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CONTEXT-DEPENDENCE OF DIAGNOSTIC SPECIES: A CASE STUDY OF THE CENTRAL EUROPEAN SPRUCE FORESTS

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Abstract: In the phytosociological literature, there are numerous different approaches to the designation of diagnostic species. Frequently, this results in discrepancies between the lists of diagnostic species published for one and the same community. We examined different approaches to determining diagnostic species using as an example *Picea abies* forests within the broader context of all Central European forests. Diagnostic species of spruce forests were determined from a data set of 20,164 phytosociological relevés of forests from the Eastern Alps, Western Carpathians, and the Bohemian Massif, which included 3,569 relevés of spruce forests. Phi coefficient of association was used to measure species fidelity, and species with the highest fidelities were considered as diagnostic. Diagnostic species were determined in four ways, including (A) comparison of spruce forests among the three mountain ranges, (B) comparison between spruce forests and other forests, performed separately in each of the mountain ranges, (C) simultaneous comparison of spruce forests of each of the mountain ranges with spruce forests of the other two ranges and with the other forests of all ranges, (D) comparison of spruce forests with the other forests, using pooled data sets from the three mountain ranges. The sets of diagnostic species of spruce forests yielded in comparisons A and B were sharply different; the set resulting from comparison C was intermediate between the first two and comparison D resulted in similar diagnostic species as comparison B. In comparison A, spruce forests of the Eastern Alps had a number of diagnostic species, while the spruce forests of the other two mountain ranges had only few diagnostic species. In comparison B, by contrast, the number and quality of diagnostic species decreased from the Bohemian Massif to the Eastern Alps. This exercise points out that lists of diagnostic species published in phytosociological literature are dependent on the context, i.e. the underlying data sets and comparisons: some of these lists are useful for identification of vegetation units at a local scale, some others for distinguishing units within a narrowly delimited community type over a large area. The thoughtless application of published lists of diagnostic species outside of the context for which they were intended should therefore be avoided.

Keywords: Bohemian Massif, Eastern Alps, Fidelity, Phytosociological database, *Picea abies*, Vegetation survey, Western Carpathians

Nomenclature: EHRENDORFER (1973), FREY et al. (1995)

INTRODUCTION

The concept of diagnostic species (also called indicator, character or differential species; WHITTAKER 1962, WESTHOFF & VAN DER MAAREL 1973, DUFRÊNE & LEGENDRE 1997, WILLNER 2001, CHYTRÝ et al. 2002) plays a key role in the classification of biotic communities. Diagnostic species can be statistically determined by measuring the fidelity, i.e. the concentration of species occurrence or abundance in relevés belonging to a given vegetation unit, and their corresponding paucity or absence in other units; species that exceed a set fidelity threshold are considered to be diagnostic. Most often, these species are determined a posteriori, i.e., after a classification is created by expert knowledge or by numerical classification methods. Diagnostic species are important namely in field surveys where they help researchers to identify community types established in existing classification systems.

Perhaps the most widespread application of the concept of diagnostic species can be found in the field of vegetation classification. A large number of papers or monographs on vegetation units in different areas have been published (MUCINA 2001), in which descriptions of particular units are often supplemented with lists of diagnostic species. The strong emphasis laid on diagnostic species by phytosociologists can be also demonstrated by the fact that the International Code of Phytosociological Nomenclature (WEBER et al. 2000) considers the names of high-rank syntaxa invalid if published without lists of diagnostic species. However, the diagnostic capacity of species in most published lists has been subjectively estimated by expert knowledge, often without sufficient data and statistical analysis. Some of these lists may be therefore unreliable.

Recently, large electronic databases of vegetation plot samples (relevés) have been created (HENNEKENS & SCHAMINÉE 2001), statistical methods suitable for determination of diagnostic species have been demonstrated (DUFRÊNE & LEGENDRE 1997, BOTTA-DUKÁT & BORHIDI 1999, BRUELHEIDE 2000, CHYTRÝ et al. 2002), and software performing these operations has been developed (MCCUNE & MEFFORD 1999, TICHÝ 2002). All of these developments make it possible to check and revise the published lists of diagnostic species by statistical data analysis. However, even if fidelity of a species to a vegetation unit is measured by statistical methods, the results are not unequivocal, depending very much on the relevé data set used for comparison. Two extreme cases can be traced in the published phytosociological literature. The first case concerns local studies whose authors are familiar with different vegetation types in a small area. These authors tend to determine diagnostic species by comparing the occurrence of a species in the given vegetation unit with its presence or absence in other units occurring in the same area. These comparisons cover a broad range of habitats but are limited geographically. For example, when determining diagnostic species of a forest community, the occurrence of the candidate species in other forest communities, but also in meadows of the same area, can be considered. This is the classical approach used by Braun-Blanquet, Tüxen, Oberdorfer and many others. The second case concerns studies focused on a single or few vegetation types that occupy a narrow range of habitats, but extend into a wider geographic area. These two alternate approaches can result in different sets of diagnostic species determined for the same community type. In the first case the diagnostic species can be termed local character species, in the second case they are closer to the traditional concept of differential species (WILLNER 2001).

