A REVIEW OF THE PLANT COMMUNITIES ASSOCIATED WITH SCOTS PINE (*Pinus sylvestris* L.) IN EUROPE, AND AN EVALUATION OF PUTATIVE INDICATOR/SPECIALIST SPECIES

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SUMMARY

Plant communities dominated by *Pinus sylvestris* (Scots pine) occur over an extraordinarily wide range of climatic and edaphic conditions. The salient features of communities from different parts of Europe are outlined, drawing mainly on phytosociological literature. The degree to which a number of specialist species (mainly mycotrophic herbs) are associated with Scots pine is assessed. We conclude that no species or species group is associated with Scots pine through all or even most of its geographic and edaphic range. It follows that separate indicators of semi-natural Scots pine-dominated communities must be sought for different regions and different habitat-types.

KEY WORDS: Pinewoods
Phytosociology

INTRODUCTION

Geography and ecology of Scots pine

Pinus sylvestris L. (Scots pine) has occupied an important place in European vegetation during the Quaternary period (the last 1.6 million years), its range expanding and contracting under the influence of climatic change (Bennett, 1995). Its distribution during the Holocene (c. the last 11,000 years) has extended from Asia to western Europe and, although it has often declined locally when faced with competition from later waves of tree expansion, it has survived in most of Europe (Huntley and Birks, 1983).

At present, *Pinus sylvestris* has the widest natural distribution of any pine species, with a range of over 10,800 km^2 between Scotland and northeast Asia (Nikolov and Helmisaari, 1992). Current European distribution (Fig. 1) covers several climatic zones;

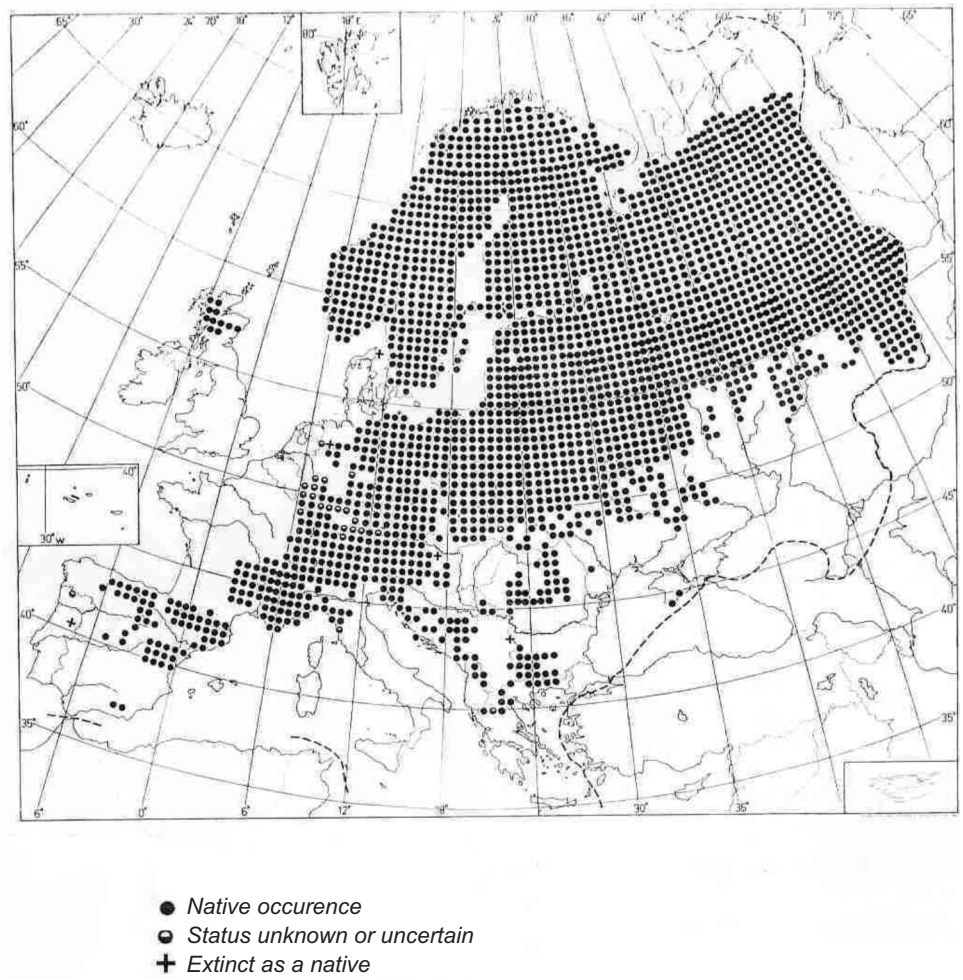

Fig. 1.–Natural distribution of *Pinus sylvestris* in Europe
Source: Jalas and Suominen (1988)
Distribución natural de Pinus sylvestris en Europa

these can be divided into oceanic, suboceanic, subcontinental, continental, alpine and Mediterranean (Ellenberg, 1988). It also grows in a variety of soil conditions. The ecology of Scots pine is largely characterised by stress tolerance. On the one hand this allows it to occupy a range of habitats that are unfavourable to other tree species, through tolerating various combinations of climatic and edaphic stress, including low temperatures, extremes of acidity and alkalinity, extremes of waterlogging and of drought. On the other

hand, Scots pine is excluded from more favourable sites through competition. Thus in central Europe its natural ecological range is restricted to dry acid, wet acid and dry alkaline soils through its inability to compete with species such as *Fagus sylvatica* (beech) and *Abies alba* (silver fir) (Ellenberg, 1988). This inability to compete successfully is seen throughout Europe and is thought to have been one of the main reasons for the contraction of its range in Britain and its extinction in Ireland (Bennett, 1995). The Irish population apparently became extinct by c. 1000 AD; the current Irish populations of *P. sylvestris* are a result of re-introductions beginning from the 17th century (Bradshaw and Browne, 1987). In Belgium, *Pinus* disappeared as a native in the mid-Holocene (Huntley and Prentice, 1993) and only reappeared as a result of afforestation beginning from the 16th century (de Kok, 1985).

The limits of *Pinus sylvestris* distribution correlate well with the –1ºC isotherm for the mean temperature of the coldest month, and the +33ºC isotherm for the mean temperature of the warmest month (Dahl, 1998). Scots pine is thought to be kept at its northern limit by summer temperatures, while *Picea abies* (Norway Spruce) is thought to be controlled more by early and late winter conditions (Engelmark, 1999). Dahl (*op. cit.*) reported that the exposure of *Picea abies* seed to frost, when snow cover was not continuous throughout the winter, might be a factor in *Pinus sylvestris* dominance over *Picea* in some areas, as *Pinus* sheds its seeds later in spring than *Picea.*

The importance of *Pinus sylvestris* in forestry has led to a great expansion in its geographical and ecological range, so that in many regions its natural distribution is difficult to establish (cf. Fig. 1). In southern Germany, for instance, some of the stands sampled as representative of the Leucobryo-Pinetum association (of acid, sandy soils) were probably on sites formerly occupied by pine-oak or birch-oak forest of the alliance Quercion robori-petraeae (Oberdorfer, 1992). This was certainly the case in the upper Rhineland, as it has been shown that pine was first introduced there in the 16th century. For some of these former Quercion sites, soil degradation through a combination of coniferization, removal of forest litter and grazing means that the Leucobryo-Pinetum today constitutes the potential natural vegetation (Oberdorfer, *op. cit.*).

Putative specialist/indicator species of Scots pine communities

Ellenberg (1988) pointed out that one of the difficulties in classifying coniferous communities is the degree to which the rather homogeneous (acid) soil conditions prevailing under the canopy allow general acid soil indicators to flourish. The result is that the presence of many plant species is primarily a reflection of the soil conditions, and bears limited relation to the type of forest canopy involved. On grounds of habitat and flora, Ellenberg (*op. cit.*) summarised the *Pinus sylvestris*-dominated communities in Central Europe in seven groups. The first four were grouped together as “southern” or “species diverse” pinewoods, whilst the other three were classed as “northern”, “species poor” or “acid-humus” pinewoods. Rodwell and Cooper (1995) also produced a summary of the *Pinus sylvestris*-dominated communities in Europe. Mire and dune pinewoods are noted as providing refuges for very weakly competitive species, now with a restricted distribution in Europe, such as members of the Pyrolaceae (Ellemberg, *op. cit.*).

