Tuexenia 33: 25–48. Göttingen 2013.
available online at www.tuexenia.de

# Differentiation of the *Piceetalia* and *Athyrio-Piceetalia* forests in Slovenia

## Differenzierung der *Piceetalia*-und *Athyrio-Piceetalia*-Wälder in Slowenien

Nina Juvan[1,*], Petra Košir[2], Aleksander Marinšek[3], Andrej Paušič[4], Andraž Čarni[4]

[1]*Anton Melik Geographical Institute, Research Centre of Slovenian Academy of Sciences and Arts, Novi trg 2, SI-1000 Ljubljana, Slovenia*
[2]*UP FAMNIT, University of Primorska, Glagoljaška 8, SI-6000 Koper, Slovenia*
[3]*Higher Vocational College for Forestry and Hunting, Ljubljanska 2, SI-6230 Postojna, Slovenia*
[4]*Jovan Hadži Institute of Biology, Research Centre of Slovenian Academy of Sciences and Arts, Novi trg 2, SI-1000 Ljubljana, Slovenia*
**Corresponding author, e-mail: nina.juven@zrc-sazu.si*

### Abstract

The article deals with Norway spruce (*Picea abies*), silver fir (*Abies alba*) and larch (*Larix decidua*) forests of the orders *Piceetalia* and *Athyrio-Piceetalia* (*Vaccinio-Piceetea*) in Slovenia. A total of 934 relevés of spruce, larch and fir forests within the *Piceetalia* and *Athyrio-Piceetalia* were collected from the literature. After resampling, 319 relevés remained, originating from 28 associations. Classification revealed two major groups of spruce, larch and fir forests, one thriving on non-carbonate bedrock and the other on carbonate. We further divided forests on non-carbonate substrate into two major groups – one thriving at high altitudes and the other in lowlands, both assigned to *Piceion abietis*. The second major group contains mesophilous, species-rich communities found mostly on carbonate bedrock. This major group can be further divided into four groups. The group of secondary forest on sites of beech forests, as well as the group of forest found in frost hollows can be assigned to *Abieti-Piceion.* The group of herb-rich, mesophilous communities forming zonal spruce and larch forests can be assigned to *Chrysanthemo-Piceion* and the group of forests on boulder scree to *Calamagrostio-Abietion.* Analysis of structural, functional, phytogeographical and geomorphological features, as well as ecological conditions estimated by bioindicator values, demonstrated the usefulness of this classification.

**Keywords:** *Abies alba,* forest communities, phytosociology, *Picea abies*, site ecology, *Vaccinio-Piceetea*

**Erweiterte deutsche Zusammenfassung am Ende des Textes**

## 1. Introduction

Coniferous forests on acidic soils of the northern hemisphere are classified within the class of *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939 (BOUBLÍK & ZELENÝ 2007, ERMAKOV & MAKHATKOV 2011, ERMAKOV & MOROZOVA 2011, LIN et al. 2012, SPRIBILLE & CHYTRÝ 2002). They include boreal types of forest and woodland that are widespread in the

Manuscript received 31 January 2013, accepted 11 June 2013
Co-ordinating Editor: Jörg Ewald

coldest parts of the northern hemisphere; in temperate regions, they are found only in mountainous areas and appear fragmentarily on the border with the Mediterranean region (GEORGIADIS et al. 2012, SPRIBILLE & CHYTRÝ 2002). The ecological optimum of the class is in areas with relatively unfavourable and cool summers and cold winters (WALLNÖFER 1993). In Europe, these forests are classified within the order *Piceetalia abietis* Pawłowski in Pawłowski et al. 1928 nom. mut. propos. on non-carbonate bedrock and *Athyrio-Piceetalia* Hadač 1969 on carbonate and base rich silicate bedrock (HADAČ et al. 1969, RODWELL et al. 2002).

In Slovenia, SFF (spruce, larch and fir forests) have been placed in one single alliance, *Vaccinio-Piceion,* divided into several sub-alliances (ZUPANČIČ 2007, ZUPANČIČ & ŽAGAR 2010). However, in recent years, the diversity of SFF on a European scale has been reflected in several ecologically based alliances (RODWELL et al. 2002, WILLNER & GRABHERR 2007). There appears a need in nature conservation to calibrate habitat types and vegetation units on a European level, in order to unify the classification system (BIONDI et al. 2012, RODWELL et al. 2002).

Soils under SFF are characterised by an accumulation of acid humus, which remains poorly mineralized because of low temperatures. Due to relatively high precipitation in Slovenia, which can exceed 2000 mm in some places (ARSO) and low evaporation due to low temperatures, water is generally abundant. Cations are consequently leached, microbial release of nitrogen and phosphorous is slow and soils are of relatively low fertility (EWALD 2000, MÁLIŠ et al. 2010).

The first studies of European coniferous forests were already carried out in the 1920s and 1930s (e.g., BRAUN-BLANQUET et al. 1939, SZAFER et al. 1923). BRAUN-BLANQUET et al. (1939) were the first to propose the assignment of coniferous forests associations to their own class *Vaccinio-Piceetea*. BECK (1906) was the first to describe spruce forests in Slovenia. Coniferous forests were later studied according to the standard Braun-Blanquet method (BRAUN-BLANQUET 1964) by many researchers, most notably Maks Wraber and Mitja Zupančič. An extensive list of publications is given in the references and in the electronic appendix.

The aim of the present work was to collect all available data and to prepare a synthetic overview of SFF in Slovenia, based on numerical analysis. We tried to discover the main groups of SFF, to identify their ecological conditions and to evaluate their floristic, structural and chorological peculiarities.

## 2. Material and methods

### 2.1 Study area

The study took place in Slovenia, which is situated at the southern outcrops of the Alps and northern outcrops of the Dinaric Alps. It lies between latitudes 45°25'N-46°53'N and longitudes 13°23'E-16°36'E. The climate is subject to alpine, mediterranean and continental influences. Precipitation varies across the country, from 800 mm in the eastern to 3000 mm in the western part. Average altitude is 557 m (PERKO & OROŽEN-ADAMIČ 1998). More than half of the area is covered by forest and more than 70% of forests are dominated by beech (ČARNI et al. 2002, ZGS 2012). The area is classified as the Euro-Siberian region, which is subdivided into the Alpine, Apennine-Balkan and Pannonian-Carpathian provinces (RIVAS-MARTÍNEZ et al. 2011).

### 2.2 Methods

A total of 934 Slovenian relevés of communities classified in the order *Piceetalia* and *Athyrio-Piceetalia* were collected from the literature and entered into a TURBOVEG (HENNEKENS & SCHAMINÉE 2001) database. Relevés with a dominance of Norway spruce (*Picea abies*), European larch (*Larix decidua*) or Silver fir (*Abies alba*) were considered. In each relevé the cover value of one above mentioned species was more than 3 (25%) on the Braun-Blanquet scale. We did not consider communities on nutrient poor and hydromorphic soils dominated by pine (*Pinetalia sylvestris* Oberd. 1957), nor subalpine krummholz communities (*Roso pendulinae-Pinetea mugo* Theurillat in Theurillat et al. 1995, ŠILC & ČARNI 2012). We executed heterogeneity-constrained resampling of the collected relevés, where the number of selected relevés was driven by beta-diversity. Thus, up to 30 relevés were chosen from each association (LENGYEL et al. 2011). After stratification 319 relevés originating from 28 associations remained. For the purpose of numerical analysis, species present in one relevé were excluded, all sub-layers were united into a single layer and certain subspecies and varieties were integrated into the level of species or aggregates (TSIRIPIDIS et al. 2007). The final dataset consisted of 863 species.

Classification was carried out on the square root-transformed matrix using Ward's method, with relative Sørensen as a distance measure. Different cluster divisions were tried, but the six-cluster solution, which was used for the next steps, was best interpretable in ecological terms. Calculations were run in the PC-ORD (MCCUNE & MEFFORD 1999).

The characteristic species of individual plot groups were determined by calculating the species' percentage frequency and fidelity and are presented in the combined synoptic table. The phi coefficient calculated in JUICE was used as a fidelity measure (TICHÝ & HOLT 2006). The threshold phi value (multiplied by 100 in JUICE) for species to be considered as characteristic was arbitrarily set at 40. We call species constant that appear in to at least 80% of the relevés and dominant that appear with cover values of 2 (5%) or higher in at least 50% of relevés.

To evaluate the ecological information content of plots with respect to light, temperature, moisture, soil reaction and nutrients, average Ellenberg indicator values (ELLENBERG et al. 1992) were calculated in JUICE. Ecological relationships among groups were presented by box plots made in STATISTICA 8 (STATSOFT 2007). Box plots were also used to compare the studied groups with respect to altitude, slope and aspect. As original sources gave no assignment of individual plots to geological units, plot clusters were interpreted with respect to prevailing bedrock type by consulting descriptions of community types.

Spectra of life forms (RAUNKIAER 1934) and chorological types (PIGNATTI et al. 2005) were calculated for each relevé and mean proportions compared between groups. CSR-strategy types were calculated for each group and presented in a Grime triangle diagram (BECKER et al. 2011, GRIME 2002, SCHMITT et al. 2010).

### 2.3 Nomenclature

The nomenclature of species of pteridophytes and spermatophytes follows MARTINČIČ et al. (1999), bryophytes MARTINČIČ (2003) and lichens WIRTH (1995). Syntaxonomical affiliation of species was taken from OBERDORFER & MÜLLER (1994). The syntaxonomical classification generally follows the synsystem proposed by ŠILC & ČARNI (2012).

## 3. Results

### 3.1 Plot database and stratified subsample

From 21 sources of literature we collected total of 934 relevés of 28 communities classified in the orders *Piceetalia* or *Athyrio-Piceetalia*. Average relevé size was around 400 m$^2$. After stratification, where up to 30 relevés were chosen from each association, 319 relevés with 863 species remained.

### 3.2 Classification and characteristic species

The Ward classification (Fig. 1) of the data set revealed two major groups of SFF. The first major group of these forests is found on non-carbonate substrates (tonalit, granit, gneiss, conglomerate, sandstone, schist, as described in ACCETTO 1986, BELEC 2009, KOŠIR 1994, MARINČEK 1975, 1980, 1995, TREGUBOV 1957, TREGUBOV & ČOKL 1957, WRABER 1958, 1959, 1963, ZUPANČIČ 1982, 1999) and consists of two groups, one of which appears as high altitudinal acidophilous SFF (Fig. 1 and Table 1, group 5) and the other lowland acidophilous SFF (Fig. 1 and Table 1, group 6). The second major group, containing SFF richer in species, found mostly on carbonate bedrock (such as limestone, dolomite, clay, alluvial sediments, as described in ACCETTO 1993, 2006, DAKSKOBLER 2003, 2006, TREGUBOV 1957, WRABER 1969, ZUPANČIČ 1980, 1999, ZUPANČIČ & ACCETTO 1994, ZUPANČIČ & ŽAGAR 2010), is made up of four groups: the first group (Fig. 1 and Table 1, group 1) represents herb-rich mesophilous SFF, constituting zonal vegetation at higher altitudes and larch forests, the second group (Fig. 1 and Table 1, group 2) contains SFF from more favourable sites, mainly of secondary origin, the third group (Fig. 1 and Table 1, group 3) SFF found in frost hollows and the fourth group (Fig. 1 and Table 1, group 4) SFF on boulder screes.

The characteristic species of the six individual groups are presented in a combined synoptic table (Table 1). There are very few species characteristic of the major group on non-carbonate bedrock (*Avenella flexuosa, Blechnum spicant*) and many for the major group on carbonate bedrock (e.g., *Ctenidium molluscum, Daphne mezereum, Valeriana tripteris*). In the following, individual groups are interpreted in detail.

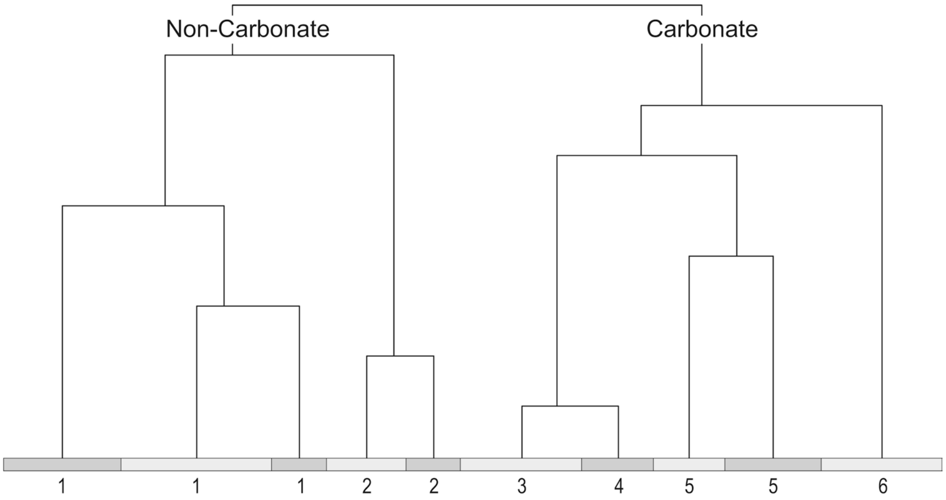

**Fig. 1.** Simplified cluster dendrogram of spruce forests data. Clusters 1–4 are found on carbonate bedrock, clusters 5–6 on non-carbonate bedrock. Legend: 1 – zonal, altimontane SFF, 2 – secondary SFF, 3 – frost hollows SFF, 4 – boulder scree SFF, 5 – altitudinal SFF, 6 – lowland SFF.

**Abb. 1.** Dendrogramm der Clusteranalyse von Daten aus Fichten-, Lärchen- und Tannenwäldern. Cluster 1-4 auf Carbonatgesteinen, Cluster 5-6 auf carbonatfreien Gesteinen. Legende: 1 – höhenzonal, 2 – sekundär, 3 – Kaltluftsenken, 4 – Blockhalden, 5 – Hochlagen 6 – Tiefland.

**Table 1.** Combined synoptic table of the Ward classification. Sources of data used for the analysis are in Appendix S1. Group numbers correspond to those in Fig. 1.