Central European spruce forests, dominated by *Picea abies*, are a suitable model to investigate this methodological issue. Their natural range is confined to higher altitudes, so it can be divided into several isolated areas in the mountains. Central European mountain ranges, such as the Alps, the Carpathians, and the Hercynic ranges north of the Alps (e.g., the Bohemian Massif), are quite different from one another in terms of phytogeographical affinities and available habitats. This makes them ideally suited for a case study of a single, though broadly defined vegetation type in several different areas. At the same time, there are abundant data representing the other vegetation types of Central Europe. These data allow a comparison of spruce forests with other vegetation types, thus demonstrating a local study analysing vegetation across many different habitats.

The objectives of the present paper are twofold. First, it will investigate the extent of differences in diagnostic species if determined from a comparison over a wider geographical range or over a wider range of habitats. Second, it will determine the main diagnostic species of the spruce forests in the Eastern Alps, Western Carpathians and the Bohemian Massif. Emphasizing mainly the methodological issues, this paper does not aim at analyzing traditional, narrowly delimited, more or less homogeneous vegetation units such as associations or alliances, but focuses instead on a broadly defined and comparatively heterogeneous vegetation unit – spruce forest. However, it is reasonable to assume that general patterns of vegetation differentiation by diagnostic species revealed in broad vegetation types will be similar to those found in narrowly delimited vegetation units.

MATERIALS AND METHODS

The determination of diagnostic species for Central European spruce forests required that a larger database including all types of Central European forests be used. For this purpose, all available relevés of natural or near-natural forest vegetation from the Austrian, Slovak and Czech national phytosociological databases were put together into a single database in the program TURBOVEG (HENNEKENS & SCHAMINÉE 2001). The data set included 20,164 relevés, with a roughly equal proportion of the relevés obtained from the Eastern Alps, Western Carpathians, and the Bohemian Massif (Table 1). Different taxonomic concepts of species and subspecies were unified and double occurrences of species in the tree and shrub layers were merged. Cryptogam records were absent in some relevés and presumably, in some other relevés, the quality of cryptogam sampling was rather poor due to omissions of all

Table 1. Basic statistics of the relevés included in the data set. Spruce forest relevés are defined as relevés with *Picea abies* cover exceeding 25% in the tree layer. For explanation of the mid-gradient forest relevés, see Materials and Methods and Fig. 1.

	Eastern Alps	Western Carpathians	Bohemian Massif	Total
No. of forest relevés, including spruce forest relevés	6,734	5,764	7,666	20,164
No. of all spruce forest relevés	1,723	432	1,414	3,569
No. of mid-gradient spruce forest relevés	580	202	495	1,277

but the most conspicuous or dominant species. Still, the cryptogams were retained in the analyses.

Next, spruce forests were identified within this larger data set. Defining spruce forest presented certain challenges. It was impossible to select relevés of particular syntaxa, because the classification systems of spruce forests used in the three countries differed considerably (JAHN 1977, MUCINA & MAGLOCKÝ 1985, MAGIC in MICHALKO et al. 1987, WALLNÖFER 1993, JIRÁSEK 1996, JIRÁSEK in NEUHÄUSLOVÁ et al. 1998, EXNER 2001, KUČERA 2001, EXNER et al. 2002, HUSOVÁ et al. 2002). Therefore we accepted a more operational definition of the studied vegetation type. We considered as spruce forests all forests in which the cover of *Picea abies* in the tree layer exceeded 25%. In many cases, it was difficult to distinguish natural spruce forests from secondary spruce plantations, namely at the higher altitudes, in the belt of mixed forests of *Fagus sylvatica*, *Abies alba* and *Picea abies*. All relevés of spruce forests from higher altitudes were therefore included into the data set. There were probably some relevés of spruce plantations from low altitudes included in the data set, but their number was negligible. In the end, 3569 relevés were considered to represent spruce forest.

Spruce forests defined in such a way were quite heterogeneous, covering a wide range of habitats. These forests are abundant on both acidic and calcareous bedrocks in the Eastern Alps and the Western Carpathians, while in the Bohemian Massif, they are only found on acidic soils due to the absence of limestones and dolomites at higher altitudes of this mountain range. By contrast, wet spruce forests are more abundant in the Bohemian Massif than in the other two mountain ranges, probably due to flatter landforms that support the development of forested peatlands.

Given this disproportional representation of different habitats in particular mountain ranges, a direct comparison of spruce forest relevés among these ranges appeared problematic. We therefore aimed at selecting a subset of relevés from the habitats that are well represented everywhere, that would enable us to compare spruce forests from corresponding habitats in the three mountain ranges. In order to thus narrow the data set, Ellenberg indicator values for vascular plants (ELLENBERG et al. 1992) were calculated for all spruce forest relevés using six ecological factors (light, temperature, continentality, moisture, soil reaction and nutrients) by unweighted averaging of species indicator values. Out of these factors, the highest variability and highest discrimination between the three mountain ranges was found for the factors moisture and reaction (Fig. 1). We selected all the relevés with moisture indicator values between 5.0–6.0 and reaction values between 3.5–5.5, because within these limits there was a considerable overlap between the relevés from the three mountain ranges. In such a way, spruce forests from the habitats underrepresented in some of the mountain ranges, such as limestone slopes or forested peatlands, were excluded, and a comparison of spruce forests from similar habitats could be made. This subset of spruce forest relevés from the above range of moisture and reaction will be hereafter referred to as mid-gradient spruce forests (Table 1). Basic characteristics of the data set in terms of constant and dominant species are summarized in Tables 2 and 3.