Ellenberg (*op. cit.*) presents lists of species associated with Central European mixed *Pinus sylvestris–Quercus* woods, ranging from the Netherlands to eastern Poland. Those which are described as «acid-tolerating needleleaved woodland plants» are listed in Table 2. Several of these species are members of the boreal element of the European flora and appear to have similar geographical distributions. These species are the basis of a hypothesis that there may be a species group which are specialists or indicators of semi-natural *Pinus sylvestris*-dominated woodland communities in Europe. One of the aims of this paper is to test this hypothesis by assessing the degree of "faithfulness" of each of these species to *Pinus sylvestris*-dominated communities.

METHODS

The present overview focuses on *Pinus sylvestris*-dominated communities that are thought to be in a natural or semi-natural condition. A survey of European phytosociological and ecological literature was undertaken. We summarise briefly the salient features of a range of communities from many parts of Europe. We concentrate on extracting information concerning species that show particular association with semi-natural pinewoods, using as a starting-point Ellenberg's (1988) list of «acid-tolerating needleleaved woodland plants». A further step was to examine whether any putative indicator / specialist species are also found in plant communities in similar habitats but dominated by other trees, *e.g. Picea abies, Betula pubescens* (downy birch) or *Quercus petraea* (sessile oak). The extent of our search is probably adequate for an overview, but by no means exhaustive. Most of our sources described vegetation using the Braun-Blanquet system of phytosociological classification and nomenclature (Westhoff and Van der Maarel, 1978; Table 1). Such data were available from sites spread across much of Europe; however, full tabular data were often not presented, and it was therefore difficult to assess how often Ellenberg's indicator species were present.

For taxonomic nomenclature, we follow Flora Europaea for vascular plants, Blockeel and Long (1998) for bryophytes and Purvis *et al.* (1992) for lichens.

RESULTS

European pinewoods and associated species: a review

Communities of broad geographical range

An overview of the phytosociological classification of European plant communities in which *Pinus sylvestris* is a significant component is presented in Table 1. Some communities are described only from a single region, but a few have broad geographical ranges.

TABLE 1

AN OVERVIEW OF SCOTS PINE COMMUNITIES IN EUROPE

Síntesis de las comunidades de Pino silvestre en Europa

Class and Order	Alliance	Association
Class Vaccinio-Piceetea (Order Vaccinio-Piceetalia)	Dicrano-Pinion *(Acid sandy-soil pinewoods)*	Leucobryo-Pinetum (syn. Dicrano-Pinetum, Myrtillo-Pinetum) Vaccinio vitis-idaeae-Pinetum sylvestris (Vaccinio-Pinetum) Cladonio-Pinetum Hylocomio-Pinetum Barbilophozio-Pinetum Bazzanio-Pinetum Cardaminopsio petraeae-Pinetum Festuco eggleri-Pinetum (syn. Festuco supinae-Pinetum, Festuco-Pinetum serpentinicum) Festuco ovinae-Pinetum Veronico-Pinetum
	Betulion pubescentis *(Birch and coniferous woodland on peat)*	Vaccinio uliginosi-Betuletum pubescentis (syn. Pino-Betuletum humilis, Pino-Betuletum pubescentis) Vaccinio uliginosi-Pinetum sylvestris (bog pinewoods)
	Pineto-Ericion juniperosum sabinae	?
Class Sedo-Scleranthetea (Order Corynephoretalia canescentis)	Corynephorion canescentis	Corynephoro-Pinetum sylvestris *(open pine woodland on dunes)*
	Koelerion glaucae	Koelerio-Pinetum sylvestris
Class Oxycocco-Sphagnetea (Order Sphagnetalia magellanici)	Sphagnion magellanici *(includes mire pinewoods)*	Eriophoro vaginati-Pinetum sylvestris
	Sphagnion fuscae *(includes mire pinewoods)*	Sphagnetum medio-rubelli pinetosum
Class Erico-Pinetea (Order Erico-Pinetalia)	Erico-Pinion *(Spring heather pinewoods)*	Erico-Pinetum sylvestris Dorycnio-Pinetum (sometimes included in Erico-Pinetum sylvestris) Carici humilis-Pinetum sylvestris Stipo-Pinetum sylvestris Convallario-Pinetum Cephalanthero-Pinetum sylvestris Molinio-Pinetum (syn. Salici-Pinetum) Molinio litoralis-Pinetum (syn. Molinietum litoralis, Calamagrostio variae-Pinetum) Cytiso nigricantis-Pinetum sylvestris
	Fraxino orni-Ostryion carpinifoliae *(Illyrian pinewoods)*	Ostryo carpinifoliae-Fraxinetum orni
Class Pulsatillo-Pinetea *(Steppe pinewoods)* (Order Pulsatillo-Pinetalia)	Cytiso ruthenico-Pinion *(Continental steppe pinewoods)* Ononido-Pinion *(Alpine steppe pinewoods)*	Pyrolo-Pinetum (syn. Peucedano-Pinetum) Ononido-Pinetum Salici elaeagni-Pinetum
Class Querco-Fagetea (Order Quercetalia robor-petraeae)	Quercion robori-petraeae	Pino-Quercetum *(Mixed oak-pine woodland)*

Principal sources: Rodwell and Cooper (1995), Ellenberg (1988), Oberdorfer (1992), Mucina *et al.* (1993).

TABLE 2

SPECIES ASSOCIATED WITH NEEDLELEAVED WOODLAND IN A SURVEY OF MIXED OAK-PINE WOODS ON DILUVIAL SANDS IN THE NORTHERN PLAIN OF CENTRAL EUROPE (AFTER ELLENBERG, 1988).

Especies asociadas con bosques aciculiformes en un estudio de bosques mixtos de pino-roble sobre arenas diluviales en la llanura norte de Europa Central (Ellenberg, 1988)

Species (Life form - Raunkiaer, 1934)	Family
I. Vascular plants.	
Calamagrostis arundinacea (Hemicryptophyte)	Gramineae
Forming stands in oak, beech and mixed montane forests. Principally in Luzulo-Fagion, also in Carpinion, more abundant in Epilobion angustifoliae; also at the tree-limit in Sorbo-Calamagrostietum (Calamagrostion). Distribution north-east Eurasian (continental). (Oberdorfer, 1979)	
Chimaphila umbellata (Herbaceous chamaephyte)	Pyrolaceae
Rare in dry pine forests, principally in younger stands. Character species of Pyrolo-Pinetum (Cytiso-Pinion), rarely also in Erico-Pinion. Distribution Eurasian-continental, circumpolar. (Oberdorfer, 1979)	
Goodyera repens (Geophyte)	Orchidaceae
In mossy pine and spruce forests. Principally under pine, supra-regional character species of Vaccinio-Piceetalia, also in Cytiso-Pinion or Erico-Pinion, spreading into coniferous plantations. Distribution North-east continental, circumpolar. (Oberdorfer, 1979)	
Monotropa hypopitys (Holosaprophytic geophyte)	Monotropaceae
Scattered in pine, fir and spruce forests, also in species-poor oak and beech forests; principally in Cytiso-Pinion and Erico-Pinion, also in Vaccinio-Piceion or Vaccinio-Abietion, in Luzulo-Fagion or Galio-Abietion. Distribution (North-eastern-) Eurasian-suboceanic. (Oberdorfer, 1979)	
Orthilia secunda (syn. Pyrola secunda). (Herbaceous chamaephyte)	Pyrolaceae
In spruce, spruce-fir and pine forests. Principally in Pyrolo-Pinetum and Vaccinio-Piceion communities, supra-regional character species of Vaccinio-Piceetalia, also in Erico-Pinion and Cytiso-Pinion, often spreading into planted/secondary coniferous forests. Distribution North-east Eurasian (Continental), circumpolar. (Oberdorfer, 1979)	
Pyrola chlorantha (Hemicryptophyte)	Pyrolaceae
Rare in dry pine forests (also mixed spruce forests). Character species of Pyrolo-Pinetum (Cytiso-Pinion), rare in Erico-Pinion. Distribution north-east Eurasian-continental (Oberdorfer, 1979)	
Rubus saxatilis (Hemicryptophyte)	Rosaceae
In open mixed coniferous forests or Tilia forests; associated with Pinus spp. in Cytiso-Pinion and Erico-Pinion; in Vaccinio-Piceetalia communities, in Tilio-Acerion, Cephalanthero-Fagion, Galio-Abietion and Calamagrostion. Distribution North-east-Eurasian (continental). (Oberdorfer, 1979)	
Trientalis europeaea (Geophyte)	Primulaceae
Mossy spruce forests, birch bogs or species-poor oak-pine forests. Principally in Vaccinio-Piceetea, also in Quercion robori-petraeae, Luzulo-Fagion or (rarely) in open Caricion ferrugineae communities. Distribution Arctic-north-eastern. (Oberdorfer, 1979)	
Vaccinium vitis-idaea (Nanophanerophyte/Woody Chamaephyte)	Ericaceae
Fairly frequent and gregarious in pine and spruce forests; in mountain heaths, bogs and alpine dwarf shrub thickets, rarely also in oak forests. Character species of Vaccinio-Piceetalia, also differential species of Pino-Quercetum (Quercion robori-petraeae), of Geniston (Vaccinio-Callunetum) and of Erico-Pinion. Distribution (Arctic-) North-east Eurasian (Continental), circumpolar (Oberdorfer, 1979)	
Viscum album subsp. *austriacum (syn. V. laxum)* (Hemiparasitic epiphyte)	Loranthaceae
Principally within the distribution of natural eastern European pine forests, rarely also in artificial pine stands; principally in Leucobryo-Pinetum and Pyrolo-Pinetum, in lesser quantity in Erico-Pinion. With *Pinus sylvestris* through the whole region. Distribution temperate continental-submediterranean (Oberdorfer, 1979)	
II. Mosses (Musci)	
Dicranum polysetum (syn. D. undulatum, D. rugosum)	Dicranaceae
On damp soil in coniferous forests, also in birch woods, heaths and raised bogs. Distribution: a mainly boreal species: Europe, Siberia, N and S America (Smith, 1978; Nyholm, 1954).	
Hylocomium splendens	Hypnaceae
Calcifuge; in woods, on heaths, moorland, sand dunes, etc. Distribution: throughout Boreal and North Temperate regions, also N. Africa and New Zealand (Smith, 1978; Nyholm, 1965).	
Ptilium crista-castrensis	Hypnaceae
Mainly in coniferous forests. Distribution: Europe, Asia, N. America (Smith, 1978; Nyholm, 1965).	