**Tabelle 1.** Kombinierte Stetigkeitstabelle der Ward-Klassifikation. Datenquellen, die für die Analyse verwendet werden, sind im Anhang S1 aufgeführt. Die Gruppennummern entsprechen denen in Abb. 1.

| Group No. | 1 | | 2 | | 3 | | 4 | | 5 | | 6 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Numbers of relevés | 30 | | 50 | | 39 | | 50 | | 91 | | 59 | |
| **Characteristic species for groups** | | | | | | | | | | | | |
| Sesleria albicans | 87 | 84,7 | 12 | --- | . | --- | . | --- | . | --- | . | --- |
| Laserpitium peucedanoides | 77 | 75,8 | 16 | --- | . | --- | . | --- | . | --- | . | --- |
| Betonica alopecuros | 70 | 66,8 | 24 | 10,3 | . | --- | . | --- | . | --- | . | --- |
| Paederota lutea | 50 | 64,1 | 4 | --- | . | --- | . | --- | . | --- | . | --- |
| Valeriana saxatilis | 47 | 63,2 | 2 | --- | . | --- | . | --- | . | --- | . | --- |
| Rhodothamnus chamaecistus | 50 | 62,5 | 6 | --- | . | --- | . | --- | . | --- | . | --- |
| Aster bellidiastrum | 60 | 61,1 | 14 | --- | 3 | --- | 4 | --- | . | --- | . | --- |
| Larix decidua | 77 | 59,8 | 30 | 9,1 | 3 | --- | . | --- | 19 | --- | 2 | --- |
| Pinus mugo | 43 | 56,8 | . | --- | . | --- | 2 | --- | 4 | --- | . | --- |
| Primula auricula | 33 | 54,2 | . | --- | . | --- | . | --- | . | --- | . | --- |
| Geranium sylvaticum | 43 | 54,1 | 10 | 1,7 | . | --- | . | --- | . | --- | . | --- |
| Phyteuma orbiculare | 50 | 53 | 12 | --- | 8 | --- | . | --- | 1 | --- | . | --- |
| Rhododendron hirsutum | 50 | 52,3 | 6 | --- | . | --- | 16 | 5,5 | . | --- | . | --- |
| Festuca stenantha | 30 | 51,3 | . | --- | . | --- | . | --- | . | --- | . | --- |
| Schistidium apocarpum | 30 | 51,3 | . | --- | . | --- | . | --- | . | --- | . | --- |
| Campanula scheuchzeri | 50 | 50,5 | 18 | 7,4 | 5 | --- | . | --- | 2 | --- | . | --- |
| Lilium martagon | 37 | 48,3 | 6 | --- | . | --- | . | --- | 2 | --- | 2 | --- |
| Salix appendiculata | 70 | 48,3 | 10 | --- | 21 | --- | 24 | --- | 5 | --- | 14 | --- |
| Lotus corniculatus | 30 | 47,1 | 4 | --- | . | --- | . | --- | . | --- | . | --- |
| Carduus crassifolius | 27 | 45,9 | 2 | --- | . | --- | . | --- | . | --- | . | --- |
| Saxifraga crustata | 27 | 45,9 | 2 | --- | . | --- | . | --- | . | --- | . | --- |
| Carex ornithopoda | 27 | 45,9 | . | --- | . | --- | 2 | --- | . | --- | . | --- |
| Convallaria majalis | 27 | 45,9 | 2 | --- | . | --- | . | --- | . | --- | . | --- |
| Hieracium villosum | 23 | 45 | . | --- | . | --- | . | --- | . | --- | . | --- |
| Campanula carnica | 23 | 45 | . | --- | . | --- | . | --- | . | --- | . | --- |
| Carex sempervirens | 23 | 45 | . | --- | . | --- | . | --- | . | --- | . | --- |
| Carex humilis | 23 | 45 | . | --- | . | --- | . | --- | . | --- | . | --- |
| Plagiochila porelloides | 23 | 45 | . | --- | . | --- | . | --- | . | --- | . | --- |
| Campanula witasekiana | 27 | 43,8 | 4 | --- | . | --- | . | --- | . | --- | . | --- |
| Aconitum lycoctonum | 30 | 42,1 | 2 | --- | 8 | 1,9 | . | --- | . | --- | . | --- |
| Festuca calva | 20 | 41,5 | . | --- | . | --- | . | --- | . | --- | . | --- |
| Mnium thomsonii | 20 | 41,5 | . | --- | . | --- | . | --- | . | --- | . | --- |
| Vicia sylvatica | 20 | 41,5 | . | --- | . | --- | . | --- | . | --- | . | --- |
| Laburnum alpinum | 37 | 40,5 | 22 | 18,4 | . | --- | . | --- | . | --- | . | --- |
| Laserpitium latifolium | 23 | 40,3 | 4 | --- | . | --- | . | --- | . | --- | . | --- |
| Alnus alnobetula | 20 | 40 | . | --- | . | --- | . | --- | 1 | --- | . | --- |
| Helleborus niger | 13 | --- | 78 | 76,7 | 3 | --- | . | --- | . | --- | . | --- |
| Euphorbia amygdaloides | 7 | --- | 70 | 65,7 | 10 | --- | 6 | --- | . | --- | 3 | --- |
| Fissidens taxifolius | . | --- | 48 | 65 | . | --- | . | --- | 1 | --- | . | --- |
| Ajuga reptans | . | --- | 44 | 55,2 | 3 | --- | . | --- | . | --- | 7 | --- |
| Aposeris foetida | 37 | 10,5 | 80 | 54,6 | 26 | --- | . | --- | 12 | --- | 3 | --- |
| Salvia glutinosa | 7 | --- | 54 | 51,2 | . | --- | 6 | --- | 1 | --- | 17 | 3,6 |
| Potentilla erecta | 3 | --- | 38 | 47,2 | . | --- | . | --- | 10 | 2,2 | . | --- |
| Campanula cochleariifolia | 10 | 3,1 | 36 | 45,8 | 3 | --- | . | --- | . | --- | . | --- |
| Brachypodium sylvaticum | . | --- | 32 | 45 | . | --- | 4 | --- | 1 | --- | 3 | --- |
| Aquilegia nigricans | 17 | 11,7 | 38 | 44,9 | . | --- | . | --- | . | --- | . | --- |
| Epipactis helleborine | . | --- | 30 | 44,5 | . | --- | 4 | --- | 1 | --- | 2 | --- |
| Digitalis grandiflora | 3 | --- | 28 | 44,1 | . | --- | . | --- | . | --- | 2 | --- |
| Fraxinus excelsior | . | --- | 30 | 43,1 | . | --- | . | --- | . | --- | 8 | 3,8 |

| Group No. | 1 | | 2 | | 3 | | 4 | | 5 | | 6 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Numbers of relevés | 30 | | 50 | | 39 | | 50 | | 91 | | 59 | |
| Knautia drymeia ssp. drymeia | 10 | --- | 42 | 42,3 | 18 | 8,8 | . | --- | . | --- | . | --- |
| Polygala chamaebuxus | 30 | 23,2 | 44 | 42 | . | --- | . | --- | 2 | --- | . | --- |
| Galium mollugo | 3 | --- | 26 | 41,8 | . | --- | 2 | --- | . | --- | . | --- |
| Hepatica nobilis | 43 | 28,9 | 54 | 41,3 | 3 | --- | 10 | --- | . | --- | . | --- |
| Dactylorhiza maculata | 3 | --- | 36 | 41 | 10 | 1,4 | 2 | --- | 4 | --- | . | --- |
| Viola reichenbachiana | 10 | --- | 52 | 41 | 18 | --- | 6 | --- | 4 | --- | 14 | --- |
| Dicranum polysetum | . | --- | 14 | --- | 79 | 66,4 | 2 | --- | 23 | 3,4 | 2 | --- |
| Rhytidiadelphus loreus | 3 | --- | 18 | --- | 87 | 55,8 | 30 | --- | 36 | 6,1 | 5 | --- |
| Calamagrostis arundinacea | 43 | 3,6 | 4 | --- | 95 | 50,7 | 4 | --- | 40 | --- | 51 | 10,4 |
| Doronicum austriacum | . | --- | 6 | --- | 62 | 49,7 | 12 | --- | 14 | --- | 17 | --- |
| Lamiastrum galeobdolon | . | --- | . | --- | 49 | 49,6 | 12 | --- | 1 | --- | 12 | --- |
| Carex pilosa | . | --- | . | --- | 33 | 49,2 | . | --- | . | --- | 5 | --- |
| Plagiothecium laetum | . | --- | . | --- | 23 | 42,6 | . | --- | . | --- | 2 | --- |
| Cladonia furcata | . | --- | . | --- | 5 | --- | 52 | 64,7 | . | --- | . | --- |
| Peltigera praetextata | . | --- | . | --- | . | --- | 40 | 59,8 | . | --- | . | --- |
| Campanula justiniana | . | --- | . | --- | 5 | --- | 42 | 56,8 | . | --- | . | --- |
| Pseudevernia furfuracea | . | --- | . | --- | . | --- | 34 | 54,8 | . | --- | . | --- |
| Mycelis muralis | . | --- | 42 | 10,9 | 28 | --- | 86 | 53,6 | 4 | --- | 24 | --- |
| Cladonia coniocraea | . | --- | . | --- | . | --- | 32 | 53,1 | . | --- | . | --- |
| Chiloscyphus polyanthos | . | --- | . | --- | . | --- | 30 | 50,1 | 1 | --- | . | --- |
| Mnium hornum | . | --- | . | --- | 3 | --- | 30 | 48,5 | . | --- | . | --- |
| Plagiomnium rostratum | . | --- | . | --- | . | --- | 26 | 47,6 | . | --- | . | --- |
| Festuca altissima | 3 | --- | . | --- | 18 | 5,3 | 50 | 46,8 | . | --- | 12 | --- |
| Bryum capillare | 17 | 11 | . | --- | . | --- | 40 | 46,7 | . | --- | . | --- |
| Plagiothecium ruthei | . | --- | . | --- | 3 | --- | 28 | 46,6 | . | --- | . | --- |
| Brachythecium rutabulum | . | --- | . | --- | . | --- | 26 | 46,3 | 1 | --- | . | --- |
| Blepharostoma trichophyllum | . | --- | . | --- | . | --- | 24 | 45,6 | . | --- | . | --- |
| Peltigera canina | 17 | 11,1 | . | --- | . | --- | 38 | 43,9 | . | --- | 2 | --- |
| Peltigera polydactyla | . | --- | . | --- | . | --- | 22 | 43,6 | . | --- | . | --- |
| Grimmia species | . | --- | . | --- | . | --- | 26 | 42 | . | --- | 5 | --- |
| Mnium stellare | . | --- | . | --- | . | --- | 20 | 41,5 | . | --- | . | --- |
| Hieracium transsylvanicum | . | --- | . | --- | . | --- | . | --- | 3 | --- | 37 | 54,4 |
| Thuidium tamariscinum | . | --- | 8 | --- | 3 | --- | 4 | --- | 3 | --- | 47 | 52,5 |
| Dryopteris dilatata | 20 | 7,5 | . | --- | 3 | --- | . | --- | 10 | --- | 53 | 49,2 |
| Rubus hirtus | . | --- | . | --- | . | --- | . | --- | 13 | 7,1 | 39 | 48,1 |
| Paraleucobryum longifolium | . | --- | . | --- | . | --- | . | --- | . | --- | 22 | 43,7 |
| Castanea sativa | . | --- | 4 | --- | . | --- | . | --- | 7 | --- | 32 | 43,6 |
| Carpinus betulus | . | --- | . | --- | . | --- | . | --- | . | --- | 20 | 41,9 |
| Hedera helix | . | --- | 2 | --- | . | --- | . | --- | . | --- | 22 | 41,1 |
| **Characteristic species for groups over carbonate bedrock** | | | | | | | | | | | | |
| Valeriana tripteris | 70 | 19,2 | 84 | 31,7 | 54 | 4,8 | 80 | 28,2 | 3 | --- | . | --- |
| Ctenidium molluscum | 73 | 17 | 78 | 21,1 | 72 | 15,6 | 98 | 39,1 | 2 | --- | 3 | --- |
| Clematis alpina | 83 | 36,3 | 58 | 13,4 | 38 | --- | 72 | 26 | 2 | --- | 5 | --- |
| Tortella tortuosa | 77 | 31,3 | 44 | 1,7 | 67 | 22,3 | 60 | 16,2 | . | --- | 5 | --- |
| Daphne mezereum | 33 | --- | 92 | 41,9 | 46 | --- | 82 | 32,9 | 7 | --- | 12 | --- |
| Rosa pendulina | 60 | 20,8 | 22 | --- | 59 | 19,9 | 82 | 41,2 | . | --- | 2 | --- |
| Asplenium viride | 77 | 35,9 | 42 | 3,9 | 44 | 5,4 | 62 | 22,4 | 2 | --- | . | --- |
| Calamagrostis varia | 73 | 35,7 | 68 | 30,7 | 13 | --- | 56 | 19,5 | 1 | --- | . | --- |
| Homogyne sylvestris | 33 | --- | 42 | 6,5 | 51 | 15,2 | 78 | 40,3 | 5 | --- | . | --- |
| Carex digitata | 27 | --- | 74 | 34,5 | 44 | 6,3 | 64 | 25,3 | 2 | --- | 10 | --- |
| Adenostyles glabra | 53 | 20,6 | 44 | 11,7 | 56 | 23,6 | 34 | 2,1 | 3 | --- | . | --- |
| Cirsium erisithales | 53 | 25,6 | 26 | --- | 41 | 13,3 | 46 | 18,3 | . | --- | . | --- |
| Mercurialis perennis | 70 | 32,4 | 52 | 15,6 | 31 | --- | 48 | 11,8 | 1 | --- | 10 | --- |
| Fissidens dubius | 67 | 40,1 | 4 | --- | 49 | 22 | 42 | 15,2 | . | --- | . | --- |
| Cyclamen purpurascens | 57 | 30,7 | 68 | 42,1 | 3 | --- | 28 | 1,6 | . | --- | 3 | --- |

| Group No. | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| Numbers of relevés | 30 | 50 | 39 | 50 | 91 | 59 |
| Neckera crispa | 33 $^{10,7}$ | 10 $^{---}$ | 28 $^{5,2}$ | 68 $^{47,4}$ | . $^{---}$ | . $^{---}$ |
| Carex alba | 7 $^{---}$ | $\boxed{74\ ^{58,5}}$ | 21 $^{---}$ | 24 $^{3,5}$ | . $^{---}$ | . $^{---}$ |
| Rubus saxatilis | 70 $^{45,3}$ | $\boxed{66\ ^{41,2}}$ | 15 $^{---}$ | 2 $^{---}$ | 1 $^{---}$ | . $^{---}$ |
| Fragaria vesca | 20 $^{---}$ | 68 $^{37,9}$ | 41 $^{11,4}$ | 36 $^{6,5}$ | 4 $^{---}$ | 7 $^{---}$ |
| Veronica urticifolia | 30 $^{3,6}$ | 50 $^{23,8}$ | 44 $^{17,3}$ | 28 $^{1,5}$ | 2 $^{---}$ | 5 $^{---}$ |
| Erica carnea | $\boxed{67\ ^{45}}$ | 44 $^{21,2}$ | . $^{---}$ | 30 $^{6,5}$ | 2 $^{---}$ | . $^{---}$ |
| Dentaria enneaphyllos | 40 $^{19,3}$ | 34 $^{12,9}$ | 33 $^{12,1}$ | 24 $^{2,1}$ | 1 $^{---}$ | . $^{---}$ |
| Gymnocarpium robertianum | 47 $^{30,3}$ | 22 $^{2,6}$ | 8 $^{---}$ | 42 $^{25}$ | . $^{---}$ | . $^{---}$ |
| Moehringia muscosa | 23 $^{5,6}$ | 28 $^{10,9}$ | 26 $^{8,2}$ | 34 $^{17,9}$ | . $^{---}$ | . $^{---}$ |
| **Characteristic species for groups over non-carbonate bedrock** | | | | | | |
| Avenella flexuosa | . $^{---}$ | 6 $^{---}$ | 36 $^{8,1}$ | 2 $^{---}$ | $\boxed{70\ ^{42,5}}$ | 53 $^{24,7}$ |
| Blechnum spicant | . $^{---}$ | 6 $^{---}$ | 3 $^{---}$ | . $^{---}$ | $\boxed{48\ ^{42,1}}$ | 32 $^{21,8}$ |
| **Common species** | | | | | | |
| Picea abies | 100 $^{5,4}$ | 100 $^{5,4}$ | 100 $^{5,4}$ | 100 $^{5,4}$ | 100 $^{5,4}$ | 92 $^{---}$ |
| Vaccinium myrtillus | 57 $^{---}$ | 86 $^{8,7}$ | 97 $^{21}$ | 90 $^{13}$ | 90 $^{13,1}$ | 47 $^{---}$ |
| Fagus sylvatica | 73 $^{---}$ | 74 $^{---}$ | 72 $^{---}$ | 88 $^{12,9}$ | 58 $^{---}$ | 88 $^{13,1}$ |
| Oxalis acetosella | 37 $^{---}$ | 84 $^{14,2}$ | 95 $^{24,8}$ | 56 $^{---}$ | 65 $^{---}$ | 80 $^{10}$ |
| Abies alba | 33 $^{---}$ | 48 $^{---}$ | 67 $^{---}$ | 100 $^{30,9}$ | 58 $^{---}$ | 100 $^{30,9}$ |

