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Forest communities of the Tatra Mountains: A classification based on a permanent plot inventory in the Tatra National Park (Poland)

Waldgesellschaften der Tatra: Eine Klassifikation auf der Basis einer permanenten Stichprobeninventur im Tatra-Nationalpark (Polen)

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Abstract

The Tatra Mts. are an area with a long tradition of phytosociological studies, as the first study using Braun-Blanquet's approach in Poland was conducted in this region in the 1920s. However, a comprehensive modern classification of the forest communities of the Tatra National Park (Polish part of the Tatra Mts.) is missing but urgently needed, for example, as a reference for forest stand conversion and restoration projects. In 2018, a systematic network of over 600 permanent research plots was sampled in the Tatra National Park using a phytosociological approach. Here, we present the first results of the numerical classification of the forest communities based on this objectively collected dataset.

Numerical classification led to the identification of eight main forest types. Seven groups were assigned to previously described alliances and sub-alliances. In addition, one group represents spruce plantations on base-rich soils. We identified two new alliances: *Aremonio-Fagion* and *Chrysanthemo rotundifolii-Piceion*, which have never been reported previously from neither the Polish part of the Tatra Mts. nor from Poland. We have related these syntaxa to the vegetation types that were previously described in the Tatra Mts. In addition, we analyzed which environmental factors drive the variability in the forest types. Soil reaction and fertility, as well as elevation and temperature, were the significant factors responsible for the differences in the species composition among the distinguished groups.

In this study, we also discuss the effects of the objective sampling design on the resulting classification. The main consequence of this sampling design is that only the forest communities that dominated the landscape of the Tatra Mts. were distinguished. There are also forest communities confined to more specific habitats that cover relatively small areas, e.g., ravine or riverine forests. For that reason, a preferential sampling scheme is required to include these communities into the classification presented in this study.

Keywords: forest communities, mountain forest, objective sampling, phytosociological classification, Poland, Tatra Mts.

Erweiterte deutsche Zusammenfassung am Ende des Artikels

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1. Introduction

The tradition of phytosociological surveys in the Tatra Mts. is very long as the first studies using Braun-Blanquet's approach (BRAUN-BLANQUET 1964, DZWONKO 2007) in Poland were conducted in this region (SZAFER et al. 1923, 1927). Since the beginning of the 20th century, dozens of papers concerning the plant communities in the Tatra Mts. have been published. However, most of them focused either on non-forest communities (BALCERKIEWICZ 1978, 1984), were limited to specific types of forest communities (ZIĘBA et al. 2018) or to selected parts of the Tatra Mts. (HORVAT et al. 1980, WOJTERSKA et al. 2005). There were several attempts to synthetize the variability of the forest communities in the Tatra Mts.; however, most of them were not supported by detailed analyses of the phytosociological relevés (MYCZKOWSKI 1976, PIĘKOŚ-MIRKOWA & MIREK 1996).

Despite 100 years having passed since the first vegetation surveys in the Tatra Mts., knowledge on the diversity of forest communities is still insufficient, and modern vegetation classification is urgently needed for both conservation and management purposes. On the one hand, some of the long-lasting disputes concerning the status of certain forest communities have recently been resolved (ZIĘBA et al. 2018). On the other hand, there are still large discrepancies among the syntaxonomic conclusions of different researchers. The best example of this is the classification of beech and silver fir forests (MATUSZKIEWICZ 1977, PIĘKOŚ-MIRKOWA & MIREK 1996). The mesic forests dominated by *Abies alba* are usually classified as *Galio-Abietetum* in the neighboring mountain ranges of the Western Carpathians (PARUSEL et al. 2004, RÓŻAŃSKI & HOLEKSA 2004), while in the Tatra Mts. they were either classified as the association *Galio-Piceetum* (MATUSZKIEWICZ 2001) or described as unidentified fir forests (*Abietetum, Abies alba-Oxalis acetosella* community) (MYCZKOWSKI 1974, PIĘKOŚ-MIRKOWA & MIREK 2003). Part of the problem is due to the fact that the majority of the forests in the lower elevations of the Tatra Mts. has been strongly transformed due to management practices, especially by the widespread planting of spruce in the 19th and early 20th centuries (LETTNER 1885, FABIJANOWSKI & DZIEWOLSKI 1996, BODZIARCZYK et al. 2019). The dominance of spruce in the canopy affected the soil properties and the composition of plants on the forest floor, partly changing the plant communities and making their discrimination more difficult (MYCZKOWSKI 1974, GODBOLD et al. 2003). Another problem is poor knowledge about the diversity of some forest types, which are limited to specific habitat conditions and thus are relatively rare in the landscape of the Tatra Mts. On the one hand, recent studies revealed that some of them should be distinguished as independent phytosociological units (ZIĘBA et al. 2018). On the other hand, the status of the others still remains unclear, for example, the maple forests of the *Tilio-Acerion* alliance.

The above-mentioned syntaxonomical problems and ambiguities are not only academic considerations, but also have far reaching consequences. The administration of the Tatra National Park has been working on stand conversion: trying to replace the spruce monocultures at lower elevations with mixed forest stands of *Fagus sylvatica*, *Abies alba* and *Picea abies* (BODZIARCZYK et al. 2019). However, to perform the conversion they need to specify the goal – which tree species should be introduced in a given place, and what should their proportions be. For that purpose it is necessary to discriminate, for example, between the fir-dominated and beech-dominated types of communities. In addition, knowledge of the diagnostic species of vegetation units could be useful as a tool to evaluate the naturalness and success of possible restoration projects. Besides problems related to stand conversion, a lack of a modern vegetation classification system brings other difficulties. For example, Tatra National Park is also a part of the Tatra Transboundary Biosphere Reserve (TTBR).

Currently, it is almost impossible to propose a standardized vegetation map and convert it into Natura 2000 habitats, as both Poland and Slovakia use very different hierarchical classifications of vegetation types.

In the years 2016–2017 a network of over 600 permanent research plots was established in the forests of the Tatra National Park (BODZIARCZYK et al. 2019). This allowed for the collection of a large amount of phytosociological data in an objective way (SCHMIEDEL et al. 2019) and for developing a new classification for the forest communities that predominate the landscape of the Tatra Mts. As learnt from earlier studies (BODZIARCZYK & PANCER-KOTEJA 2004, PARUSEL et al. 2004), forest communities occurring in small patches are usually either absent or heavily underrepresented in datasets resulting from surveys conducted in regularly distributed sample plots, thus they are not the subject of this research. Specifically, the aims of this study were to: (1) provide objective numerical classification of forest communities dominating the landscape of the Tatra Mts; (2) define sets of diagnostic species for distinguished forest associations; (3) analyze the main gradients responsible for diversity in the main forest types; (4) discuss the diversity of the main forest types in the Tatra Mts. in a broader geographical context.

2. Methods

2.1 Study areas

The Tatra Mts. are the highest mountain range in the Carpathians (highest peaks: in Slovakia - Gerlach 2655 m a.s.l., in Poland - Rysy 2499 m a.s.l.). They are situated on the border between Poland and Slovakia. The total area of the Tatra Mts. is ca. 79,000 ha. Based on geomorphological criteria, they are divided into three parts: Western Tatras, High Tatras and Belianske Tatras. They are a biodiversity hotspot with ca. 1300 species of vascular plants and ca. 6000 species of animals (MIREK 1996, PIĘKOŚ-MIRKOWA & MIREK 2003, MRÁZ & RONIKIER 2016). In view of the above mentioned attributes, they are a National Park (IUCN category: II), Transboundary MaB Unesco Reserve and belong to the Natura 2000 network (KOUTNÁ & CHOVANCOVÁ 2010).

The research was performed in the Polish part of the Tatra Mts. and covered the entire forest area of the Polish Tatra National Park (ca. 12,900 ha). Lower parts of these areas are mainly built out of sedimentary rocks (limestones, dolomites and flysch), only locally covered by glacial moraines with crystalline rocks. Higher parts of the mountains consist mostly of crystalline rocks (gneisses, granodiorites and granites) (PIOTROWSKA et al. 2015). The lower parts (up to 1250 m a.s.l.) of the Tatra Mts. lay in a zone of moderate cool climate (mean annual temp.: +5 °C) (HESS 1996) and are dominated by a mixed beech-fir forest. Nonetheless, large areas of these forests were converted in the 19th century or earlier into artificial Norway spruce (*Picea abies*) monocultures. Slightly less fertile and more humid habitats are covered by European fir (*Abies alba*) forests, whereas most acidic soils are covered by mixed *Abies alba* and *Picea abies* stands. Additionally, the most inaccessible dolomite and limestone rocks have surviving Scots pine (*Pinus sylvestris*) woodlands, whereas wet sites at the bottom of valleys are covered by small patches of grey alder (*Alnus incana*) forests. Furthermore, on the steep and rocky gullies, patches of sycamore (*Acer pseudoplatanus*) forests have developed (PIĘKOŚ-MIRKOWA & MIREK 1996).

The upper montane belt (mean annual temp.: +3 °C) (HESS 1996) is dominated by Norway spruce. In the more fertile habitats, on limestone and dolomite bedrock, grow relatively species-rich calcareous spruce forest communities. Nonetheless, the majority of this zone is covered by subalpine acidophilous spruce forests (PIĘKOŚ-MIRKOWA & MIREK 1996). The timber line runs across the Polish Tatra Mts. at the elevation of 1550 m a.s.l. (mean annual temp.: +2 °C) (HESS 1996, PIĘKOŚ-MIRKOWA & MIREK 1996). In some parts of the mountains, along the timberline survive Swiss stone pine (*Pinus cembra*) forests (ZIĘBA et al. 2018). Between 1550 m a.s.l. and 1850 m a.s.l. (mean annual temp.: +1 °C) grow dense shrubs of *Pinus mugo*, which are traditionally divided, based on the soil properties, into two associations – calcareous and silicolous (PIĘKOŚ-MIRKOWA & MIREK 1996).

2.2 Sampling design and dataset

The data were collected from permanent plots, located on a systematic sampling grid (500 m × 500 m) throughout the whole of the Polish Tatra Mts. (BODZIARCZYK et al. 2019). The entire grid consists of 848 sampling plots (from 817 m a.s.l. to 2405 m a.s.l.), whereas 669 (817 m – 1801 m) are located in forest ecosystems and *Pinus mugo* shrubs (Fig. 1). At each plot a relevé of 100 m^2 was taken (circular plot with a radius r = 5.64 m). The Braun-Blanquet scale (BRAUN-BLANQUET 1964, DZWONKO 2007) was used to estimate the cover of each species in every layer, including trees, shrubs and herbs. Mosses and lichens were not identified. The majority of the relevés were collected in 2018, with only 11 were taken in 2017. On the basis of expert knowledge, every relevé was tentatively characterized by assigning to the phytosociological unit, preferably to association or alliance. Some of the plots designated by a systematic grid were located in places where heterogeneous communities could have a transitional character, and therefore it could be identified with more than one phytosociological unit (e.g., *Sambuco-Salicion*/*Dentario glandulosae-Fagetum* or *Seslerion tatrae/Polysticho-Piceetum*). All of the relevés were stored in the Turboveg database (HENNEKENS & SCHAMINÉE 2001). The collected dataset is included in the Forest Database of Southern Poland (PIELECH et al. 2018).

