

## Delimitation of syntaxa in northern Europe - a case study

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**ABSTRACT.** - This study is concerned with some basic problems connected to the delimitation of syntaxa in northern Europe, using 20 relevés of mesotrophic deciduous forest from Öland in the Boreo-nemoral zone of Sweden as an example.

Vegetation science in northern Europe has not followed one particular approach, but has proceeded along a number of paths. The Zürich-Montpellier school has only recently been applied in a few studies. Therefore, the syntaxonomy of North European plant communities has remained largely unknown. Besides, it can be difficult to assign northern community types to existing syntaxa of the Braun-Blanquet system which has basically been developed, and adapted to the vegetational differentiation, in central and southern Europe. Further problems concern the loss of diagnostic species among vascular plants, the change in species behaviour with respect to environmental preferences and amplitudes, and, in the case of deciduous forests, the heterogeneity in the floristic composition of stands due to the decrease and split up of the deciduous forest area.

Four suggestions are made to overcome some of the problems mentioned: (1) the delimitation of the Boreo-nemoral zone as a "phytosociological region", and the consistent use of regional associations and character species, (2) the acceptance of a formation-specific character species concept, (3) the use of environmental information for assigning plant community types to syntaxa, and, finally, (4) the recognition of bryophytes and fungi as diagnostic species.

**KEY WORDS** - Boreo-nemoral zone, Braun-Blanquet system, deciduous forest, diagnostic species, formation, northern Europe, regional character species, syntaxonomy

### INTRODUCTION

The taxonomic treatment of plant communities in northern Europe is a difficult task. This paper aims to point out some of the problems connected to the delimitation of northern syntaxa, and to give suggestions to overcome these problems. Deciduous hardwood forests will serve as an example to elucidate both problems and proposed solutions.

In northern Europe, deciduous hardwood forests are restricted to the Nemoral zone in southernmost Sweden and Norway, the westernmost parts of Norway and the Boreo-nemoral zone in SE Norway, S Sweden and SW Finland. In the Boreo-nemoral zone, the forests are mainly composed of *Acer platanoides*, *Fraxinus excelsior*, *Quercus robur* (*Q. petraea* less common), *Tilia*

*cordata* and *Ulmus glabra* (on Öland and Gotland also *U. minor*), forming species-rich communities: in a study of altogether 367 relevés of about 225 m<sup>2</sup> size, the average species number of different community types varied between 22 and 51, similar to or even exceeding corresponding figures of many deciduous forest communities in central Europe (Diekmann 1994). Despite this species richness, community differentiation is comparatively less diverse. Four main forest types are distinguished: oligotrophic oak forests, mesotrophic (mixed) deciduous forests, eutrophic elm-ash forests, and eutrophic alder-ash forests. Except for the oligotrophic oak forests, the stands are geographically concentrated to areas with calcareous bedrock and/or deposits and to climatically favourable (warm) localities in SE Norway, eastern Sweden and close to the big Swedish inland lakes.

Mesotrophic forests represent the most widespread and characteristic forest type within the Boreo-nemoral zone, without floristically similar counterparts in the Nemoral zone. Therefore, relevés of this forest type (from Öland) will be used for describing and discussing the syntaxonomic problems concerning North European vegetation (Table 1). The 20 relevés were first published by Diekmann (1994; Table 10, no. 1-20) and referred to the *Quercus robur-Euonymus europaeus* community, *Tilia cordata* sub-community, *Filipendula ulmaria* form. With an average total species number of 51, they represent the floristically richest deciduous forest community type in the Boreo-nemoral zone of northern Europe (see above). The stands grow on level or slightly sloping ground. The soil type usually is a rather shallow, mesotrophic, loamy or clayey brown earth with a mull humus layer (Diekmann 1994).

#### SYNTAXONOMIC PROBLEMS

##### *General considerations*

The framework of the Zürich-Montpellier phytosociological school (Braun-Blanquet approach) has mainly been developed in central and southern Europe. In large areas of these regions, broad-leaved hardwood forests represent the potential natural vegetation, and several of their main phytosociological units (syntaxa) were recognized early, e.g. the class *Quercus-Fagetea* and the order *Fagetalia*, as well as many alliances and associations. Also in northern Europe, vegetation science has a long tradition, but it has not followed one particular approach, neither regarding methodology of sampling nor with respect to syntaxonomic classification. In Sweden, the "Uppsala school" played a prominent role, but it has become more a tradition than a well-defined method (see Trass and Malmer 1973 for a detailed review). In contrast to the Zürich-Montpellier school, it has not resulted in a generally accepted system of hierarchically structured vegetation units. From the beginning, the interest of vegetation scientists in northern Europe was mainly

