees resembled that of the paludified sub-xeric mineral soil forests (Fig. 3).

4. Discussion

4.1. The condition of forested mire margin sites in relation to drainage

The largest part of the area of peatlands drained for forestry in Finland is presently undergoing the third drainage phase of post-drainage succession (Tomppo 1999, Reinikainen et al. 2000, Hökkä *et al.* 2002). According to the sample plots of this study (Table 1), forested mire margin communities are almost equally distributed into the third and the fourth drainage phases. Most of the sites in this study represent oligo-mesotrophy and oligotrophy (fertility levels III and IV) in the third drainage phases. Sites in the fourth drainage phase are mostly represented by meso-eutrophy and oligo-mesotrophy (levels I–II, III), oligotrophic sites were few. The results of this study indicated that the sites with the highest production potential were drained first (Korpela 1999), and, also, that the most nutrient-rich sites have reached the final phase of post-drainage succession in a shorter time than the nutrient-poor sites (see Hotanen and Vasander 1992, Laine *et al.* 1995, Hotanen *et al.* 1999).

The fact that the peat layer of the pristine mire sites is thinner than on the drained sites might be due to the selection criteria of the sample plots of this study or it might indicate that only the sites with the thinnest peat layer have been left undrained. At the time of drainage the drained sites may also have been site types with much thicker peat layer than now. Also, the possible ground water level draw-down caused by drainage of areas surrounding pristine sites may have affected the thickness of the peat layer of these undrained remnants of forested mire margins, which usually cover small areas (Ohlsson *et al.* 1997, Aapala 2001). The fact that drainage has been more intensive in southern Finland is also evident in this study (cf Tomppo 1999, Reinikainen *et al.* 2000, Aapala 2001).

4.2. Changes in field and bottom layer structure

In the field layer vegetation the greatest effects of drainage were on the nutrient-rich, meso-eutrophic sites of forested mire margin communities (Korpela 1999). The increase in the mean cover of the field layer was a consequence of the increase of forest herbs, forest dwarf-shrubs and forest grasses (Korpela 1999, see also Laine *et al.*1995, Reinikainen *et al.* 2000) and even of forest graminoid species, which indicate marsh and spring influence (Korpela 1999, Reinikainen *et al.* 2000).

The most drastic changes occurred in the mean cover of growth form groups in the ground layer. There was a clear trend of decrease of the cover of total ground layer and bryophytes, especially the cover of *Sphagnum* mosses (Korpela 1999, Korpela and Reinikainen 1996c), and a simultaneous increase of the cover of forest carpet mosses or other Bryidae-mosses towards the final post-drainage succession phase (e.g. Laine *et al.* 1995, Korpela and Reinikainen 1996c, Hotanen *et al.* 1999, Reinikainen *et al.* 2000). The decrease of the mean cover of the bottom layer was most drastic in the meso-eutrophic fertility level due to the increased cover of the field layer and also due to increased growth of shrubs and trees.

4.3. Effect of drainage and site fertility on the tree size distribution

Tree size distribution between undrained and drained forested mire margin sites of corresponding fertility levels were similar to other studies made on forest structure in undrained and drained forested peatlands (e.g. Hökkä and Laine 1988, Uuttera *et al.* 1996, 1997, Sarkkola *et al.* 2003a). An uneven-age structure, which is a typical feature of old-growth forests, has been found to be typical in undrained spruce mires (Heikurainen 1971, Gustavsen and Päivänen 1986, Hörnberg *et al.* 1995, Segertsröm *et al.* 1994, Segertsröm and Bradshaw 1996, Norokorpi 1997). In this study the uneven-aged structure was most obvious of forested mire sites in the undrained phase. This was found both in the analyses of the diameter distribution and the canopy layer structure. The results also indicated that no tree harvesting had been conducted on these undrained forested mires sites. Although, when comparing the size distributions of undrained and drained forested peatlands, selective cuttings may have been conducted even on undrained forested peatlands in Finland (Gustavsen and Päivänen 1986).