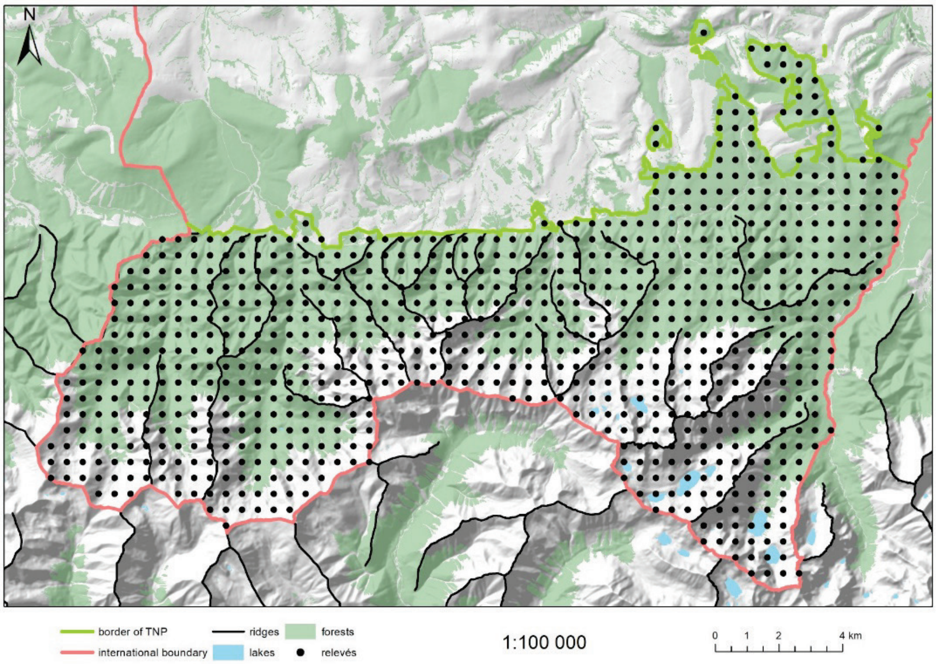

Fig. 1. Map presenting distribution of 848 permanent plots located on systematic sampling grid (500 m × 500 m) in Tatra National Park (Poland). In this study, 669 plots located in forest ecosystems and *Pinus mugo* shrubs were considered.

Abb. 1. Karte mit der Verteilung von 848 Dauerflächen auf einem systematischen Stichprobenraster (500 m × 500 m) im Tatra-Nationalpark (Polen). In dieser Studie wurden 669 Parzellen in Waldökosystemen und *Pinus mugo*-Gebüschen berücksichtigt.

Data describing the habitat conditions in the sampled plots, such as elevation [m a.s.l.], inclination [°] and exposure [°], were taken from the digital elevation model (DEM), with a terrain pixel resolution of 5 m. In addition, the DEM was used to calculate the potential solar radiation, which describes the amount of solar energy (expressed in kWh/m^2) that can potentially reach each place. Other site variables (soil and geology - bedrock) were taken from soil (scale 1:20 000, SKIBA 2002) and geological (scale 1:30 000, BAC-MOSZASZWILI et al. 1979) maps. Furthermore, to determine the impact of disturbance on the forest communities of the Tatra Mts., we analyzed each plot regarding the occurrence of disturbance events since 1999. The data were derived from aerial and satellite images in the GIS environment, based on photointerpretation (CIOŁKOSZ et al. 1999). Two types of disturbances were distinguished: 1) natural: windfalls, bark beetle outbreaks, avalanches, landslides, floods and 2) human-induced: different types of cutting, including salvage cutting (predominant) and cutting in the course of forest conversion.

Out of the initial dataset of 669 relevés, only plots located in forests were used and the plots representing *Pinus mugo* shrubs were excluded. In addition, prior to the statistical analyses, a pre-selection of the sample plots was made to exclude heavily disturbed or heterogeneous plots. First, all plots with tree cover lower than 20% were excluded. Second, based on tentative phytosociological diagnoses, we excluded plots with a significant contribution of non-forest vegetation type (e.g., plots characterized as *Seslerion tatrae/Polysticho-Piceetum* or *Calamagrostietum/Vaccinio-Pinetum cembre*). The final dataset included 307 relevés.

2.3 Statistical analyses

The classification was performed in the Juice program (TICHÝ 2002). All other statistical analyses were performed and graphically presented in R (ver. 3.6.1, R CORE TEAM 2019) with packages 'vegan' (OKSANEN et al. 2019), 'ggplot2' (WICKHAM 2016) and 'ggpubr' (KASSAMBARA 2019). Prior to the statistical analyses, in Juice we combined the layers from all relevés and merged all narrowly defined species into their broadly defined taxonomic units (see Appendix 1 for details). For classification, we used a modified TWINSPAN algorithm (ROLEČEK et al. 2009) with the total inertia as a measure of cluster heterogeneity. We set six cut levels to reflect the differences in species abundances based on the Braun-Blanquet scale and defined divisions into 30 clusters as a rule for stopping a divisive procedure in TWINSPAN. The resulting clusters were then analyzed and placed into the hierarchical system proposed by MUCINA et al. (2016). We attempted to assign the distinguished groups at the level of (sub)alliance, but whenever possible, we also referred to the association level.

All distinguished forest types were characterized by a set of diagnostic species. In this step, we excluded forest plantations (monocultures of *Picea abies*) and used only identified syntaxa.

We used a phi coefficient (CHYTRÝ et al. 2002) as a statistical measure of fidelity and used standardization that accounted for differences in the sizes of the analyzed clusters (TICHÝ & CHYTRÝ 2006). In addition, we used Fisher's exact test to test for the significance ($\alpha = 0.001$) of the fidelity measures (CHYTRÝ et al. 2002). We selected the minimum thresholds of phi coefficients for diagnostic and highly diagnostic species, which were 25 and 50, respectively. In addition, we defined sets of constant and dominant species for all distinguished associations. Species that reach 40% and 80% frequencies were designated as constant and highly constant, respectively. Finally, dominant and highly dominant species were defined as those that exceed 25% cover in 5% and 10% of plots in the analyzed group, respectively. The thresholds used in this study are consistent with other regional studies from Central Europe (CHYTRÝ 2013, PIELECH 2015). In addition, a synoptic table was generated to show the differences among the associations.

A Kruskal-Wallis test followed by post-hoc test were used to analyze differences in elevation, slope, aspect and solar radiation. The same statistical procedures were then used to compare the diversity indices among associations, species richness, Shannon's and Simpson's diversity indices, and evenness. In addition, we calculated community weighted means of Ellenberg's Indicator Values (EIVs) for light, temperature, moisture, reaction and nitrogen (fertility), and then compared them among the distinguished associations using a permutation test with EIVs randomization (ZELENÝ & SCHAFFERS

2012); we ran this test with 10,000 iterations. Finally, we used non-metric multidimensional scaling (NMDS) to explore the distinctiveness of the analyzed groups. To better interpret the distribution of the associations along the main environmental gradients, we passively fitted environmental variables using the *envfit* function from the 'vegan' package.

3. Results

3.1 Classification

Based on the results of the TWINSPAN analysis (Fig. 2), we identified eight main forest types. Seven clusters were identified as previously described forest types representing five alliances. In addition, one cluster represents monocultures of *Picea abies* planted on base-rich soils. Below we present a description for all distinguished groups with comments on their phytosociological affinities and lists of diagnostic, constant and dominant species. Species that have crossed the upper thresholds, i.e., highly diagnostic, highly constant and highly dominant, are given in bold. In addition, the synoptic table (Supplement S1) presents the differences in the species composition of the seven distinguished forest types. The descriptions mentioned above are followed by a list of identified syntaxa presented in a hierarchical order. The distribution of plots assigned to each forest type in presented in Figure 3.

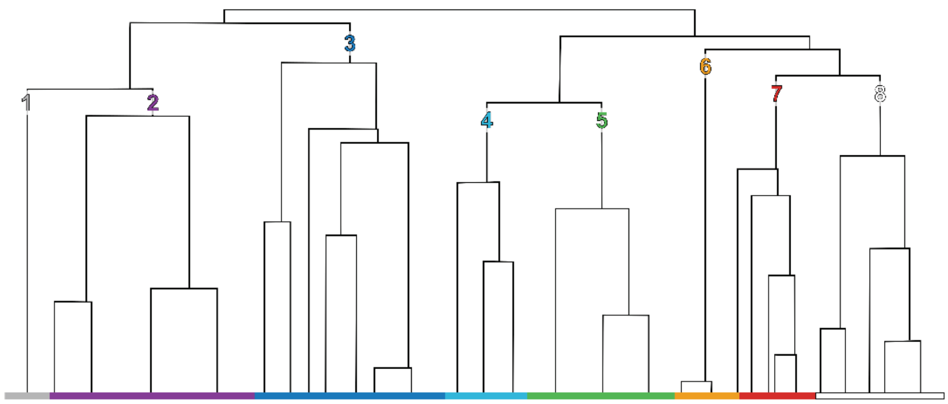

Fig. 2. Dendrogram presenting results of TWINSPAN classification. Explanations: 1 – *Piceion excelsae*, subalpine Swiss stone pine (*Pinus cembra*) forests; 2 – *Piceion excelsae*, subalpine spruce forests; 3 – *Abieti-Piceion*; 4 – *Chrysanthemo rotundifolii-Piceion*; 5 – *Aremonio-Fagion*; 6 – *Fagion sylvaticae*, beech and mixed fir-beech forests (*Eu-Fagenion* and mesic *Galio-Abietenion*); 7 – *Fagion sylvaticae*, hygrophilous fir forests (hygrophilous *Galio-Abietenion*); 8 – spruce plantations on base-rich soils.

Abb. 2. Dendrogramm mit Ergebnissen der TWINSPAN-Klassifizierung. Erläuterungen: 1 – *Piceion excelsae*, subalpine Zirbenwälder (*Pinus cembra*); 2 – *Piceion excelsae*, subalpine Fichtenwälder; 3 – *Abieti-Piceion*; 4 – *Chrysanthemo rotundifolii-Piceion*; 5 – *Aremonio-Fagion*; 6 – *Fagion sylvaticae*, Buchen- und Tannen-Buchnmischwälder (*Eu-Fagenion* and mesophytisches *Galio-Abietenion*); 7 – *Fagion sylvaticae*, hygrophile Tannwälder (hygrophiles *Galio-Abietenion*); 8 – Fichtenforsten auf basenreichen Böden.

Group 1

Number of relevés: 15

Vegetation type: Swiss stone pine (*Pinus cembra*) forests

Phytosociological affinity: *Piceion excelsae* Pawłowski et al. 1928 p.p.