Southern Finland has several *Pinus sylvestris*-dominated communities on mineral soils, distinguished as *Cladina* type, *Calluna* type, *Vaccinium* type and Myrtillus type (Kalliola, 1973). Several of the dwarf shrubs appear to mirror the presence of *Pinus,* particularly *Arctostaphylos uva-ursi, Empetrum nigrum* agg. and *Vaccinium vitis-idaea.* None of these fare well in *Picea*-or *Betula* -dominated communities. *Dicranum polysetum* appears to be strongly associated with *Pinus,* and particularly with the Ericaceae-dominated communities. *Pyrola chlorantha* appears in the *Calluna* type and *Vaccinium* type communities and *Goodyera repens* is associated with the Myrtillus type community. Other species in the putative indicator set appear not to be strongly associated with *Pinus.* Several lichen species are strongly associated with *Pinus,* particularly in the *Cladina* type community; these include *Cladonia alpestris, C. arbuscula, C. cornuta, C. rangiferina, C. gracilis* and *C. deformis* *.

Inland sand dunes in North Karelia (SE Finland) are chiefly covered by Scots pine forests. On south-facing slopes the ground layer is usually dominated by lichen-rich communities, with *Cladina* spp. predominating; on north-facing slopes it is usually dominated by moss-rich communities, with *Pleurozium schreberi* predominating. An analysis using an agglomerative minimum variance method distinguished seven noda, of which six are dominated by Scots pine (Oksanen, 1983). *Vaccinium vitis-idaea* and *Dicranum polysetum* are constant species throughout. *Hylocomium splendens* is characteristic of "moss-rich north slope forests" and is rare in lichen-rich forest. Other putative indicator species are recorded in the moss-rich noda only: *Calamagrostis arundinacea, Trientalis europaea, Ptilium crista-castrensis* and single records each of *Pyrola chlorantha, Orthilia secunda* and *Monotropa hypopitys.*

On peatlands in the region *Vaccinium vitis-idaea* is more strongly associated with *Picea abies,* while *Calluna vulgaris, Vaccinium uliginosum, Pinguicula villosa, Drosera rotundifolia,* and several other species are associated with Scots pine. *Trientalis europaea* occurs on spruce bogs. *Dicranum polysetum* occurs in both pine and spruce bogs, while *Hylocomium splendens* is more frequently associated with spruce (Kalliola, 1973).

Sweden

More than half (55%) of the land area of Sweden is under forest. The forest estate is dominated by two species, *Picea abies* (46.1% of the growing stock volume) and *Pinus sylvestris* (39.1%) (Engelmark and Hytteborn, 1999). «Pine and spruce occur in mixed stands, but may also form pure stands. Pine is a weaker competitor than spruce on mesic and intermediate nutrient-rich soil. In successional stands following disturbance pine can, however, dominate at such sites. At nutrient-poor sites, in very dry or very wet places, and on calcareous bedrock with a thin soil layer, pine competes successfully with spruce» (Engelmark and Hytteborn, 1999). In the boreal region, the distribution of pine and spruce is chiefly related to soil texture but shows much regional variation. «In many parts of northern Sweden, pine prevails in the valleys, with their drier climate and coarser soils,

(*) The "reindeer lichens", with a disappearing, granular, primary thallus, have been assigned by some authors to a separate genus *Cladina.* Recent studies find this group to be more appropriately treated as a subgenus within *Cladonia* (Purvis *et al.* 1992).

and spruce on the hillsides and upland, with a moister climate, excessive snow and above all, more fine-grained material in the tills.» (Sjörs, 1965).

A range of Scots-pine dominated communities are outlined by Engelmark and Hytteborn (1999), using an informal nomenclature. The "*Pinus*-lichen community" is characterised by an open tree layer of scattered pines and an abundant lichen mat. The field layer has a very low diversity and consists almost exclusively of dwarf shrubs, the two most common being *Calluna vulgaris* and *Vaccinium vitis-idaea.* Mats of *e.g. Cladonia arbuscula, C. rangiferina, C. stellaris, C. uncialis, Cetraria islandica* and *Stereocaulon paschale* cover the ground. Bryophytes are sparse; the putative indicator *Dicranum polysetum* is among the species that may occur. This community is found on dry and nutrient-poor sites; the soils are distinctly podzolized, usually with a thin mor humus layer. Pine-lichen forests are much more extensive in the boreal region (Sjörs, *op. cit.*).

The "pine forest on rocky ground" is a mosaic of different communities on acid bedrock. «Scattered pines occur which root in crevices of the bedrock with sufficient soil for the pine to survive dry periods. The annual growth rate is very low, and the trees are small in stature, but can reach quite and advanced age. In small depressions without drainage, mire fragments with, for instance, *Calluna vulgaris, Vaccinium uliginosum* and *Sphagnum capillifolium* develop» (Engelmark and Hytteborn, *op. cit.*). The first invading plants on the bare rocks are lichens and bryophytes that are attached to the rock. «Such mats of lichens and bryophytes are sensitive to trampling and erosion and can be blown or washed away and thereafter the succession starts again».

In the *"Pinus-Vaccinium vitis-idaea* community", *V. vitis-idaea* is usually the most prominent species in the field layer, but other dwarf shrubs, such as *V. myrtillus, Calluna* and *Empetrum nigrum* can dominate. The number of herbs is low. *Pyrola chlorantha* is an uncommon, but characteristic species of this community and *Orthilia secunda* also occurs. The ground layer is characterised by a high cover of bryophytes and dominated by *Pleurozium schreberi* and *Hylocomium splendens; Dicranum fuscescens, D. polysetum, D. scoparium, Polytrichum juniperinum* and the lichens *Cladonia arbuscula* and *C. rangiferina* may occur frequently. «Soil water and nutrient availability are higher than in the above-mentioned communities, which favours the growth of bryophytes at the expense of lichens, particularly in northern areas with reindeer grazing... The soil is acid and podsolized and the humus type is a mor, usually slightly thicker than in the pine-lichen community» (Engelmark and Hytteborn, *op. cit.*).

The *"Pinus-Calluna-Vaccinium uliginosum* community" is usually dominated by pine, but spruce and birch also occur. The tree layer is sparse. The field layer is dominated by *Calluna, Vaccinium myrtillus* and *V. uliginosum;* other species include *Betula nana, Andromeda polifolia* and *Carex globularis.* The ground layer includes *Sphagnum capillifolium* and *S. russowii;* more typical forest mosses may occur in drier patches. «The humus layer has built up to a thick peat-like layer. The development of this community is probably a result of drainage problems and poor nutrient conditions» (Engelmark and Hytteborn, *op. cit.*). This community is stated to be of limited distribution in Sweden but to occur commonly in Norway.