Diagnostic species were determined by fidelity calculations, with the phi coefficient of association (SOKAL & ROHLF 1995, CHYTRÝ et al. 2002) as the fidelity measure. This coefficient ranges from -1 to 1 and increases with increasing fidelity, zero meaning no fidelity

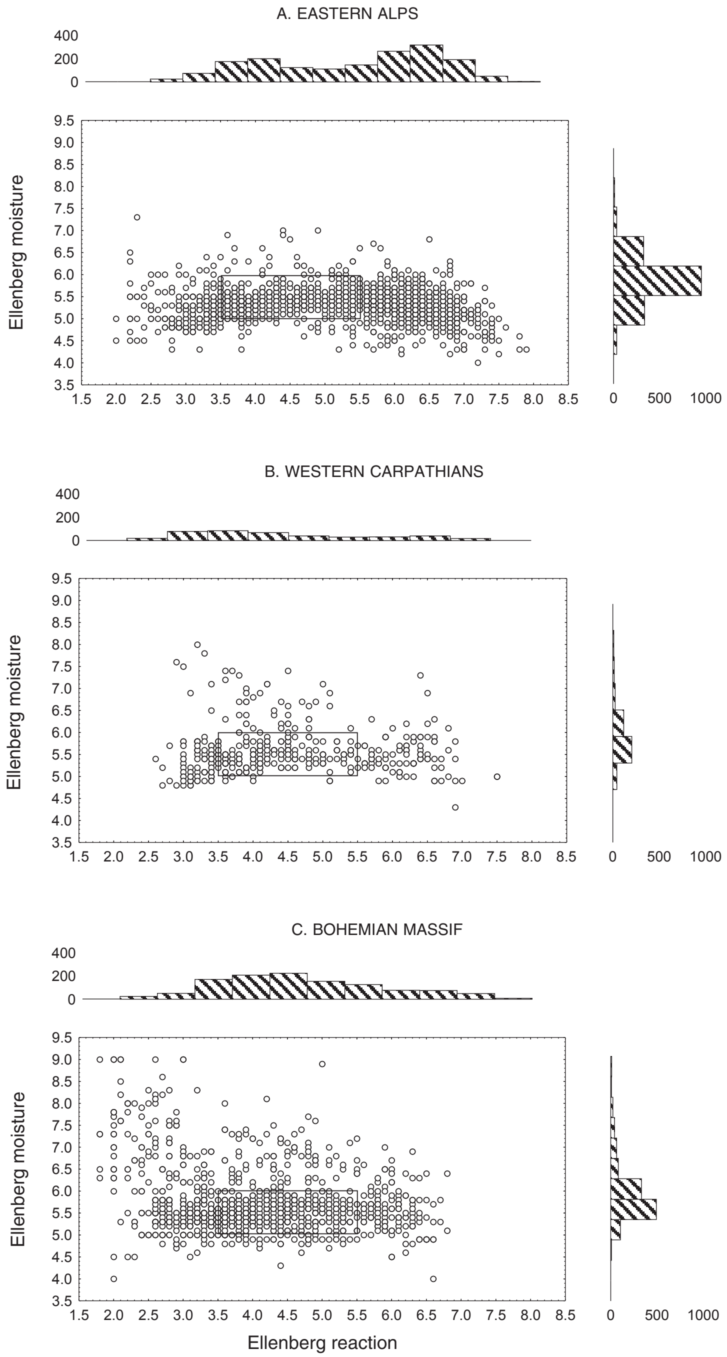

Fig. 1. Scatter plots of Ellenberg indicator values for soil reaction and moisture for the spruce forests of the Eastern Alps (A), Western Carpathians (B), and Bohemian Massif (C). Histobars are scaled in absolute frequencies per each category. Frames within the plots delimit the mid-gradient spruce forests.

Table 2. Constant species of spruce forests in the three mountain ranges, defined as species with occurrence frequency > 50%. Numbers are percentage occurrence frequencies. Species constant in all the mountain ranges are set in bold.