Diagnostic species: *Calluna vulgaris*, *Huperzia selago*, *Lycopodium annotinum*, ***Pinus cembra***, ***P. mugo***, ***Vaccinium vitis-idaea***

Constant species: *Athyrium distentifolium*, *Calamagrostis villosa*, *Deschampsia flexuosa*, *Dryopteris dilatata* agg., *Homogyne alpina*, *Huperzia selago*, *Lycopodium annotinum*, *Oxalis acetosella*, ***Picea abies***, *Pinus cembra*, ***P. mugo***, *Rubus idaeus*, ***Sorbus aucuparia***, ***Vaccinium myrtillus***, ***V. vitis-idaea***

Dominant species: *Athyrium distentifolium*, ***Calamagrostis villosa***, *Deschampsia flexuosa*, *Lycopodium annotinum*, ***Picea abies***, ***Pinus cembra***, ***P. mugo***, *Sorbus aucuparia*, ***Vaccinium myrtillus***, ***V. vitis-idaea***

Group 2

Number of relevés: 67

Vegetation type: Subalpine Norway spruce forests on nutrient-poor soils

Phytosociological affinity: *Piceion excelsae* Pawłowski et al. 1928

Diagnostic species: *Deschampsia flexuosa*

Constant species: *Calamagrostis villosa*, ***Deschampsia flexuosa***, ***Dryopteris dilatata* agg.**, *Homogyne alpina*, *Oxalis acetosella*, ***Picea abies***, ***Sorbus aucuparia***, ***Vaccinium myrtillus***

Dominant species: ***Calamagrostis villosa***, *Deschampsia flexuosa*, *Oxalis acetosella*, ***Picea abies***, ***Vaccinium myrtillus***

Group 3

Number of relevés: 62

Vegetation type: Mountain mesophilous forests of silver fir and Norway spruce

Phytosociological affinity: *Abieti-Piceion* (Br.-Bl. in Br.-Bl. et al. 1939) Soó 1964

Diagnostic species: *Chamaenerion angustifolium*, *Luzula luzuloides*

Constant species: *Athyrium distentifolium*, *Deschampsia flexuosa*, *Dryopteris dilatata* agg., *Gentiana asclepiadea*, ***Homogyne alpina***, *Luzula luzuloides*, *L. sylvatica*, ***Oxalis acetosella***, ***Picea abies***, *Rubus idaeus*, *Senecio nemorensis* agg., ***Sorbus aucuparia***, ***Vaccinium myrtillus***

Dominant species: *Abies alba*, *Athyrium distentifolium*, *Deschampsia flexuosa*, ***Oxalis acetosella***, ***Picea abies***, ***Vaccinium myrtillus***

Group 4

Number of relevés: 27

Vegetation type: Subalpine herb-rich Norway spruce forests on rich calcareous soils

Phytosociological affinity: *Chrysanthemo rotundifolii-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962

Diagnostic species: *Aconitum variegatum*, *Asplenium viride*, ***Astrantia major***, *Bellidiastrum michelii*, ***Campanula polymorpha***, *Cardaminopsis arenosa* agg., *Carduus glaucus*, *Carex brachystachys*, *C. flacca*, *C. sempervirens*, *Carlina acaulis*, *Cirsium erisithales*, *Clematis alpina*, *Coeloglossum viride*, *Corallorhiza trifida*, *Crepis jacquinii*, *Digitalis grandiflora*, *Epipactis atrorubens*, *Festuca carpatica*, *F. versicolor*, ***Fragaria vesca***, ***Galium anisophyllum***, *G. mollugo* agg., *Gentianella lutescens*, *Geranium sylvaticum*, *Heracleum sphondylium*, *Hypericum maculatum*, ***Hieracium murorum***, ***Leontodon hispidus* agg.**, *Linum catharticum*, *Listera ovata*, *Moneses uniflora*, *Monotropa hypopitys*, *Mycelis muralis*, *Parnassia palustris*, *Pedicularis verticillata*, *Petasites kablikianus*, *Phyteuma orbiculare*, *P. spicatum*, *Pimpinella major*, *Poa nemoralis*, ***Polystichum lonchitis***, *Primula elatior*, *Prunella vulgaris*, *Ranunculus oreophilus*, *Salix caprea*, ***Scabiosa lucida***, ***Sesleria tatrae***, *Soldanella carpatica* agg., *Swertia perennis*, *Thymus alpestris*, ***Tofieldia calyculata***, *Trisetum alpestre*, *Vaccinium vitis-idaea*, *Valeriana tripteris*, *Viola biflora*

Constant species: *Acer pseudoplatanus*, *Asplenium viride*, *Astrantia major*, *Athyrium filix-femina*, ***Calamagrostis arundinacea***, *Campanula polymorpha*, *Chaerophyllum hirsutum*, *Cirsium erisithales*, *Clematis alpina*, *Crepis paludosa*, *Deschampsia flexuosa*, ***Fragaria vesca***, *Galeobdolon luteum*, *Galium anisophyllum*, *Gentiana asclepiadea*, *Gymnocarpium dryopteris*, ***Hieracium murorum***, ***Homogyne alpina***, *Hypericum maculatum*, *Leontodon hispidus* agg., *Leucanthemum waldsteinii*, *Listera ovata*, *Luzula sylvatica*, *Maianthemum bifolium*, *Mycelis muralis*, ***Oxalis acetosella***, *Phyteuma spicatum*, ***Picea abies***, *Pimpinella major*, *Polygonatum verticillatum*, *Polystichum lonchitis*, *Prenanthes purpurea*, *Primula elatior*, *Rubus idaeus*, *Salix caprea*, *Scabiosa lucida*, *Senecio nemorensis* agg., ***Soldanella carpatica* agg.**, *Solidago virgaurea*, ***Sorbus aucuparia***, ***Vaccinium myrtillus***, *V. vitis-idaea*, *Valeriana tripteris*, *Viola biflora*

Dominant species: ***Calamagrostis arundinacea***, ***C. varia***, *Festuca versicolor*, ***Oxalis acetosella***, ***Picea abies***, ***Vaccinium myrtillus***

Group 5

Number of relevés: 48

Vegetation type: Montane herb-rich beech forests on base-rich bedrock typical of N Alps and Western Carpathians

Phytosociological affinity: *Aremonio-Fagion* (Horvat 1950) Borhidi in Török et al. 1989

Diagnostic species: *Abies alba*, *Acer pseudoplatanus*, *Actaea spicata*, *Ajuga reptans*, *Asplenium viride*, *Athyrium filix-femina*, *Bellidiastrum michelii*, *Calamagrostis arundinacea*, *C. varia*, ***Cardamine trifolia***, ***Carex digitata***, *C. ornithopoda*, *Cirsium erisithales*, ***Clematis alpina***, *Crepis paludosa*, *Daphne mezereum*, *Dentaria glandulosa*, *Digitalis grandiflora*, *Dryopteris filix-mas*, *Euphorbia amygdaloides*, *Fagus sylvatica*, *Fragaria vesca*, *Fraxinus excelsior*, *Galium schultesii*, *Gentiana asclepiadea*, *Hieracium murorum*, *Hordelymus europaeus*, *Lilium martagon*, *Listera ovata*, *Maianthemum bifolium*, ***Mercurialis perennis***, *Mycelis muralis*, *Orthilia secunda*, *Paris quadrifolia*, *Phyteuma spicatum*, *Polygonatum verticillatum*, *Polystichum aculeatum*, *Prenanthes purpurea*, *Ranunculus platanifolius*, *Rosa pendulina*, *Sanicula europaea*, *Solidago virgaurea*, *Thalictrum aquilegifolium*, ***Valeriana tripteris***

Constant species: ***Abies alba***, ***Acer pseudoplatanus***, *Asplenium viride*, *Athyrium filix-femina*, ***Calamagrostis arundinacea***, *Cardamine trifolia*, *Carex digitata*, *Chaerophyllum hirsutum*, *Clematis alpina*, *Crepis paludosa*, *Dentaria glandulosa*, *Digitalis grandiflora*, *Dryopteris dilatata* agg., *D. filix-mas*, ***Fagus sylvatica***, *Fragaria vesca*, *Galeobdolon luteum*, ***Gentiana asclepiadea***, *Gymnocarpium dryopteris*, ***Hieracium murorum***, *Homogyne alpina*, *Listera ovata*, *Lonicera nigra*, *Luzula sylvatica*, *Maianthemum bifolium*, ***Mercurialis perennis***, *Mycelis muralis*, ***Oxalis acetosella***, *Paris quadrifolia*, *Petasites albus*, *Phyteuma spicatum*, ***Picea abies***, ***Polygonatum verticillatum***, ***Prenanthes purpurea***, *Ranunculus platanifolius*, *Rubus idaeus*, *Sanicula europaea*, *Senecio nemorensis* agg., *Soldanella carpatica* agg., *Solidago virgaurea*, ***Sorbus aucuparia***, *Vaccinium myrtillus*, ***Valeriana tripteris***

Dominant species: ***Abies alba***, *Acer pseudoplatanus*, ***Calamagrostis arundinacea***, *C. varia*, ***Fagus sylvatica***, ***Oxalis acetosella***, ***Picea abies***, *Sanicula europaea*, *Vaccinium myrtillus*

Group 6

Number of relevés: 20

Vegetation type: Montane basiphytic beech and fir-beech forests

Phytosociological affinity: *Fagion sylvaticae* Luquet 1926, *Eu-Fagenion* Oberdorfer 1957 and mesic part of *Galio-Abietenion* Oberdorfer 1962

Diagnostic species: *Abies alba*, *Acer pseudoplatanus*, *Aegopodium podagraria*, *Asarum europaeum*, ***Circaea alpina***, *Dentaria glandulosa*, *Dryopteris filix-mas*, *Fagus sylvatica*, *Galeobdolon luteum*, *Phegopteris connectilis*, *Polygonatum verticillatum*, *Prenanthes purpurea*, *Sanicula europaea*, ***Viola reichenbachiana***

Constant species: ***Abies alba***, ***Acer pseudoplatanus***, *Asarum europaeum*, *Athyrium filix-femina*, *Calamagrostis arundinacea*, *Circaea alpina*, *Dentaria glandulosa*, *Dryopteris carthusiana*, *D. dilatata* agg., *D. filix-mas*, ***Fagus sylvatica***, ***Galeobdolon luteum***, *Gentiana asclepiadea*, *Gymnocarpium dryopteris*, *Homogyne alpina*, *Maianthemum bifolium*, ***Oxalis acetosella***, *Petasites albus*, *Phegopteris connectilis*, ***Picea abies***, *Polygonatum verticillatum*, ***Prenanthes purpurea***, *Rubus idaeus*, *Sanicula europaea*, *Senecio nemorensis* agg., *Soldanella carpatica* agg., *Sorbus aucuparia*, *Vaccinium myrtillus*, *Viola reichenbachiana*

Dominant species: ***Abies alba***, *Acer pseudoplatanus*, *Athyrium distentifolium*, *Calamagrostis arundinacea*, *C. villosa*, ***Fagus sylvatica***, *Gymnocarpium dryopteris*, *Homogyne alpina*, *Oxalis acetosella*, *Petasites albus*, ***Picea abies***, *Rosa pendulina*, *Rubus idaeus*, ***Sanicula europaea***, *Sorbus aucuparia*, *Stellaria nemorum*, *Vaccinium myrtillus*

Group 7

Number of relevés: 26

Vegetation type: Montane wet forests dominated by silver fir

Phytosociological affinity: *Fagion sylvaticae* Luquet 1926; *Galio-Abietenion* Oberdorfer 1962 p.p.