The "basicole pine forest community" is characterised, in its most typical form, as herb- and grass-rich forest on calcareous or base-rich bedrock with a thin soil layer. The tree layer is often sparse; *Pinus sylvestris* is the commonest species but *Picea abies, Betula pubescens* and *Sorbus aucuparia* may also occur. This type of vegetation has a

limited distribution in Scandinavia; in Sweden it occurs most frequently on the islands of Gotland and Öland. The commonest variant on Gotland has a field layer dominated by *Arctostaphylos uva-ursi,* with many other species attaining high abundance, *e.g. Anemone pratensis, Calamagrostis varia, Helianthemum nummularium* and *Sesleria caerulea* (Engelmark and Hytteborn, *op. cit.*).

Commercial tree-cutting started in Sweden in the 1600s. Only 3% of the productive forest land has escaped intensive harvesting (Engelmark and Hytteborn, *op. cit.*). Managed forests are usually aged between 80 and 130 years before cutting. Some plants which are rare in Sweden, e.g. the orchids *Calypso bulbosa* and *Listera cordata,* depend on old-growth forest as they require periods of 60-80 years before re-establishment after clearfelling (Sjöberg and Lennartson, 1995). Swedish boreal forest was not commercially logged before 1800; when surveyed prior to logging it was found to be dominated by stands of large trees over 200 years in age. Since then the architecture of pine and spruce stands has changed completely, with habitats for rare species becoming less frequent (Linder and Östlund, 1998). The tendency towards denser, darker forests has reduced the numbers of herb species such as *Chimaphila umbellata* and *Anemone vernalis.* Retention of old-growth features was recommended for the conservation of these species (Linder and Östlund, *op cit.)*

Norway

A basiphilous pine forest from southern Norway was described as the Convallario-Pinetum association (Bjørndalen, 1980). The sites studied were located on shallow calcareous soil, either on limestone or shales. This is a herb-rich association with affinities to the Querco-Fagetea communities of Central Europe; it was placed in the Trifolion medii alliance by Bjørndalen *(op. cit.)* but transferred to the Erico-Pinion alliance by Rodwell and Cooper (1995). The Convallario-Pinetum is found in Norway, Sweden and Finland, with floristic trends related to gradients in moisture and nutrients (Rodwell and Cooper, *op. cit.*). The vegetation includes *Vaccinium vitis idaea, Trientalis europaea, Rubus saxatilis* and *Hylocomium splendens* (Table 3). Four main variants were recognised: a xerophilous variant dominated by *Arctostaphylos uva-ursi* and *Festuca ovina;* a more acidophilous variant dominated by *Calluna vulgaris;* a herb-rich variant dominated by *Convallaria majalis, Brachypodium sylvaticum* and *Calamagrostis epigeios;* and a mesophilous variant dominated by *Molinia caerulea, Briza media* and *Inula salicina.* Pine forests dominated by *Molinia litoralis* (*Molinia caerulea sensu lato*) seem related to the mesophilous variant of Convallario-Pinetum in Grenland and are also placed in the class Erico-Pinetea (Bjørndalen, *op. cit.*).

Some other basiphilous pine forests are species poor and are dominated by *Vaccinium myrtillus* and *V. vitis-idaea* but differ from acidophilous forests by having a number of demanding species. *Picea abies* is often co-dominant and so the community can be placed into the association Melico-Piceetum in the Vaccinio-Piceion alliance.

The other pine forest alliances in Fennoscandia, Dicrano-Pinion and Phyllodoco-Vaccinion, have markedly acidophilous communities. A transitional pine-spruce woodland exists at higher altitudes in Scandinavia, the Barbilophozio-Pinetum. This community includes moisture loving species including several species of *Barbilophozia* (liverworts) (Rodwell and Cooper, 1995). In western Norway there are heathy pinewoods, the Bazzanio-

Pinetum, growing beyond the range of *Picea* where the oceanic climate allows bryophytes to form an important part of the community (Rodwell and Cooper, 1995).

Eastern Europe

Latvia

Latvia is in the hemiboreal zone, and up to 25% of its forested area can be classified as wetland. Included in these are forested wetlands of the Dicrano-Pinion which Prieditis (1997) divides into four variants. Of the putative indicator/specialist species only *Vaccinium vitis-idaea* was recorded in these communities; other species present included *V. myrtillus, V. uliginosum, Pyrola rotundifolia* and *Pleurozium schreberi.* Latvian forest also includes «typical forest bog where *Pinus sylvestris* and Oxycocco-Sphagnetea species predominate».

The other Latvian wetland forest community which contains significant amounts of *Pinus sylvestris* also belongs to the Vaccinio-Piceetea, but is dominated instead by *Picea abies.* Three communities are distinguished. The putative indicator species are infrequent, although one of them, *Hylocomium splendens,* is a diagnostic species for two associations in which *Pinus sylvestris* is infrequent. *Vaccinium vitis-idaea, V. myrtillus* and *Pleurozium schreberi* are all present but do not appear to have a particular association with *Pinus sylvestris. Orthilia secunda* is present but infrequent.

Poland

The coniferous forests of Bialowieza forest in eastern Poland include the forest types Pino-Quercetum, Peucedano-Pinetum and Vaccinio uliginosi-Pinetum with some Cladonio-Pinetum and Sphagno-Piceetum (Falinski, 1986).

In the Pino-Quercetum there is a rich herb layer which Falinski (*op. cit.*) classified into four groups; these included some typical coniferous forest species including *Vaccinium myrtillus, V. vitis-idaea, Orthilia secunda, Pyrola chlorantha, P. minor, Trientalis europaea, Goodyera repens* and *Ptilium crista-castrensis. Calamagrostis arundinacea* was also present.

The Querco-Piceetum spruce forest (alliance Vaccinio-Piceion) has less pine than the Pino-Quercetum; it also includes *Vaccinium myrtillus* and *V. vitis-idaea* in abundance (Falinski, *op. cit.*). *Hylocomium splendens* and *Pleurozium schreberi* occur where the deciduous litter does not accumulate. The Sphagno girgensohnii-Piceetum, in which spruce absolutely dominates the community in both canopy and shrub layer, also has both *Vaccinium* species.

The Pyrolo-Pinetum (syn. Peucedano-Pinetum) pine forest has a greater number of species and includes a component of spruce in this site which sometimes becomes dominant. The commonest components of the shrub layer are *Vaccinium myrtillus, Vaccinium vitis-idaea, Calluna vulgaris* and *Chamaecytisus ratisbonensis ssp. ruthenicus.* Of the putative indicator species, *Orthilia secunda, Pyrola chlorantha, Chimaphila umbellata, Calamagrostis arundinacea* and *Goodyera repens* occur. Mosses include *Hylocomium splendens, Dicranum polysetum, Ptilium crista-castrensis* and *Pleurozium schreberi.*

The Cladonio-Pinetum, almost entirely developed on sand, has occasional *Vaccinium myrtillus,* many lichens and some mosses but none of the putative indicator species.

The bog pine forest Vaccinio uliginosi-Pinetum has a small spruce and birch component but is dominated by pine in the canopy layer. Hummocks are dominated by a shrub layer of *Vaccinium myrtillus, V. vitis-idaea, V. uliginosum* and *Ledum palustre.* Mosses include *Pleurozium schreberi, Hylocomium splendens, Dicranum polysetum* and *Polytrichum strictum. Sphagnum* spp. fill the hollows. The Sphagnetum medio-rubelli pinetosum (Class Oxycocco-Sphagnetea) is composed of low forest and *Sphagnum* spp., with some herbs and Ericaceae.

Bernadzki *et al.* (1998) studied succession in Bialowieza National Park. They found that both *Pinus* and (particularly) *Picea* were declining and suggested this may be linked to a milder climate and atmospheric deposition of nitrogen.

A phytosociological outline of the Ojców National Park is presented by Medwecka-Kornás and Kornás (1963). They distinguish three variants of Pino-Quercetum; all occur over beds of loess, upon which decalcified, acid podzolic soils (pH 3.5-5.5) have developed. The Pino-Quercetum luzuletosum, *Fagus sylvatica* variant is restricted to shallow loess on upper slopes and the Pino-Quercetum luzuletosum, *Abies alba* variant to moister and cooler sites. The Pino-Quercetum, *Pinus sylvestris* variant is widely distributed on drier sites, but the dominance of pine in its stands is sometimes a result of disturbance. Of the putative indicators, *Orthilia secunda* is constant in all three variants and *Calamagrostis arundinacea* is present in all three. *Trientalis europaea* is recorded from the *Pinus* and *Abies* variants, but *Monotropa hypopitys* from the *Fagus* variant only.