Group 1 – altimontane and subalpine SFF on carbonate bedrock: Diagnostic species for this group are, e.g*., Sesleria caerulea, Laserpitium peucedanoides, Betonica alopecurus,* mainly originating from the alpine and subalpine calcareous swards of *Elyno-Seslerietea* and tall herb vegetation of higher altitudes of *Mulgedio-Aconitetea.* Constant species of these communities are *Picea albies* and *Clematis alpina* and dominant *Larix decidua*. Bedrock is mainly limestone, sometimes dolomite and moraines. The relevés originate from the Julian Alps and Karavanke (Karawanken). Plots classified in this group were originally assigned to *Adenostylo glabrae-Piceetum, Seslerio albicantis-Piceetum* or *Rhodothamno-Laricetum*.

Group 2 – secondary SFF: Diagnostic species for this group are, e.g., *Helleborus niger, Euphorbia amygdaloides, Ajuga reptans*, the majority of them originating from beech forests of *Carpino-Fagetea*. The constant species are *Picea abies, Hiercium murorum, Vaccinium myrtillus, Valeriana tripteris* and *Oxalis acetosella* that appear as constant species in nearly all *Picea abies*-dominated communities, except *Variana tripteris* that is common on crevices and rock cliffs of *Asplenietea*. The dominant species in this forest is *Picea abies*. The bedrock is mainly limestone and dolomite, occasionally also breccia, moraines and alluvial sediments. The relevés originate from Julian Alps, Kamnik-Savinja Alps and Karavanke. Original assignments of plots in this group were in *Aposerido-Piceetum, Laburno alpini-Piceetum, Rhamno fallici-Piceetum, Petasiti-Piceetum, Erico-Piceetum*.

Group 3 – frost hollow SFF: The characteristic species for this group are, e.g., *Dicranum polysetum, Rhytidiadelphus loreus, Calamagrostis arundinacea, Doronicum austriacum,* originating from tall herb vegetation of higher altitudes *Mulgenio-Aconitetea* and mosses that indicate cold and humid habitat. Constant species are *Picea abies*, *Vaccinium myrtillus*, *Oxalis acetosella*, *Gentiana asclepiadea* and *Sorbus aucuparia*. Dominant species are *Picea abies* and *Calamagrostis arundinacea*. Bedrock of the area is composed mainly of limestone and dolomite, but at the bottom of frozen holes, we can find some chert, clay or moraines. *Calamagrostis arundinacea* is a species of non-carbonate bedrock, in the frozen holes it is found because of colluviums of chert above the limestone bedrock. Plots are found in the Dinaric Alps. Plots in this group were originally assigned to *Hacquetio-Piceetum, Stellario montanae-Piceetum, Lonicero caeruleae-Piceetum.*

Group 4 – boulder scree SFF: Diagnostic species for this group are *Cladonia furcata, Peltigera praetextata, Ctenidium molluscum* which are characteristic of skeletal soils with thin humus layer. Constant species are *Picea abies, Abies alba, Vaccinium myrtillus, Fagus sylvatica and Daphne mezereum*. Dominant species are *Picea abies* and *Abies alba*. Plots of this association were found in the Dinaric Alps. Plots were originally assigned to *Campanulo justinianae-Piceetum, Calamagrostio-Abietetum, Neckero-Abietetum*, *Asplenio-Piceetum, Ribeso alpinae-Piceetum.*

Group 5 – acidophilous high elevation SFF: There are two diagnostic species *Avenella flexuosa* and *Blechnum spicant*. Constant species are *Picea abies* and *Vaccinium myrtilus*, whereas *Picea abies* is also dominant species. Bedrock is composed of various non-carbonate bedrock, such as breccia, chert, conglomerate, sandstone, schist etc. The relevés originate from Julian Alps, Kamnik-Savinja Alps, Karavanke and above all from Pohorje that is the only mountain range that is in major part built of non-carbonate bedrock. The associations classified in this group are *Mastigobryo-Piceetum, Sphagno-Piceetum, Rhytidiadelpho lorei-Piceetum, Prenantho purpureae-Piceetum, Avenello flexuosae-Piceetum, Luzulo sylvaticae-Piceetum*.

Group 6. – lowland SFF: the diagnostic species for this group are, e.g., *Hieracium transsylvanicum, Dryopteris dilatata, Thuidium tamariscinum, Castanea sativa, Carpinus betulus,* which indicate lower altitudes and/or acid sites. Bedrock is mainly non-carbonate (tonalite, granite, gneiss, schist, sandstone etc.) that are sometimes mixed with carbonates. The associations classified in this group are *Galio rotundifolii-Abietetum, Bazzanio-Abietetum, Luzulo albidae-Abietetum, Hieracio rotundati-Abietetum, Paraleucobryo-Abietetum, Polysticho setiferi-Abietetum*, *Dryopterido-Abietetum.*

### 3.3 Ellenberg indicator values (Fig. 2)

Ellenberg indicator values show that the highest light availability is in the subalpine SFF and the lowest in frost hollows and lowland acidophilous SFF. Temperatures are the highest in lowland SFF and in secondary SFF. The lowest are in subalpine and altimontane SFF, frost hollows and acidopihlous high altitudinal SFF. Moisture is higher in acidophilous high elevation and lowland SFF and in frost hollow SFF, where we can find impermeable bedrock. On carbonate humidity is much lower. Soil reaction is high on SFF over carbonate bedrock, the lowest within this group is in frost hollows, but lower in acidophilous SFF. Nutrient poor stands can be found at high elevation: in altimontane and subalpine and acidophilous high elevation SFF. The nutrients richest are acidophilous lowland SFF.

### 3.4 Geomorphology and diversity (Fig. 3)

Altimontane and subalpine SFF and high altitudinal acidophilous SFF appear at the highest altitudes while lowland acidophilous SFF and secondary SFF appear at the lowest altitudes. Lowland acidophilous SFF, which appear in special microecological conditions such as in ravines, and altimontane and subalpine spruce forests, occur on steeper slopes.

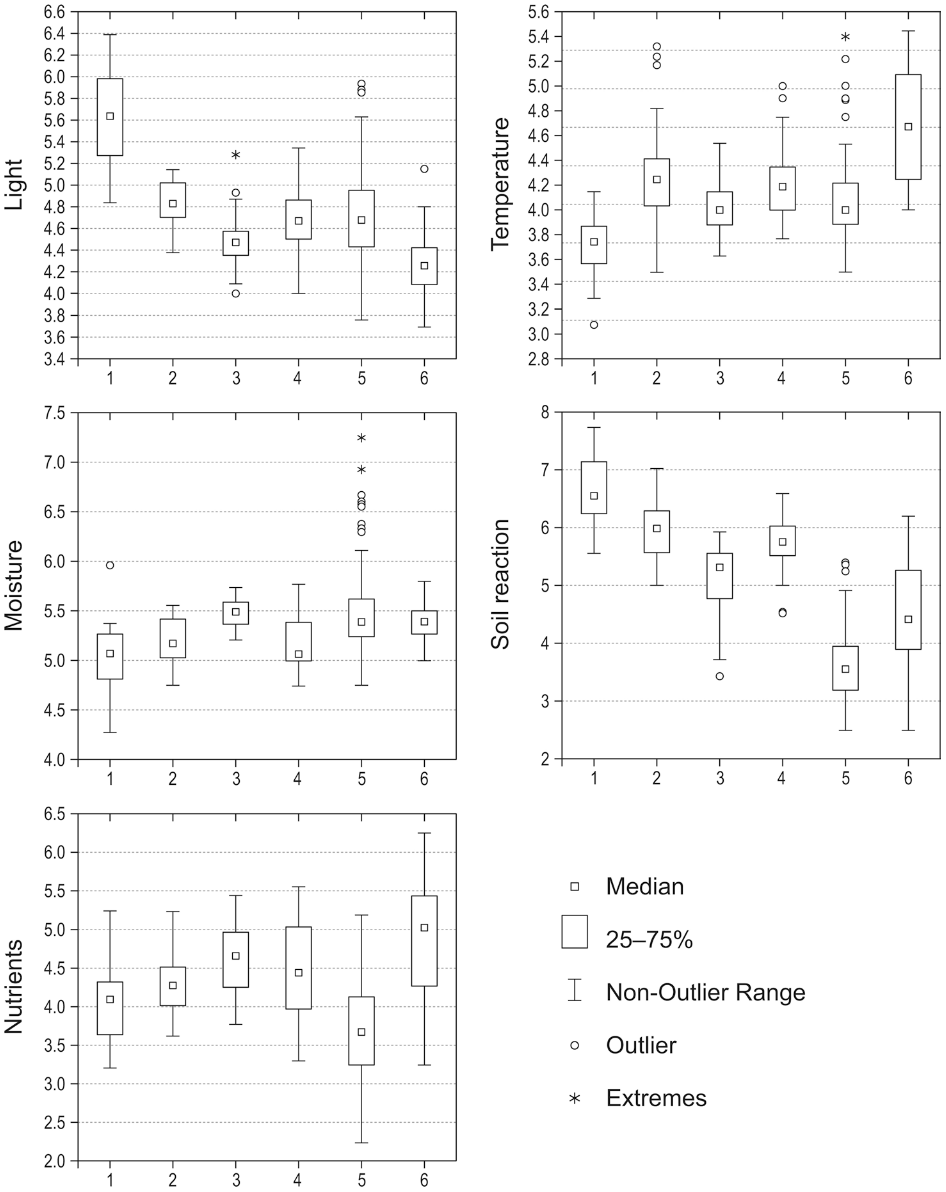

**Fig. 2.** Comparison of average Ellenberg indicator values. Median values, interquartile distance, maximum and minimum, outliers and extreme values are shown. Group numbers correspond to those in Fig. 1.

**Abb. 2.** Vergleich der mittleren Ellenberg-Zeigerwerte. Medianwerte, Interquartilsabstand, Maximum und Minimum, Ausreißer- und Extremwerte werden dargestellt. Die Gruppennummern entsprechen denen in Abb. 1.

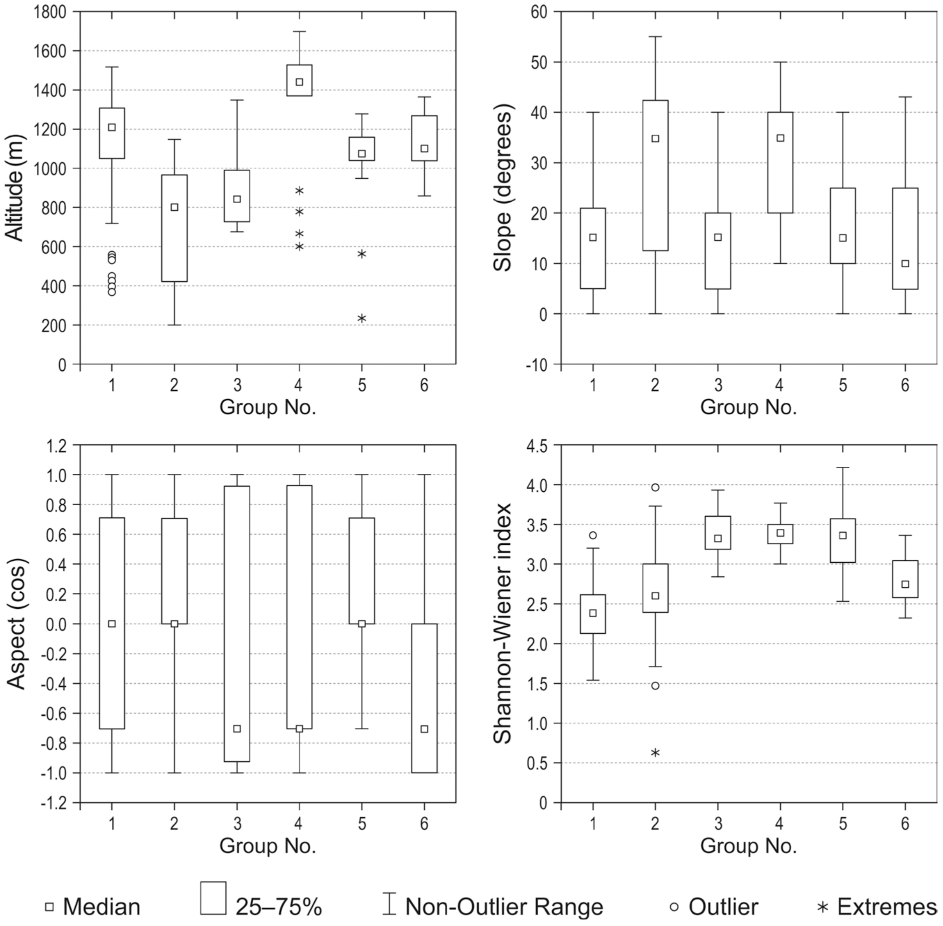

**Fig. 3.** Comparison of altitude, slope, aspect and Shannon-Wiener index for studied groups. Median values, interquartile distance, maximum and minimum, outliers and extreme values are shown. Group numbers correspond to those in Fig. 1.