TABLE 1

20 relevés of mesotrophic mixed deciduous forest from Öland. Low-frequent species are omitted. For alliance character species within the order *Fagetalia*, the following abbreviations were used: *Alno-Ulmion* (AU), *Fagion* (FG), *Tilio-Acerion* (TA). Other abbreviations: regional association character species within the Boreo-nemoral zone (RA), local association character species on Öland (LA), formation-specific association character species within the Boreo-nemoral zone (FA), bryophyte (B), differential species (d).

Running number		12345678911111111112
		01234567890
<b>Upper tree layer:</b>		
<i>Quercus robur</i>		4433331+22+123113232
<i>Fraxinus excelsior</i>		+21222343322.2+2++32
<i>Tilia cordata</i>	RA	1132+.2+2.43234.+...
<i>Acer platanoides</i>	TA	+.+.+.+.+.+.+.131.+3
<i>Ulmus glabra</i>	TA	+.+.+.+.+.+.+.2.+2
<b>Lower tree layer:</b>		
<i>Ulmus glabra</i>	TA	2+111.+.+.+.2+11.22+21
<i>Tilia cordata</i>	RA	+33133312.22121.+.+. .
<i>Acer platanoides</i>	TA	.222322+2+...211.+++
<i>Fraxinus excelsior</i>		+.+.+.+.+.+.1.+.+.+. .
<i>Quercus robur</i>		+.+.+.+.+.+.+.+.+.+. .
<b>Shrub layer:</b>		
<i>Crataegus</i> spp.		2121122+++r2++r32+12
<i>Ulmus glabra</i>	TA	.r2+1.+.+.11.12r12111
<i>Corylus avellana</i>		3313..24131.42+2343.
<i>Tilia cordata</i>	RA	.1+1+2122211+.rr..
<i>Fraxinus excelsior</i>		rr2+.1+1+.2.2r.+.+. .
<i>Cornus sanguinea</i>		+.r+1r+12..r..2.+3
<i>Acer platanoides</i>	TA	+.1121rr...+r1rr+. .
<i>Lonicera xylosteum</i>		..21r2+111...21r..2.
<i>Ribes alpinum</i>	TA	r.r+++r.rr..r...rr..
<i>Sorbus aucuparia</i>		r.rr+r.+.r.rr+.+.+. .
<i>Viburnum opulus</i>	d AU	+...r..rr...+.+.+. .
<i>Malus sylvestris</i>		....r.r...r...r...r... .
<i>Euonymus europaeus</i>		....r..r1.....r
<b>Field layer:</b>		
Character and differential species of <i>Alno-Ulmion</i>		
<i>Geum rivale</i> d		3+1+2223442124r.2223
<i>Elymus caninus</i>		r1.+22222222.....+2.
<i>Plagiomnium undulatum</i> B		+122+11233212+2+2.2
<i>Gagea lutea</i>		+.r..rr.....r+212+
<i>Rubus caesius</i> d		1r.r+.1r.....r
<i>Festuca gigantea</i>		....+.+.+.+.+.+. .
<i>Ulmus minor</i>		+.+.+.+.+.+.+.+.+. .
<i>Angelica sylvestris</i> d		....FFF.....
<i>Viburnum opulus</i> d		++rrr.+r+.+.+.+.r..
<i>Allium scorodoprasum</i> d		.....2.....1.....
<i>Stachysylvatica</i>		+.....

TABLE 1 (continued)