Bulgaria

Ingean (1996) described three associations with Scots pine using an *ad hoc* nomenclature. The *Pinus sylvestris-Picea abies-Vaccinium myrtillus-Lerchenfeldia flexuosa* community included *Vaccinium vitis-idaea, Calamagrostis arundinacea, Pyrola chlorantha* and *Orthilia secunda* (Table 3). The *Pinus sylvestris-Picea abies-Vaccinium myrtillus- Calamagrostis arundinacea* community and the *Picea abies-Vaccinium myrtillus- Calamagrostis arundinacea* community both included *Vaccinium vitis-idaea* and *Calamagrostis arundinacea.*

Central Europe

Czech Republic

Neuhäusl and Neuhäuslová-Novotná (1979) summarised the natural forest communities of the Zelezné Hory mountains in eastern Bohemia. In the Abieto-Quercetum there was some *Pinus sylvestris* and *Calamagrostis arundinacea;* however the latter appeared to associate more with *Quercus petraea* than *Pinus* or *Abies.* There was also a very small amount of *P. sylvestris* and *C. arundinacea* in the Luzulo pilosae-Abietetum. *Calamagrostis* also occurred in the *Abies alba-Calamagrostis arundinacea* community with a very high frequency, and at low frequency in the Luzulo-Fagetum, Abietetum hercynicum, Aceri-Carpinetum and Dentario enneaphylli-Fagetum. Although *Pinus sylvestris* occurred

in the Luzulo albidae-Quercetum, *Pinus sylvestris-Quercus petraea* variant, none of the putative indicator species did. However, in the *Pinus sylvestris-Festuca cinerea* variant, *Vaccinium vitis-idaea* and *Calamagrostis arundinacea* both occur. In the Equiseto-Piceetum, both *Pinus sylvestris* and *Vaccinium vitis-idaea* occur (Table 3).

The same authors (1968) studied mesophilous and sub-xerophilous forests in Central Bohemia. The grass *Calamagrostis arundinacea* was recorded in a range of broadleaved forest communities on relatively poor or wet soils (Galio-Carpinetum, Galio rotundifolii-Quercetum, Tilio-Quercetum and Potentillo-Quercetum).

Rybnicek *et al.* (1984) summarised the peatland vegetation communities of the former Czechoslovakia, including the association Eriophoro vaginati-Pinetum sylvestris (Class Oxycocco-Sphagnetea). This association contained *Vaccinium vitis-idaea.* However, *V. vitis-idaea* and *Hylocomium splendens* were also included as diagnostic species of the association Pino rotundatae-Sphagnetum.

Austria

Austria contains a diversity of Scots pine-dominated communities corresponding to different combinations of altitude, rock type, topography and drainage conditions (Mucina *et al.,* 1993).

Communities of acid soils

The Scots pine-dominated communities of free-draining, non-calcareous soils belong to the Dicrano-Pinion. The following associations are described by Mucina *et al.* (1993): Dicrano-Pinetum (syn. Leucobryo-Pinetum; *Dicranum polysetum* is among the diagnostic species); Vaccinio vitis-idaeae-Pinetum (diagnostic species include *Vaccinium vitis-idaea* and *Hylocomium splendens);* Cardaminopsio petraeae-Pinetum; Festuco ovinae-Pinetum; and Festuco eggleri-Pinetum (constant species include *Vaccinium vitis-idaea).* The last two associations are characteristic of serpentine areas, and their flora includes edaphically specialised elements.

Two associations are distinguished on acid peat (Mucina *et al.,* 1993). The Vaccinio uliginosi-Betuletum pubescentis is developed on the margins of raised bogs and on transitional mires. The open canopy is dominated by *Betula pubescens,* with an admixture of Scots pine, especially in more continental areas. *Frangula alnus* dominates in the shrub layer. The field layer is commonly dominated by *Molinia caerulea* or *Vaccinium uliginosum.* Common mosses include *Hylocomium splendens, Pleurozium schreberi, Polytrichum commune, Sphagnum magellanicum* and *S. angustifolium* (syn. *S. recurvum* var. *tenue).* The Vaccinio uliginosi-Pinetum sylvestris differs from the preceding in the greater admixture of species typical of raised bog, *e.g. Eriophorum vaginatum, Sphagnum magellanicum, S. capillifolium, Vaccinium oxycoccus.* The low, open canopy is generally dominated by Scots pine, but this is replaced by Norway spruce at montane and subalpine levels. *Vaccinium vitis-idaea* is among the constant species.

Communities of base-rich soils (Erico-Pinetea)

Erico-Pinion communities (Spring heather-Scots pine forest) are found on more or less lime-rich dry slopes and gravel beds, at foothill to montane levels, where they may

have an important role in protection against erosion. None of the putative indicator species was recorded among the diagnostic species listed by Mucina *et al.* (1993).

The Erico-Pinetum sylvestris is dominated by Scots pine, with lesser amounts of *Picea abies, Larix decidua, Quercus petraea* and *Sorbus aria. Juniperus communis* may be sub-dominant, or there may be an open shrub layer of warmth-demanding species such as *Berberis vulgaris, Amelanchier ovalis* and *Viburnum lantana.* The field layer is rich in species; among the species that become sub-dominant are *Erica herbacea* (syn. *E. carnea), Calamagrostis varia, Carex alba* and *Sesleria albicans.* The community is widely distributed at submontane and montane levels, most frequently on dolomite, also on limestone and serpentine. The sites are mostly dry, on steep, south-facing slopes; soils are of rendzina type (Mucina *et al.,* 1993).

The Dorycnio-Pinetum develops in the valleys of the northern Alps on the gravels or terraces of calcareous alpine rivers, at levels no longer subject to inundation (Mucina *et al.,* 1993). Scots pine forms an open canopy in these riparian pinewoods. On sand deposits the soils have greater water-holding capacity; this facies is characterised by the presence of *Alnus incana* and *Molinia arundinacea.* The association lacks characteristic species, and is included in the Erico-Pinetum by Oberdorfer (1992).

The Carici humilis-Pinetum sylvestris includes the open Scots pine-dominated woods that develop on ridges at subalpine levels in the inner Alps. These woodlands also develop in warm, low-rainfall localities at montane levels. Typical sites are extremely dry, with shallow soils on rocky south-facing slopes. *Carex humilis* dominates the herb layer. This may be either a permanent community or a pioneer phase leading to the Erico-Pinetum sylvestris, with which it is linked by numerous species in common (Mucina *et al.,* 1993).

The Molinio litoralis-Pinetum (syn. Calamagrostio-Pinetum) is a pioneer or permanent community on steep marl slopes, with shallow, lime-rich, humus-poor soils, *e.g.* pseudogleys. The heavy soils, poorly aerated during wet periods, may become hard as stone on drying out. The moderately open canopy is dominated by Scots pine, with some *Picea abies* and *Sorbus aria.* The field layer is dominated by grasses and sedges (especially *Molinia caerulea* subsp. *arundinacea* and *Calamagrostis varia)* (Mucina *et al.,* 1993). In southern Germany this community exists only in small stands (Oberdorfer, 1992).The Cephalanthero-Pinetum lies close to the preceding, but edaphic conditions are less extreme (Mucina *et al., op. cit.*)

The Ostryo carpinifoliae-Fraxinetum orni is represented in Austria by outlying, relict stands. The sites are always well-protected, with a favourable local climate and humidity, *e.g.* in ravines. The subsoil is formed by carbonate rocks such as limestone and dolomite. The canopy is dominated by *Ostrya carpinifolia* and *Fraxinus ornus,* but *Pinus sylvestris* and *P. nigra* are widespread (Mucina *et al.,* 1993).

Communities of low-rainfall sites

The continental Pulsatillo-Pinetea is represented by two associations. The Ononido-Pinetum is a xerothermic woodland of colline to montane altitudes, with its centre of distribution in the dry valleys of the inner Alps. The open canopy is composed almost exclusively of Scots pine; the trees are low-growing and broad-crowned, and frequently bear *Viscum album* subsp. *austriacum. Juniperus communis* is frequent in the shrub layer (Mucina *et al.,* 1993).

The Salici elaeagni-Pinetum is found principally on alluvial gravels. Usually a thin layer of raw humus or moder overlies a slightly alkaline mineral horizon. The species-poor ground flora contains a mixture of calcicole and calcifuge elements, the latter including the putative indicators *Goodyera repens, Orthilia secunda* and *Pyrola chlorantha,* The thick moss carpet is composed of *Pleurozium schreberi, Rhytidiadelphus triquetrus, Hylocomium splendens, etc.* This association occupies a marginal position in the Pulsatillo-Pinetea, being transitional to the Erico-Pinetea (Mucina *et al.* 1993).