**Abb. 3.** Vergleich von Höhe, Hangneigung, Exposition und Shannon-Wiener-Index der Untersuchungsgruppen. Medianwerte, Interquartilsabstand, Maximum und Minimum, Ausreißer- und Extremwerte werden dargestellt. Die Gruppennummern entsprechen denen in Abb. 1.

Secondary and boulder scree SFF show a preference for south-exposed slopes; other groups show no aspect preference. The most species-rich SFF are on carbonate bedrock, while acidophilous communities are less species-rich.

### 3.5 Life forms (Fig. 4)

The differences in species richness between forests on non-carbonate and those on carbonate bedrock can be specifically attributed to the greater contribution of hemicriptophytes, chamaephytes and geophytes in the latter groups. Geophytes are most abundant in secondary SFF. Phanerophytes are abundant in lowland SFF, where tree species from neighbouring forests can be found. Only a small number of therophytes and nano-phanerophytes can be found in all forests concerned.

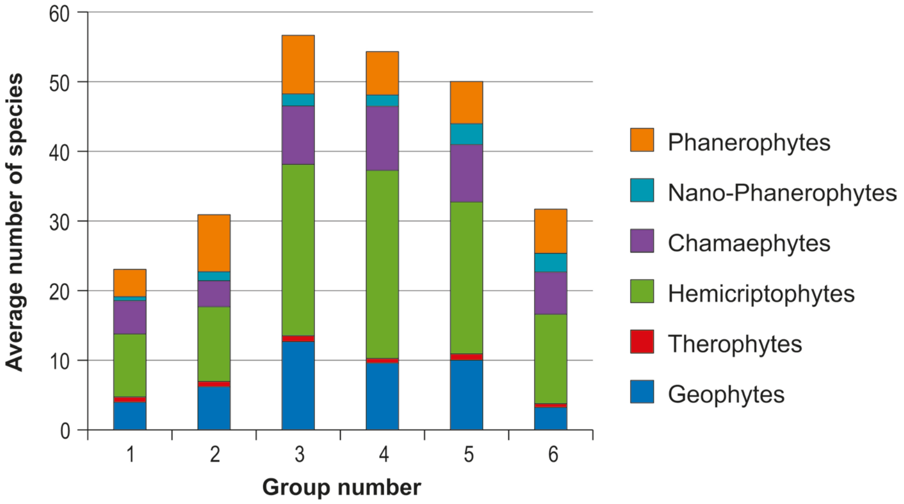

**Fig.4.** Life form structure in the SFF. Group numbers correspond to those in Fig. 1.

**Abb. 4.** Struktur der Lebensform in der Fichten-, Lärchen- und Tannenwälder. Die Gruppennummern entsprechen denen in Abb. 1.

### 3.6 Chorological spectrum (Fig. 5)

The proportion of boreal, arctic and alpine, as well as of widely distributed species is higher in SFF on non-carbonate bedrock. In forests on carbonate bedrock, more oreophytes with south European and Mediterranean affinity appear. "Mediterranean" species are here defined in the widest sense, including submediterranean, mediterranean-montane etc. Eurasian species are most frequent in secondary SFF, while Atlantic species are rare in all forests.

### 3.7 Life strategy types (Fig. 6)

The strategy type diagram shows that the most severe ecological conditions are found in zonal SFF, since stress-tolerators prevail there. The most advantageous conditions are within lowland acidophilous SFF, where many competitors can be found. Conditions are intermediate in other SFF.

## 4. Discussion

The main differentiation that appeared in the material is between groups 1 to 4 and groups 5 to 6. This level reflects the bedrock, since groups 1-4 appear on carbonate bedrock, whereas the other communities, groups 5-6, appear on acidic soils. Figure 2 shows that stands on acid soils are most humid and rich in organic material. Decomposition is slow due to a lack of cations, low temperature and high ground water, whereas the carbonate bedrock is drier, warmer and rich in cations. It is well known that bedrock is the most important factor in the division of SFF (BADOREK et al. 2011, EXNER et al. 2002, KUTNAR 2012, WILLNER & GRABHERR 2007).

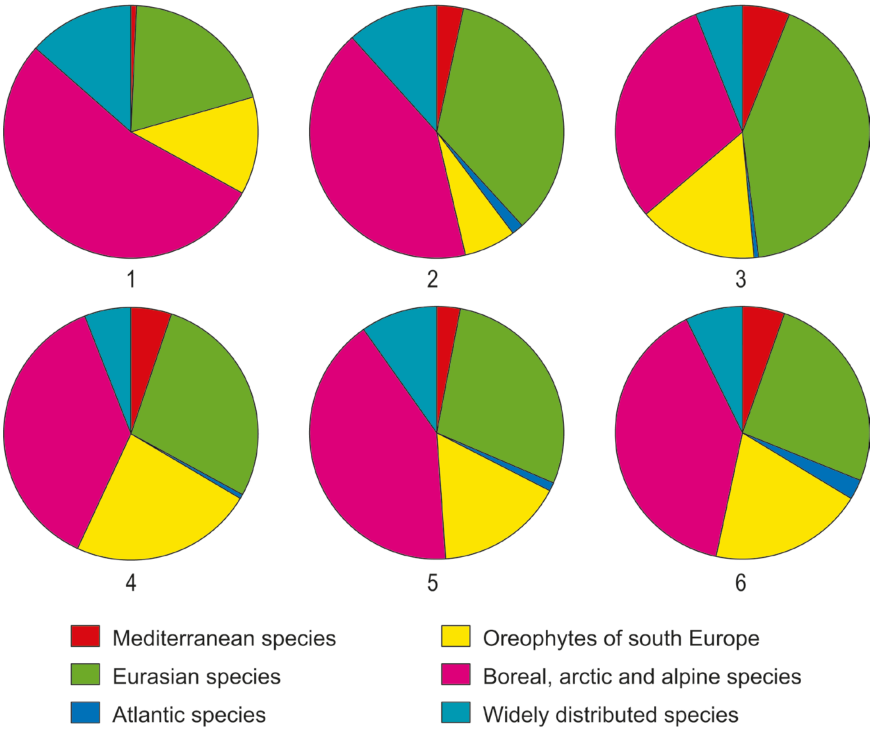

**Fig. 5.** Proportion of chorotypes in the SFF. Group numbers correspond to those in Fig. 1.

**Abb. 5.** Anteil der Chorotypen in den sechs Typen von Fichten-, Lärchen- und Tannenwälder. Die Gruppennummern entsprechen denen in Abb. 1.

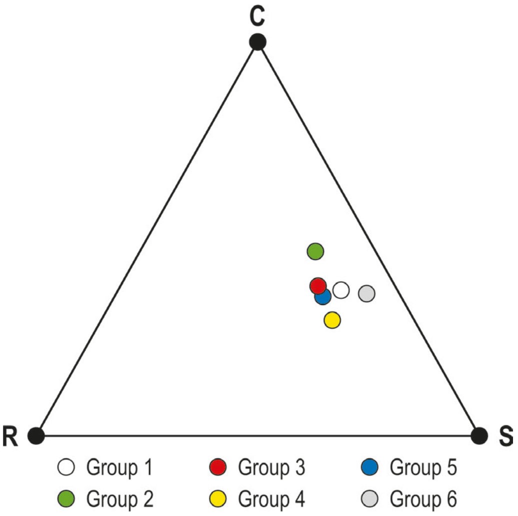

**Fig. 6.** Position of groups in the Grime triangle model of C, S and R strategies. Group numbers correspond to those in Fig. 1.

**Abb. 6.** Lage der Gruppen im Grime-Dreiecksmodell der C-, S- und R-Strategien. Die Gruppennummern entsprechen denen in Abb. 1.

Group 1 contains SFF associations that are found on carbonate bedrock at high altitudes. Forests of this type can only be found in the northern part of Slovenia; the timberline in the southern part is composed of beech forests (MARINŠEK et al. 2013, WRABER 1966). Larch communities, which have been studied by DAKSKOBLER (2006), are considered as secondary forests on sites of beech forests (ZUPANČIČ & ŽAGAR 2007). The *Adenostylo glabrae-Piceetum* is the zonal community of the Julian Alps, Karavanke and Kamnik-Savinja Alps and cannot be found in the Dinaric Alps. It appears above beech forest (*Anemone-Fagetum*) and below *Pinus mugo*-dominated communities (WRABER 1966). It could be related to the association *Homogyno sylvestis-Piceetum* (POLDNI & BRESSAN 2007). *Seslerio-Piceetum* is represented by only one relevé from a secondary forest on a steep slope (ZUPANČIČ 1999).

Altimontane and subalpine forests are found at high altitudes (above 1400 m) on relatively steep slopes. The chorological spectrum shows a high proportion of Southern European oreophytes and a low proportion of Eurasian species characteristic of beech forests. Unfavourable site conditions are reflected by the high proportion of chamaephytes and more stress-tolerant species than in other SFF. Diagnostic species are from the group of alpine and subalpine dry grasslands and tall-herb species of high altitudes (VITTOZ et al. 2010, ZUPANČIČ 1999).

The secondary spruce forests of group 2 appear on lower elevation sites with carbonate bedrock. These communities are not recent spruce plantations, but have developed over centuries of introduction and support of spruce in the region (ČARNI et al. 2011). The constituent associations *Aposerido-Piceetum, Rhamno falacis-Piceetum, Petasiti-Piceetum* and *Erico-Piceetum* are considered as secondary *Picea*-dominated forests on sites of beech forests (ZUPANČIČ 1999).

ZUPANČIČ (1999) regards the association *Laburno alpini-Piceetum* as a primary spruce forest, although its sites are encroached by beech and a high proportion of species from beech forests places this association within the group of secondary spruce forests – a result which is congruent with the opinion of WILLNER & GRABHERR (2007) who think it is of secondary origin.

There is only scarce material from the associations *Petasiti-Piceetum* (3 relevés) and *Erico-Piceetum* (1 relevé). Therefore, the affiliation of the latter relevé with the *Erico-Piceetum* Schweingruber 1972 as a geographical variant with *Helleborus niger* subsp. *niger* (ZUPANČIČ 1999) requires further evaluation.

These forests grow at lower altitudes, on moderate slopes, species with competitor strategy are more abundant and their stands are the most species-rich of all types considered here. The life history spectrum shows a higher proportion of geophytes that is characteristic for beech forest, where they build an early spring aspect (HEINRICHS et al. 2012). The high growth potential places secondary spruce forests among the most valuable for forestry in the region. While their diagnostic species originate from beech forests (ZUPANČIČ & ŽAGAR 2010), secondary spruce forest have some additional species not common in beech forests, which lends them remarkable species richness (MÁLIŠ et al. 2012).

Group 3 comprises mainly SFF found in frost hollows on carbonate bedrock. Frost hollows are a phenomenon that appears in the karst landscapes of Southern Slovenia and Croatia (DAKSKOBLER et al. 2008). In this limestone region the acidophytic species *Calamagrostis arundinacea* is diagnostic of frost hollows (ZUPANČIČ 1980). Frost hollows are found in depressions with a microclimate that deviates markedly from the surrounding zonal beech forest vegetation. In clear nights, heavy cold air flows into these depressions and, since they are protected from wind, accumulates in them. As the surrounding air warms during daytime, it becomes lighter and mixes poorly with the cold air sitting in the hollows, causing extended periods of cold. Beech cannot survive in such climatic conditions and is replaced by SFF (HORVAT et al. 1974). Communities of this type have been sampled in the Dinaric Alps: *Lonicero-Piceetum* in subalpine belt in Trnovski gozd, Snežnik, around Postojna and in Kočevski Rog, *Stellario-Piceetum* in Trnovski gozd and *Hacquetio-Piceetum* in Snežnik area (ZUPANČIČ 1980).

These forests occur in the moistest and most acid sites among the groups on carbonate bedrock. They are found on moderate slopes, the proportion of nanophanerophytes shows that the canopy is not closed. Among diagnostic species, species with a higher moisture demand, above all bryophytes, can be found. These forests have been originally described by ZUPANČIČ (1980) in his study about frost hollows in the Slovenian part of the Dinaric Alps, and later on adapted to the international standard of nomenclature (WEBER et al. 2000). Similar forests can also be found towards the south in Croatia (VUKELIĆ et al. 2010a).

Group 4 comprises SFF on boulder scree habitats. The communities appear along the lower edges of precipices, on rocky reefs and terraced slopes. The sites are exposed to wind and insolation and subject to large daily and yearly temperature oscillations (ACCETTO 2006, TREGUBOV & ČOKL 1957). The community types *Calamagrostio-Abietetum* and *Neckero-Abietetum* were first described in the Snežnik mountain range (TREGUBOV & ČOKL 1957). ZUPANČIČ & ACCETO (1994) described the association *Ribeso alpine-Piceetum* and pointed out its floristic and ecological similarity to *Neckero-Abietetum*. The *Asplenio-Piceetum* (ACCETTO 1993) was originally described as a community of frost hollows, but was placed within boulder scree communities according to its floristic composition. ZUPANČIČ (1999) propose to classify this association within subalpine SFF, as a member of the alliance *Chrysanthemo-Piceion*. This association, found in the Kočevsko region certainly needs further syntaxonomical treatment.

The communities of group 4 are found on moderate slopes of southern aspect. The number of species per relevé is lower than in the other SFF types over carbonate bedrock. In the chorological spectrum more Southern European oreophytes and Mediterranean species (in the widest sense) are found. Diagnostic species are few, indicating variable and severe site conditions. These forests thrive from the montane up to the subalpine belt on limestone and dolomite boulder scree (HORVAT 1962). Similar communities can be found further to the south, where the proportion of species characteristic of beech forest becomes higher (VUKELIĆ et al. 2010b)

The acidophilous group of SFF is made up of high altitude and lowland SFF. Spruce and fir are strong competitors at cold, extremely poor and/or wet sites, where the dominance of zonal beech forests is reduced. Within the high altitude group of SFF, communities dominated by spruce and larch are found, whereas the lowland group SFF is mainly dominated by fir. This is a result of the fact that fir is more sensitive to winter frost than spruce (LEBOURGEOIS et al. 2010, EWALD et al. 2011).

Acidophilous high altitude SFF (group 5) comprises spruce forests of various origins. *Mastigobryo-Piceetum*, *Sphagno-Piceetum, Rhytidiadelpho lorei-Piceetum* were recorded from smaller or larger depression with impermeable non-carbonate bedrock (KUTNAR 2012, ZUPANČIČ 1999). *Prenantho purpureae-Piceetum* and *Avenello flexuosae-Piceetum* are secondary forests on sites of beech forests (ZUPANČIČ 1999), whereas *Luzulo sylvaticae-Piceetum* (WRABER 1963, ZUPANČIČ 1999) forms zonal altimontane/subalpine vegetation on non-carbonate bedrock. These forests are very poor in species, and thrive on soils rich in moisture and organic material, with moderate slope inclination. The majority of species are of boreal, arctic and alpine origin; there is lack of diagnostic species, which may be due to the smaller pools of acidophilous forest species in Europe (EWALD 2003). The non-carbonate bedrock and colder climate are decisive factors for appearance of this group.