The increase in stand density, caused by improved growth conditions after drainage (Roy *et al.* 2000), continues for some decades after drainage (Hökkä and Laine 1988, Sarkkola *et al.* 2003a) and maintains an uneven-aged and uneven-sized stand structure characterized by a reversed J-shape diameter distribution (Hökkä and Laine 1988). The reversed J-shape diameter distribution was obvious in all fertility levels also on the drained sites of this study. The most static diameter distribution occurred on the most spruce dominant, oligo-mesotrophic sites. The effect of drainage on this fertility level could better be observed with canopy layer structure analysis and with the changes in tree species proportions than by the shape of diameter distribution (see also Uuttera *et al.* 1996, 1997). Owing to several factors, the uneven-aged and uneven-sized structure may even be emphasized during the first decades after drainage (Hökkä and Laine 1988, Uuttera *et al.* 1996). The former feature was most obvious in the diameter distributions of the most nutrient-rich meso-eutrophic sites in the fourth drainage phase and on nutrient-poorer, oligotrophic, sites in the third drainage phase. In the present study a slight increase in mean diameter and a slight change in diameter distribution in pine dominated sites of oligotrophic fertility level in the fourth drainage phase was observed, which is also due to the tree stand age. However, there is evidence that the diameter distributions may become less skewed as the drainage age increases (Hökkä and Laine 1988, Sarkkola *et al.* 2003a). In this study the few number of plots in undrained phase, especially in the most nutrient-rich sites, made the comparison of diameter distribution in each forest development class in each drainage phase and fertility level group difficult (see Päivänen 1999).

In this study there was no information available of the drainage age of the studied sites. When comparing the shape of diameter distribution curves of different drainage ages of drained, unmanaged, pine dominated peatland sites of a longitudinal data set (see Sarkkola *et al.* 2003b), the drainage age of 50 years matched with the oligotrophic sites. A drainage age from 10 to 30 years with light tree stand treatments (see Sarkkola *et al.* 2003a) seemed to match with the meso-eutrophic sites in the fourth drainage phase of this study. Neither was there any available information of possible improvement cuttings made in connection with the drainage. Although the criterion for including the sample plots in this study e.g. that the tree stand ought to have been untreated at least ten years before the inventory, there might still have been some sample plots included where the tree stand had been treated in connection with drainage. In general, though, the considerable cover of the suppressed and undergrowth trees in the fourth drainage phase are similar to untreated tree stands (see e.g. Päivänen 1999). The diameter distribution of the forested mire margin sites of this study both in the undrained and drained phases resembled that of the spruce and pine mire sites in the cross-sectional data of the whole 8th National Forest Inventory, 1986–1994 (Hökkä *et al.* 2002).

4.4. Effect of drainage and fertility on structural diversity

According to the present study, drainage or site fertility had no effect on the number of canopy layers in forested mire margin communities. This also indicates that the great variation of age and size remains during the first decades after drainage (Hökkä and Laine 1988, Uuttera *et al.* 1996, 1997, Päivänen 1999, Sarkkola *et al.* 2003a, b). The number of tree and shrub species differed by site fertility in all drainage phases, which indicates that diversity in stand structure by type groups, as in this study, depends on the fertility of the sites (e.g. Uuttera *et al.* 1997). It is known that the numerical values of diversity indices (as Shannon's diversity index H') rise as the number of species increases and their occurrences become more even (Kouki 1993). In this study, this former feature was most evident in the diversity of the understorey vegetation, but there were no clear differences between the diversity indices of the tree and shrub species. It should be noted that diversity indices as such are not entirely suitable for application in forestry, because tree size and its variation and many other important stand parameters are not recorded (e.g. Lähde *et al.* 1999). However, they can be useful tools when interpreting results obtained by other analytical methods.

The effect of drainage was apparent in the change of the tree and shrub species composition and in the structural diversity expressed by percentage covers of different canopy layers. After drainage the main change in the tree layer structure was the increased cover of the dominant trees in all fertility classes. The changes are explained by the competitive advantage obtained by the existing individual trees after drainage. Even the suppressed individual trees benefit from the change in the water regime and nutrient availability, and continue to grow to the upper tree canopy (Hånell 1984). Together, the dominant tree layer, the suppressed tree layer, and regenerated saplings (Hånell 1984) use the improved biological productivity (Hökkä 1997, Uuttera *et al.* 1996, 1997).