Germany

Detailed accounts of the vegetation of both plantations and semi-natural forest dominated by Scots pine are presented for southern Germany by Oberdorfer (1992) and for Brandenburg by Hofmann (1964a,b). An overview of the vegetation of Central European pinewoods is presented by Hofmann (1991).

Communities of acid soils

Pinewoods of podzolised sandy soils are widespread, especially in eastern Germany. Hofmann (1991) distinguishes the associations Vaccinio-Pinetum sylvestris, Calluno-Pinetum sylvestris and Cladonio-Pinetum sylvestris. For southern Germany, Oberdorfer (1992) includes all such communities within a broadly-circumscribed Leucobryo-Pinetum association.

In southern Germany, the Vaccinio uliginosi-Betuletum pubescentis consists of low birch woodland over peat, with an admixture of Scots pine (Oberdorfer, 1992). The author notes that this is a permanent community in the suboceanic part of its range, but that in more continental regions it is a successional stage leading to bog pinewoods. (Vaccinio uliginosi-Pinetum sylvestris). The Eriophoro vaginati-Pinetum sylvestris is a low, open pine woodland on raised bog sites where water tables are high for long periods; characteristic species include *Eriophorum vaginatum, Ledum palustre, Vaccinium oxycoccus* and *Sphagnum* spp. (Hofmann, 1991).

Communities of base-rich sites (Erico-Pinetea)

The Erico-Pinetum sylvestris (described above under Austria) occurs in montane to submontane regions over calcareous rock (Oberdorfer, 1992). Of the putative indicator species, only *Hylocomium splendens* was frequent (Table 3). The Molinio-Pinetum (syn. Salici-Pinetum) occurs principally in the prealpine region, on the alluvial terraces of rivers with lime-rich, oligotrophic waters. It consists of open stands of Scots pine with a grassy field layer dominated by *Molinia caerulea* subsp. *arundinacea, Brachypodium rupestre* or *B. pinnatum,* and *Calamagrostis varia.* Of the putative indicators only *Hylocomium splendens* was frequent

A different community with a similar name, the Molinio caeruleae-Pinetum sylvestris, is recorded by Hofmann (1991) as growing on poor gley podzols. Stands of Scots pine, intermingled with *Betula pubescens,* are accompanied by *Molinia caerulea* and the undershrub *Ledum palustre.*

TABLE 3

DISTRIBUTION OF PUTATIVE INDICATOR SPECIES IN COMMUNITIES DOMINATED BY SCOTS PINE AND RELATED COMMUNITIES

Distribución de especies indicadoras putativas en comunidades dominadas por Pino silvestre y en las comunidades relacionadas

	Calamagrostis arundinacea	*Chimaphila umbellata*	*Goodyera repens*	*Monotropa hypopitys*	*Orthilia secunda*	*Pyrola chlorantha*	*Rubus saxatilis*	*Trientalis europaea*	*Vaccinium vitis-idaea*	*Viscum album austriacum*	*Dicranum polysetum*	*Hylocomium splendens.*	*Ptilium crista-castr.*	*Indicator count*
I. Communities dominated by Scots pine														
Ia. Acid sandy-soil pinewoods (Dicrano-Pinion)														
1. Leucobryo-Pinetum sensu lato	I	I	I	I	I	I		I	IV	I	V	III	I	12
2. Leucobryo-Pinetum			I					I	I		I	I		5
3. Leucobryo-Pinetum cladonietosum												+	+	2
4. Cladonio-Pinetum			I								III	I	I	4
5. *P. sylvestris-Hylocomium splendens* woodland			II					I	IV			V	III	5
Ib. Bog pinewoods														
6. Vaccinio uliginosi-Pinetum sylvestris			I					I	IV		II	II	I	6
7. Vaccinio uliginosi-Pinetum sylvestris									+		+	+		3
8. Eriophoro vaginati-Pinetum									+			+		2
Ic. Spring heather pinewoods (Erico-Pinion)														
9. Convallario-Pinetum							+	+	+			+		4
10. Erico-Pinetum					I	I	I		I		I	II		6
11. Molinio-Pinetum			I				I				I	II	I	5
12. Molinio litoralis-Pinetum				I	I		II					III		4
13. Coronillo-Pinetum				I	II		III							3
14. Cytiso-Pinetum				I	I		II				I	I		5
15. Stipo-Pinetum (as Carici-Pinetum)											II			1
Id. Steppe pinewoods														
16. Pyrolo-Pinetum		IV	II	II	III	III			I	II	III	III		9
Overall frequency in Scots pine forest (%)	6,3	12,5	43,8	31,3	37,5	18,8	37,5	31,3	56,3	12,5	62,5	87,5	37,5	
II. Related communities dominated by other conifers														
17. *P. sylvestris-Picea abies-Vaccinium myrtillus-Lerchenfeldia* community	+				+	+			+					4
18. Pino rotundatae-Sphagnetum									+			+		2
19. Vaccinio uliginosae-Pinetum rotundatae									V		III	III		3
20. Sphagnum girgensohnii-Piceetum									+			+		3
21. Querco-Piceetum					+				+			+		2
22. Equiseto-Piceetum									+				+	2
23. Melico-Piceetum					+		+		+		+	+		4
24. Calamagrostio villosae-Piceetum								II	I		(+)	I	I	5
25. Vaccinio-Abietetum	I			I	(+)				II		I	IV	I	7
26. Luzulo-Abietetum	I								I		(+)	III	I	5

TABLE 3 *(cont.)*

DISTRIBUTION OF PUTATIVE INDICATOR SPECIES IN COMMUNITIES DOMINATED BY SCOTS PINE AND RELATED COMMUNITIES

Distribución de especies indicadoras putativas en comunidades dominadas por Pino silvestre y en las comunidades relacionadas

	Calamagrostis arundinacea	*Chimaphila umbellata*	*Goodyera repens*	*Monotropa hypopitys*	*Orthilia secunda*	*Pyrola chlorantha*	*Rubus saxatilis*	*Trientalis europaea*	*Vaccinium vitis-idaea*	*Viscum album austriacum*	*Dicranum polysetum*	*Hylocomium splendens.*	*Ptilium crista-castr.*	*Indicator count*
27. Dicrano-Juniperetum									I		III	I		3
28. *Juniperus communis ssp. communis-Oxalis acetosella woodland*							I		III				I	3
Overall frequency in related communities dominated by other conifers (%)	25,0	0,0	0,0	8,3	33,3	8,3	16,7	8,3	100,0	0,0	41,7	75,0	41,7	
III. Related communities of broadleaved forest														
29. *Quercus petraea-Betula pubescens-Dicranum majus* woodland			I					I				IV	I	4
30. Betulo-Quercetum roboris									I		I			2
31. Erico-Betuletum pubescentis									I		I			2
32. *Betula pubescens-Sorbus aucuparia* community	III										I	V	III	4
33. Genisto tinctoriae-Quercetum	I			I							II	I		4
34. Vaccinio uliginosi-Betuletum								I	III		II	II		4
35. Luzulo-Fagetum	(+)				(+)									2
Overall frequency in related broadleaved forest communities (%)	45,0	0,0	15,0	15,0	15,0	0,0	0,0	30,0	45,0	0,0	70,0	60,0	29,0	

Frequency of a species is the percentage of a given set of sample plots in which the species is present. «V» = present in 80-100% of sample plots, «IV» = 60-79%, «III» = 40-59%, «II» = 20-39%, «I» = <20%; «(+)» = single occurrence; «+» = frequency unspecified. Sources: 1,6,10-14,16,19,24-26;32-34: S. Germany (Oberdorfer, 1992); 15: E. Germany (Hofmann, 1964b); 2,4,27,30,31: The Netherlands (Stortelder *et al.,* 1999); 3: France (Rodwell and Cooper, 1995); 5,28,29: Scotland (Rodwell, 1991); 7: Poland (Rodwell and Cooper, 1995); 20,21: Poland (Falinski, 1986); 8, 35: Czech Rep. (Moravec *et al.,* 1982); 18: Czech Rep. (Rybnicek *et al.,* 1984), 22: Czech Rep. (Neuhäusl and Neuhäuslová-Novotná, 1979); 9,23: Norway: (Bjørndalen, 1980); 17: Bulgaria (Ingean, 1996).

The Coronillo-Pinetum forms small stands on shallow rendzina soils on steep, rocky, exposed slopes (Oberdorfer, 1992). The low, open canopy is dominated by Scots pine, intermingled with *Sorbus aria.* The herb layer is dominated by graminoids, especially *Sesleria albicans* and *Carex humilis,* and is rich in light- and warmth-demanding species. Among the putative indicators, only *Rubus saxatilis* was very frequent and *Orthilia secunda* moderately frequent (Table 3). The Cytisonigricantis-Pinetum occurs on dry, well-illuminated, south-facing sites, on shallow soils of rendzina type over calcareous substrata. The sparse canopy is composed of Scots pine, *Sorbus aria* and *Fagus sylvatica.* The shrub layer includes warmth-loving shrubs such as *Cytisus nigricans.* In the field layer, *Carex humilis* and *Sesleria albicans* again predominate.