Eastern Alps		Western Carpathians		Bohemian Massif	
I. All spruce forests					
Oxalis acetosella	80	***Oxalis acetosella***	83	***Vaccinium myrtillus***	77
Vaccinium myrtillus	65	***Vaccinium myrtillus***	80	***Oxalis acetosella***	64
Hieracium sylvaticum	56	*Dryopteris carthusiana* agg.	70	*Avenella flexuosa*	62
		Athyrium filix-femina	56	*Dryopteris carthusiana* agg.	60
		Avenella flexuosa	53	*Calamagrostis villosa*	58
		Senecio nemorensis agg.	52	*Polytrichum formosum*	55
		Rubus idaeus	52	*Dicranum scoparium*	54
II. Mid-gradient spruce forests					
Oxalis acetosella	94	***Vaccinium myrtillus***	96	***Oxalis acetosella***	93
Vaccinium myrtillus	78	***Oxalis acetosella***	92	***Vaccinium myrtillus***	76
Hieracium sylvaticum	69	***Dryopteris carthusiana*** **agg.**	85	***Dryopteris carthusiana*** **agg.**	76
Avenella flexuosa	68	***Avenella flexuosa***	63	*Polytrichum formosum*	67
Luzula luzuloides	66	*Rubus idaeus*	59	***Avenella flexuosa***	64
Dryopteris carthusiana **agg.**	64	*Senecio nemorensis* agg.	54	*Calamagrostis villosa*	60
Polytrichum formosum	60	*Athyrium filix-femina*	54	*Maianthemum bifolium*	53
Homogyne alpina	58			*Dicranum scoparium*	53
Abies alba	52				

Table 3. Dominant species of spruce forests in the three mountain ranges, defined as species whose cover exceeds 25% in > 5% of relevés. Numbers are percentages of relevés in which the species cover exceeds 25%. Species dominant in all the mountain ranges are set in bold.

Eastern Alps		Western Carpathians		Bohemian Massif	
I. All spruce forests					
Vaccinium myrtillus	14	***Vaccinium myrtillus***	19	*Calamagrostis villosa*	20
Oxalis acetosella	14	***Oxalis acetosella***	19	***Vaccinium myrtillus***	19
Fagus sylvatica	11	*Calamagrostis arundinacea*	7	***Oxalis acetosella***	13
Abies alba	8	*Athyrium distentifolium*	7	*Avenella flexuosa*	10
Avenella flexuosa	5	*Calamagrostis villosa*	6	*Polytrichum formosum*	9
				Dicranum scoparium	6
				Sphagnum girgensohnii	5
				Athyrium distentifolium	5
				Abies alba	5
II. Mid-gradient spruce forests					
Oxalis acetosella	23	***Oxalis acetosella***	27	***Oxalis acetosella***	22
Vaccinium myrtillus	15	***Vaccinium myrtillus***	20	***Calamagrostis villosa***	18
Calamagrostis villosa	9	*Athyrium distentifolium*	11	*Athyrium distentifolium*	14
Avenella flexuosa	9	*Calamagrostis arundinacea*	8	***Vaccinium myrtillus***	13
Abies alba	8	***Calamagrostis villosa***	5	*Polytrichum formosum*	11
Fagus sylvatica	6			*Avenella flexuosa*	8
Polytrichum formosum	5			*Fagus sylvatica*	6
				Abies alba	6

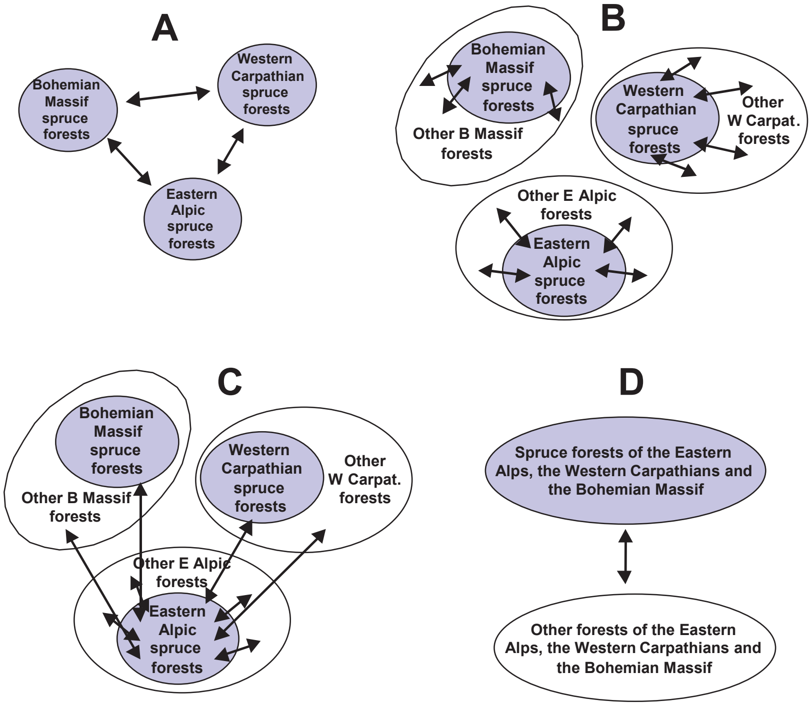

Fig. 2. Schemes of the four comparisons used for determination of diagnostic species. In C, only comparison of the Eastern Alpic with the other forests is shown, but analogous comparisons were also done for the Western Carpathian and the Bohemian Massif spruce forests.

and negative values indicating negative fidelity, i.e. a tendency of the species to avoid the given vegetation unit. An advantage of the phi coefficient as a fidelity measure is its independence of the data set size, which implies that the results obtained from data sets of different sizes can be directly compared. It is also little affected by the relative size of the vegetation unit within the data set. This was important in our case because the number of spruce forest relevés from the Western Carpathians was lower than from the other two mountain ranges. We performed a few trial analyses with equal numbers of relevés in all the mountain ranges, after random deletion of superfluous relevés from the Alps and the Bohemian Massif. As the results of these trials did not substantially differ, we present here the results of the analyses with the full data set.