Diagnostic species: *Caltha palustris* agg., *Chaerophyllum hirsutum*, *Deschampsia cespitosa*, *Equisetum sylvaticum*, ***Leucanthemum waldsteinii***, *Luzula luzulina*, *Lysimachia nemorum*, *Myosotis palustris*, *Myosoton aquaticum*, *Phegopteris connectilis*, *Stellaria nemorum*

Constant species: *Abies alba*, *Athyrium filix-femina*, *Calamagrostis arundinacea*, *Chaerophyllum hirsutum*, *Deschampsia cespitosa*, *Dryopteris dilatata* agg., *Galeobdolon luteum*, *Gentiana asclepiadea*, *Gymnocarpium dryopteris*, *Homogyne alpina*, ***Leucanthemum waldsteinii***, *Luzula luzulina*, *L. sylvatica*, *Maianthemum bifolium*, ***Oxalis acetosella***, *Petasites albus*, *Phegopteris connectilis*, ***Picea abies***, *Prenanthes purpurea*, *Rubus idaeus*, *Senecio nemorensis* agg., *Soldanella carpatica* agg., ***Sorbus aucuparia***, ***Vaccinium myrtillus***

Dominant species: ***Abies alba***, ***Athyrium distentifolium***, ***Chaerophyllum hirsutum***, ***Oxalis acetosella***, ***Picea abies***, ***Rubus idaeus***, *Sorbus aucuparia*, *Vaccinium myrtillus*

Group 8

Number of relevés: 42

Vegetation type: Norway spruce plantations on base-rich soils

Phytosociological affinity: --

Based on the phytosociological units described above, we propose the following core classification system for forest communities in the Tatra Mts.:

Cl. *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939
- O. *Piceetalia excelsae* Pawłowski et al. 1928
  - All. *Piceion excelsae* Pawłowski et al. 1928
    - Subalpine Swiss stone pine (*Pinus cembra*) forests (group 1)
    - Subalpine Norway spruce forests on nutrient-poor soils of the higher montane zone (group 2)
- O. *Athyrio filicis-feminae-Piceetalia* Hadač in Hadač et al. 1969
  - All. *Abieti-Piceion* (Br.-Bl. in Br.-Bl. et al. 1939) Soó 1964
    - Mountain mesophilous forests of silver fir and Norway spruce (group 3)
  - All. *Chrysanthemo rotundifolii-Piceion* (Krajina 1933) Březina et Hadač in Hadač 1962
    - Subalpine herb-rich Norway spruce forests on rich calcareous soils (group 4)

Cl. *Carpino-Fagetea sylvaticae* Jakucs ex Passarge 1968
- O. *Fagetalia sylvaticae* Pawłowski 1928
  - All. *Aremonio-Fagion* (Horvat 1950) Borhidi in Török et al. 1989
    - Suball. *Lonicero alpigenae-Fagenion* Oberdorfer et Müller 1984
      - Montane herb-rich beech forests on base-rich bedrock typical of Northern Alps and Western Carpathians (group 5)
  - All. *Fagion sylvaticae* Luquet 1926
    - Montane basiphytic beech and fir-beech forests – *Eu-Fagenion* Oberdorfer 1957 and mesic part of *Galio-Abietenion* Oberdorfer 1962 p.p. (group 6)
    - Montane wet forests dominated by silver fir – *Galio-Abietenion* Oberdorfer 1962 p.p. (group 7)

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Abb. 3. Verteilung der Plots, die acht Waldtypen in der Tatra zugeordnet sind. Schwarze Kreise sind Plots, die den einzelnen Waldtyp darstellen, und schwarze Punkte sind alle verbleibenden Waldplots. Erläuterungen s. rechts und Abb. 2.

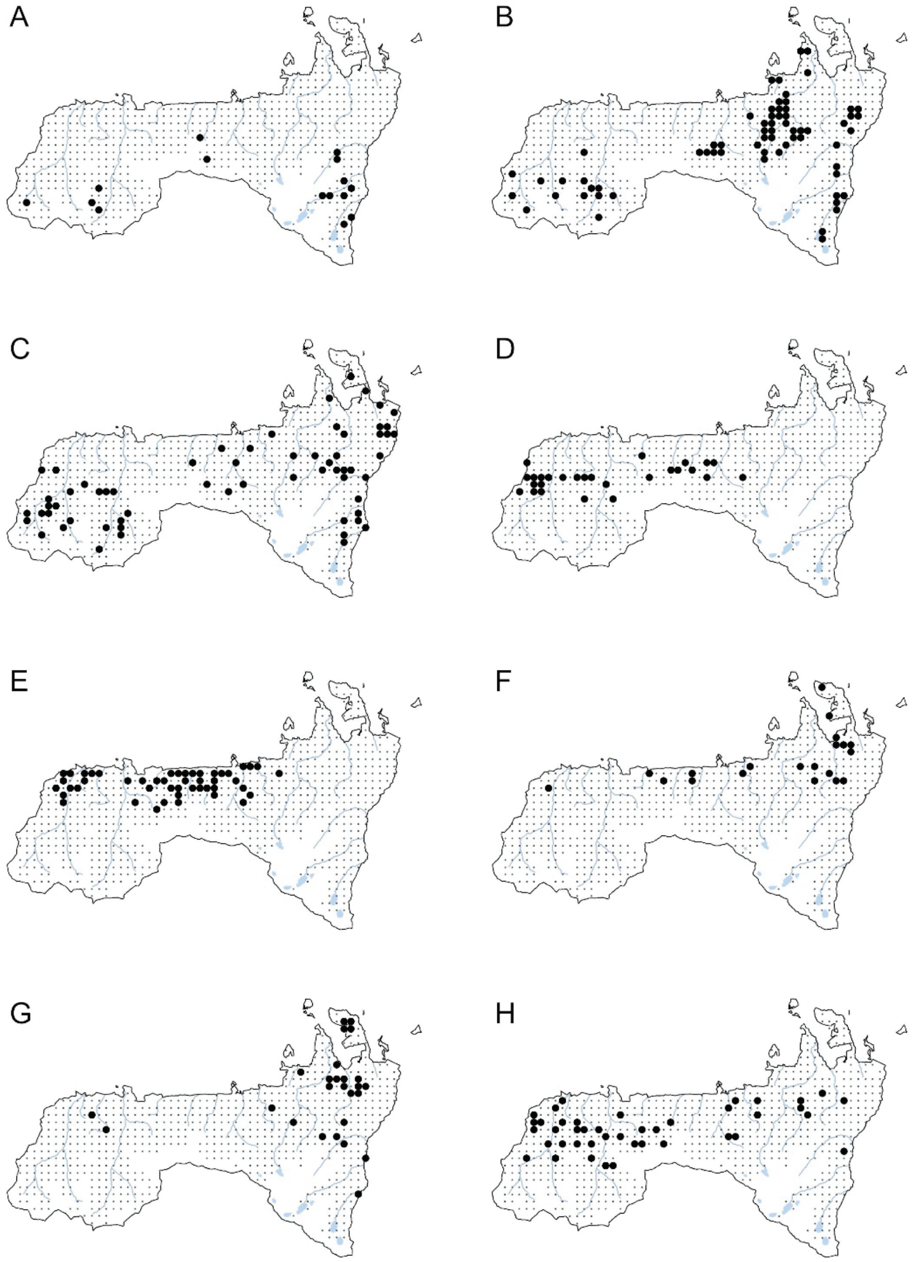

Fig. 3. Distribution of plots assigned to eight forest types in Tatra Mts. Black circles are plots that represent each forest types and black dots are all remaining forest plots. A – Subalpine Swiss stone pine (*Pinus cembra*) forests (group 1, *Piceion excelsae* p.p.); B – Subalpine Norway spruce forests (group 2, *Piceion excelsae* p.p.); C – Mesophilous forests of silver fir and Norway spruce (group 3, *Abieti-Piceion*); D – Subalpine Norway spruce forests on calcareous soils (group 4, *Chrysanthemo rotundi-folii-Piceion*); E – Beech forests on base-rich bedrock (group 5, *Aremonio-Fagion*); F – Basiphytic beech and fir-beech forests (group 6, *Eu-Fagenion* and *Galio-Abietenion* p.p.); G – Wet silver fir forests (group 7, *Galio-Abietenion* p.p.), H – Norway spruce plantations on base-rich soils.

3.2 Species diversity of main forest types in Tatra Mts.

There are strong and significant differences in the plant species richness and Shannon diversity index among the seven distinguished groups. Coniferous forests on poor soils and located at higher mountain elevations (*Piceion excelsae*, *Abieti-Piceion*) are characterized by the lowest richness and diversity; while, the forests typical of base-rich calcareous soils (*Aremonio-Fagion*, *Chrysanthemo rotundifolii-Piceion*) are the richest and the most diverse forest types in the Tatra Mts. (Fig. 4). The forest of the *Fagion sylvaticae* alliance, including both hygrophilous and mesic beech-fir forests, are characterized by mean species richness and Shannon diversity index values. A comparison of the Simpson diversity indices and evenness showed less clear results, but generally, mountain coniferous forests on poor soils showed lower values than those indices for other forest types.

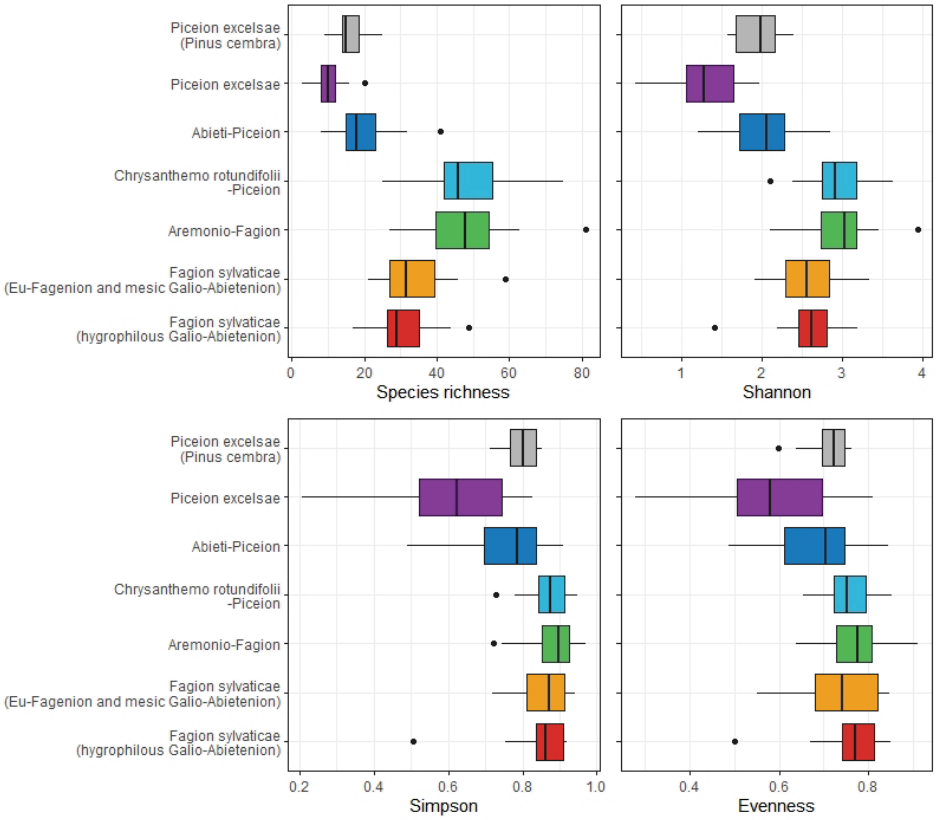

Fig. 4. Comparison of plant species richness, diversity and evenness indices among five forest association in the Tatra Mts.