Communities of low-rainfall sites

The continental Pyrolo-Pinetum sylvestris (syn. Peucedano-Pinetum) occurs in southern Germany as scattered relict stands on dry, warm sites with low rainfall (Oberdorfer, 1992). Putative indicator species are numerous: *Chimaphila umbellata, Pyrola chlorantha, Orthilia secunda, Dicranum polysetum* and *Hylocomium splendens* are frequent in the samples and *Viscum album* ssp. *austriacum. Monotropa hypopitys, Goodyera repens and Vaccinium vitis-idaea* also occur (Table 3). Oberdorfer *(op. cit.)* adds that this is an endangered community in southern Germany; although most stands are protected, an impoverishment in species has been noted in recent years, with a striking decline in *Chimaphila umbellata.*

Another community with continental characteristics is described from central Europe on lime-rich sands in low-rainfall areas, such as the lower valley of the Oder; it was classified as Carici-Pinetum in Hofmann (1964b) but as Stipo-Pinetum sylvestris in Hofmann (1991). It includes continental species such as *Stipa capillata, Potentilla arenaria, Pulsatilla pratensis, etc.* and the xerophilous sedges *Carex humilis* and *C. supina.* The only putative indicator listed by Hofmann (1964b) was *Dicranum polysetum.*

The Koelerio-Pinetum sylvestris occurs on mesotrophic sandy soils that still retain some lime in the subsoil, and dry out strongly in summer. This continental community reaches its westernmost outposts in the lower reaches of the Oder. The community contains numerous warmth-loving species; *Dianthus arenarius* and *Koeleria glauca* are character species (Hofmann, 1991).

The Corynephoro-Pinetum sylvestris is a low, open pine woodland occurring on very dry, very nutrient-poor sands, e.g. on inland dunes. Diagnostically important species in the ground flora include the grass *Corynephorus canescens,* the sedge *Carex arenaria* and the moss *Polytrichum piliferum* (Hofmann, 1964b, 1991).

Western Europe

The Netherlands

Stortelder *et al.* (1999) present detailed accounts of Scots pine-dominated vegetation in the Netherlands. The Cladonio-Pinetum sylvestris association is characteristic of dry, nutrient-poor, acid, sandy soils; in this habitat it forms the first stage in woodland devel-

opment. The authors distinguish a cladinetosum subassociation, rich in *Cladonia* spp., and a dicranetosum polyseti subassociation, richer in bryophytes and herbs.

The Leucobryo-Pinetum has less extreme soil characteristics and is distinguished by a podzol or micropodzol profile, mostly with a thick layer of raw humus on account of the very slow decomposition rate of the litter (Stortelder *et al., op. cit.*). The authors distinguish four sub-associations. The first three may be interpreted as a successional series: deschampsietosum, dominated by the grass *Deschampsia flexuosa,* then vaccinietosum, distinguished by the abundance of *Vaccinium myrtillus* and *V. vitis-idaea,* then empetretosum, dominated by *Empetrum nigrum.* The fourth subassociation, molinietosum, is distinguished by the abundance of *Molinia caerulea;* it is found in relatively moist sites.

France

Muller (1992) studied forest vegetation on sandstone in the Bitcherland, NE France and identified three communities in which Scots pine was prominent: Luzulo-Quercetum, with *Pinus sylvestris* frequent, and *Hylocomium splendens* and *Ptilium crista-castrensis* occurring at low frequencies; Leucobryo-Pinetum cladonietosum, on very dry soil, with the ground vegetation dominated by *Cladonia* spp. and a mixture of grasses and mosses (including *H. splendens* at low frequency); and Vaccinio uliginosi-Pinetum, on very wet peaty soil. The Leucobryo–Pinetum of the Bitcherland is similar to pinewoods further east, i.e. in the eastern Vosges Mountains, the major difference being the absence of *Vaccinium vitis-idaea.*

Closely related associations contained some of the other possible specialist/indicator species, including *Calamagrostis arundinacea* in Calamagrostido–Quercetum oak–pine forest towards the mid-part of the valley of the river Main (Muller, *op. cit.*). The author also indicated the place of *Pinus sylvestris* in the different climatic zones from Atlantic to continental, with its importance increasing from west to east.

Great Britain

Semi-natural *Pinus sylvestris* woodland occurs in Scotland. This is community W18 (*Pinus sylvestris-Hylocomium splendens* woodland) of British Plant Communities and corresponds with the Hylocomio-Pinetum (Alliance Dicrano-Pinion) (Rodwell, 1991). The vegetation has three constant components: the grass *Deschampsia flexuosa,* ericoids (including *Vaccinium myrtillus, Vaccinium vitis-idaea* and *Calluna vulgaris*) and bryophytes. The mosses *Hylocomium splendens, Dicranum scoparium, Pleurozium schreberi, Plagiothecium undulatum* and *Rhytidiadelphus loreus* are all very common; *Ptilium crista-castrensis* is very frequent under all but the densest canopies and is particularly distinctive of this community. A set of herbs are described as generally infrequent in pinewoods but especially characteristic of the *Pinus-Hylocomium* woodland: of these, *Listera cordata* and *Goodyera repens* are widespread whilst *Pyrola minor, P. media, P. rotundifolia, Moneses uniflora* and *Orthilia secunda* are occasional or rare. Five sub-communities are distinguished.

Spain

An overview of the vegetation of the Iberian peninsula was produced by Rivas-Goday (1956). An alliance in the class Vaccinio–Picetea was described as Pineto–Ericion juniperosum sabinae; it included the association Sabino-Pinetum sylvestris (Rivas-Martínez *et al.,* 1987). This association included *Pinus sylvestris*-dominated vegetation on limestone. *Pyrola chlorantha* is a character species of the alliance.

Veronico-Pinetum dominates in the Central and Western Pyrenees with *Juniperus communis, Veronica officinalis* subsp. *hemisphaerica, Deschampsia flexuosa* and *Agrostis capillaris* (Rodwell and Cooper, 1995). Rivas-Martínez *et al.* (1987) described dwarf juniper scrub vegetation (Vaccinio myrtilli–Juniperetum nanae association) in the northern Iberian mountains, which included a pinetosum sylvestris subassociation. This contained none of the putative indicator/specialist species of central European needleleaved forest (Table 2).

In Mediterranean Spain some Vaccinio-Juniperetum contains *Pinus sylvestris* with *Juniperus communis, Cytisus purgans, Vaccinium myrtillus, Calluna vulgaris, Erica arborea* and *Deschampsia flexuosa* (Rodwell and Cooper, 1995).

Martínez García (1998) undertook a comprehensive survey of *Pinus sylvestris* woods in central Spain. Again, none of Ellenberg's (1988) proposed indicator species was recorded. The most frequently occurring species were: *Pinus sylvestris,* 100% of all plots, *Arenaria montana* 73%, *Rumex acetosella* 67%, *Festuca rubra* agg. 56%, *Deschampsia flexuosa* 55%, *Teesdalia nudicaulis* 52%, and *Luzula lactea* 50%. The samples were divided into two groups by "TWINSPAN" (Two-way indicator species analysis; Hill, 1979): one group of pinewoods on siliceous soils, the other of calcicole pinewood. The former had *Arnoseris minima, Micropyrum tenellum, Cytisus oromediterraneus, Cerastium ramosissimum, Cruciata glabra* and *Viola riviniana* as indicator species, while the latter had *Koeleria vallesiana* subsp. *vallesiana* as an indicator species. The siliceous pinewoods were further subdivided along a gradient from xerophile to mesophile.

Microcommunities on special substrata

Epiphytic communities

Little information was traced on the epiphytes of *Pinus sylvestris.* The distribution of epiphytic lichen and bryophyte species was studied on a range of host tree species in boreal Finland by Kuusinen (1996). Most of the epiphytes showed some preference for one or two host species. The epiphyte flora of *Pinus sylvestris* was most similar to that of *Picea abies.* Both species were similar in having a bark pH less than pH 4. Most of the trees were over 100 years old. The number of bryophyte and lichen species on the trees varied between the southern and middle boreal areas, and for *Picea* and *Pinus* the total number was lower in the southern area. *Pinus* had two and five "faithful" species in the southern and middle boreal areas respectively, while *Picea* was found to have five and nine. *Pinus* had a very low total species richness and diversity and only a few specific species, probably because of the unfavourable physical characteristics of its flaking bark as well as the unfavourable chemistry. Kuusinen *(op. cit.)* concluded that the few unique features of the epiphyte flora on *Pinus* will be maintained in managed forests.