Lowland SFF (group 6) occur in the zone of beech forests. They thrive on sites that are unfavourable for the development of beech forest, at moist sites in ravines or on extremely acid soils (DAKSKOBLER & MARINŠEK 2009, WRABER 1958, 1959). The majority of forest of this type can be found in lowlands of the eastern part of Slovenia and also in the non-carbonate Pohorje mountain range. Not restricted to a certain altitudinal zone, such communities can be sporadically found also elsewhere in the country (MARINČEK & ČARNI 2002).

The characteristics of these communities are similar to the previous, but less pronounced. Diagnostic species originate from neighbouring beech forests. The proportion of beech forest species can be quite abundant locally, so that these forests have sometimes been classified within beech forests (BOUBLÍK 2010).

Clusters were largely homogenous in respect to bedrock and habitat as described in original sources. Communities described locally in original papers stay intact in the clusters formed by numerical analysis. Nevertheless, the analysis shows some inconsistencies that need further elaboration in the future.

### 4.1 General view over *Piceetalia* and *Athyrio-Piceetalia* forests

The majority of *Piceetalia* and *Athyrio-Piceetalia* forests are dominated by spruce. *Abies alba* appears as a dominant tree species in forests on carbonate boulder scree (group 4) and in lower altitudes on non-carbonate bedrock (group 2). We can find *Larix decidua* in secondary forests on carbonate bedrock at higher altitudes (group 1).

Spruce forests form zonal vegetation in the northern part of Slovenia. It appears in high elevations on carbonate (*Adenostylo-Piceetum*) as well as on non-carbonate bedrock (*Luzulo sylvaticae-Piceetum*). However, spruce does not form zonal vegetation in the Dinaric Alps, where a milder, mediterraean-atlantic climate favours beech forests up to the timberline. The milder climate with higher temperature and precipitation in the form of rain accelerates decomposition and does not allow formation of mor humus required by spruce forest species. Moreover the bedrock in Slovenia is composed mainly of carbonates, which are permeable for water and inhibit acidification. In contrast, spruce forests are adapted to continental climate with cool summers and cold winters with a deep snow cover.

In the Dinaric Alps spruce forests appear only in frozen hollows and on boulder scree, where they are co-dominated by fir. Here more severe meso- and microclimatic conditions allow the development of spruce forests.

Secondary spruce forests can be found on carbonate as well as on non-carbonate bedrock. On carbonate bedrock they form an individual cluster (group 2), whereas on non-carbonates these forests are classified along with other spruce forest, as the small species pool on these substrates allows less differentiation. On non-carbonate bedrock spruce forests are found in high elevations, but also in wet and extremely acid sites, where they are dominated by fir in the lowlands.

### 4.2 Syntaxonomical assignment

We place all associations within the class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939 and the orders *Piceetalia abietis* Pawłowski in Pawłowski et al. 1928 and *Athyrio-Piceetalia* Hadač 1969. While the division between species-rich spruce forests on carbonate and species-poor ones on acidic bedrock is widely accepted, authors apply it at different levels of the hierarchy.

In the traditional system, all SFF are assigned to the order *Piceetalia* and to the alliance *Piceion* with suballiances *Vaccinio-Piceenion* over non-carbonate and *Abieti-Piceenion* over carbonate bedrock (ZUPANČIČ 1980, 1999). WILLNER & GRABHERR (2007) propose a division of the order *Piceetalia* into two alliances *Abieti-Piceion* and *Vaccinio-Piceion,* changing the syntaxonomical level of the former suballiances.

RODWELL et al. (2002) and WALLNÖFER (1993) distinguish the order *Athyrio-Piceetalia* over carbonate bedrock with montane alliance *Abieti-Piceion* and subalpine alliance *Chrysanthemo rotundifolii-Piceion* and order *Piceetalia* with alliance *Piceion excelsae* over non-carbonate bedrock - a solution that reflects the results of numerical analysis of the Slovenian material best (Table 2).

ZUPANČIČ (1999) suggest to reserve higher syntax for geographical differentiation and points out the possibility to distinguish a separate regional order *Cardamino trifoliae-Piceetalia* over carbonate bedrock with alliance *Homogyno sylvestris-Piceion.* It could be further divided into the suballiances *Anemono trifoliae-Piceenion* and *Betonico alopecuri-Piceenion* representing subalpine and montane SFF, being parallel to montane *Abieti-Piceion* and subalpine *Chrysanthemo-Piceion*.

In this study we classified SFF according to the results of numerical analysis and obtained floristically and ecologically homogenous units. As shown in Table 2 these clusters broadly correspond to alliances or, in the case of the *Abieti-Piceion*, to groups of related associations within alliances.

Cluster 1 presents altimontane and subalpine spruce and larch forests, which can be classified within the *Chrysanthemo rotundifolii-Piceion*. This unit is also recognised by EUNIS (2013) as subalpine spruce and larch forest over base- and lime-rich substrate. However, this does not match with traditional treatment of larch forests that are classified within *Abieti-Piceion* (ZUPANČIČ & ŽAGAR 2007). The predominant association forming zonal subalpine vegetation in the Northern Slovenian Alps is the *Adenostylo glabrae-Piceetum*, which is also reported as zonal vegetation from Germany (EWALD 1999) and Austria (EXNER et al. 2002).

The secondary spruce forests (cluster 2) over carbonate bedrock form an individual group within the *Abieti-Piceion* alliance. These stands appear at lower altitudes than the previous group; they replace former beech forests that influence the present floristic composition. All associations were described by ZUPANČIČ (1999) and treated already then as secondary forests on sites of beech forests (except *Laburno-Piceetum*). Although well-differentiated against other SFF, their syntaxonomic status is problematic because of their close affinity to beech forests. Thus, secondary plantations outside the natural distribution area of *Picea abies* have been subjected to a separate classification into so-called *culto-Piceeta* (ZERBE 1994). In a similar vein, EWALD (2005) classified spruce forests at beech sites within the natural distribution area of *Picea* as "*sylvofacies*", which were interpreted as anthropogenic variants of *Fageta*. On the other hand, EXNER et al. (2002) as well as BOU-

**Table 2.** Affiliation of numerical clusters of spruce-fir-forests (in bold letters) to the syntaxonomical system; associations predominant in Slovenia are underlined; doubtful association in brackets.

**Tabelle 2.** Einordnung der numerisch ermittelten Cluster von Fichten-Tannen-Wäldern (fett gedruckt) in das pflanzensoziologische System; in Slowenien vorherrschende Assoziationen sind unterstrichen; zweifelhafte Assoziationen in Klammern.

- *Vaccinio-Piceetea*
  - *Athyrio-Piceetalia* (carbonate bedrock)
    - *Chrysanthemo-Piceion*
      - **Cluster 1 (subalpine)**
        - *Adenostylo glabrae-Piceetum p.p.*
        - *Rhodothamno-Laricetum*
        - *Seslerio albicantis-Piceetum*
    - *Abieti-Piceion*
      - **Cluster 2 (secondary)**
        - *Aposerido-Piceetum*
        - *Rhamno fallici-Piceetum*
        - *Laburno alpini-Piceetum*
        - *Petasiti-Piceetum*
        - *Erico-Piceetum*
        - *Adenostylo glabrae-Piceetum p.p.*
        - *(Rhytidiadelpho lorei-Piceetum p.p.)*
      - **Cluster 3 (frost hollows)**
        - *Hacquetio-Piceetum*
        - *Stellario montanae-Piceetum*
        - *Lonicero caeruleae-Piceetum p.p.*
        - *Prenantho purpureae-Piceetum p.p.*
        - *Ribeso alpini-Piceetum p.p.*
    - *Calamagrostio-Abietion*
      - **Cluster 4 (boulder scree)**
        - *Calamagrostio-Abietetum*
        - *Neckero-Abietetum*
        - *Campanulo justinianae-Piceetum*
        - *Asplenio-Piceetum*
        - *Ribeso alpini-Piceetum p.p.*
  - *Piceetalia* (acidic bedrock)
    - *Piceion*
      - **Cluster 5 (high elevation)**
        - *Luzulo sylvaticae-Piceetum*
        - *Mastigobryo-Piceetum*
        - *Sphagno-Piceetum*
        - *Rhytidiadelpho lorei-Piceetum p.p.*
        - *Avenello flexuosae-Piceetum*
        - *Prenantho purpureae-Piceetum p.p.*
        - *Bazzanio-Abietetum p.p.*
        - *Galio rotundifolii-Abietetum p.p.*
        - *Lonicero caeruleae-Piceetum p.p.*
      - **Cluster 6 (low elevation)**
        - *Luzulo albidae-Abietetum*
        - *Hieracio rotundati-Abietetum*
        - *Paraleucobryo-Abietetum*
        - *Polysticho setiferi-Abietetum*
        - *Galio rotundifolii-Abietetum p.p.*
        - *Bazzanio-Abietetum p.p.*

BLÍK & ZELENÝ (2007) classified secondary *Picea*- and *Abies*-stands as *Piceeta* and *Abieteta*. In Slovenia, where secondary SFF on carbonate are the most species-rich group, the latter approach has yielded a remarkable diversity of associations.

With their mixture of boreal-subalpine and montane diagnostic species, SFF from frost hollows (cluster 3) are also placed in the *Abieti-Piceion* Br.-Bl. in Br.-Bl. et al. 1939. The *Lonicero caeruleae-Piceetum* seems is the most prominent association in the original material.

Cluster 4 (boulder scree SFF) may be assigned to the *Calamagrostio-Abietion* Horvat 1962 nom. invers. propos. These communities have been assigned to a remarkable diversity of associations in the past.

We place the acidophilous associations from groups 5 and 6 into the *Piceion abietis* Pawłowski et al. 1928 nom. mut. propos. Due to the paucity in species, the floristic differentiation of the constituent clusters appears too weak to warrant further formal subdivision. With respect to original associations, there is some overlap with cluster 3 of frost hollows (*Lonicero caeruleae-Piceetum*, *Prenantho purpureae-Piceetum*), and imperfect separation of clusters 5 and 6 (*Galio rotundifolii-Abietetum*, *Bazzanio-Abietetum*). Within cluster 5, the *Luzulo-Piceetum* appears as the regionally dominant type of zonal subalpine spruce forest of acidic bedrock in Slovenia. Cluster 6 is best represented by the associations *Luzulo-Abietetum* and *Galio-Abietetum*. In cluster 6, problems of differentiating against adjacent deciduous forests as discussed for cluster 2 must be expected.

We tried to classify the material presenting the order *Piceetalia* and *Athyrio-Piceetalia* in Slovenia. We established six floristically well-established groups that show clear ecological affiliations and can be tentatively placed into alliances. The original material reveals a remarkable diversity of associations (Table 2). As some associations are poorly presented by relevé material, we refrained from formal revisions below the level of clusters/alliances. Several associations have their centres of distribution beyond our region and should be treated based on a broader material.

## 5. Conclusion

The study gives an overview of *Piceetalia and Athyrio-Piceetalia* -communities in Slovenia. Despite its position on the edge of spruce forest distribution, we found a remarkable diversity that can be placed into the existing syntaxonomical system of alliances.

Numerically derived clusters yields six groups that possess common floristic, structural and ecological characteristics and appear in well-defined habitats, the majority of them also found elsewhere in the temperate distribution area of the dominant tree species. This finding suggests to prefer a system of broad alliances over a finer geographic division. The remarkable abundance of associations found in original sources from Slovenia is also well represented by numerical clusters, but requires revision which will have to take account of data from surrounding areas and make comparisons with adjacent deciduous forests.

## Erweiterte deutsche Zusammenfassung

**Einleitung** – Nadelwälder auf sauren Böden in der nördlichen Hemisphäre werden in die Klasse *Vaccinio-Piceetea* eingeordnet. Sie umfassen boreale Waldtypen, die in den kältesten Teilen der nördlichen Hemisphäre weit verbreitet sind. In temperaten Regionen kommen sie fast nur in gebirgigen Regionen vor und erscheinen an der Grenze zur mediterranen Region nur fragmentarisch. Das ökologische Optimum der Klasse liegt in Gebieten mit relativ unvorteilhaften und kühlen Sommern und kalten Wintern. In Europa werden die Nadelwälder in die Ordnungen *Piceetalia abietis* auf carbonatfreien Substraten und *Athyrio-Piceetalia* auf Carbonatgesteinen sowie basenreichen Silikatgesteinen eingeordnet (WALLNÖFER 1993).

In den vergangenen Jahren spiegelte sich die Diversität von Fichten-, Tannen- und Lärchenwäldern auf europäischer Ebene in zahlreichen ökologisch basierten Verbänden wider. Es besteht ein Bedarf, die in Slowenien vorkommenden Vegetationseinheiten innerhalb des europäischen Rahmens zu kalibrieren, um letztlich das Klassifikationssystem zu vereinheitlichen (RODWELL et al. 2002).

Ziel der vorliegenden Arbeit war es, alle verfügbaren Daten zu sammeln und eine synthetische Übersicht der Fichten-, Tannen- und Lärchenwälder in Slowenien auf der Basis einer numerischen Analyse zu erstellen. Wir haben versucht, die Hauptgruppen dieser Wälder zu finden, ihre ökologischen Bedingungen zu identifizieren und ihre floristischen, strukturellen und chorologischen Eigenheiten herauszuarbeiten.

**Material und Methoden** – Die Studie wurde in Slowenien durchgeführt, das an den südlichen Vorposten der Alpen und den nördlichen Vorposten der dinarischen Alpen liegt. Das Klima ist alpin, mediterran und kontinental beeinflusst. Der Niederschlag variiert im Land, von 800 mm pro Jahr im östlichen bis 3000 mm im westlichen Teil. Mehr als die Hälfte des Gebietes ist von Wäldern bedeckt, und mehr als 70 % der Wälder werden von Rotbuchen (*Fagus sylvatica*) dominiert (MARINČEK & ČARNI 2002).

Insgesamt 934 slowenische Vegetationsaufnahmen wurden aus der Literatur gesammelt und in eine Datenbank eingegeben. Wir führten eine eine ‚Heterogenitäts-limitierte' Auswahl der gesammelten Aufnahmen durch, in der die Zahl der ausgesuchten Aufnahmen von der Beta-Diversität bestimmt wurde (heterogeneity-constrained random resampling, LENGYEL et al. 2011). Auf diese Weise wurden 30 Aufnahmen von jeder Assoziation ausgesucht. Nach einer Stratifikation verblieben 319 Aufnahmen von 28 Assoziationen. Die Klassifikation wurde mit einer Quadratwurzel-transformierten Matrix unter Verwendung der Ward-Methode durchgeführt, mit relativem Sørensen als Distanzmaß (Abb. 1). Die charakteristischen Arten der einzelnen Gruppen wurden durch Kalkulation der prozentualen Stetigkeit und Treue bestimmt (TICHÝ & HOLT 2006) und werden in einer kombinierten synoptischen Tabelle (Tab. 1) präsentiert.