Fidelity calculations were performed based on four comparisons (Fig. 2): (A) spruce forests compared among the three mountain ranges; (B) spruce forests compared with the other forests, separately in each of the three mountain ranges; (C) spruce forests of each of the mountain ranges, compared simultaneously with the spruce forests of the other two mountain ranges and with the other forests of all the three mountain ranges; (D) spruce forests compared with the other forests, using pooled data from all the mountain ranges. Each of these comparisons was run twice, once based on all spruce forests and once based on mid-gradient spruce forests. For the analyses of the mid-gradient spruce forests, the relevés of

Table 4. Diagnostic species of spruce forests in the three mountain ranges. Only spruce forests are compared (Fig. 2A). Numbers are phi coefficients of association between the species and spruce forests of particular mountain ranges.

Eastern Alps		Western Carpathians		Bohemian Massif	
I. All spruce forests					
Larix decidua	.480	(no species exceeded the threshold phi=.296)		*Polytrichum commune*	.346
Adenostyles glabra	.401			*Calamagrostis villosa*	.342
Calamagrostis varia	.372			*Trientalis europaea*	.339
Solidago virgaurea	.350				
Daphne mezereum	.345				
Ctenidium molluscum	.342				
Hieracium sylvaticum	.326				
Phyteuma spicatum	.326				
Ranunculus nemorosus	.324				
Campanula rotundifolia agg.	.316				
Luzula luzulina	.306				
Plagiochila asplenioides	.306				
Valeriana tripteris	.304				
Melampyrum sylvaticum	.298				
Primula elatior	.296				
II. Mid-gradient spruce forests					
Larix decidua	.492	*Lonicera nigra*	.273	*Streptopus amplexifolius*	.316
Luzula luzuloides	.431	*Galium schultesii*	.243	*Athyrium distentifolium*	.314
Luzula luzulina	.333	*Soldanella carpatica*	.234	*Trientalis europaea*	.301
Plagiochila asplenioides	.327			*Plagiothecium laetum*	.296
Rhytidiadelphus triquetrus	.316			*Rumex alpestris*	.240
Hieracium sylvaticum	.312				
Gentiana asclepiadea	.289				
Huperzia selago	.280				
Abies alba	.270				
Veratrum album	.267				
Melampyrum sylvaticum	.252				
Cardamine trifolia	.245				
Blechnum spicant	.245				
Hylocomium splendens	.244				
Homogyne alpina	.228				

spruce forests excluded from the mid-gradient category were included in the group of the other forests.

Due to different designs of the comparisons, we did not set any universally applied threshold fidelity (phi) value for species to be diagnostic. Instead, for comparisons A–C, we listed 15 species with the highest phi-value in that mountain range, where the phi-values were the highest. Then, we used the phi-value of the least faithful of these 15 species as a threshold for the other two mountain ranges. For comparison D, we only listed the 20 most faithful species. Due to lacking or incomplete cryptogam records in some relevés, fidelity values and diagnostic capacity of the cryptogams may be generally underestimated. However, fidelity of the cryptogams can be compared at least among themselves.

Table 5. Diagnostic species of spruce forests in the three mountain ranges. Spruce forests are compared with the other forests, separately in each of the mountain ranges (Fig. 2B). Numbers are phi coefficients of association between the species and spruce forests of particular mountain ranges.

Eastern Alps		Western Carpathians		Bohemian Massif	
I. All spruce forests					
(no species exceeded the threshold phi=.268)		*Vaccinium myrtillus*	.521	*Calamagrostis villosa*	.499
		Avenella flexuosa	.487	*Vaccinium myrtillus*	.467
		Calamagrostis villosa	.422	*Dicranum scoparium*	.438
		Dicranum scoparium	.392	*Sphagnum girgensohnii*	.386
		Vaccinium vitis-idaea	.365	*Trientalis europaea*	.374
		Trientalis europaea	.327	*Homogyne alpina*	.372
		Sphagnum girgensohnii	.312	*Polytrichum formosum*	.360
		Luzula pilosa	.300	*Polytrichum commune*	.352
		Dryopteris carthusiana agg.	.298	*Luzula sylvatica*	.339
		Pleurozium schreberi	.282	*Dryopteris carthusiana* agg.	.331
				Avenella flexuosa	.326
				Bazzania trilobata	.301
				Athyrium distentifolium	.290
				Plagiothecium laetum	.272
				Plagiothecium undulatum	.268
II. Mid-gradient spruce forests					
Avenella flexuosa	.341	***Vaccinium myrtillus***	.435	*Athyrium distentifolium*	.469
Luzula luzuloides	.328	*Avenella flexuosa*	.402	*Streptopus amplexifolius*	.411
Polytrichum formosum	.297	*Athyrium distentifolium*	.310	*Luzula sylvatica*	.310
Dryopteris carthusiana **agg.**	.283	*Luzula sylvatica*	.308	*Rumex alpestris*	.306
Soldanella hungarica	.269	*Trientalis europaea*	.308	***Homogyne alpina***	.293
Luzula pilosa	.255	***Calamagrostis villosa***	.297	***Calamagrostis villosa***	.288
Calamagrostis villosa	.251	***Homogyne alpina***	.287	***Dryopteris carthusiana*** **agg.**	.275
Homogyne alpina	.238	***Dryopteris carthusiana*** **agg.**	.266	*Polytrichum formosum*	.272
Gymnocarpium dryopteris	.224	*Dicranum scoparium*	.227	*Oxalis acetosella*	.267
Oxalis acetosella	.217	*Carex pilulifera*	.219	***Vaccinium myrtillus***	.252
Carex pilulifera	.206	*Calamagrostis arundinacea*	.206	*Dicranum scoparium*	.234
Vaccinium myrtillus	.204			*Trientalis europaea*	.216
Calamagrostis arundinacea	.198				
Blechnum spicant	.198				
Hieracium sylvaticum	.196				