4.5. Changes in species composition in the overstorey

The tree layer of oligo-mesotrophic spruce mires already in pristine phase resembles that of mesic mineral soil forests, in which spruce is dominant but pine and birch are also present (Heikurainen and Pakarinen 1982). This was seen also in the present study, there were no noticeable differences in composition of trees in different layers between undrained oligo-mesotrophic spruce mires and mesic paludified mineral soil forests. The most nutrient-rich, meso-eutrophic forested mire sites in pristine phase have usually closed and well established tree stand, spruce as codominant with some deciduous trees (birch, alder etc.), sometimes even *Alnus glutinosa* (Heikurainen and Pakarinen 1982). The former describtion matches with the undrained, most nutrient-rich sites of this study and even *Alnus glutinosa* could be found in the dominant tree layer. In the pristine phase of oligotrophic, forested mires, as in this study, pine canopy is well developed and in spruce pine swamps also spruce and birch is present in the dominant tree layer (Heikurainen and Pakarinen 1982, Laine and Vasander 1996).

Minerotrophic mire sites, as all fertility levels in this study, will develop to mixed stands of pubescent birch (*Betula pubescens*), Norway spruce (*Picea abies*) and Scots *pine* (*Pinus sylvestris*) after drainage (Päivänen 1999). The more nutrient-poor sites support mainly Scots pine (Keltikangas *et al.* 1986). In general, in drained peatlands, pubescent birch is a typical pioneer tree species, which can quickly occupy sites that for some reason have free space as result of ditching or cutting (Päivänen 1999). The increase of pubescent birch in this study was greatest in the drained nutrient-rich sites. The increase of deciduous trees, especially pubescent birch, has been found to be greatest in drained spruce swamps, which were hardwood-spruce fens at the time of ditching (Keltikangas *et al.* 1986). In these nutrient-rich composite types, large increases in the quantity of small diameter pubescent birch slows when the stands reach full density (Päivänen 1999).

It's known that the proportions of pubescent birch and deciduous trees increase in undrained spruce mires towards northern Finland from about 18 % in South-Central Finland to about 30 % in Lapland (Heikurainen 1971, Mattila and Penttilä 1987, Norokorpi *et al.* 1997). Regarding the present study area, which comprises the whole country except northern Finland, and also according to mean temperature sums among the groups, the effect of drainage best explained the increase of pubescent birch.

5. Conclusions

Changes in the structural diversity of understorey vegetation caused by drainage were greater in the most nutrient-rich, meso-eutrophic sites of forested mire margin communities. Drainage changed most drastically the composition and cover of the ground layer species. The changes indicated the succession from the diverse mixture of mire and forest vegetation towards more forest-like vegetation in corresponding fertility levels. This was more obvious in changes of proportions of species groups than in species diversity measures. The relationship between the structural and species diversity of the overstorey and the structural and species diversity of the understorey vegetation, as depending on the same main ecological variables (fertility and drainage), was most obvious (see also Pitkänen 1997). How the overstorey effects on the understorey on mire margin sites needs to be solved in further studies.

The effect of drainage was more obvious in the change of tree and shrub species composition and percentage covers than the tree size distributions. In drained sites the percentage cover of the dominant trees was increased in all fertility levels, while variation of the cover of lower tree layers was more related to the interaction of site fertility and drainage phase. The increased percentage cover of pubescent birch, was typical for the drained sites, especially the drained meso-eutrophic sites. Site fertility affected on tree and shrub species number, which was highest in meso-eutrophic sites. The number of deciduous tree species and presence of certain deciduous species (i.e. *Betula* spp., *Alnus* spp. and *Populus* spp.) and also the cover of the shrub layer was still considerable in forested mire margin communities also after drainage (see Norokorpi *et al.* 1997), altought, the cover of species like *Alnus glutinosa* in the upper layers was decresed.