Abb. 4. Vergleich des Pflanzenartenreichtums, der Diversitäts und Evenessindices zwischen fünf Waldassoziationen in der Tatra.

3.3 Main factors driving diversity in forest associations

We found significant differences in the topography among the five distinguished forest associations (Fig. 5). The analysis of the vertical distribution confirmed previously known patterns: beech and fir-beech forests (*Fagion sylvaticae*, *Aremonio-Fagion*) occur mostly at lower elevations (lower montane zone), while higher elevations (upper montane zone) is dominated by Norway spruce or spruce-fir forests (*Piceion excelsae*, *Abieti-Piceion* and *Chrysanthemo rotundifolii-Piceetum*). Wet forests dominated by silver fir occurred at the lowest elevations, mostly below 1000 m a.s.l. In addition, it is typical of places with the lowest slope that allows for the accumulation of moisture. On the other side, Swiss stone pine forests (part of *Piceion excelsae*) occured on the steepest slopes and the highest elevations close to the timberline.

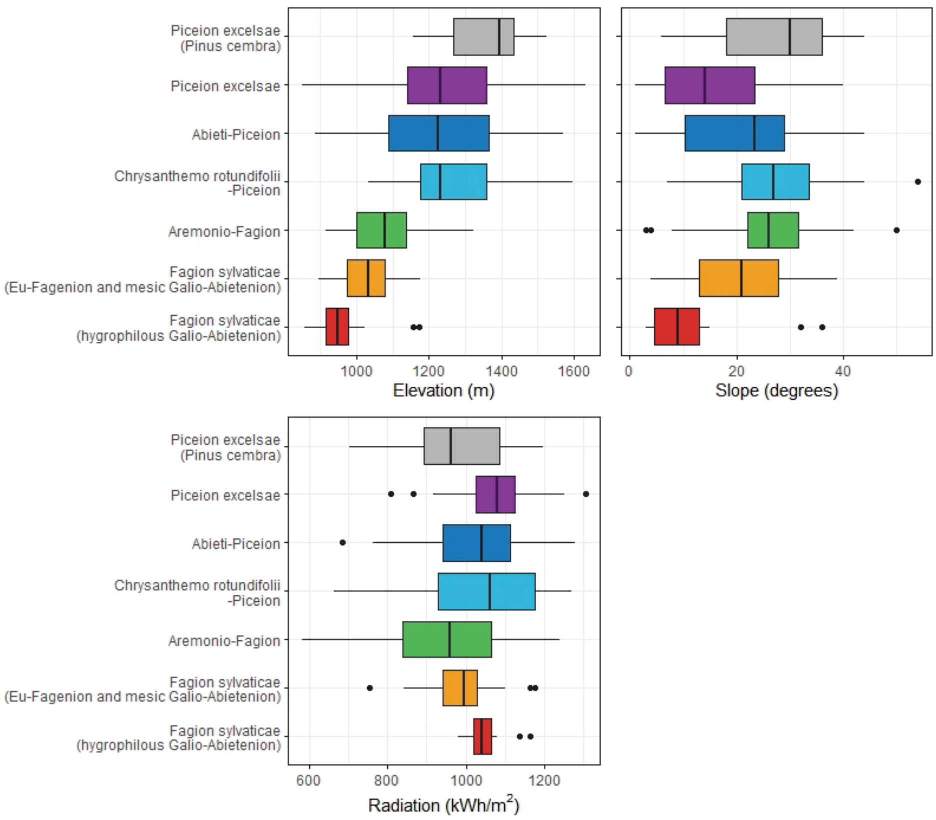

Fig. 5. Comparison of topographic conditions, including elevation, slope and topography-related potential solar radiation, among five forest associations in Tatra Mts.

Abb. 5. Vergleich der topographischen Bedingungen einschließlich Höhenlage, Hangneigung und Topographie-bezogener Sonneneinstrahlung zwischen fünf Waldassoziationen in der Tatra.

The comparison of the community weighted means of the EIVs revealed the strongest significant differences in reaction, but differences in fertility and temperature were also significant (Table 1). The non-metric multidimensional scaling analysis showed a clear segregation of the distinguished forest types in the ordinal space (Fig. 6a). Plotting the environmental variables into an ordinal space (Fig. 6a, Table 2) revealed that the main gradient responsible for the variability of the forest communities in the Tatra Mts. was generated due to differences in the soil reaction. This gradient refers to the co-occurrence of acidic and calcareous bedrocks in the Tatra Mts. The second NMDS axis is strongly correlated with the EIV for moisture and light; however, the segregation of the distinguished units along the second axis is rather weak.

Table 1. Comparison of community weighted-means of EIVs among seven distinguished forest types.

Tabelle 1. Vergleich von gewichteten Ellenberg-Zeigerwerten zwischen sieben unterschiedenen Waldtypen.

	Sum of sq	Mean sq	*F* value	*p*	sign.
Light	32.4	5.3	21.7	0.296	
Temperature	35.3	5.9	66.6	0.026	*
Moisture	13.9	2.3	13.8	0.274	
Reaction	213.3	35.5	82.0	< 0.001	***
Fertility	112.7	18.8	45.0	0.030	*

Table 2. Correlation of passively fitted environmental variables with first and second ordination axes.

Tabelle 2. Korrelation von passiv angepasster Umgebungsvariablen mit der ersten und zweiten Ordinationsachse.

	Label	NMDS1	NMDS2	*r*
Elevation	Elev	-0.897	-0.442	0.134
Slope	Slope	0.798	-0.602	0.075
Light (EIV)	EIV.L	-0.379	-0.925	0.319
Temperature (EIV)	EIV.T	0.999	0.037	0.585
Moisture (EIV)	EIV.M	-0.349	0.937	0.023
Reaction (EIV)	EIV.R	0.996	0.091	0.773
Fertility (EIV)	EIV.F	0.642	0.767	0.672

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Abb. 6. a) Spinnenplots, die die Verteilung der verschiedenen Waldgesellschaften im Ordinationsraum der NMDS darstellen. Graue gestrichelte Linien kennzeichnen Fichtenforsten. Erklärungen: 1 – *Piceion excelsae*: subalpine Zirbenwälder; 2 – *Piceion excelsae*: subalpine Fichtenwälder; 3 – *Abieti-Piceion*; 4 – *Chrysanthemo rotundifolii-Piceion*; 5 – *Aremonio-Fagion*; 6–7 – *Fagion sylvaticae* (Spinnenplots für zwei Untergruppen überlappten sich stark und wurden daher der Klarheit halber zusammengefügt); 8 – artenreiche Fichtenforste mit nährstoffreichen Substraten. **b)** Orinations-Biplot mit passiv angepassten Umgebungsvariablen, dargestellt durch Pfeile. Der Pfeil für EIV.T war stark korreliert und überlappte mit EIV.R und wird daher nicht dargestellt.

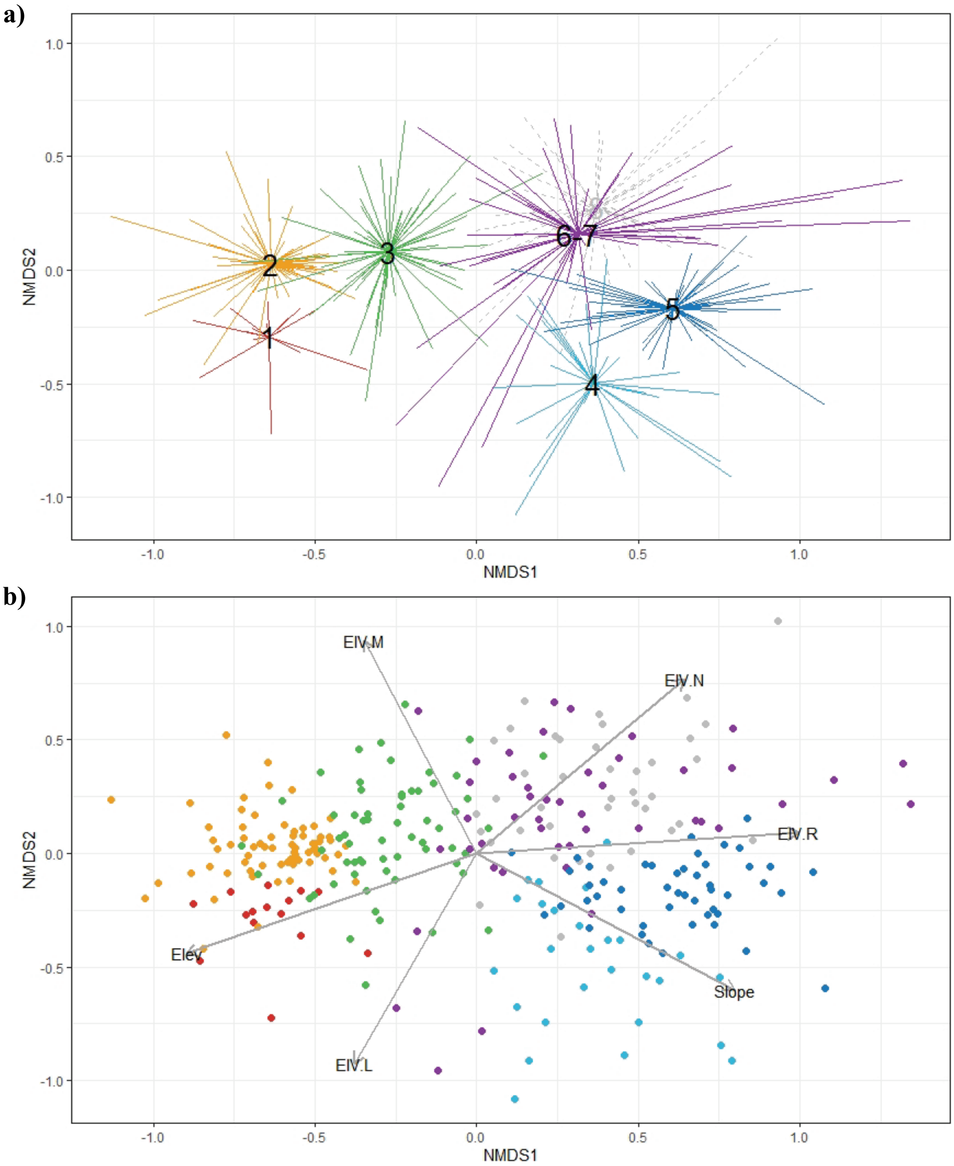

Fig. 6. Panel **a)** Spider plots presenting distribution of distinguished forest communities in ordinal space of NMDS. Grey dashed lines denote Norway spruce plantations. Explanations: 1 – *Piceion excelsae*: subalpine Swiss stone pine forests; 2 – *Piceion excelsae*: subalpine Norway spruce forests; 3 – *Abieti-Piceion*; 4 – *Chrysanthemo rotundifolii-Piceion*; 5 – *Aremonio-Fagion*; 6–7 – *Fagion sylvaticae* (spider plots for two subgroups strongly overlapped and therefore were joined for sake of clarity); 8 – species rich Norway spruce plantations of fertile substrates. Panel **b)** Ordination biplot with passively fitted environmental variables represented by arrows. Arrow for EIV.T was strongly correlated and overlapped with EIV.R, and is not presented.