Data set editing, calculations of Ellenberg indicator values and of the phi coefficients were performed in the program JUICE 5.0 (Tichý 2002; see also web site www.sci.muni.cz/botany/juice.htm). Scatter plots of indicator values were drawn in STATISTICA 5.5 (StatSoft 2000).

RESULTS

Diagnostic species yielded from the comparison of only spruce forests among the three mountain ranges (Comparison A, Fig. 2A, Table 4) were numerous for the Eastern Alps, but rather few for the Bohemian Massif and particularly for the Western Carpathians. When all spruce forests were compared, many of the diagnostic species for the Alps were basiphilous species, confined to limestone or dolomite, such as *Adenostyles glabra*, *Calamagrostis varia*,

Table 6. Diagnostic species of spruce forests in the three mountain ranges. Spruce forests of each mountain range are simultaneously compared with the other forests of the same mountain range and with all the forests of the other mountain ranges (Fig. 2C). Numbers are phi coefficients of association between the species and spruce forests of particular mountain ranges.

Eastern Alps		Western Carpathians		Bohemian Massif	
I. All spruce forests					
Larix decidua	.317	(no species exceeded the threshold phi=.206)		*Calamagrostis villosa*	.390
Luzula luzulina	.281			*Trientalis europaea*	.377
Homogyne alpina	.281			*Sphagnum girgensohnii*	.348
Melampyrum sylvaticum	.278			*Polytrichum commune*	.338
Plagiochila asplenioides	.268			*Avenella flexuosa*	.276
Hylocomium splendens	.237			*Vaccinium myrtillus*	.271
Adenostyles glabra	.235			*Galium harcynicum*	.263
Gentiana asclepiadea	.229			*Dicranum scoparium*	.263
Rhytidiadelphus triquetrus	.226			*Polytrichum formosum*	.261
Vaccinium myrtillus	.225			*Plagiothecium laetum*	.243
Veratrum album	.218			*Streptopus amplexifolius*	.214
Ctenidium molluscum	.214			*Dryopteris carthusiana* agg.	.213
Ranunculus nemorosus	.209			*Lophozia ventricosa*	.211
Solidago virgaurea	.206			*Athyrium distentifolium*	.206
Blechnum spicant	.206				
II. Mid-gradient spruce forests					
Homogyne alpina	.242	*Athyrium distentifolium*	.162	*Streptopus amplexifolius*	.337
Blechnum spicant	.203			*Athyrium distentifolium*	.332
Luzula luzulina	.199			*Calamagrostis villosa*	.234
Avenella flexuosa	.197			*Trientalis europaea*	.226
Larix decidua	.190			*Polytrichum formosum*	.199
Gentiana asclepiadea	.186			*Dryopteris carthusiana* agg.	.180
Polytrichum formosum	.185			*Plagiothecium laetum*	.177
Luzula luzuloides	.177			*Avenella flexuosa*	.166
Rhytidiadelphus loreus	.176			*Rumex alpestris*	.158
Vaccinium myrtillus	.174				
Veratrum album	.173				
Gymnocarpium dryopteris	.161				
Luzula sylvatica	.161				
Soldanella hungarica	.160				
Luzula pilosa	.158				

and *Ctenidium molluscum*. These species were eliminated by restricting the comparison to the mid-gradient spruce forests. However, even then the Alpic spruce forests were better characterized in terms of diagnostic species than the spruce forests of the Carpathians or the Bohemian Massif.

The results were sharply different when the spruce forests were compared with the other forests, separately in each of the mountain ranges (Comparison B, Fig. 2B, Table 5). For all spruce forests, the Bohemian Massif and the Western Carpathians had many more diagnostic species than the Eastern Alps. For the mid-gradient spruce forests, the number of diagnostic species was roughly equal for the three mountain ranges. Still, the diagnostic species of the Bohemian Massif and Western Carpathians had on average higher phi values, implying a higher diagnostic capacity.