Running number	12345678911111111112 01234567890
Character and differential species of <i>Tilio-Acerion</i>	
Acer platanoides	r2++1211.+...++221+21
Ulmus glabra	..r1.rr.++.+.++++
Ribes alpinum	..r.r1r.r...r...rr..
Geranium robertianum d	.....r.....
<i>Quercio-Fagetea</i> and <i>Fagetalia</i> character species	
Anemone nemorosa	333333322r3333232233
Anemone ranunculoides	23222222+212222222
Hepatica nobilis	122222212+2221132322
Fraxinus excelsior	122122+121+2+22r2112
Poa nemoralis	r+11+31+1221223r12+2
Ranunculus auricomus agg.	212rr1.++2+1++13+++2
Convallaria majalis	23113+3322+r2+...+rr1
Carex sylvatica	+1+.11+232++r1+1.r+2
Viola mirabilis	..+2+22r1...+1+r+22
Campanula trachelium	.r.rrr+2.rrrr+r1r+r+
Cardamine bulbifera	r1+112+rr..1+2+.221.
Paris quadrifolia	2+r...r+r1r1r..r1.+
Mercurialis perennis	+412..2+.r...+23+222
Tilia cordata	.+r.r.r++++1r.r.+.
Ranunculus ficaria	32...1...222112.r122
Milium effusum	rr22+.+.+.12+2.r1..
Melica uniflora	.r+r..1...+r2..+2222
Cornus sanguinea	r..r2+r+.1...+.+r2
Brachypodium sylvaticum	.1r11.11+12.r...r.+.
Euonymus europaeus	r..r+++r+r.....rr
Corylus avellana	r+...r+r+r.r...rr...
Viola reichenbachiana	.1.r.r.....1+++11.+
Hedera helix	.12+.12.r...+2....++
Pulmonaria officinalis	+. ...2rr.r.....r.1+
Bromus benekenii	..+.1+r..1.....+. .
Polygonatum multiflorum	...r+++r1.....
Malus sylvestris	..+.rr+...r.....r...
Lonicera xylosteum	..+.+.+.r...+.+.+.r
Quercus robur	.r.r.....r+...r...r
Scrophularia nodosa	r.....+.+.+.+.+.+
Lathyrus vernus	..r.+...r...r.....
Lathyrus niger	..r.+...r...r.....
Companions	
Crataegus spp.	1++r+++rr.++r+11+++1
Primula veris	..r+1+++r++1+1121r11
Deschampsia cespitosa	1+r.1++11+1r...r+r
Fragaria vesca	.rr.2++r.+1rr1r+.+r
Vicia sepium	..+.1.r++121+lrr2.2
Allium oleraceum	..+r1r...22r11++r.r

TABLE I (conclusion)

Running number	12345678911111111112 01234567890
<i>Filipendula ulmaria</i>	2...1.r2122...lr.r.+r
<i>Viola riviniana</i>	2.+r+1...+1+1...r+
<i>Rubus saxatilis</i>	+...r21.12.12+++...1
<i>Geranium sylvaticum</i>	1+1+111+r...2...r
<i>Melampyrum pratense</i>	.r.+2.1.+...r+1..rr+
<i>Sorbus aucuparia</i>	.+r++...+r..rrr...r.
<i>Melampyrum sylvaticum</i>	...r+...r.122+r.+2..
<i>Carex digitata</i>	.1+r+...r..r.r...r..
<i>Geum urbanum</i>	..1..1....r+...r1...11
<i>Anthriscus sylvestris</i>	...r.....r.r.1212.+
<i>Listera ovata</i>	r.....r+r.r.r.r.+
<i>Maianthemum bifolium</i>	.r....+21+1..2.....
<i>Aegopodium podagraria</i>	..r3.2++22.....
<i>Veronica chamaedrys</i>	.....r12..++..+..
<i>Laserpitium latifolium</i> FA	...rr1..r....+1....
<i>Orchis mascula</i>	.....r.+rr1...+....
<i>Dactylorhiza fuchsii</i>	.....+r1.+r.....r
<i>Taraxacum officinale</i> agg.	...r+...r.....r+
<i>Melica nutans</i>	..r...1....+.....r.
<i>Melampyrum nemorosum</i> FA	...2.12..r.....
<b>Bryophytes:</b>	
<i>Eurhynchium hians</i>	r122222322+1+2+2r212
<i>Brachythecium rutabulum</i>	..+.++r++1++..rr.r1..
<i>Rhytidiadelphus triquetrus</i>	..+r+...2123+...2.r
<i>Plagiomnium affine</i>	..r+r...+.1112...1..
<i>Fissidens taxifolius</i>	.r.+rr22+.....
<i>Fissidens cristatus</i> FA	...r+r...r..r.....r.
<i>Scleropodium purum</i>	.....+r.+...r.r+....
<i>Eurhynchium striatum</i>	12.r.....r.r.....
<i>Plagiochila asplenioides</i>	+.r.r.r...r.....
<i>Eurhynchium praelongum</i>	.....+1.2...rr.....
<i>Cirriphyllum piliferum</i>	.....+.....1r.....r.
<i>Brachythecium velutinum</i> FA	.....r.....r.r+....

focused on plant geographic aspects and the ecology of widely distributed types of vegetation, such as coniferous forests and mires. On contrary, deciduous forests, fairly rare and only occurring in the southern parts of Fennoscandia, were not paid much attention to. In general, only few phytosociological investigations have been carried out (for a literature review, see Diekmann 1994), and first since the beginning of the 1970's, the Braun-Blanquet approach was applied in studies on deciduous forests, mainly by Norwegian authors, e.g. Bjørnstad (1971), Fremstad (1979) and Kielland-Lund (1981).