4. Discussion

4.1 Phytosociological classification, newly recognized syntaxa and links to other regions

Based on the analyzed material, we were able to distinguish eight groups representing different forest types that predominate in the Polish part of the Tatra Mts. One group (8) represents Norway spruce plantations and constitutes a legacy of former intensive forest management in the Tatra Mts. that took place before the Tatra National Park was established. The seven remaining groups (1–7) represent natural forest communities and we were able to assign them to previously described syntaxa.

Regarding the TWINSPAN classification, the first order division refers to the distinction between coniferous forests of the class *Vaccinio-Piceetea* and broadleaved or mixed forests that represent the *Carpino-Fagetea sylvaticae* class. Differences between these groups are driven by the variability in the elevation and fertility; coniferous forests of *Vaccinio-Piceetea* are typical of the higher elevations and usually grow on poor to moderately fertile soils. On the contrary, the mixed and broadleaved forests of *Carpino-Fagetea sylvaticae* grow at a lower elevation (lower mountain zone) and typically develop on base-rich soils. The only exception from this general pattern is the herb-rich Norway spruce forests on rich calcareous soils, here classified as *Chrysanthemo rotundifolii-Piceion*. They are traditionally included in the *Vaccinio-Piceetea* class; however, as they grow on nutrient-rich calcareous soils, they share many forest species with the beech and mixed beech-fir forests of *Fagetalia sylvaticae*. Therefore, in the TWINSPAN dendrogram, the forests of *Chrysanthemo rotundifolii-Piceion* are closer to the beech forests than to the coniferous forests of the *Vaccinio-Piceetea* class.

As mentioned in the introduction, the tradition of phytosociological studies in the Polish part of the Tatra Mts. is very long, but this region is still missing comprehensive modern classification. Many authors still use anachronic or illegitimate names of syntaxa that were introduced by influential studies published many decades ago. With this work, we have recognized and identified several new syntaxa that have never been reported from Poland and we have attempted to relate them to previously identified vegetation types from this region.

For the first example, we have recognized high elevation Norway spruce forests on calcareous substrates as representing the *Chrysanthemo rotundifolii-Piceion* alliance. This alliance embraces montane spruce forests on nutrient-rich soils of Central and Northern Europe (MUCINA et al. 2016), and has been reported from many countries, including neighboring Slovakia (FAJMONOVÁ 1986, EXNER et al. 2002, KUČERA 2010, JUVAN et al. 2013). This subalpine calcareous Norway spruce forest is one of the most unique forest types in Poland. Initially known as a subassociation of a broadly defined unit of mountain Norway spruce forests under the name *Piceetum tatricum normale* Szafer, Pawłowski & Kulczyński 1923, it was then described as an association of *Polysticho-Piceetum* (Szafer, Pawłowski & Kulczyński) W. Matuszkiewicz (1967) 1977. Within the alliance *Chrysanthemo rotundifolii-Piceion*, Slovak authors identified several narrowly defined associations, including *Chrysanthemo rotundifolii-Piceetum* Krajina 1933 Hadač et al. 1969, *Adenostylo alliariae-Piceetum excelsae* Březina et Hadač in Hadač et al. 1969, *Cortuso-Piceetum* Fajmonová 1986 and *Seslerio variae-Piceetum* Fajmonová 1978 (FAJMONOVÁ 1986, KUČERA 2010). Their occurrence in the Polish part of the Tatra Mts. should be a subject of a more detailed study.

Another problem that needs attention is the classification of beech and fir-beech forests. All beech forests that developed on base-rich soils in the Polish Carpathians have been traditionally classified as one association *Dentario glandulosae-Fagetum* W. Matuszkiewicz 1964 ex Guzikowa et Kornaś 1969. However, the actual variability of beech forests within this region is much broader and cannot be constrained within a frame of one association. What is more, recent synthesis of the variability of beech forests in Europe showed that the northern part of the Carpathians falls within a range of the *Aremonio-Fagion* alliance (WILLNER et al. 2017). This unit includes basiphilous beech forests that coincided with glacial refuge areas of beech. Forests of *Aremonio-Fagion* are defined as the Alpine-Dinaric ('Illyric'); however, WILLNER et al. (2017) showed that some of the associations also extend to the Carpathians. The recent revision of beech forests in Slovakia has confirmed the occurrence of this forest type in the Western Carpathians, including the Tatra Mts. (UJHÁZYOVÁ et al. 2021). In this study, we also confirmed the occurrence of the *Aremonio-Fagion* forests in the Polish part of the Tatra Mts. They are floristically well defined by a long list of diagnostic species, including *Asplenium viride*, *Bellidiastrum michelii*, *Calamagrostis varia*, *Cardamine trifolia*, *Cirsium erisithales*, *Clematis alpina*, *Phyteuma spicatum*, *Polystichum aculeatum*, *Ranunculus platanifolius*, *Rosa pendulina*, *Thalictrum aquilegifolium*, *Valeriana tripteris* and others. Most of these species are usually absent in the forests of *Fagion sylvatice,* which typically occur on the Carpathian flysch. In Slovakia, this type of beech forest has been assigned to the narrowly defined alliance *Lonicero alpigenae-Fagion sylvaticae* Dierschke 1998 (UJHÁZYOVÁ et al. 2021). This approach seems to be fully supported by the fact that the basiphilous beech forests of the Carpathians and Eastern Alps are closely related, but distinct from the basiphilous beech forests of southern Europe. In this study, however, our data did not allow for a judgment between these broad and narrow approaches. As we generally adopted a broad European classification of vegetation as a framework for this study, we classified the mountain basiphilous beech forest in the Tatra Mts. to the *Lonicero alpigenae-Fagenion* suballiance subordinated to *Aremonio-Fagion*.

In this study, we aimed to examine the variability of forest types at the alliance level. However, in some cases, a low order division in the TWINSPAN classification corresponded to the syntaxa of a level lower than alliance. Therefore, we decided to analyze and interpret these clusters as independent groups. One example are the Swiss stone pine (*Pinus cembra*) forests, which are separated from the other forests of *Piceion excelsae*. Some authors claim that *Pinus cembra* forests could be distinguished as a separate alliance *Pinion cembrae* (RIVAS-MARTÍNEZ 2011); however, the set of diagnostic species shows their similarity to the *Piceion excelsae* forests. This was also confirmed by a similarity analysis between *Pinus cembra* forests, *Picea abies* forests and *Pinus mugo* krummholz (ZIĘBA et al. 2018). Such a statement is presented in the description of *Piceion excelsae* as European boreo-montane spruce forests and subalpine open pine woods on nutrient-poor podzolic soils (MUCINA et al. 2016).

Wet forests dominated by silver fir is another group that was separated in the TWINSPAN classification at the relatively low order of divisions. This is due to the high share of species characterized by high moisture demands, including *Caltha palustris*, *Chaerophyllum hirsutum*, *Deschampsia caespitosa*, *Equisetum sylvaticum*, *Leucanthemum waldsteinii* and *Myosotis palustris*. We recognized this forest type as belonging to the *Galio-Abietenion* suballiance within the *Fagion sylvatice* alliance. Presumably, this group represents *Equiseto silvaticae-Abietetum* Moor 1952 (*Stellario nemorum-Abietetum albae* Kučera 2019), and this association has never been reported, neither from the Polish Tatra Mts. nor from the territory of Poland (although ŚWIERKOSZ et al. (2014) suggested that some relevés from Poland might represent this unit). This association was reported from Slovakia and other countries (HUSOVÁ 1998, KUČERA 2009, 2019). On the other hand, similar communities are sometimes identified as a hygrophilous subtype of *Galio rotundifolii-Abietetum albae* (PARUSEL et al. 2004, BOUBLÍK & ZELENÝ 2007, BOUBLÍK 2010, CHYTRÝ 2013).

4.2 Species richness, species diversity and habitat characteristics

All distinguished forest types differ significantly in terms of species diversity and habitat conditions. Considering species richness and diversity, coniferous forests of the *Vaccinio-Piceetea* were generally poor, and the mean number of species per plot ranged from 10 to 19. This was also reflected in the relatively low values in the diversity indices. Contrary to this, broadleaved and mixed forests of the *Carpino-Fagetea sylvaticae* class harbor many more species, and the mean species richness ranged from 31 to 47. The only exception is *Chrysanthemo rotundifolii-Piceion*; although included in the *Vaccinio-Piceetea* class, relevés representing this alliance showed the highest mean species richness (49).

The analysis of elevational ranges confirmed previously known patterns: beech and mixed beech-fir forests (*Fagion sylvaticae, Aremonio-Fagion*) are typical of the lower montane zone and only rarely exceed an elevation as high as 1250 m a.s.l. The subalpine zone is dominated by coniferous forests of *Vaccinio-Piceetea*. The Swiss stone pine forests, which are sometimes considered a transition between subalpine forests and *Pinus mugo* shrubs, occur at the highest and the steepest sites (ZIĘBA et al. 2019). On the contrary, hygrophilous fir forests occur in flat places at the lowest locations.

Both NMDS and a comparison of the EIVs showed that gradient was responsible for the variability in the forest communities in the Tatra Mts., and this was generated due to differences in the soil reaction. This gradient refers to the co-occurrence of acidic and calcareous bedrocks in the Tatra Mts. Therefore, there is a clear distinction between the species-rich and species-poor forest communities. In addition, elevation and related climatic conditions are essential drivers of the variability in the forest vegetation in the Tatra Mts. The above-mentioned differences in altitudinal ranges are also reflected in the significant differences in the community-weighted means of the temperature indicator values (EIV.T).

4.3 Effect of (objective) sampling design on results of classification

The results of the forest classification presented here are strongly influenced by the sampling design and need detailed discussion. The systematic sampling design is based on a grid, and when coupled with objective unsupervised classification allowed the identification of only those forest types that predominate in the landscape of the studied area. However, there are also other forest communities that cover small areas and are limited to specific habitat conditions. We expect that there are at least three more forest communities covering small areas and occurring in scattered patches in the Tatra Mts., including Scots pine forests, riparian grey alder forests and ravine Sycamore maple forests. Those forest types were either omitted by the sampling based on a systematic grid or were represented in the dataset by a very small number of plots, and thus were included in the clusters that could not be identified as an independent forest community. Our study also showed that the surveying of the above-mentioned communities, which were represented by relatively small patches in specific habitat conditions, requires a rather preferential sampling design. Nevertheless, we found that grid-based objective sampling may be very useful for analyzing the main forest types at the higher level of syntaxonomical resolution. In this study, we successfully identified new alliances that has never been reported from the study area previously.

A systematic sampling design also resulted in a big share of heterogeneous plots. This heterogeneity could be a result of microhabitat heterogeneity (e.g., presence of groundwater discharge, proximity to stream, rock outcrop) or disturbances (e.g., windthrows, bark beetle outbreaks, avalanches) that are common in the Tatra Mts. In addition, numerous plots that were selected for sampling were influenced by historical forest management. Most of the forests in the lower montane zone had been heavily managed and transformed by logging and planting spruce monocultures in past centuries (LETTNER 1885, LIBERAK 1924, SOKOŁOWSKI 1936). Therefore, only a portion of the initially sampled plots was used to elaborate on the characteristics of the natural forest vegetation. Out of the 669 sampled plots, only 307 relevés (45.9%) met the initial criteria (homogeneity and absence of strong disturbances), and were therefore used in the analyses. Moreover, 42 relevés were classified as anthropogenic Norway spruce plantations. Only 265 sample plots – which constitutes a little more than one-third of the initial dataset – were used to characterize the distinguishing syntaxa and to define sets of diagnostic species.