Table 7. Diagnostic species of Central European spruce forests. Relevés of the three mountain ranges were pooled and spruce forests compared with the other forests (Fig. 2D). Numbers are phi coefficients of association between the species and spruce forests.

I. All spruce forests		II. Mid-gradient spruce forests	
Vaccinium myrtillus	.405	*Avenella flexuosa*	.283
Calamagrostis villosa	.365	*Athyrium distentifolium*	.282
Dicranum scoparium	.363	*Vaccinium myrtillus*	.274
Avenella flexuosa	.335	*Calamagrostis villosa*	.273
Polytrichum formosum	.314	*Dryopteris carthusiana* agg.	.272
Homogyne alpina	.304	*Homogyne alpina*	.267
Dryopteris carthusiana agg.	.272	*Polytrichum formosum*	.266
Sphagnum girgensohnii	.256	*Streptopus amplexifolius*	.260
Trientalis europaea	.255	*Oxalis acetosella*	.229
Luzula sylvatica	.241	*Luzula sylvatica*	.222
Bazzania trilobata	.227	*Luzula pilosa*	.201
Oxalis acetosella	.226	*Dicranum scoparium*	.200
Polytrichum commune	.224	*Carex pilulifera*	.175
Luzula pilosa	.216	*Trientalis europaea*	.167
Hylocomium splendens	.208	*Gymnocarpium dryopteris*	.164
Plagiothecium undulatum	.201	*Blechnum spicant*	.163
Melampyrum sylvaticum	.200	*Thelypteris phegopteris*	.156
Pleurozium schreberi	.184	*Gentiana asclepiadea*	.153
Rhytidiadelphus loreus	.183	*Plagiothecium undulatum*	.152
Blechnum spicant	.182	*Maianthemum bifolium*	.150

The comparison of spruce forests of particular mountain ranges with all the other forests (Comparison C, Fig 2C, Table 6) yielded a result which was a sort of compromise between the two previous comparisons. The set of diagnostic species for the spruce forests of the Eastern Alps was more similar to the set resulting from the Comparison A of only spruce forests between the three mountain ranges. For the Western Carpathians, diagnostic values of species were very low. This result was similar for all and mid-gradient spruce forests.

The comparison of spruce forests with the other forests, using pooled data from the three mountain ranges (Comparison D, Fig. 2D, Table 7) gave a similar result as the Comparison B of spruce with the other forests for the Bohemian Massif and the Western Carpathians. Again, the resulting diagnostic species were roughly similar for all and mid-gradient spruce forests.

DISCUSSION

Differentiation of spruce forests in the Central European mountain ranges

Picea abies is known to homogenize habitats for plants of the field layer through the accumulation of slowly decomposing, acidic coniferous litter (JAHN 1977, ELLENBERG 1996). Such conditions are suitable only for a few plants, such as *Avenella flexuosa*, *Dryopteris carthusiana* agg., *Oxalis acetosella*, and *Vaccinium myrtillus*. These species and a few others with similar ecological requirements are widespread in most spruce forests (Table 2) and some of them can be considered as diagnostic of spruce forests if the spruce forests are compared with the other forests of the same area (Tables 5 and 7). However, they can hardly be used for discrimination between different types of spruce forests (WALLNÖFER 1993, ELLENBERG 1996).

The comparison among the spruce forests in the three mountain ranges (Fig. 2A, Table 4) clearly shows that the centre of floristic diversity of the Central European spruce forests is in the Alps. Alpic spruce forests were positively differentiated by many species, not only in the comparison based on all spruce forests, where basiphilous species formed a substantial part of the diagnostic species group, but also in the comparison based on mid-gradient spruce forests, with calcareous habitats largely eliminated from the data set. This pattern was already documented by JAHN (1977, 1985), although she used a much smaller data set.

The remarkable floristic richness of the Alpic spruce forests is perhaps partly due to the peculiar situation in the dry and continental valleys of the Central Alps, where beech (*Fagus sylvatica*) is absent, and the soils which would otherwise be occupied by this strongly competitive deciduous tree are dominated by spruce (MAYER 1974, JAHN 1977, WALLNÖFER 1993, ELLENBERG 1996). While the species composition of the tree layer is mainly determined by macroclimate, the herb layer has a more favourable microclimate, and its species composition is more dependent on soil conditions. On suitable soils, many species typical of deciduous forests grow under a spruce canopy, and some of these species positively differentiate Alpic spruce forests against the spruce forests in the other ranges. In the subcontinental transition zone between the Outer and the Central Alps, species of deciduous forests are abundant in natural coniferous forests even on siliceous bedrock (MAYER 1969, ZUKRIGL 1973). In this zone, *Abies alba* is a naturally dominating tree species, whereas in more oceanic regions like the Bohemian Massif, spruce is mostly associated with beech. Thus, *Abies* is a differential species of Alpic spruce forests (Table 4).