Um den ökologische Informationsgehalt der Gruppen hinsichtlich Licht, Temperatur, Feuchtigkeit, Bodenreaktion und Nährstoffen zu beurteilen, wurden mittlere Ellenberg-Zeigerwerte (ELLENBERG et al. 1992) berechnet (Abb. 2). Mittels Box Plots wurden die untersuchen Gruppen hinsichtlich Meereshöhe, Exposition und Inklination verglichen. Spektren von Lebensformen (Abb. 4) und chorologische Typen nach PIGNATTI et al. (2005) (Abb. 5) wurden für jede Aufnahme berechnet und mittlere Anteile zwischen den Gruppen verglichen. CSR-Strategietypen für jede Gruppe werden in einem Grime-Dreiecks-Diagramm (GRIME 2002) präsentiert (Abb. 6).

**Ergebnisse und Diskussion** – Wir fanden sechs floristisch gut begründete Gruppen, die klare ökologische Zugehörigkeiten zeigen und vorläufig Verbänden zugeordnet werden können (Abb. 1.). Das Originalmaterial zeigt sechs Gruppen, die eine bemerkenswerte Diversität von Assoziationen enthalten. Die vorgeschlagene Klassifikation ist in Tabelle 2 gezeigt.

Die wesentliche Differenzierung im Aufnahmematerial besteht zwischen den Gruppen 1–4 und den Gruppen 5–6. Diese Ebene spiegelt das Ausgangsgestein wider, da die Gruppen 1–4 auf Carbonatgestein vorkommen (1 – zonale und hochmontane Fichten- und Lärchenwälder, 2 – sekundäre Fichten wälder, 3 – Kaltluft-Fichtenwälder, 4 – Blockschutt-Fichten- und Tannenwälder), während auf sauren Böden die Gruppen 5 und 6 gefunden werden (5 – Hochlagen-Fichtenwälder, 6 – Tieflands-Fichtenwälder).

Der Großteil der Wälder wird von Fichten (*Picea abies*) dominiert. Die Tanne (*Abies alba*) erscheint als dominante Baumart in Wäldern auf Kalk-Blockschutt (Gruppe 4) sowie in niedrigen Höhenlagen auf nicht-carbonatischem Gestein (Gruppe 2). Die Lärche (*Larix europaea*) findet sich in Sekundärwäldern auf Carbonat in höheren Lagen (Gruppe 1).

Fichtenwälder bilden die zonale Vegetation im nördlichen Teil Sloweniens. Sie treten in großen Höhen auf Carbonat- wie auf carbonatfreiem Substrat auf. In den dinarischen Alpen bilden Fichtenwälder jedoch nicht die zonale Vegetation; hier begünstigt ein milderes, mediterran-atlantisches Klima Buchenwälder bis zur Baumgrenze. Das mildere Klima mit höheren Temperaturen und Niederschlägen als Regen fördert den Streuabbau und erlaubt nicht die Bildung von Rohhumus, der von den Fichtenwald-Arten benötigt wird. Außerdem besteht das Ausgangsgestein in Slowenien vorherrschend aus Carbonaten, die durchlässig für Wasser sind und Versauerung verhindern. Im Gegensatz dazu sind Fichtenwälder an kontinentales Klima mit kühlen Sommern und kalten Wintern mit hoher Schneebedeckung angepasst.

In den dinarischen Alpen kommen Fichtenwälder nur in Kaltluft-Mulden und auf Blockschutthalden vor, wo sie von Tannen mitdominiert werden und strengere meso- und mikroklimatische Bedingungen ihre Entwicklung erlauben.

Sekundäre Fichtenwälder sind sowohl auf Carbonat- wie auf carbonatfreiem Substrat zu finden. Auf Carbonatgestein bilden sie ein indiviuelles Cluster (Gruppe 2). Demgegenüber werden solche Wälder auf carbonatfreiem Gestein zusammen mit anderen Fichtenwäldern klassifiziert, weil der kleine Artenpool auf diesen Substraten weniger Differenzierung erlaubt. Auf carbonatfreiem Gestein wachsen Fichtenwälder in großen Höhenlagen, aber auch auf nassen und extrem sauren Standorten, wo sie in den Tieflagen von Tannen dominiert werden.

## Acknowledgements

The authors acknowledge financial support from the state budget through the Slovenian Research Agency (P1-0236) and the European Social Fund. We thank Iztok Sajko, who kindly elaborated all graphics. We owe thanks also to Jörg Ewald, Thilo Heinken and unknown reviewers for comments and suggestions on previous versions of the manuscript.

## Supplements and Appendices

**Additional supporting information may be found in the online version of this article.**

**Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.**

**Appendix S1.** Sources of data used for the analysis in Table 1.

**Anhang S1.** Herkunft der Daten für die Analyse in Tabelle 1.

## References

ACCETTO, M. (1986): Nova geografska variant združbe jelke in okroglolistne lakote na Bohorju (*Galio-Abietetum* M. Wrab. 59 var. geogr. nova *Dentaria polyphyllos*) (The new geographical variant of the *Galio-Abietetum* M. Wrab. 59 association (*Galio-Abietetum* M. Wrab. 59 var. geogr. nova *Dentaria polyphyllos*) in the Bohor mountains) [in Slovenian]. – Zbornik gozdarstva in lesarstva 27: 89–105.

ACCETTO, M. (1993): The frost-pocket norway spruce forests (*Asplenio-Piceetum* R. Kuoch 1954 var. geogr. *Omphalodes verna* var. geogr. nova) in the dolines of Kočevsko (SE Slovenia). – Gozdarski vestnik 51: 426–445.

Accetto, M. (2006): *Campanulo justinianaea-Piceetum abietis* var. ass. nov. v Dinarskem gorstvu južne Slovenije (*Campanulo justinianaea-Piceetum abietis* var. ass. nov. in the Dinaric mountains of the southern Slovenia) [in Slovenian]. – Razprave 4. razreda SAZU 47: 65–101.

ARSO, Slovenian environment agency – URL: http://www.arso.gov.si/vreme/podnebje [accessed 2013-01-26].

Badorek, T., Tuittila, E.S., Ojanen, P. & Minkkinen, K. (2011): Forest floor photosynthesis and respiration in a drained peatland forest in southern Finland. – Plant Ecol. Biodivers. 4: 227–241.

Beck, G. (1906): Die Umkehrung der Pflanzenregionen in den Dolinen des Karstes. – Sitzungber. Akad. Wiss.Wien, Mathem.-naturw. Kl. 115 (1–10): 3–19.

Becker, T., Andres, C. & Dierschke, H. (2011): Junge und alte Steppenrasen im NSG "Badraer Lehde-Großer Eller" im Kyffhäusergebirge. – Tuexenia 31: 173–210.

Belec, Z. (2009): Fitocenološka analiza in zgodovina jelovih gozdov na Pohorju (Phytocenological analysis and history of silver fir forests on Pohorje) [in Slovenian]. Doktorska disertacija. – Ljubljana, Univerza v Ljubljani, Biotehniška fakulteta, Oddelek za biologijo: 198 pp.

Biondi, E., Casavecchia, S., Pesaresi, S. & Zivkovic, L. (2012): Natura 2000 and Pan-European ecological network: a new methodology for data integration. – Biodivers. Conserv. 21: 1741–1754.

Boublík, K. (2010): Formalized classification of vegetation of *Abies alba*-dominated forests in the Czech Republik. – Biologia 65: 822–831.

Boublík, K. & Zelený, D. (2007): Plant communities of silver fir (*Abies alba*) forests in southeastern Bohemia. – Tuexenia 27: 73–90.

Braun-Blanquet, J. (1964): Pflanzensoziologie. Grundzüge der Vegetationskunde. 3rd ed. – Springer, Berlin: 865 pp.

Braun-Blanquet, J., Sissingh, G. & Vlieger, J. (1939): Prodromus der Pflanzengesellschaften. Fasz. 6. Klasse der *Vaccinio-Piceetea* (Nadelholz- und Vaccinienheiden-Verbände der eurosibirisch-nordamerikanischen Region). – Mari-Lavit, Montpellier: 124 pp.

Čarni, A., Juvan, N., Košir, P., Marinšek, A., Paušič, A. & Šilc U. (2011): Plant communities in gradients. – Plant Biosystems 145, suppl. 1: 54–64.

Čarni, A., Marinček, L. Seliškar, A. & Zupančič, M. (2002): Vegetation map of forest communities of Slovenia in a scale of 1:400 000. – ZRC Publishing, Ljubljana.

Dakskobler, I. (2003): Pionirsko smrekovje nad sedanjo (antropogeno) zgornjo gozdno mejo v južnih Julijskih Alpah (primer iz zgornje Baške doline) (Pioneer spruce stands above the actual (anthropogenic) upper forest line in the southern Julian Alps (an example from the upper Bača Valley) [in Slovenian]. – Hacquetia 2: 19–52.

Dakskobler, I. (2006): Asociacija *Rhodothamno-Laricetum* (Zukrigl 1973) Willner & Zukrigl 1999 v Julijskih Alpah (The asssociation *Rhodothamno-Laricetum* (Zukrigl 1973) Willner & Zukrigl 1999 in the Julian Alps) [in Slovenian]. – Razprave IV. razreda SAZU 47: 117–192.

Dakskobler, I. & Marinšek, A. (2009): A review of silver fir sites in Slovenia. – Zbornik gozdarstva in lesarstva 89: 43–54.

Dakskobler, I., Sinjur, I., Veber, I. & Zupan, B. (2008): Locatities and sites of *Pulsatilla vernalis* in the Julian Alps. – Hacquetia 7: 47-69.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulißen, D. (1992): Zeigerwerte von Pflanzen in Mitteleuropa. – Scripta Geobot. 18: 1–248.

Ermakov, N. & Makhatkov, I. (2011): Classification and ordination of north boreal light-coniferous forests of the West Sibirian Plain. – Plant Biosystems 154, suppl. 1: 199–207.

Ermakov, N. & Morozova, O. (2011): Syntaxonomical survey of boreal oligotrophic pine forests in northern Europe and Western Siberia. – Appl. Veg. Sci. 14: 524–536.

EUNIS (2013): Habitat types. European Environment Agency – URL: http://eunis.eea.europa.eu/habitats/ [accessed 2012-04-20].

Ewald, J. (1999): Soziologie und Standortbindung subalpiner Fichtenwälder in den Bayerischen Alpen. – Tuexenia 19: 107–125.

Ewald, J. (2000): The influence of coniferous canopies on understory vegetation and soil in mountain forests of the northern Calcareous Alps. – Appl. Veg. Sci. 3: 123–134.

Ewald, J. (2003): The calcareous riddle: Why are there so many calciphilous species in the central European flora? – Folia Geobot. 38: 357–366.

Ewald, J. (2005): Schlusswaldgesellschaften des Werdenfelser Landes (Bayerische Alpen). – Hoppea 66: 377–406.

EWALD, J., JEHL, H., BRAUN, L. & LOHBERGER E. (2011): Die Vegetation des Nationalpark Bayerischer Wald als Ausdruck von Standort und Walddynamik. – Tuexenia 31: 9–38.

EXNER, A., WILLNER, W. & GRABHERR, G. (2002): *Picea abies* and *Abies alba* forests of the Austrian Alps: numerical classification and ordination. – Folia Geobot. 37: 383–402.

GEORGIADIS, N., PETREMANN, J., SCHRÖDER, E. & SPYROGLOU, G. (2012): Contribution to the assessment of the conservation status of spruce forest in Greece. – J. Biol. Res. 17: 57–67.

GRIME, J.P. (2002): Plant strategies, vegetation processes and ecosystem properties. – John Wiley & Sons Ltd., Chichester: 456 pp.

HADAČ, E., BŘEZINA, P., JEŽEK, V., KUBIČKA, J., HADAČOVÁ, V. & VONDRÁČEK, M. (1969): Die Pflanzengesellschaften des Tales „Dolina Siedmich pramenov" in der Belaer Tatra. – Vegetácia ČSSR 2. – SAV, Bratislava: 343 pp.

HEINRICHS, S., SCHULTE, U. & SCHMIDT, W. (2012): Eisbruch im Buchenwald – Untersuchungen zur Vegetationsdynamik der Naturwaldzell "Ochsenberg" (Eggegebirge/Nordrhein-Westfalen). – Tuexenia 32: 7–29.

HENNEKENS, S.M., & SCHAMINÉE, J.H.J. (2001): TURBOVEG, a comprehensive database management systeme for vegetation data. – J. Veg. Sci. 12: 589–591.

HORVAT, I. (1962): Vegetacija planina zapadne Hrvatske (Vegetation of the montains of West Croatia) [in Croatian]. – Prirodoslovna istraživanja, Jugoslovenska akademija znanosti i umjetnosti, Zagreb, Acta Biologica 2: 5–179.

HORVAT, I., GLAVAČ, V. & ELLENBERG, H. (1974): Vegetation Südosteuropas. – G. Fischer, Stuttgart: 768 pp.

KOŠIR, Ž. (1994): Ekološke in fitocenološke razmere v gorskem in hribovitem jugozahodnem obrobju Panonije (Ecological and phytosociological circumstances in the montane and hilly edge of southwestern Pannonia) [in Slovenian]. – Ljubljana, Zveza gozdarskih društev Slovenije: 149 pp.

KUTNAR, L. (2012): Growth characteristics of Norway spruce in the Pokljuka mires and forests. – Folia Biol. Geol. 53: 141–150.

LEBOURGEOIS, F., RATHGEBER, C.B.K. & ULRICH, E. (2010): Sensitivity of French temperate coniferous forests to climate variability and extreme events (*Abies alba, Picea abies* and *Pinus sylvestris*). – J. Veg. Sci. 21: 364–376.

LENGYEL, A., CHYTRÝ, M. & TICHÝ, L. (2011): Heterogeneity-constrained random resampling of phytosociological databases. – J. Veg. Sci. 22: 175–183.

LIN, C.-T., LI, C.-F., ZELENÝ, D., CHYTRÝ, M., NAKAMURA, Y., CHEN, M.-Y., CHEN, T.-Y., HSIA, Y.-J., HSIEH, C.-F., LIU, H.-Y., WANG, J.-C., YANG, S.-Z., YEH, C.-L. & CHIOU, C.-R. (2012): Classification of the High-Mountain Coniferous Forests in Taiwan. – Folia Geobot. 47: 373–401.

MÁLIŠ, F., UJHÁZY, K., VODÁLOVÁ, A., BARKA, I., ČABOUN, V. & SITKOVÁ, Z. (2012): The impact of Norway spruce planting on herb vegetation in the mountain beech forests on two bedrocks. – Eur. J. For. Sci. 131: 1551–1569.