The sets of the diagnostic species presented here have to also be interpreted in the context of the above-mentioned sampling scheme. Due to the lack of a broad context (non-forest vegetation and other forest types with small areas in the Tatra Mts.), some of the diagnostic species might be somewhat surprising. For example, some of the species with higher moisture demands are diagnostic for hygrophilous fir forests, while in the broader context should be treated as characteristics of riparian forests. This is due to the fact that hygrophilous forests of the *Galio-Abietenion* occur in the wettest locations when considering all the distinguished associations. Similarly, *Chrysanthemo rotundifolii-Piceion* was distinguished by numerous species typical of calcareous alpine grasslands.

4.4 New classification of forest communities and problems of stand conversion

Using the old and simplified classification of forest communities of the Tatra National Park has led to some controversial decisions concerning stand conversion, including planting beech seedlings under mature secondary spruce stands throughout the lower elevations. The new classification clearly indicates that the extent of the fertile beech forests of the alliance *Aremonio-Fagion* in the Tatra Mts. is limited to the western and central part of the Tatra National Park. Low-elevation forests in the eastern part of the park forest communities that represent the *Eu-Fagenion* and *Galio-Abietenion* alliances should be dominated by silver fir, with European beech playing only a minor role. Our study also confirmed, that even in low elevations forests, representing the *Piceion excelsae* or *Abieti-Piceion* alliances, Norway spruce should play the role of dominant or co-dominant species, so there is no need to eliminate or strongly reduce the share of spruce in the process of stand conversion. The list of diagnostic species for each syntaxonomical unit could be a useful tool for guiding further stand conversion processes.

Erweiterte deutsche Zusammenfassung

Einleitung – Die Tradition pflanzensoziologischer Untersuchungen im Tatra-Gebirge ist sehr lang, da in dieser Region die ersten Studien mit dem Ansatz von Braun-Blanquet (BRAUN-BLANQUET 1964, DZWONKO 2007) in Polen durchgeführt wurden (SZAFER et al. 1923, SZAFER et al. 1927). Seit Beginn des 20. Jahrhunderts sind Dutzende von Arbeiten über die Pflanzengesellschaften in der Tatra veröffentlicht worden. Obwohl seit den ersten Vegetationserhebungen in der Tatra 100 Jahre vergangen sind, ist das Wissen über die Vielfalt der Waldgesellschaften immer noch unzureichend, und eine moderne Vegetationsklassifizierung ist sowohl für Naturschutz- als auch für Bewirtschaftungszwecke dringend erforderlich.

In den Jahren 2016–2017 wurde in den Wäldern des Tatra-Nationalparks ein Netzwerk von über 600 permanenten Forschungsflächen eingerichtet (BODZIARCZYK et al. 2019). Dies ermöglichte die objektive Erfassung einer großen Menge pflanzensoziologischer Daten und die Erarbeitung einer neuen Klassifikation für die Waldgesellschaften, die die Landschaft der Tatra dominieren. Die Ziele dieser Studie waren: (1) Bereitstellung einer objektiven numerischen Klassifikation der Waldgesellschaften, die die Landschaft der Tatra dominieren; (2) Definition von diagnostischen Arten für die unterschiedenen Waldassoziationen; (3) Analyse der Hauptgradienten, die für die Vielfalt der Haupt-Waldtypen verantwortlich sind; (4) Diskussion der Vielfalt der Haupt-Waldtypen in der Tatra in einem breiteren geografischen Kontext.

Material und Methoden – Die Forschung wurde im polnischen Teil der Tatra durchgeführt und umfasste die gesamte Waldfläche des polnischen Tatra-Nationalparks (ca. 12.900 ha). Die Daten wurden von 100 m^2 großen Dauerflächen gesammelt, die sich in einem systematischen Stichprobenraster (500 m × 500 m) in der gesamten polnischen Tatra befanden, insgesamt 669 Plots (817 m – 1801 m) in Waldökosystemen und Pinus mugo-Gebüschen (Abb. 1). Für die Vegetationsaufnahmen wurde die Braun-Blanquet-Skala verwendet, um die Bedeckung jeder Art in jeder Schicht (Bäume, Sträucher und Kräuter) abzuschätzen. Daten, die die Standortsbedingungen in den untersuchten Flächen beschreiben, wie Höhe, Neigung und Exposition, wurden dem digitalen Höhenmodell (DEM) entnommen. Darüber hinaus wurde das DEM verwendet, um die potenzielle Sonnenstrahlung zu berechnen, die die Menge an Sonnenenergie beschreibt, die potenziell jeden Ort erreichen kann.

Vom Gesamtdatensatz wurden nur die Plots in Wäldern verwendet, während diejenigen von *Pinus mugo*-Gebüschen ausgeschlossen wurden. Vor den statistischen Analysen wurde eine Vorauswahl getroffen, um stark gestörte oder heterogene Plots auszuschließen. Dies betraf zum einen alle Parzellen mit einer Baumbedeckung von weniger als 20 %. Zum anderen haben wir, basierend auf vorläufigen pflanzensoziologischen Diagnosen, Plots mit einem signifikanten Anteil vom Typ der Nichtwaldvegetation ausgeschlossen. Der endgültige Datensatz enthielt 307 Flächen.

Zur Klassifizierung verwendeten wir einen modifizierten TWINSPAN-Algorithmus (ROLEČEK et al. 2009) mit der Gesamtträgheit als Maß für die Clusterheterogenität. Die resultierenden Cluster wurden dann analysiert und in das hierarchische System von MUCINA et al. (2016) eingestuft. Wir haben versucht, die unterschiedenen Gruppen auf der Ebene des (Unter-)Verbands zuzuordnen. Alle verschiedenen Waldtypen wurden durch eine Reihe diagnostischer Arten charakterisiert. Dafür verwendeten wir den Phi-Koeffizienten (CHYTRÝ et al. 2002) als Maß für die Treue sowie eine Standardisierung, die Unterschiede in der Größe der analysierten Cluster berücksichtigte (TICHÝ & CHYTRÝ 2006). Zusätzlich haben wir den exakten Fisher-Test verwendet, um die Signifikanz der Treuegrade zu testen (CHYTRÝ et al. 2002). Schließlich wurden auch Gruppen konstanter und dominanter Arten für alle unterschiedlichen Assoziationen definiert.

Ein Kruskal-Wallis-Test, gefolgt von einem Post-hoc-Test, wurde verwendet, um Unterschiede in Höhe, Neigung, Exposition und Sonneneinstrahlung zu analysieren. Die gleichen statistischen Verfahren wurden dann verwendet, um die Diversitätsindizes zwischen Assoziationen zu vergleichen, einschließlich Artenreichtum, Shannons und Simpsons Diversitätsindizes und Evenness. Zusätzlich berechneten wir gewichtete Mittelwerte der Ellenberg-Indikatorwerte (EIVs) für Licht, Temperatur, Feuchtigkeit, Reaktion und Stickstoff (Nährstoffversorgung) und verglichen sie dann unter Verwendung eines Permutationstests mit Randomisierung der EIVs zwischen den verschiedenen Assoziationen (ZELENÝ & SCHAFFERS 2012). Schließlich verwendeten wir eine nichtmetrische mehrdimensionale Skalierung (NMDS) mit passiv angepassten Umgebungsvariablen, um die Unterscheidungskraft der analysierten Gruppen zu untersuchen.

Ergebnisse – Basierend auf den Ergebnissen der TWINSPAN-Analyse (Abb. 2) haben wir acht Hauptwaldtypen identifiziert. Sieben Cluster wurden als zuvor beschriebene Waldtypen identifiziert, die fünf Verbände repräsentieren. Darüber hinaus repräsentiert ein Cluster Monokulturen von *Picea abies*, die auf basenreichen Böden gepflanzt wurden. In Abschnitt 3.1 präsentieren wir Beschreibungen und Karten (Abb. 3) für alle unterschiedlichen Gruppen mit Kommentaren zu ihren pflanzensoziologischen Affinitäten und Listen diagnostischer, konstanter und dominanter Arten.

Es gibt starke und signifikante Unterschiede im Pflanzenartenreichtum und im Shannon-Diversitäts-Index zwischen den sieben verschiedenen Gruppen. Nadelwälder auf armen Böden und in größeren Gebirgshöhen (*Piceion excelsae*, *Abieti-Piceion*) zeichnen sich durch den geringsten Artenreichtum und die geringste Vielfalt aus; die für basenreiche Kalkböden typischen Wälder (*Aremonio-Fagion*, *Chrysanthemo rotundifolii-Piceion*) sind die reichsten und vielfältigsten Waldtypen in der Tatra (Abb. 4). Die Wälder des Verbandes Fagion sylvaticae, der sowohl hygrophile als auch mesophytische Buchen-Tannen-Wälder umfasst, zeichnen sich durch mittleren Artenreichtum und mittlere Shannon-Diversitäts-Indexwerte aus.

Wir fanden signifikante Unterschiede in der Topographie zwischen den fünf unterschiedenen Waldverbänden (Abb. 5). Die Analyse der vertikalen Verteilung bestätigte bisher bekannte Muster: Buchen- und Tannen-Buchenwälder (*Fagion sylvaticae*, *Aremonio-Fagion*) treten meist in tieferen Lagen (untere Montanzone) auf, während höhere Lagen von Fichten- oder Fichten-Tannenwäldern dominiert werden (*Piceion excelsae*, *Abieti-Piceion* und *Chrysanthemo rotundifolii-Piceetum*). Wälder Nasser Standorte, die von Weißtannen dominiert werden, traten in den niedrigsten Lagen auf, meist unter 1000 m ü.M. Darüber hinaus sind sie typisch für Orte mit der niedrigsten Neigung, an denen sich Feuchtigkeit ansammelt. Auf der anderen Seite traten zum *Piceion excelsae* zählende Zirbenwälder an den steilsten Hängen und den höchsten Erhebungen nahe der Waldgrenze auf.

Der Vergleich der gewichteten Mittelwerte der EIV ergab die stärksten signifikanten Unterschiede in der Reaktion, aber auch Unterschiede in Nährstoffversorgung und Temperatur waren signifikant (Tab. 1). Die nichtmetrische mehrdimensionale Skalierung zeigte eine klare Trennung der verschiedenen Waldtypen im Ordnungsraum (Abb. 6a). Die Darstellung der Umgebungsvariablen in einem Ordnungsraum (Abb. 6a, Tab. 2) ergab, dass der Hauptgradient, der für die Variabilität der Waldgemeinschaften in der Tatra verantwortlich ist, aufgrund von Unterschieden in der Bodenreaktion erzeugt wurde. Dieser Gradient kommt durch das gleichzeitige Auftreten von sauren und kalkhaltigen Grundgesteinen in der Tatra zustande.