When, in general, high stand diversity means richness of tree species and wide variation in tree size, age, and genotype within each species and when diversity increases with increasing number of tree species (Buongiorno *et al.* 1994, Norokorpi *et al.* 1994), according to this study the effect of drainage was not directly decreasing the stand diversity. However, after drainage the dynamics and development of tree stand might slowly lead to more even-size structure by self-thinning process, but mostly by different kinds of cuttings, which are usually followed after drainage.

Since the nutrient-rich sites in the pristine phase are very rare, they are or should be protected as threatened biotopes (e.g. Heikkilä and Lindholm 2000). Also the pristine, intermediate fertility level spruce swamps should be protected as remaining fragments of old-growth swamp forests, which have become very important to serve as a reference for the managed forests (Hanski & Hammond 1995).

References

Aapala, K. 2001. Korpien ekologiset ominaispiirteet ja suojelutilanne (Ecological features and the state of conservation of spruce mires in Finland). In: Aapala, K. (ed.) Soidensuojelualueverkon arviointi (Evaluation of the mire conservation network in Finland, in Finnish). Suomen ympäristökeskuksen julkaisuja, (Publications of the Finnish Environment Institute) 490: 87-149.

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968. Vegetation zones and their sections in northern Europe. Annales Botanici Fennici 5:169-211.

Buongiorno, J., Dahr, S., Lu, H.-Ch. & Lin, Ch.-R. 1994.Tree size diversity and economic returns in uneven-aged forest stands. Forest Science 40(1): 83-103.

Cajander, A. K. 1926. The theory of forest types. Acta Forestalia Fennica 29(3): 1 - 108.

Camp, O. 1994. Critical elements of forestry sustainability. International Journal of Ecoforestry 10(1): 7-10.

Eurola, S., Hicks, S. & Kaakinen, E. 1984. Key to Finnish mire types. In: Moore, P.D. (ed.), European mires: 11-117.Academic Press, London.