MÁLIŠ, F., VLADOVIČ, J., ČABOUN, V. & VODÁLOVÁ, A. (2010): The influence of *Picea abies* on herb vegetation in forest plant communities of the Veporské vrchy Mts. – J. For. Sci. 56: 58–67.

MARINČEK, L. (1975): Gozdna vegetacija Moravške doline na miocenskih kamninah (The forest vegetation of the Moravče valley on Miocene bedrock) [in Slovenian]. – Razprave 4. razreda SAZU 18: 1–28.

MARINČEK, L. (1980): Gozdne združbe na klastičnih sedimentih v jugovzhodni Sloveniji (The forest vegetation in Southeast Slovenia on clastic sediments) [in Slovenia]. – Razprave 4. razreda SAZU 23: 44–185.

MARINČEK, L. (1995): Urwald Šumik in Slowenien. – Sauteria 6: 57–74.

MARINČEK, L. & ČARNI, A. (2002): Commentry to the vegetation map of forest communities of Slovenia in a scale of 1:400 000. – ZRC Publishing, Ljubljana.

MARINŠEK, A., ŠILC, U. & ČARNI, A. (2013): Geographical and ecological differentiation of *Fagus* forest vegetation in SE Europe. – Appl. Veg. Sci. 16: 131–147.

MARTINČIČ, A. (2003): Annotated check-list of the moses of Slovenia. – Hacquetia 2: 91–166.

MARTINČIČ, A., WRABER, T., JOGAN, N., RAVNIK, V., PODOBNIK, A, TURK, B. & VREŠ, B. (1999): Mala flora Slovenije. Ključ za določanje praprotnic in semenk (Small flora of Slovenia. Determination key for *Pteridophyta* and *Spermatophyta*) [in Slovenian]. – Tehniška založba Slovenije, Ljubljana: 845pp.

MCCUNE, B. & MEFFORD, M.J. (1999): PC-ORD. Multivariate Analysis of Ecological Data, Version 4. – MjM Design, Glenden Beach: 237 pp.

OBERDORFER, E. (1994): Pflanzensoziologische Exkursionsflora 7 ed. – Ulmer, Stuttgart: 1050 pp.

PERKO, D. & OROŽEN-ADAMIČ, M. (Ed.) (1998): Slovenija – pokrajine in ljudje (Slovenia – regions and people) [in Slovenian]. – Založba Mladinska knjiga, Ljubljana: 735 pp.

PIGNATTI, S., MENEGONI, P. & PIETROSANTI, S. (2005): Valori di bioindicazione delle piante vascolari della flora d`Italia (Bioindicator values of vascular plants of the Flora of Italy) [in Italian]. – Braun-Blanquetia 39: 1–97.

POLDINI, L. & BRESSAN, E. (2007): I boschi ad abete rosso ed abete bianco in Friuli (Italia nord-orientale) (Norway Spruce and European Silver-fir woods in Friuli (NE-Italy)) [in Italian]. – Fitosociologia 44: 15−54.

RAUNKIAER, C. (1934): The life forms of plants and statistical plant geography. – Charendon Press, Oxford: 632 pp.

RIVAS-MARTÍNEZ, S., RIVAS SÁEN, S. & PENAS MERINO, S. (2011): Worldwide bioclimatic classification system. – Global Geobot. 1: 1–634.

RODWELL, J.R., SCHAMINEE, J.H.J., MUCINA, L., PIGNATTI, S., DRING, J. & MOSS, D. (2002): The diversity of European vegetation. An overview of phytosociological alliances and their relationship to EUNIS habitats. – Report EC-LNV nr. 2002/054, Wageningen: 168 pp.

SCHMITT, B., FARTMANN, T. & HÖLZEL, N. (2010): Vergesellschaftung und Ökologie der Sumpf-Siegwurz (*Gladiolus palustris*) in Südbayern. – Tuexenia 30: 105–127.

ŠILC, U. & ČARNI, A. (2012): Conspectus of vegetation syntaxa in Slovenia. – Hacquetia 11: 113–164.

SPRIBILLE, T. & CHYTRÝ, M. (2002): Vegetation survey in the circumboreal coniferous forest. A review. – Folia Geobot. 37: 365–382.

STATSOFT, INC. (2007): STATISTICA, data analysis system, version 8. – StatSoft, Stuttgart, Wien.

SZAFER, W., PAWŁOWSKI, B. & KULCZYŃSKI, S. (1923): Die Pflanzenassoziationen des Tatra-Gebirges I. Teil: Die Pflanzenassoziationen des Chochołowska-Tales. – Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B, Sci. Nat., Suppl.: 1–66.

TICHÝ, L. & HOLT, J. (2006): JUICE, program for management, analysis and classification of ecological data. – Masaryk University, Vegetation Science Group, Brno: 97 pp.

TREGUBOV, V. (1957): Elaborat za osnovo gojitvenega in melioracijskega načrta gozdov, gozdnih zemljišč in pašnikov za področje Zgornje Savske doline. (Ausarbeitung als Grundlage des Hege- und Meliorationsplanes der Wälder, Waldböden und Weideflächen für das Gebiet des oberen Savetales) [in Slovenian]. – OLO Kranj, Uprava za gozdarstvo: 23–41.

TREGUBOV, V. & ČOKL, M. (Ed.) (1957): Prebiralni gozdovi na Snežniku. Vegetacijska in gozdnogospodarska monografija (Forests of the Snežnik. Phytosociological and forestry monograph). [in Slovenian]: 23–65. Inštitut za gozdno in lesno gospodarstvo Slovenije, Ljubljana.

TSIRIPIDIS, I., BERGMEIER, E. & DIMOPOULOS, P. (2007): Geographical and ecological differentiation in Greek *Fagus* forest vegetation. – J. Veg. Sci. 18: 743–750.

VITTOZ, P., CAMENISCH, M., MAYOR, R., MISERERE, L., VUST, M. & THEURILLAT, J. P. (2010): Subalpine-nival gradient of species richness for vascular plants, bryophytes and lichens in the Swiss Inner Alps. – Bot. Helv. 120: 139–149.

VUKELIĆ, J., ALLEGRO, A. & ŠEGOTA, V. (2010a): Altimontane-subalpine spruce forests with *Laserpitium krapfii* (*Laserpitio krapfii-Piceetum abietis* ass. nova) na sjevernom Velebitu (Hrvatska). – Šumarski list 84: 211–228.

VUKELIĆ, J., ALLEGRO, A., ŠEGOTA, V., ŠAPIĆ, I. (2010b) Nomenclatural-phytocoenotical revision of the association *Calamagrostio variae-Piceetum dinaricum* Bertović 1975, nom.illeg. in Croatia. – Šumarski list 84: 559–568.

WALLNÖFER, S. (1993): *Vaccinio-Piceetea*. – In: MUCINA, L., GRABHERR, G. & WALLNÖFER, S. (Eds.): Die Pflanzengesellschaften Österreichs. Teil III. Wälder und Gebüsche: 241–275. G. Fischer Verlag, Jena.

WEBER, H.E., MORAVEC, J. & THEURILLAT, J.P. (2000): International Code of Phytosociological Nomenclature. 3rd edition. – J. Veg. Sci. 11: 739–768.

WILLNER, W. & GRABHERR, G. (Eds.) (2007): Die Wälder und Gebüsche Österreichs. – Spektrum Akademischer Verlag, München: 608 pp.

WIRTH, V. (1995): Flechtenflora. – Ulmer, Stuttgart: 661 pp.

WRABER, M. (1958): Predalpski jelov gozd v Sloveniji (*Bazzanieto-Abietetum* Wraber 1953 praealpinum subass. nova) (The prealpine fir forest in Slovenia) [in Slovenian]. – Biološki vestnik 6: 36–45.

WRABER, M. (1959): Gozdna združba jelke in okroglolistne lakote v Sloveniji (*Galieto rotundifolii-Abietetum* Wraber 1955) (The forest community of fir and *Galium rotundifolium* in Slovenia) [in Slovenian]. – Prirodoslovno društvo v Ljubljani, Posebne izdaje 1: 1–20.

WRABER, M. (1963): Gozdna združba smreke in gozdne bekice v slovenskih Vzhodnih Alpah (*Luzulo sylvaticae-Piceetum* Wraber 1953) (The forest community of spruce and *Luzula sylvatica* in the Slovenian Eastern Alps) [in Slovenian]. – Razprave 4. razreda SAZU 7: 79–175.

WRABER, M. (1966): Das *Adenostylo glabrae-Piceetum*, eine neue Fichtenwaldgesellschaft in den slowenischen Alpen. – Angew. Pflanzensoziol. (Wien) 18/19: 93–101.

WRABER, M. (1969): Subalpinski smrekov gozd na Kočevskem in njegova horološko-ekološka problematika (Der subalpine Fichtenwald im Karstgebiet von Kočevje und seine chorologisch-ökologische Problematik) [in Slovenian]. – Varstvo narave 6: 91–104.

ZERBE, S. (1994): Das *Galio harcynici-Culto-Piceetum* als Fichten-Forstgesellschaft bodensaurer Waldstandorte im deutschen Mittelgebirgsraum. – Tuexenia 14: 73–82.

ZGS (2012): Poročilo Zavoda za gozdove Slovenije o gozdovih za leto 2011 (Report of Slovenia Forest Service for year 2011) [in Slovenian]. – Zavod za gozdove Slovenije, Ljubljana: 133 pp.

ZUPANČIČ, M. (1980): Die Fichtenwälder der Forstlagen im dinarischen Gebiete Sloweniens. – Dela 24, Slovenska akademija znanosti in umetnosti, razred za naravoslovne vede, Ljubljana: 262 pp.

ZUPANČIČ, M. (1982): *Sphagno-Piceetum* R. Kuoch 1954 v Sloveniji. Predhodno obvestilo (*Sphagno-Piceetum* R. Kuoch 1954 in Slovenia (Preliminary report)) [in Slovenian]. – Biološki vestnik 30: 137–150.

ZUPANČIČ, M. (1999): Spruce forests of Slovenia. – Dela 36, Slovenska akademija znanosti in umetnosti, razred za naravoslovne vede, Ljubljana: 222 pp.

ZUPANČIČ, M. (2007): Syntaxonomic problems of the classes *Vaccinio-Piceetea* and *Erico-Pinetea* in Slovenia. – Fitosociologia 44: 3–13.

ZUPANČIČ, M. & ACCETTO, M. (1994): *Ribeso alpine-Piceetum* ass. nova v Dinarskem gorstvu Slovenije (*Ribeso alpine-Piceetum* ass. nova in the Slovenian Dinaric mountains) [in Slovenian]. – Razprave 4. razreda SAZU 35: 151–175.

ZUPANČIČ, M. & ŽAGAR, V. (2007): Comparative analysis of phytocoenoses with larch: (*Rhodothamno-Rhododendretum* var. geogr. *Paederota lutea laricetosum*, *Rhodothamno-Laricetum*). – Razprave 4. razreda SAZU 48: 307–335.

ZUPANČIČ, M. & ŽAGAR, V. (2010): An overlooked sub-association in secondary spruce association. – Folia Biol. Geol. 51: 109–130.

**Appendix S1.** Sources of data used for the analysis in Table 1. Group numbers refer to Table 1.

**Anhang S1.** Herkunft der Daten für die Analyse in Tabelle 1. Die Gruppennummern beziehen sich auf Tabelle 1.

### Group 1

Zupančič 1999, *Adenostylo glabrae-Piceetum,* Table 9 (relevés 2, 3), Dakskobler 2003, *Adenostylo glabrae-Piceetum,* Table 2 (relevés 2, 3, 6, 7, 8, 9, 10, 13, 16, 17), Dakskobler 2006, *Rhodothamno-Laricetum*, Table 2 (relevés 1, 15, 33, 35), Table 3 (relevés 3, 8, 19, 15, 37, 38), Table 4 (relevés 1, 8, 12, 14, 17, 21, 26), Zupančič 1999, *Seslerio albicantis-Piceetum*, Table 17 (relevé 3).

### Group 2

Zupančič 1999, *Rhytidiadelpho lorei-Piceetum*, Table 4 (relevé 93), Zupančič 1999, *Adenostylo glabrae-Piceetum,* Table 8 (relevés 6, 8, 12, 16, 18), Zupančič 1999, *Aposerido-Piceetum*, Table 11 (relevés 2, 4, 5, 9, 12, 14, 18, 19, 20, 22, 23, 24, 25), Zupančič 1999, *Rhamno fallici-Piceetum*, Table 15 (relevés 1, 2, 3, 4, 5, 6, 7, 8, 9, 10), Zupančič 1999, *Laburno alpini-Piceetum*, Table 13 (relevés 1, 4, 5, 6, 8, 9, 12, 14, 16), Zupančič 1999, *Laburno alpini-Piceetum*, Table 14 (relevés 1, 2, 3, 5, 6), Zupančič 1999, *Petasiti-Piceetum*, Table 16 (relevés 1, 2, 3), Zupančič 1999, *Erico-Piceetum*, Table 20 (relevé 2), Zupančič & Žagar 2010, *Aposerido-Piceetum*, Table 1 (relevés 2, 4), Marinček & Marinšek unpubl., (1 relevé).

### Group 3

Zupančič 1999, *Prenantho purpureae-Piceetum,* Table 5 (relevés 35, 37), Zupančič 1980, *Lonicero caeruleae-Piceetum*, Table 1 (relevés 3, 15, 19, 24, 26, 28, 30, 31, 32, 37, 38), Zupančič & Accetto 1994, *Ribeso alpini-Piceetum*, Table 1 (relevés 2, 4, 5), Zupančič 1980, *Hacquetio-Piceetum*, Table 3 (relevés 3, 4, 6, 7, 8, 9, 11, 12, 14, 15, 17), Zupančič 1980, *Stellario montanae-Piceetum*, Table 2 (relevés 2, 3, 6, 9, 10, 11, 12, 14, 15, 16, 17), Wraber 1969, *Lonicero caeruleae-Piceetum.* p. 95 (1 relevé).

### Group 4

Zupančič & Accetto 1994, *Ribeso alpini-Piceetum*, Table 1 (relevés 6, 7, 8, 12, 14, 15, 17, 18, 19, 22), Accetto 2006, *Campanulo justinianae-Piceetum*, Table 1 (relevés 1, 2, 3, 4, 6, 7, 8, 9, 10, 11, 13, 14, 15, 16), Tregubov 1957, *Calamagrostio-Abietetum*, Table 10 (relevés 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20), Tregubov 1957, *Neckero-Abietetum*, Table 10 (relevés 1, 2, 3, 4, 5, 6, 7, 8, 9), Accetto 1993, *Asplenio-Piceetum*, Table 1 (relevés 1, 2, 3, 5, 6, 7).