Consequently, any attempt to assign deciduous forest community types in northern Europe to already existing syntaxa of the Braun-Blanquet system is difficult: it meets a system that, in most parts of Europe, is since long established, generally accepted and successfully applied in many respects. Northern community types not fitting into this system may be looked upon as geographic outliers (marginal communities) at the northern border of deciduous hardwood forests in Europe. A critical revision of several syntaxa of the Braun-Blanquet system might be necessary; however, such a revision cannot be based on the relatively poor community differentiation in northern Europe, as it appears natural to set up the system where it is most diverse, i.e. in southern and central Europe. In the following, the specific problems of syntaxonomic delimitation of northern community types will be discussed in detail.

#### *Loss and intermixture of diagnostic species*

It was pointed out earlier that deciduous forests in northern Europe form species-rich communities. However, moving northwards in Europe, one observes a successive loss of species in general, and of diagnostic species in particular. The latter especially concerns species on the levels of alliance and association, while class and order character species are still common. Within the order *Fagetalia*, the loss of character and differential species is most pronounced for *Carpinion*, *Fagion* and *Tilio-Acerion*, whereas many *Alno-Ulmion* species are fairly common even in the north of Fennoscandia. Here, it must be emphasized that the deciduous forests in northern Europe do not possess any own endemic character species which could compensate for this loss of diagnostic species. No general character species *sensu* Westhoff and van der Maarel (1973) — i.e. character species valid for and geographically restricted to the total area of the syntaxa — are thus available for the delimitation of associations restricted to northern Europe.

In Table 1, *Quercus-Fagetea* and *Fagetalia* species are well represented and characterize the stands as mesophytic broad-leaved forests. *Carpinion* and *Fagion* species are almost absent, and particularly the two most distinctive species of these alliances are completely lacking, i.e. *Carpinus betulus* and *Fagus sylvatica*, respectively. *Tilio-Acerion* and *Alno-Ulmion*, on the other hand, are both represented by a few species. The composition of the tree layer — *Acer platanoides* and *Ulmus glabra* are occurring constantly — suggests to refer the relevés to the *Tilio-Acerion*. In contrast, in the field layer, diagnostic species of the *Alno-Ulmion* (*Geum rivale*, *Elymus caninus*, etc.) are much more frequent, although those character species that indicate very wet soil conditions are absent (while otherwise common in northern Europe), such as *Chrysosplenium alternifolium*, *Equisetum pratense*, *E. sylvaticum*, *Matteuccia struthiopteris* and *Stellaria nemorum*. Thus, by simply “counting” character

species, the relevés cannot with certainty be assigned to either of the two alliances. In northern Europe, this intermixture of species of different alliances is probably not an exception, as it has also been observed in thermophilous forest-edge communities (*Geranium sanguinei* vs. *Trifolium medii*, see Diekmann 1990).

#### *Change in species behaviour*

Species may show different ecological behaviour in different geographic areas. This may concern shifts both in optimum and amplitude. Possible mechanisms for the change in ecological behaviour are the existence of separate ecotypes and the presence or absence of potential competitors. The geographic variation in habitat response can sometimes be explained by compensation for difference in climate, according to the law of relative habitat constancy (Walter and Walter 1953), but the mechanisms underlying these geographic changes have not yet been understood very well. Many examples for ecological shifts of species were given by Westhoff and van der Maarel (1973). With respect to the transition from central to northern Europe, changes in species behaviour were recently demonstrated by Gustafsson (1994) and Diekmann (1995). These are probably most pronounced regarding soil reaction: for instance, some species that serve as indicators of calcareous soils in central Europe (*Campanula persicifolia*, *Polygonatum odoratum*, *Laserpitium latifolium*) can in Scandinavia abundantly be found also on fairly acid soils.