Communities of dead timber

Among the most fundamental changes to the forest ecosystem resulting from commercial silviculture is the removal of dead wood. Old-growth forest with an ample supply of coarse woody debris in the form of logs, stumps and dead standing trees are important for the diversity of birds, invertebrates and cryptogams. In Sweden, it has been estimated that up to 47% of forest species depend on dead wood for their survival (Berg *et al.,* 1994). More than 450 species of fungi and about 1000 insect species are confined to old-growth stands (Engelmark and Hytteborn, 1999),

Dead wood is a vital habitat for many bryophyte and lichen species. For the boreal and boreo-nemoral zones of Sweden, Engelmark and Hytteborn (*op. cit.*) list 53 lichens, 9 liverworts and 6 mosses that are almost totally dependent on decomposing wood; an additional *ca.* 50 lichens, 18 liverworts and 7 mosses occur mostly on decomposing wood but also on other substrates. In Sweden many bryophytes were found to grow only on large sized logs found late in the successional history of stands (Söderström, 1987), and it was concluded that bryophytes are more dependent than vascular plants on old growth forests (Söderström and Jonsson, 1992).

The ecology of Scots pine communities: other factors

The effects of grazing

Grazing response of vegetation is an important factor in determining floristic composition. In boreal communities, increased grazing of lichens by reindeer has reduced the cover of late-successional lichen species such as *Cladonia stellaris* in favour of more rapidly-colonizing lichens and of bryophytes (cf. Väre *et al.,* 1985; Engelmark and Hytteborn, 1999). Cattle and sheep grazing is, or was, an important factor affecting the basicole pine forest community on Gotland and Öland (Engelmark and Hytteborn, *op. cit.*). Spring heather-Scots pine (Erico-Pinion) communities are used as forest grazing for sheep and cattle in some parts of Austria (Mucina *et al.,* 1993). In some regions, e.g. Sierra de Guadarrama (Spain), silviculture with Scots pine is intimately combined with the raising of domestic livestock; in others (e.g. Ireland), silvicultural policy has aimed to exclude large herbivores from conifer plantations as far as possible.

Fire ecology

Pinus is subject to a moderate-severity fire regime which may or may not influence forest dynamics, depending on the frequency at which fire occurs (Agee, 1998). In Europe *Pinus sylvestris* is often found on regularly burnt sites with a dry continental climate, as in northern Sweden, while *Picea abies* dominates on sites where fires occur rarely or not at all, e.g. at high altitude or in maritime areas in Sweden or western Norway (Engelmark, 1999). *Picea abies* does not burn often and, when it does, crown fires usually kill it. *Pinus sylvestris'* habit of strong self-pruning reduces its vulnerability to crown fire; *P. sylvestris* forests burn at a lower level, with the field layer and ground lichens constituting an important part of the fuel (including *Empetrum, Vaccinium* and *Cladonia* spp.).

In northern Sweden, «the great forest fires of the past have had a considerable influence on tree distribution, favouring pine as the more fire-resistant and the more rapidly colonizing species. Old pines with fire-scars are often seen, being survivors from one or several fires, and now surrounded by younger forest.» (Sjörs, 1965).

Over sixty species of vascular plants, fungi, lichens and invertebrates in Fennoscandia are considered fire dependent. Several components of the understorey are adapted to burning, e.g., *Vaccinium vitis-idaea* and *V. myrtillus* can both regenerate by sprouting from rhizomes (Agee, 1998; Engelmark, 1999). Esseen *et al.* (1992) considered *Anemone patens, Anemone vernalis, Chimaphila umbellata, Geranium bohemicum* and *Geranium languinosum* as fire dependent; other species favoured by fire include *Chamerion angustifolium* and a number of mosses.

DISCUSSION

Clearly the ecological and climatic range occupied by Scots pine is remarkably wide, and hence the plant communities associated with the tree are highly diverse. Species richness increases along a gradient from north to south; also along a gradient from base-poor to base-rich soils. The natural range of Scots pine is clearly concentrated (a) in boreal and continental regions (Fig. 1) and (b) on acid, podzolic soils over siliceous substrata. Within this core range, the most constant associated species are the undershrubs *Calluna vulgaris, Vaccinium myrtillus, V. vitis-idaea* and *Empetrum nigrum,* the grass *Deschampsia flexuosa,* the mosses *Pleurozium schreberi, Hylocomium splendens* and *Dicranum scoparium* and the lichens *Cladonia rangiferina* and *C. sylvatica.* Most of these occur with more or less equal frequency under Norway spruce.

Our survey is largely supportive of Ellenberg's (1988) list of «acid-tolerating needleleaved woodland plants» (Tables 2, 3). Most of these species are also frequent in forest dominated by other conifers, especially Norway spruce. The orchid *Goodyera repens* appears to have the strongest association with Scots pine; however, it is generally present only at low frequencies (Tables 2, 3). It spreads readily into coniferous plantations (Oberdorfer, 1979; Rodwell, 1991). *Rubus saxatilis* appears to show an association with Scots pine forest on relatively base-rich soils (Table 3); Oberdorfer (1979) records it as being associated with *Pinus* spp. in the Cytiso-Pinion and Erico-Pinion, but as also occurring in a wide range of forest communities, both coniferous and deciduous (Table 2). The "odd one out" in Ellenberg's list is the grass *Calamagrostis arundinacea;* our survey did not support an association of this species with coniferous forest (Table 3), and other authors record it as being associated mainly with oak (Falinski, 1986; Oberdorfer, 1992) and beech (Oberdorfer, 1992). The moss *Hylocomiun splendens* also has too wide an ecological range to be ranked as a specialist species (Tables 2, 3).

Most of the needleleaved woodland specialists have significant physiological characteristics in common, notably mycotrophy (*i.e.,* the roots have an obligate association with a mycorrhizal fungus, on which they show varying degrees of dependence for their nutrition). *Monotropa* represents the extreme of specialisation, the plant being devoid of chlorophyll and reliant on the mycorrhiza for all nutrition, *i.e.* it is a holosaprophyte (Mabberley, 1987). The Pyrolaceae, a particularly well-represented group *(Pyrola, Orthilia, Chimaphila),* are largely hemisaprophytic. Ericaceae and Orchidaceae are also

mycotrophic. The relationships between these species, the canopy trees, and the fungi with which both are associated merits deeper investigation.

The main difficulty in utilising these species as indicators of site/stand condition, old growth or historical continuity lies in the extraordinary ecological range of *Pinus sylvestris.* There does not appear to be any vascular plant, bryophyte or lichen species that could provide an indication of site quality for Scots pine-dominated communities on a Europe-wide basis. This is because (a) none of the specialist species has as wide an ecological or climatic range as Scots pine and (b) most of the specialist species are also more or less frequently found in association with other tree species. The likelihood that one or more species will provide good indicators of site conditions on a regional basis remains valid. We suggest that, within a given region, a suite of plant species may be recognised as linked with mature, semi-natural coniferous woodland and, *ipso facto,* with sites of high biological value.

The gaps in our knowledge are many. Further research is required to tease out the relations between specialist species and site conditions at a regional level. It is also needed to assess the effects of different successional stages and of different management strategies on these specialist species, and on plant biodiversity in general. In particular, we need more information on the effects on plant biodiversity of:

(a) different grazing regimes - including the absence of grazing;
(b) different fire régimes - including the effects of fire prevention;
(c) the effects of the removal of dead timber;
(d) the effects of different timber harvesting strategies.

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RESUMEN

Revisión de las comunidades vegetales asociadas al pino silvestre (*Pinus sylvestris* L.) en Europa y evaluación de las especies indicadoras/especialistas putativas

Las comunidades vegetales dominadas por *Pinus sylvestris* (pino silvestre) se encuentran en un rango de distribución extraordinariamente amplio de condiciones climáticas y edáficas. En este trabajo se resaltan las características principales de las comunidades de distintas partes de Europa. También se evalúa el grado en que se asocian con el pino silvestre diversas especies especialistas (principalmente hierbas micotróficas). Se concluye que no existen especies o grupos de especies asociadas con el pino silvestre en todo o en la mayoría de su rango geográfico o edáfico. Por tanto, se deben buscar indicadores separados de comunidades seminaturales dominadas por pino silvestre para las diferentes regiones y tipos de habitat.

PALABRAS CLAVE: Pinares
Fitosociología

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