Another typical feature of the valleys in the Central Alps is the widespread occurrence of *Larix decidua*, a species with the highest fidelity to the Alpic spruce forests. Although *Larix* is also found in the continental central ranges of the Western Carpathians (MICHALKO et al. 1987), it is much less widespread there than in the Alps. From the data we have, spruce forests of the Western Carpathians appear to be surprisingly poor in diagnostic species. Our trial analyses have shown that this is not an artefact of the lower number of spruce forest relevés from the Western Carpathians. A possible explanation is the transitional species composition of the Western Carpathian spruce forests between those of the Eastern Alps and of the Bohemian Massif (see also Fig. 1).

The comparison of the spruce forests with the other forests yielded similar groups of diagnostic species in all the three mountain ranges, namely in the variant where mid-gradient spruce forests were used as the basis of comparison (Fig. 2B, Table 5). Although realized through similar groups of diagnostic species, this differentiation is strongest in the Bohemian Massif and weakest in the Eastern Alps. There are two possible complementary explanations. First, the gentle topography of the Bohemian Massif results in altitudinal vegetation belts that are spatially extensive and rather homogeneous. Mosaics of natural spruce and beech or fir forests are therefore much rarer in the Bohemian Massif than in the rugged topography of the other two ranges; occurrence of beech forest species in spruce forests and vice versa is therefore less frequent in the Bohemian Massif. This is in accordance with the results of EWALD (2000) who found only small differences in the species composition of the herb layer between spruce and beech forests of the northern Calcareous Alps. Second, deciduous forest species occurring in spruce forests of the beech-free continental valleys of the Central Alps level off the floristic differences between spruce and other forests on the scale of the whole of the Eastern Alps.

Generally, diagnostic species yielded by comparisons of spruce forests with the other forests (Tables 5 and 7) are in good accordance with published lists (e.g. JAHN 1977, WALLNÖFER 1993, MORAVEC et al. 1995). Some species reported in the literature as diagnostic of the Central European spruce forests, however, were not ranked among the most faithful in our analyses. This concerns for example *Vaccinium vitis-idaea*, *Orthilia secunda* and *Lycopodium annotinum* which are also commonly found in pine, acidophilous oak or acidophilous beech forests, the liverworts *Barbilophozia lycopodioides* and *B. floerkei* which may be overlooked by some researchers, and rare species such as *Corallorhiza trifida*, *Listera cordata* and *Moneses uniflora*. Still, all the above mentioned species do show a preference for spruce forests. On the other hand, species of the genus *Pyrola* were not indicated as preferential for spruce forests, perhaps partly due to their rare occurrence, and partly due to their preference of pine or acidophilous oak forests.

General remarks on the interpretation of diagnostic species

A comparison of species occurrence within and outside a vegetation unit is necessary for the determination of its diagnostic status. The comparisons performed in this paper simulated two different approaches which are used by phytosociologists: (A) narrowing the ecological and extending the geographical range of the comparative data (Fig. 2A), and (B) narrowing the geographical and extending the ecological range (Fig. 2B).

Our results show that in Comparison A, Alpic spruce forests were very well positively differentiated, while this was not the case of spruce forests in the other mountain ranges. In Comparison B, however, the pattern was reversed: spruce forests of the Bohemian Massif and of the Western Carpathians were better differentiated than the Alpic spruce forests.

These results suggest that published lists of diagnostic species must be interpreted with caution. Unless we know what community types were used for comparison by the author of the list of diagnostic species, we can hardly use these species for practical identification of vegetation units. Often the comparative data set is published in phytosociological tables. Very often, however, authors who work locally but have a broad geographical background subjectively estimate diagnostic capacity of species, combining both geographical and local ecological perspectives. This approach is similar to Comparison C (Fig. 2C) made in the current paper, which could be superior to the above two. Unless the considered factors are explicitly stated, however, there are hidden unknowns concerning the weighting of these two perspectives and the influence of the author's knowledge on the result. This is also the case with national vegetation surveys that are based on literature review rather than on data analysis, such as MUCINA et al. (1993) or MORAVEC et al. (1995), to name two examples from the countries covered by the current study. Diagnostic species in these surveys are usually taken over from specialized studies which greatly vary in putting the emphasis on either geographical or local ecological context.

A reconciliation of the geographical and local ecological perspectives could be found in a comparison of each vegetation unit with all the other units, simultaneously over a large geographical area and a broad environmental gradient, as simulated in Comparison C of the current study. However, even though we compiled one of the largest phytosociological data sets ever used for a single analysis, its geographical and ecological extent was nonetheless limited. First, it lacked data from the natural range of spruce forests in northern Europe and in the other mountain ranges of Central and southeastern Europe. Second, it did not include treeless vegetation, although the species composition of some treeless vegetation types may be quite similar to the spruce forests (e.g. *Vaccinium* heaths, forest clearings or subalpine tall-forb vegetation). This highlights the difficulties of obtaining universally valid comparisons.

Clearly, the context-dependence of diagnostic species, particularly the divergence between local ecological and broader geographical perspectives, will continue to dominate phytosociology even in the era of large electronic vegetation-plot databases. In general, the focused application of only one of the perspectives will provide the most efficient means of practical identification of vegetation units in a given context. It is therefore critical that care be taken to apply published lists of diagnostic species only in the context used by the original author.

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