Shifts in ecological behaviour can also be observed among some of the alliance character species present in Table 1. In northern Europe, the *Alno-Ulmion* species *Elymus caninus*, *Gagea lutea* and *Plagiomnium undulatum* are not restricted to wet or moist sites, but occur frequently also in forest communities on mesic soils (cf. Diekmann 1994). The same applies to *Prunus padus*, which is rare on Öland but occurs commonly in mesotrophic deciduous forests on the Swedish mainland and in Norway. On the other hand, the *Tilio-Acerion* species *Acer platanoides* and *Ulmus glabra* are abundant in eutrophic alder-ash forests assigned to the *Alno-Ulmion* (Kielland-Lund 1981, Diekmann 1994). Compared with central Europe, the species mentioned have extended (or at least changed) their ecological amplitude as well as their community spectrum. Consequently, indicative function and diagnostic/syntaxonomic value of these species in northern Europe are reduced or altered. Therefore, the taxa in question do not fulfill the criteria of general character species. To give a further example: *Gymnocarpium dryopteris* and *Thelypteris phegopteris* are generally treated as character species of the *Fagion* which is restricted to the southernmost parts of Sweden and Norway. Still, the two fern species can be found in the whole of Fennoscandia even north of the polar circle (Hultén 1971). Changes in species behaviour can also be observed in other community types than forests. Obviously, it is necessary to geographically limit the

diagnostic value and validity of certain species. This is the well-known problem of geographic fidelity of character taxa (cf. Westhoff and van der Maarel 1973).

### *Decrease and split up of the deciduous forest area*

The area of deciduous forest in Boreo-nemoral Fennoscandia has decreased to a small fraction of its prehistoric size, first due to climatic deterioration since the early Sub-boreal time (about 3000 B.C), and later caused by millennia of anthropogenic cultivation and exploitation (cf. Diekmann 1994). The originally large and partly continuous area of deciduous forest has been split up into more or less isolated patches, the more so as some sub-areas rich in deciduous forest are naturally separated from other sub-areas due to geographic or topographic isolation, e.g. the Baltic islands of Öland and Gotland, and several fiord districts in western Norway. The concentration of stands to a few sub-areas entails a heterogeneity in the relevé material, since transitions between stands of different sub-areas are few or lacking. Vegetational differentiation becomes difficult to interpret, because it may not only be caused by differences in environmental factors, but also by local phenomena connected to vegetation (forest) history and anthropogenic impact, or simply by random effects. How to syntaxonomically deal with this heterogeneity?

Two examples shall be mentioned. The two islands Öland and Gotland are both characterized by a largely calcareous bedrock and a fairly warm and dry climate. Nevertheless, the mesotrophic deciduous forests on these islands are very different from each other (Diekmann 1994), and the stands on Öland (Table 1) do not have real counterparts on Gotland. A comparison reveals that the mesotrophic forests on the two islands can hardly be assigned to the same community. However, it also seems unreasonable to form two separate associations, based on local floristic differences. In western Norway, the differences in the forest vegetation between isolated sub-areas with deciduous forest are even more pronounced. This has resulted in a description of a fairly large number of regional (local) associations (e.g. Øvstedal 1985, Kielland-Lund 1994), distinguished from each other only by regional character species (a regional character species is defined as a taxon with fidelity for the total area of the syntaxon, but with its area exceeding that of the syntaxon, see Westhoff and van der Maarel 1973), but without being characterized by general character species. The following questions arise: is it desirable to create a number of regional and/or local associations according to the considerable vegetational differentiation, by this risking an inflation of syntaxa (cf. Pignatti 1968)? Is it preferable to only accept general character species and associations, thereby forming a number of marginal and fragmentary communities without specific rank? Or is an intermediate concept between these two the best solution to the problem?



## PROPOSED SOLUTIONS

### *Regional associations*

By applying a strict concept of general character species valid throughout the whole range of a syntaxon, no associations of deciduous hardwood forest could be formed in northern Europe. Neither could associations be formed of other southern vegetation types lacking endemics, such as thermophilous forest-edge, meadow and weed communities. Note that, according to this concept, also the beech forests in the northern parts of central Europe just represent fragmentary forms of more southerly distributed communities (Dierschke 1992, 1994). However, the former are generally treated as separate associations (e.g. Dierschke 1985, 1989), based on the explicit or implicit use of regional character species. In fact, regional associations have since long been generally accepted, not only in northern Europe and other marginal areas of Europe, but also in its central parts (e.g. Oberdorfer 1968). Many "good" associations are actually based on regional character species occurring even beyond the range of "their" association.