Eurola, S., Aapala, K., Kokko, A. & Nironen, M. 1991. Mire type statistics in the bog and southern aapa mire areas of Finland (60-66°N). Annales Botanici Fennici 28: 15-36.
Franzreb, K. E. 1978. Tree species used by birds in logged and unlogged mixed coniferous forests. Wilson Bulletin 90(2): 221-238.
Frey, T. E. A. 1973. The Finnish school and Forest-Site Types. In: Whittaker, R. H. (ed.), Ordination and classification of communities: 405-433. The Hague.
Gustavsen, H. & G., Päivänen, J. 1986. Luonnontilaisten soiden puustot kasvullisella metsämaalla 1950-luvun alussa. Summary: Tree stands on virgin forested mires in the early 1950´s. Folia Forestalia 673: 1-27.
Hånell, B. 1984. Skogsdikningsboniteten hos Sveriges torvmarker. Sveriges lantbruksuniversitetet. Raporter i skogsekologi och skoglig marklära 50: 1-125.
— 1988. Post-drainage forest productivity of peatlands in Sweden. Canadian Journal of Forest Research 18: 1443-1456.
Hanski, I. & Hammond, P. 1995. Biodiversity on boreal forests. Trend. Ecol. Evolut. 10: 5-6.
Heikkilä, R. 1994a. Soidensuojelu Suomessa. Abstract: Mire conservation in Finland. Terra 106(3): 226-231.
— 1994b. Threatened types of peatland. In: Forestry Environment Guide. Finnish Forest and Park Service, Helsinki. Appendix 3.
— & Lindholm, T. 2000. Conservation of the biodiversity of mires in Finland. In: Rochefort, L. & Daigle, J-Y (eds.). Sustaining Our Peatlands, Proceedings of Quebec 2000, the 11th International Peat Congress August 6-12. 2000, Quebec-city, Canada, Volume II, pp. 1038-1043. CSPP, IPS.
Heikurainen, L. 1971. Virgin peatland forests in Finland. Acta Agr. Fenn. 123: 11 - 26.
— & Pakarinen, P. 1982. Mire vegetation and site types. In: Laine, J. (ed.), Peatlands and their utilization in Finland, pp. 14 - 23. Finnish Peatland Society. Helsinki. ISBN 951-99402-9-4.
Heino, R. & Hellsten, E. 1983. Climatological statistics in Finland 1961-1980. Supplement to the Meteorological Yearbook of Finland 80 (1a): 1-560. ISBN 951-697-195-4.
Hökkä, H. 1997. Models for predicting growth and yield in drained peatland stands in Finland. The Finnish Forest Research Institute, Research papers 651: 1-45.
— & Laine, J. 1988. Suopuustojen rakenteen kehitys ojituksen jälkeen Summary: Post-drainage development of structural characteristics in peatland forest stands. Silva Fennica 22(1): 45-65.
—, Kaunisto, S., Korhonen, K.T., Päivänen, J., Reinikainen, A. & Tomppo, E. 2002. Suomen suometsät 1951-1994. Metsätieteen aikakauskirja 2B: 201-357 (In Finnish). Metsäntutkimuslaitos, Suomen Metsätieteellinen Seura.
Holmen, H. 1964. Forest ecological studies on drained peatland in the province of Uppland, Sweden. Parts I-III. Studia Forestalia Suecica 16: 1-236.
Hörnberg, G., Ohlsson, M. & Zackrisson, O. 1995. Stand dynamics, regeneration patterns and long-term continuity in boreal old-growth Picea abies swamp forests. Journal of Vegetation Science 6: 291-298.
Hotanen, J-P. & Vasander, H. 1992. Eteläsuomalaisten metsäojitettujen turvemaiden kasvillisuuden numeerinen ryhmittely. Summary: Post-drainage development of vegetation in southern Finnish peatlands studied by numerical analysis. Suo 43(1): 1-10.
—, Nousiainen, H. & Paalamo, P. 1999. Vegetation succession and diversity on Teuravuoma experimental drainage area in northern Finland. Suo 50(2): 1-55.
Huikari, O. 1974. Site quality estimation on forest land. In: Heikurainen, L. (ed.), Proceedings of the International Symposium on Forest Drainage, 2nd-6th September, 1974. Jyväskylä-Oulu, Finland, pp. 15-24.
Ilvessalo, Y. 1957. Suomen suot. Valtakunnan metsien inventointiin perustuva kuvaus. Summary: The mires of Finland. A survey based on the 3rd National Forest Inventory. Suo 8: 51-61.
Kalliola, R. 1973. Suomen yleisimpien metsätyyppien floristinen rakenne. (The floristic composition of the most common forest site types in Finland) pp. 260-267. Suomen kasvimaantiede (Plant geography of Finland, in Finnish). WSOY, Helsinki. ISBN 951-0-05731-2.
Kalela, A. 1961. Waldvegetationszonen Finnlands und ihre klimatischen paralleltypen. Archivum Societatis Zoologicae Botanicae Fennicae 'Vanamo' 16 (Suppl.): 65-83.
Keltikangas, M., Laine, J., Puttonen, P. & Seppälä, K. 1986. Vuosina 1930-1978 metsäojitetut suot: Ojitusalueiden inventoinnin tuloksia. Summary: Peatlands drained for forestry during 1930-1978: Results from field surveys of drained areas. Acta Forestalia Fennica 193:1-94.
Korpela, L. 1999. Diversity of vegetation in pristine and drained forested mire margin communities in Finland. International Peat Journal 9: 94-117. ISBN 0782-7784.
— & Reinikainen, A. 1996a. A numerical analysis of mire margin forest vegetation in South and Central Finland. Annales Botanici Fennici 33: 183-197.
— & Reinikainen A. 1996b. Patterns of diversity in boreal mire margin vegetation. Suo 47(1): 17-28.

— & Reinikainen, A. 1996c. Sphagnum communities before and during post-drainage succession of boreal forested mire margin sites. Proceedings of the Second International Symposium on the Biology of Sphagnum (IAB), Université Laval, Québec city, Canada, July 12th-13th 1996, p.38. Faculté des sciences de l'agriculture et de l'alimentation Université Laval, Québec Canada.