### Group 5

Tregubov & Čokl 1957, *Mastigobryo-Piceetum,* Table p. 31 (relevés 18, 34, 80, 95, 126, 173, 207, 210, 212, 214, 219, 221), Wraber 1958, *Bazzanio-Abietetum*, Table in appendix (relevé 3), Marinček & Marinšek unpubl., *Bazzanio-Abietetum*, Table 1 (5 relevés), Zupančič 1999, *Avenello flexuosae-Piceetum*, Table 18 (relevés 2, 5, 8, 12, 13, 14, 25, 28, 32, 34, 45, 48, 50, 51), Wraber 1959, *Galio rotundifolii-Abietetum,* Table in appendix (relevé 10), Zupančič 1999, *Rhytidiadelpho lorei-Piceetum*, Table 4 (relevés 4, 8, 16, 18, 19, 21, 36, 37, 40, 41, 45, 56, 86, 91), Zupančič 1999, *Prenantho purpureae-Piceetum,* Table 5 (relevés 1, 3, 6, 9, 23, 24, 25, 27, 39, 41, 42), Zupančič 1999, *Luzulo sylvaticae-Piceetum,* Table p. 62 (relevé 1), Wraber 1963, *Luzulo sylvaticae-Piceetum,* Table p. 90 (relevés 1, 10, 11, 15, 21, 22, 23, 27, 33, 38, 39, 41), Tregubov 1957, *Lonicero caeruleae-Piceetum*, Table 11 (relevés 2, 3, 4, 64), Zupančič 1999, *Luzulo sylvaticae-Piceetum,* Table 6 (relevés 2, 8, 14), Zupančič 1982, *Sphagno-Piceetum*, Table 1 (relevés 1, 2, 3, 4, 14, 15, 16, 17, 18, 26, 28, 38, 47).

### Group 6

Wraber 1959, *Galio rotundifolii-Abietetum*, Table in appendix (relevés 6, 7, 37), Košir 1994, *Luzulo albidae-Abietetum*, Table 6 (relevés 1, 3, 4, 5, 7, 9, 10, 14, 16, 17, 19, 20, 21, 22), Marinček 1995, *Hieracio rotundati-Abietetum*, Table 2 (relevés 1, 2, 3, 4, 5, 7, 8, 9, 10), Belec 2009, *Paraleucobryo-Abietetum,* Table 23 (relevés 1, 2, 3), Marinček 1975, *Bazzanio-Abietetum*, Table p. 21 (relevé 1), Marinček 1980, *Galio rotundifolii-Abietetum*, Table 2 (relevés 1, 4, 7, 12, 15, 18), Wraber 1958, *Bazzanio-Abietetum*, Table (relevé 5), Accetto 1986, *Galio rotundifolii-Abietetum*, Table 5 (relevés 11), Marinček & Košir unpubl., *Galio rotundifolii-Abietetum*, Table 1 (relevés 1, 3, 9, 16, 20, 22), Košir 1994, *Polysticho setiferi-Abietetum*, Table 5 (relevés 2, 3, 4, 5, 7), Marinšek unpubl. (9 relevés).

## References used only in appendix

MARINČEK, L. & KOŠIR, P. (unpubl.): Geographical differentiation of the association *Galio rotundifolii-Abietetum* Wraber (1955) 1959 in Slovenia.

MARINČEK, L. & MARINŠEK, A. (unpubl.): Unpublished relevés.

MARINŠEK, A. (unpubl.): Unpublished relevés.

Tuexenia 34: 501–504. Göttingen 2014.
available online at www.tuexenia.de

# Erratum to JUVAN et al. (2013) in Tuexenia 33

In JUVAN et al. (2013), a post-acceptance publication error resulted in printing wrong Figures 1, 3, 4, 5 and 6. We publish the corrected Figures and their captions below.

## Erratum zu JUVAN et al. (2013) in Tuexenia 33

In JUVAN et al. (2013) resultierte ein Fehler nach der Annahme des Manuskripts zum Druck falscher Abbildungen 1, 3, 4, 5 und 6. Wir publizieren die korrigierten Abbildungen mit ihren Unterschriften im Folgenden.

JUVAN, N., KOŠIR, P., MARINŠEK, A., PAUŠIČ, A. & ČARNI, A. (2013): Differentiation of the *Piceetalia* and *Athyrio-Piceetalia* forests in Slovenia. – Tuexenia 33: 25–48.

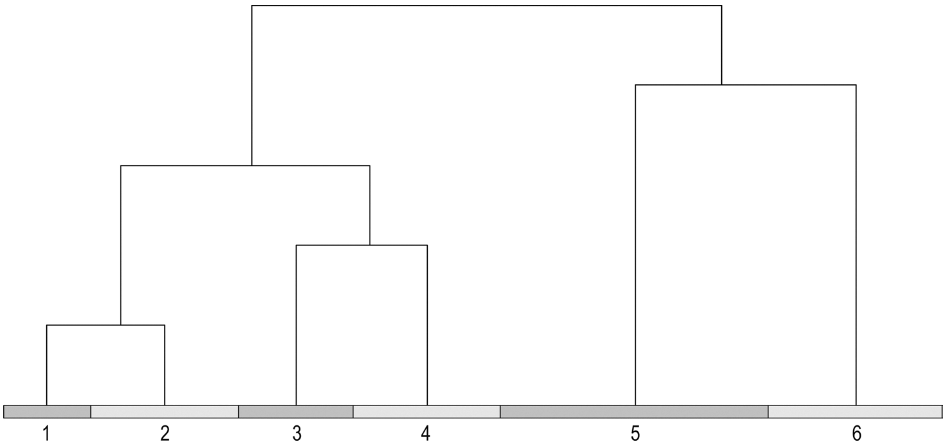

**Fig. 1.** Simplified cluster dendrogram of spruce forests data. Clusters 1–4 are found on carbonate bedrock, clusters 5–6 on non-carbonate bedrock. Legend: 1 – zonal, altimontane SFF, 2 – secondary SFF, 3 – frost hollows SFF, 4 – boulder scree SFF, 5 – altitudinal SFF, 6 – lowland SFF.

**Abb. 1.** Dendrogramm der Clusteranalyse von Daten aus Fichten-, Lärchen- und Tannenwäldern. Cluster 1-4 auf Carbonatgesteinen, Cluster 5-6 auf carbonatfreien Gesteinen. Legende: 1 – höhenzonal, 2 – sekundär, 3 – Kaltluftsenken, 4 – Blockhalden, 5 – Hochlagen 6 – Tiefland.

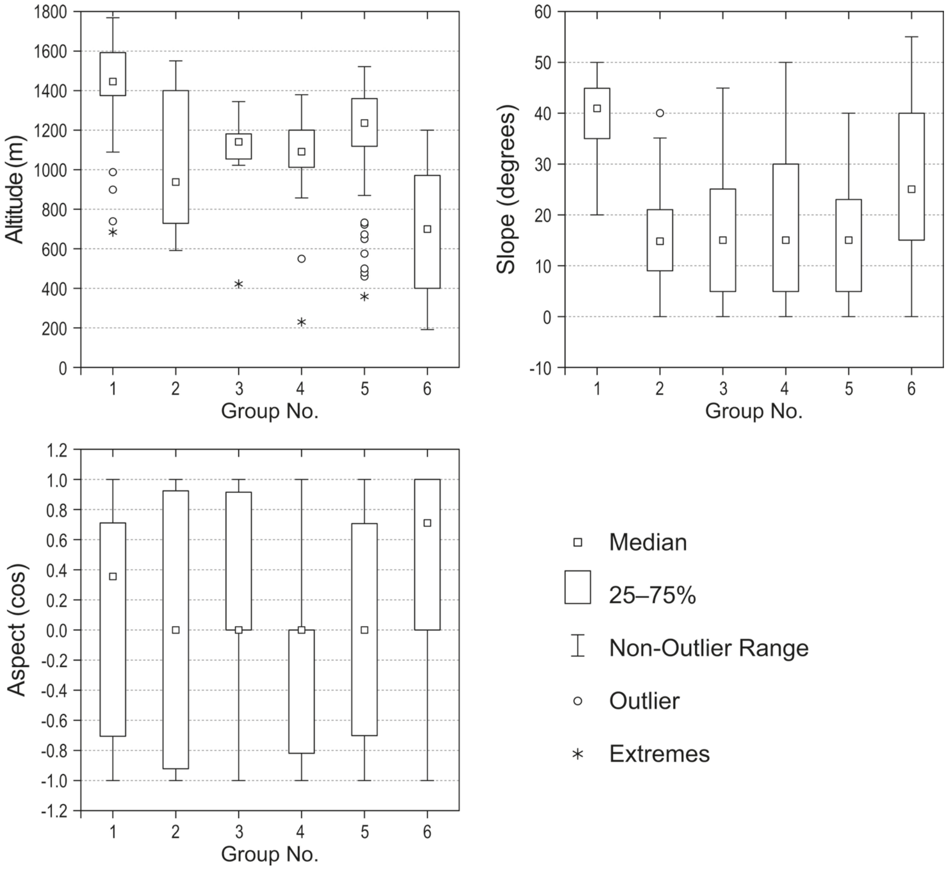

**Fig. 3.** Comparison of altitude, slope and aspect for studied groups. Median values, interquartile distance, maximum and minimum, outliers and extreme values are shown. Group numbers correspond to those in Fig. 1.

**Abb. 3.** Vergleich von Höhe, Hangneigung und Exposition der Untersuchungsgruppen. Medianwerte, Interquartilsabstand, Maximum und Minimum, Ausreißer- und Extremwerte werden dargestellt. Die Gruppennummern entsprechen denen in Abb. 1.

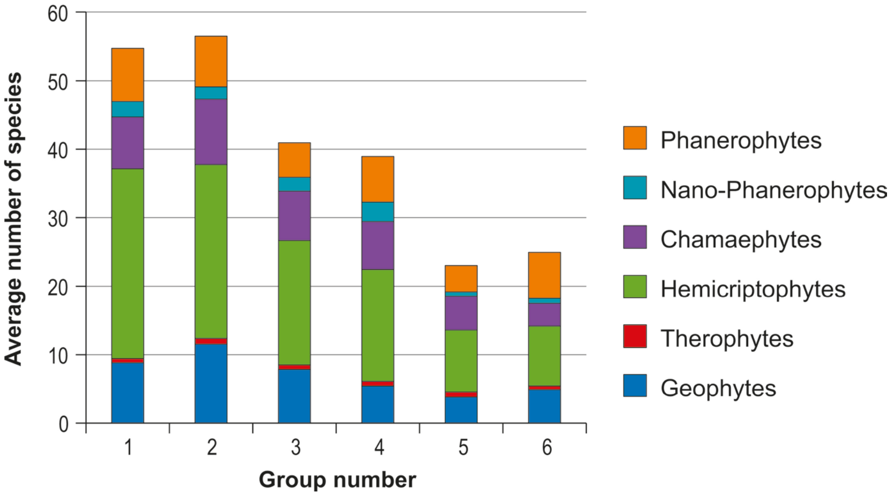

**Fig.4.** Life form structure in the SFF. Group numbers correspond to those in Fig. 1.

**Abb. 4.** Struktur der Lebensform in der Fichten-, Lärchen- und Tannenwälder. Die Gruppennummern entsprechen denen in Abb. 1.

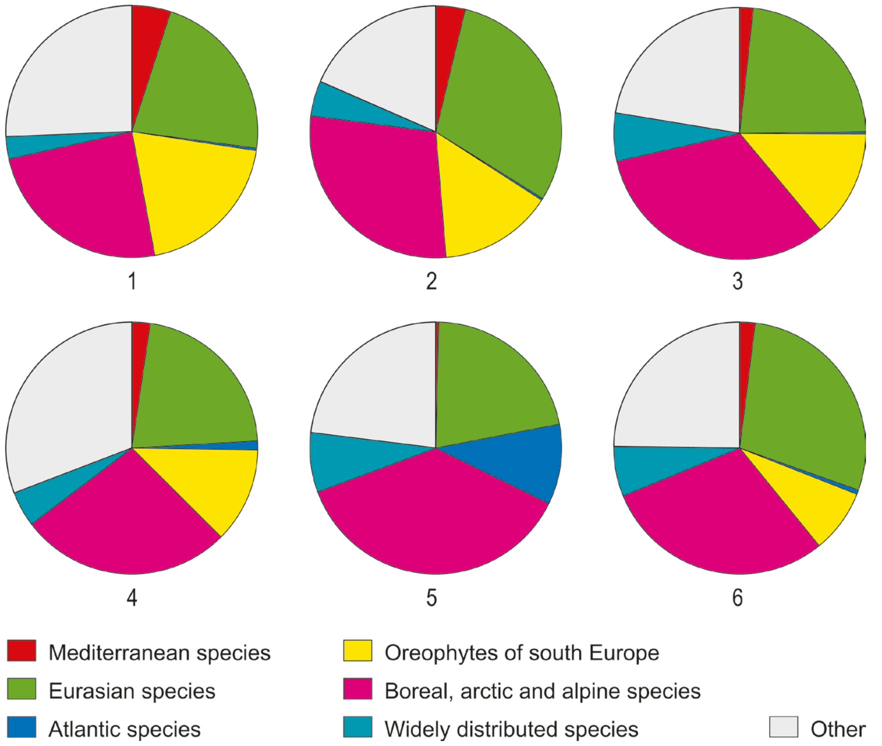

**Fig. 5.** Proportion of chorotypes in the SFF. Group numbers correspond to those in Fig. 1.

**Abb. 5.** Anteil der Chorotypen in den sechs Typen von Fichten-, Lärchen- und Tannenwälder. Die Gruppennummern entsprechen denen in Abb. 1.

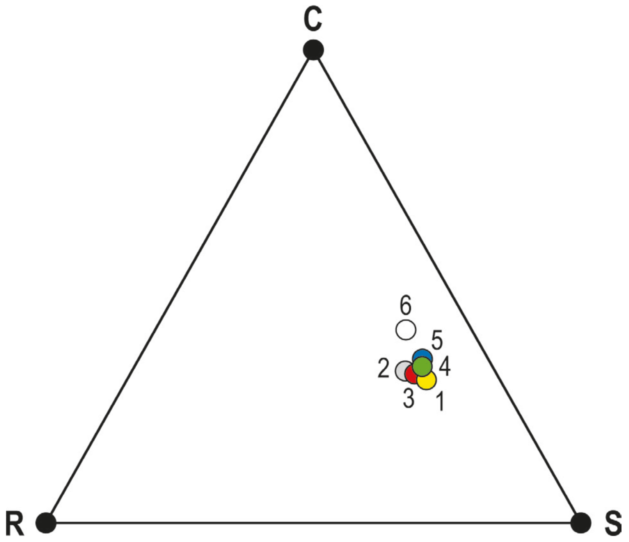

**Fig. 6.** Position of groups in the Grime triangle model of C, S and R strategies. Group numbers correspond to those in Fig. 1.

**Abb. 6.** Lage der Gruppen im Grime-Dreiecksmodell der C-, S- und R-Strategien. Die Gruppennummern entsprechen denen in Abb. 1.