If a species changes its ecological and sociological behaviour within its distribution area in such a way that it is not faithful to one particular syntaxon in all parts of its area, it cannot serve as general character species in the strict sense. This means that species such as *Gagea lutea*, *Elymus caninus* and *Prunus padus* actually are regional character species of the *Alno-Ulmion* within central Europe, because they are not restricted to this alliance in northern Europe. In the same way, *Acer platanoides* and *Ulmus glabra* are regional character species of the *Tilio-Acerion* in central Europe. A large number of units of the Braun-Blanquet system could not be maintained without accepting regional character species.

If we geographically limit the validity of character species, the problem remains which geographic units we should choose (cf. Dierschke 1992). Phytosociologists have not yet agreed upon this, but usually apply a floristic definition of units. While some have chosen a division into larger regions (whole subcontinents or countries), others have preferred smaller units. Two ways of defining "phytosociological regions" appear to be most logical:

(1) to define these regions according to the major phytogeographical units, i.e. vegetation zones. These differ considerably with respect to their forest vegetation, and it is between these zones the changes in species behaviour are most pronounced. Regional associations (or higher phytosociological units) can thus be defined separately for the Mediterranean, Nemoral and Boreo-nemoral zone.

(2) to define the "syntaxonomical range" of a character species by means of the hierarchical system of phytosociological units. Bergmeier *et al.* (1990) proposed that a taxon can only be accepted as character species if it fulfills the necessary criteria within the range of the next higher main unit (association

within the range of the alliance, alliance within the range of the order, etc.). However, applying this principle to deciduous forests in northern Europe (or in the northern parts of central Europe), no association character species will be found, simply because the four alliances within the order *Fagetalia* have a very wide distribution. Dierschke (1992, 1994) therefore proposed to use the next higher intermediate unit, for example the suballiance when dealing with association character species. Divisions of *Fagion* and *Carpinion* into suballiances using geographic differential species have recently been suggested by Dierschke (1990) and Müller (1990), respectively. With respect to northern Europe, *Alno-Ulmion* and *Tilio-Acerion* are of particular interest, but for these, no subdivisions have yet been proposed. However, the eutrophic and mesotrophic deciduous forests of this region differ from those in central Europe to such an extent (cf. Diekmann 1994) that the formation of particular suballiances seems to be well substantiated. Several taxa may serve as geographic differential species, such as *Veronica chamaedrys*, *Geranium sylvaticum*, *Rubus saxatilis* and *Allium oleraceum*, as well as a number of bryophytes.

In both division (1) and (2), the Boreo-nemoral zone is delimited as a separate phytosociological region. For the mesotrophic deciduous forests in Table 1 (and for corresponding forests on the Swedish mainland and in SE Norway), the following regional character species are now available: *Tilia cordata*, *Lathyrus vernus*, *L. niger*, *Brachypodium sylvaticum* and *Bromus benekenii*. *Viola reichenbachiana* is largely restricted to Öland and can thus serve as a local character species of mesotrophic deciduous forests. The taxa mentioned are true forest species and rare both in oligotrophic and eutrophic forests. Especially *Tilia cordata* is characteristic for mesotrophic forests that have only moderately been influenced by human activity. Thereby, these forests can be assigned to a regional association (*Ulmo-Tilietum* Kielland-Lund in Seibert 69 em. Diekmann 94) for which two geographic races (Öland, Swedish mainland/SE Norway) have been distinguished (Diekmann 1994). On Gotland, the anthropogenic impact on the landscape in general and on the forest vegetation in particular has been so strong that no primarily natural or semi-natural forests can be found any longer. The mesotrophic forests on this island are structurally and compositionally very different from those on Öland and on the mainland: the tree layer is dominated by *Quercus robur* and *Fraxinus excelsior*, and diagnostic species such as *Tilia cordata* and *Lathyrus niger* are largely lacking. They are best assigned to a fragmentary community ("Restgesellschaft", cf. Brun-Hool 1966), by Diekmann (1994) referred to as *Quercus robur-Fraxinus excelsior* community. Regional character species can also be distinguished in other forest types. Concerning the eutrophic elm-ash forests in the Boreo-nemoral zone, for example, *Corydalis bulbosa* and *Allium ursinum* become character species of the regional association *Ulmo-Fraxinetum* Sjögren 71 ex Diekmann 94.