Kouki, J. 1993. Biodiversity in boreal forests: a review on ecological research needs and conservation possibilities (In Finnish with English summary). Publications of the National Board of Finland, Series A, 11. Vantaa, Finland.

Kutnar, L. & Martinčič, A. 2003. Ecological relationships between vegetation and soil-related variables along the mire margin-mire expanse gradient in the eastern Julian Alps, Slovenia. Annales Bot. Fennici 40: 177-189.

Kuusela, K. & Salminen, S. 1969. The 5th National Forest Inventory in Finland. General design, instructions for field work and data processing. Communicationes Instituti Forestalis Fenniae (CIFF) 69(4): 1-72.

Lähde, E., Laiho, O., Norokorpi, Y. & Saksa, T. 1999. Stand structure as the basis of diversity index. Forest Ecology and Management 115: 213-220.

Laine, J. & Vasander, H. 1996. Ecology and vegetation gradients of peatlands. In: Vasander, H. (ed.), Peatlands in Finland, pp. 10-19. Finnish Peatland Society, Helsinki, Finland. ISBN 952-90-7971-0.

—, Vasander, H. & Laiho, R. 1995. Long-term effects of water level drawdown on the vegetaion of drained pine mires in Southern Finland. Journal of Applied Ecology 32: 785-802.

Lehto, J. 1978. Käytännön metsätyypit (In Finnish). Kirjayhtymä, Helsinki. 98 p. ISBN 951-26-1479-0.

Leppäniemi, P., Hallikainen, V., Mikkola, K., Puoskari, J. & Sepponen, P. 1998. Forest structure classes in Central Finnish Lapland. Scandinavian Journal of Forest Research 13: 442-450.

Lindholm, T. & Tuominen, S. 1989. Vanhojen luonnonmetsien rakennetyypit eräillä eteläboreaalisilla luonnonsuojelualueilla. Summary: The structure classes of southern boreal natural forests in some Finnish nature protection areas. In: Poikajärvi, H., Sepponen, P., Varmola, M. (eds.), Research activities on the nature conservation areas. Folia Forestalia 736(7): 46-52.

MacArthur, R. H. 1965. Pattern in species diversity. Biological Review 40: 510-533.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princenton University Press, 179 p. Great Britain. ISBN 0-691-08485-8, ISBN 0-691-08491-2 (pbk.).

Malmström, C. 1928. Våra torvmarker ur skogsdiknings synpunkt. (English summary: Our peat areas from the point of forest-draining). Meddelanden från statens skogsforskningsinstitut 24: 251-372.

Mattila, E. & Penttilä, T. 1987. Lapin ja Koillis-Suomen metsälautakuntien suometsät vuosina 1952-1984 (Peatland forests of Lappi and Koillis-Suomi forestry board districts, North Finland, 1952-1984). Folia Forestalia 703: 1-49.

Norokorpi, Y., Lähde, E., Laiho, O. & Saksa, T. 1997. Stand Structure, Dynamics, and Diversity of Virgin Forests on Northern Peatlands. In: Trettin, C., Jurgensen, M. F., Grigal, D. F., Gale, M. R., and Jeglum, J. (eds.), Northern Forested Wetlands, Ecology and Management p. 73-87. Lewis Publishers, Florida. 486 p. ISBN 1-56670-177-5.

Ohlsson, M. 1990. Dikning av näringsrika sumpskog - ett hot mot våra mest artrika skogsekosystem. Skogsfakta Flora, Fauna, Miljö: 14. The Swedish University of Agricultural Sciences, Uppsala.

—, Söderström, L., Hörnberg, G., Zackrisson, O. & Hermansson, J. 1997. Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. Biological Conservation 81: 221-231.

Paavilainen, E. & Päivänen, J. 1995. Peatland Forestry. Ecology and Principles. Ecological Studies 111. Springer-Verlag, Berlin-Heidelberg, 248 p. ISBN 3-540-58252-5.

Päivänen, J. 1999. Tree stand structure on pristine peatlands and changes after forest drainage. International Peat Journal 9: 66-72. ISBN 0782-7784.

Peet, R.K. 1974. The measurement of species diversity. Annual Review of Ecology and Systematics 5: 285-307.

Pitkänen, S. 1997. Correlation between stand structure and ground vegetation : an analytical approach. Plant Ecology 131: 109-126.

Prieditis, N. 1999. Status of wetland forests and their structural richness in Latvia. Environmental Conservation 26(4): 332-346.

Reinikainen, A., Hotanen, J-P., Mäkipää, R. & Vanha-Majamaa, I. 2000 (eds.). Kasvit muuttuvassa metsäluonnossa. Summary: Changes in the frequency and abundance of forest and mire plants in Finland since 1950. Tammi, Helsinki. ISBN 951-31-1963-7.

Rice, J., Anderson, R. W. & Ohmart, R.D. 1984. Comparison of the importance of different habitat attributes to avian community organization. Journal of Wildlife Management 49(3): 895-911.

Roy, V., Ruel, J.-C. & Plamondon, A.P. 2000. Establishment, growth and survival of natural regeneration after clearcutting and drainage on forested wetlands. Forest Ecology and Management 129: 253-267.

Ruuhijärvi, R. 1982. Mire complex types in Finland. In: Laine, J. (ed.), Peatlands and their utilization in Finland, 24-28. Finnish Peatland Society, Helsinki. ISBN 951-99402-9-4.

Sarasto, J. 1961. Über die Klassifierung der für Walderziehung entwässerten Moore. Acta Forestalia Fennica 74(5): 1-57.

Sarkkola, S., Alenius, V., Hökkä, H., Laiho, R., Päivänen, J. & Penttilä, T. 2003a. Changes in structural inequality in Norway spruce stands on peatlands sites after water-level drawdown. Canadian Journal of Forest Research 33: 222-231.

Sarkkola, S., Hökkä, H. & Penttilä, T. 2003b. Size-structural development of uneven-aged and non-managed Scots pine dominated peatland stands following drainage. Proceedings of IUFRO International Interdisciplinary Conference of Uneven-aged Forest Management: Alternative Forms, Practices, and Constraints. June 8-17, 2003, Espoo, Finland.

Segerström, U., Hörnberg, G. & Bradshaw, R. 1996. The 9000 year history of vegetation development and disturbance patterns of a swamp-forest in Dalarna, northern Sweden. The Holocene 6 (1): 37-48.

—, Bradshaw, R., Hörnberg, G. & Bohlin, E. 1994. Disturbance history of a swamp forest refuge in northern Sweden. Biological Conservation 68: 189-196.

Siitonen, J. Martikainen, P., Kaila, L., Nikula, A. & Punttila, P. 1995. Kovakuoriaislajiston monimuotoisuus eri tavoin käsitellyillä metsäalueilla Suomessa ja Karjalan tasavallassa. In: Hannelius, S. & Niemelä, P. (eds.). Monimuotoisuus metsien hoidossa. Finnish Forest Research Institute, Research Notes 564: 43-64.

Tomppo, E., 1999. Forest Resources of Finnish Peatlands in 1951-1994. International Peat Journal 9: 38-44. ISBN 0782-7784.

—, Varjo, J., Korhonen, K., Ahola, A., Ihalainen, A., Heikkinen, J., Hirvelä, H., Mikkelä, H., Mikkola, E., Salminen, S. & Tuomainen, T. 1997. Country report for Finland. In: Study on European Forestry Information and Communication Systems. Reports on forestry inventory and survey systems. Vol. 1. European Commission: 145-226. ISBN 92-827-9847-X.

Tuhkanen, S. 1980. Climatic parameters and indices in plant geography. Acta Phytogeographica Suecica 67: 1-105.

Uuttera, J., Maltamo, M. & Hotanen, J-P. 1996. Stand structure of undrained peatland forests in central Finland. Suo 47(4): 125-135.

— 1997. The structure of forest stands in virgin and managed peatlands: a comparison between Finnish and Russian Karelia. Forest Ecology and Management 96: 125-138.

Wilson, M. F. 1974. Avian community organization and habitat structure. Ecology 55: 1017-1029.

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