In order not to contribute to an "inflation" of syntaxa, no local

associations within parts of the Boreo-nemoral zone (e.g. SE Norway, Gotland) should be delimited. The situation is somewhat difficult in western Norway which is very diverse in its environmental conditions and vegetation, and which cannot easily be assigned to a particular vegetation zone (cf. Diekmann 1994). However, if one distinguishes this region as an own Western broad-leaved and pine forest region, it might be justified to recognize regional associations (e.g. Kielland-Lund 1994).

#### *Restriction of character species to structural vegetation types*

Species may occur in more than one type of vegetation or formation. Many common forest species actually thrive better at half-shady forest margins or in gaps where the light conditions are somewhat more favourable, and are therefore assigned to communities of forest-edges (*Trifolio-Geranietea*, *Glechometalia hederaceae*) or clearings (*Epilobietea angustifolii*). On the other hand, many common meadow species serve as character species of communities within the class *Molinio-Arrhenatheretea*, although they are originally native to forests, e.g. *Cirsium oleraceum*, *Angelica sylvestris* and *Crepis paludosa* (cf. Ellenberg 1986). The extension in ecological and sociological amplitude has largely been caused by the activity of man. This has led to the syntaxonomic problem that a species either lost its diagnostic value, or had to be assigned to only one particular syntaxon.

If one conceives forest vegetation and open vegetation as basically different from each other regarding structure, habitat conditions and internal interactions (cf. Dierschke 1992), it is near at hand to restrict the validity of character species to these basic formations. This idea has first been proposed by Bergmeier *et al.* (1990) who suggested three classes of formations: (1) woodlands and scrub, dominated by phanerophytes, (2) meadows, dwarf shrubs, weed communities, freshwater vegetation, and other vegetation types dominated by non-phanerophyte vascular plants, and (3) cryptogam communities. By using structural elements, the new concept of formation-specific character species solves many syntaxonomic problems and improves the structural and ecological homogeneity of syntaxa (Dierschke 1992).

By applying this concept to Boreo-nemoral forest communities, many character species of forest-edge communities — usually treated as differential species within forests — may also serve as character taxa within the “woodland and scrub” formation: *Laserpitium latifolium* and *Melampyrum nemorosum* become exclusive (“true”) character species of mesotrophic deciduous forests (*Ulmo-Tilietum*, Table 1). Note that the latter species has even earlier been treated as character species of both a forest community (*Carpinion*) and a forest-edge community (*Trifolio-Melampyretum nemorosii*). Other elements of forest fringes may serve as character species of eutrophic elm-ash forests (e.g. *Alliaria petiolata*) and oligotrophic oak forests (*Lathyrus*

*montanus*, *Hieracium* spp.). Particularly eutrophic alder-ash forests (*Alno-Ulmion*) would profit by "receiving" elements from *Montio-Cardaminetea*, *Calthion*, *Filipendulion* and *Glechometalia* (cf. also Bergmeier *et al.* 1990, Dierschke 1992). New taxa become also available for *Alnetea glutinosae* and *Vaccinio-Piceetea*, from *Phragmitetea* and *Oxycocco-Sphagnetea*, respectively.

### *Environmental information*

A fundamental principle of the Zürich-Montpellier school has been that plant communities or syntaxa are recognized by their floristic composition alone (Westhoff and van der Maarel 1973). However, in practice, it has turned out that this often is a difficult task, due to the scarcity or lack of diagnostic species, the intermixture of diagnostic species of different communities, vegetation dynamics, etc. Therefore, other information than floristic has often been used for recognition of syntaxa.

The floristic-sociological characters of a syntaxon are supposed to reflect other characters as well, such as physiognomy, spatial structure and environment. A syntaxon should therefore floristically and structurally be more or less uniform. However, this has not always been the case (e.g. for the *Vaccinio-Piceetea*) which has sometimes led to some syntaxonomic refinements (cf. Westhoff and van der Maarel 1973). The proposed restriction of character taxa to formation classes takes the idea of structural uniformity into account. Syntaxa also have an ecological meaning, which is one of the basic practical applications of phytosociology. When we talk about a particular syntaxon, we do not only implicitly presume a certain floristic composition, but at the same time also certain environmental conditions. The word *Alno-Ulmion*, for example, tells us both about structure and species composition (the frequent occurrence of *Quercus-Fagetalia*, *Fagetalia* and *Alno-Ulmion* species and the relative scarcity of species of other vegetation types) and about the environment (moist to wet, more or less eutrophic forest soil). Consequently, when diagnostic species are rare or absent, syntaxa may be recognized by the ecological conditions. The significance of an ecological characterization of syntaxa was recently emphasized by Pignatti *et al.* (1995).

The mesotrophic deciduous forests on Öland (Table 1) could not with certainty be referred to an alliance as both *Alno-Ulmion* and *Tilio-Acerion* taxa were present in a few species (which, moreover, partly showed a change in ecological behaviour as compared with central Europe). Here, environmental conditions help to decide upon which alliance the forests should be referred to. In Boreo-nemoral Fennoscandia, mesotrophic forests with high frequency of *Tilia cordata* (assigned to the *Ulmo-Tilietum*) are found in areas with a fairly warm and dry macroclimate (as on Öland and in the area of Lake Mälaren) and/or on more or less unstable, preferably S-/SW-facing screes and slopes favoured by a warm local climate (as on the plateau-like hills in the province

of Västergötland). The stands are thus associated with "thermophilous" forest sites. In central Europe, corresponding sites are occupied by forests that are referred to the *Tilio-Acerion*, such as the *Aceri platanoidis-Tilietum platyphyllis* and *Quercus petraeae-Tilietum platyphyllis*. Only in spring when the soils can be wet or even waterlogged, northern mesotrophic forests remind of eutrophic alder-ash forests (*Alno-Ulmion*) of the same region. However, the soils usually dry out during summer, in contrast to *Alno-Ulmion* forests. A high groundwater level in spring is a general feature of northern deciduous forests and may explain the high species number and cover degree of geophytes (*Gagea lutea*, *Ranunculus auricomus*, *Anemone ranunculoides*, etc.). It might be added that the "thermophilous" character of mesotrophic forests is also obvious in the frequent occurrence of southern species expressed in a high average of Ellenberg indicator values for temperature (cf. Diekmann 1994). To sum up, the forests are best assigned to the *Tilio-Acerion*.

### *Cryptogams*

Deciduous forests in northern Europe form species-rich communities, but at the same time suffer from a decrease in species, in particular of diagnostic taxa, as compared with central Europe. This seeming discrepancy can be explained by the fact that the loss of species mainly concerns true forest species among vascular plants which is compensated by a higher frequency of companions and bryophytes (cf. Diekmann 1994). In Boreo-nemoral deciduous forests, the bottom layer is usually well developed, and several bryophyte taxa are more common than in Nemoral forests, e.g. *Eurhynchium hians*, *E. angustirete* and *Rhytidiadelphus triquetrus*.

With respect to *Fagetalia* communities, bryophytes have only exceptionally been used as diagnostic species (e.g. *Plagiomnium undulatum* as *Alno-Ulmion* character species). Considering their richness in northern communities, mosses and liverworts should be used as character and differential species to a greater extent. In mesotrophic deciduous forests on Öland (Table 1), *Brachythecium velutinum* and *Fissidens cristatus* can frequently be found. In oligotrophic and eutrophic deciduous forests, on the other hand, the two species are clearly less common. They can thus be used as differential species for mesotrophic forests, or — by applying the formation-specific character species concept — even as character species. However, the knowledge about the ecological and sociological preferences and amplitudes of many bryophyte species is still too incomplete to allow to assign these to particular syntaxa.

Fungi represent another group of cryptogams that has not received much attention as part of forest communities dominated by vascular plants, for several reasons: only fruitbodies of macrofungi — but no microfungi — are visible, the macrofungi are often difficult to identify, and they show a strong

seasonal periodicity. Thus, the analysis of terrestrial macrofungi requires a high time effort which has prevented most phytosociologists to treat these organisms in more detail. However, Bujakiewicz (1992) studied the soil macrofungi of deciduous forests and showed differences in species composition between *Alnetea glutinosae* and *Quercio-Fagetea*, as well as between alliances within the order *Fagetalia*. The *Alno-Ulmion*, for example, is distinguished by a number of saprophytic fungi indicative of fertile and humid habitats. The *Tilio-Acerion* is less well distinguished, but the *Ulmo-Tilietum* in Norway is according to Bujakiewicz (1992) characterized by a high frequency and abundance of *Camarophyllus pratensis* and *Hygrocybe coccinea*.

Again, information on the ecological and sociological optima and amplitudes of fungi is scarce, although their species number is very high. Hallingbäck (1994) recently published a list of about 3200 macrofungi in Sweden, of which more than 25% have a preference for deciduous hardwood forests. It may therefore be worth to place more emphasis on the study of this organism group.

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