Diskussion – Wir konnten acht Gruppen unterscheiden, die verschiedene im polnischen Teil der Tatra vorherrschende Waldtypen repräsentieren. Eine Gruppe (8) umfasst Fichtenforsten und ist ein Erbe der ehemaligen intensiven Waldbewirtschaftung in der Tatra. Dies geschah vor der Gründung des Tatra-Nationalparks. Die sieben verbleibenden Gruppen (1–7) repräsentieren natürliche Waldgemeinschaften, und wir konnten sie zuvor beschriebenen Syntaxa zuordnen. Wir haben mehrere Syntaxa identifiziert, die noch nie aus Polen beschrieben wurden, und wir haben versucht, sie mit zuvor beschriebenen Vegetationstypen aus dieser Region in Beziehung zu setzen. So haben wir hochgelegene Fichtenwälder auf kalkhaltigen Substraten als Vertreter des *Chrysanthemo rotundifolii-Piceion* erkannt. Dieser Verband umfasst montane Fichtenwälder auf nährstoffreichen Böden Mittel- und Nordeuropas (MUCINA et al. 2016) und wurde aus vielen Ländern, einschließlich der benachbarten Slowakei, beschrieben (FAJMONOVÁ 1986, EXNER et al. 2002, KUČERA 2010, JUVAN et al. 2013). Dieser subalpine Fichtenwald kalkhaltiger Böden ist einer der einzigartigsten Waldtypen in Polen, der zuvor als *Polysticho-Piceetum* (Szafer, Pawłowski & Kulczyński) W. Matuszkiewicz (1967) 1977 beschrieben wurde. In dieser Studie haben wir auch das Vorkommen von Wäldern des *Aremonio-Fagion* im polnischen Teil der Tatra bestätigt. Sie sind floristisch durch eine lange Liste diagnostischer Arten gut definiert. In der Slowakei wurden solche Buchenwälder einem eng definierten Verband *Lonicero alpigenae-Fagion sylvaticae* Dierschke 1998 (UJHÁZYOVÁ et al. 2021) zugeordnet. In unserer Studie haben wir ein breiteres Konzept übernommen und den basiphilen Bergbuchenwald in der Tatra dem *Lonicero alpigenae-Fagenion*-Unterverband zugeordnet, der dem *Aremonio-Fagion* untergeordnet ist.

Das systematische Stichprobendesign basiert auf einem Raster und ermöglichte in Verbindung mit einer objektiven unbeaufsichtigten Klassifikation nur die Identifizierung der Waldtypen, die in der Landschaft des Untersuchungsgebiets vorherrschen. Es gibt jedoch auch andere Waldgesellschaften, die kleine Flächen abdecken und auf bestimmte Standortsbedingungen beschränkt sind. Wir erwarten, dass es mindestens drei weitere Waldgesellschaften in kleinen und verstreuten Arealen der polnischen Tatra gibt, darunter Waldkiefernwälder, Grauerlen-Auwälder und Bergahorn-Schluchtwälder. Diese Waldtypen wurden entweder bei der Stichprobe auf der Grundlage eines systematischen Rasters ausgelassen oder durch eine sehr kleine Anzahl von Plots im Datensatz dargestellt und somit in diejenigen Cluster aufgenommen, die nicht als unabhängige Waldgemeinschaft identifiziert werden konnten. Unsere Studie hat auch gezeigt, dass die Erfassung der oben genannten Gesellschaften von Sonderstandorten ein eher bevorzugtes Stichprobendesign erfordert. Wir haben jedoch festgestellt, dass gitterbasierte objektive Stichproben sehr nützlich sein können, um die Hauptwaldtypen auf höherer Ebene der syntaxonomischen Auflösung zu analysieren.

Dedication

This paper is dedicated to the memory of Paweł Kauzal (1986–2020), our friend and co-author of this paper. Paweł was employed at the Tatra National Park and was devoted to both nature conservation and ecological research. He significantly contributed to this paper by collecting large portion of data and thoroughly discussing the first version of the manuscript. During the revision of the text we got the sad news that Paweł tragically died after falling from a rock while monitoring rare plants in the Tatra Mountains.

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Author contributions

Study concept: JS, JB, AZ, TZK, RP; field sampling: AZ, TZK, PK; data management: AZ, RP, WR, KF; statistical analyses: RP, WR, JS, KF; manuscript drafting: RP, JS, AZ, TZK, PK, KF; manuscript revision: RP, AZ, TZK, JS, WR, KF

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Supplements

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.

Supplement E1. Combined synoptic table of frequency (%) and fidelity for five associations of forests in the Polish part of the Tatra Mts.

Anhang E1. Kombinierte synoptische Tabelle der Frequenz (%) und Treue für fünf Waldverbände im polnischen Teil der Tatra.

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Supplement S1. Combined synoptic table of frequency (%) and fidelity for five associations of forests in the Polish part of the Tatra Mts. *Phi* coefficient values for diagnostic (φ > 0.25) and highly diagnostic (φ > 0.5) species are marked light- and darkgray background, respectively. Diagnostic species are sorted according to their diagnostic value in each group. Significant values of fidelity (*phi* coefficient multiplied by 100) are given in superscript. Frequencies for constant (> 40%) and highly constant (> 80%) are also marked by light- and darkgray background, respectively. Species with freqencies lower than 10% in all associations are excluded.

Explanations: *Pic exc – Piceion excelsae* : group with *Pinus cembra* (no. 1) refers to Swiss stone pine forests, also narrowly defined as *Pinion cembrae* , *Abi-Pic – Abieti-Piceion* , Chry-Pic – *Chrysanthemo rotundifolii-Piceion* ; *Are-Fag – Aremonio-Fagion* ; *Fag syl – Fagion sylvaticae* : group no. 6 includes mesic forests of *Eu-Fagenion* and *Galio-Abietenion* , while group no 7 encompasses hygrophilous fir forests of *Galio-Abietenion* .

Beilage S1. Kombinierte synoptische Tabelle der Frequenz (%) und Treue für fünf Waldverbände im polnischen Teil der Tatra. Werte der p*hi* Koeffizienten für diagnostische (φ > 0,25) und hochdiagnostische (φ > 0,5) Arten sind hell- bzw. dunkelgrau hinterlegt. Diagnostische Arten werden in jeder Gruppe nach ihrem diagnostischen Wert sortiert. Signifikante Werte der Treue (p*hi* -Koeffizient multipliziert mit 100) sind hochgestellt. Frequenzen für konstante (> 40%) und hoch konstante (> 80%) Arten sind ebenfalls hell- bzw. dunkelgrau hinterlegt. Arten mit Häufigkeiten unter 10 % in allen Verbänden sind nicht aufgeführt.

Erläuterungen: *Pic exc – Piceion excelsae* : Gruppe mit *Pinus cembra* (Nr. 1) bezeichnet Zirbenwälder, auch eng definiert als *Pinion cembrae* , *Abi-Pic – Abieti-Piceion* , *Chry-Pic – Chrysanthemo rotundifolii-Piceion* ; *Are-Fag – Aremonio-Fagion* ; *Fag syl – Fagion sylvaticae* : Gruppennr. 6 umfasst mesophytische Wälder des *Eu-Fagenion* und *Galio-Abietenion* , während Gruppe Nr. 7 hygrophile Tannenwälder des *Galio-Abietenion* umfasst.

No.	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Syntaxon	***Pic exc (P. cembra)***	***Pic exc***	***Abi-Pic***	***Chry-Pic***	***Are-Fag***	***Fag syl* (mesic)**	***Fag syl* (wet)**
No. of relevés	**15**	**67**	**62**	**27**	**48**	**20**	**26**
D.S. *Piceion excelsae* (*Pinus cembra* forests)							
Pinus mugo	87 ^{83}	1	.	15	.	.	.
Pinus cembra	53 ^{65}	1	2	.	.	.	4
Huperzia selago	60 ^{47}	10	5	30	8	5	.
Lycopodium annotinum	47 ^{40}	12	5	26	4	.	.
Calluna vulgaris	20 ^{38}	.	.	4	.	.	.
D.S. *Piceion excelsae*							
Deschampsia flexuosa	80	85 ^{26}	68	59	29	15	35
D.S. *Abieti-Piceion*							
Luzula luzuloides	27	7	50 ^{30}	30	12	5	12
Chamaenerion angustifolium	7	9	35 ^{27}	7	12	5	15
D.S. *Chrysanthemo rotundifolii-Piceion*							
Scabiosa lucida	.	.	.	44 ^{62}	2	.	.
Leontodon hispidus agg.	.	.	.	48 ^{60}	8	.	.
Astrantia major	.	.	.	48 ^{54}	19	.	.
Galium anisophyllum	.	.	.	41 ^{53}	4	5	.
Sesleria tatrae	.	.	.	33 ^{53}	2	.	.
Polystichum lonchitis	.	.	.	44 ^{52}	17	.	.
Campanula polymorpha	13	.	5	59 ^{51}	27	.	.
Tofieldia calyculata	.	.	.	33 ^{51}	4	.	.
Phyteuma orbiculare	.	.	.	26 ^{48}	.	.	.
Primula elatior	.	.	2	63 ^{48}	40 ^{23}	15	8
Pimpinella major	.	.	2	41 ^{47}	12	5	.
Heracleum sphondylium	.	.	.	26 ^{46}	2	.	.
Carlina acaulis	.	.	.	22 ^{44}	.	.	.
Thymus alpestris	.	.	.	22 ^{44}	.	.	.
Gentianella lutescens	.	.	.	22 ^{42}	2	.	.
Coeloglossum viride	.	.	2	37 ^{41}	15	5	4
Ranunculus oreophilus	.	.	.	19 ^{40}	.	.	.
Carduus glaucus	.	.	.	19 ^{40}	.	.	.
Parnassia palustris	.	.	.	26 ^{40}	8	.	.
Corallorhiza trifida	.	.	.	26 ^{40}	8	.	.
Soldanella carpatica agg.	13	6	34	96 ^{40}	69 ^{17}	50	65
Carex flacca	.	.	.	22 ^{40}	4	.	.
Festuca carpatica	.	.	.	19 ^{38}	2	.	.
Carex brachystachys	.	.	.	22 ^{38}	6	.	.
Cardaminopsis arenosa agg.	7	.	2	33 ^{37}	17	.	.
Aconitum variegatum	.	.	.	33 ^{37}	17	5	4
Viola biflora	.	1	3	44 ^{37}	31 ^{21}	.	15
Carex sempervirens	.	.	.	15 ^{36}	.	.	.
Festuca versicolor	.	.	.	15 ^{36}	.	.	.
Geranium sylvaticum	.	.	.	15 ^{36}	.	.	.
Petasites kablikianus	.	.	.	37 ^{36}	21	15	.
Hypericum maculatum	.	1	8	56 ^{35}	35	20	23
Epipactis atrorubens	.	.	.	22 ^{34}	10	.	.
Monotropa hypopitys	.	.	.	15 ^{33}	2	.	.
Linum catharticum	.	.	.	19 ^{31}	8	.	.
Crepis jacquinii	.	.	.	11 ^{31}	.	.	.
Pedicularis verticillata	.	.	.	11 ^{31}	.	.	.
Trisetum alpestre	.	.	.	11 ^{31}	.	.	.
Galium mollugo agg.	.	.	.	11 ^{31}	.	.	.
Alchemilla glaucescens	.	.	.	11 ^{31}	.	.	.
Prunella vulgaris	.	.	3	33 ^{31}	19	5	12
Salix caprea	.	.	10	44 ^{31}	23	15	23
Moneses uniflora	.	.	5	26 ^{30}	10	.	8
Poa nemoralis	.	.	5	26 ^{29}	10	10	.
Swertia perennis	7	.	.	19 ^{28}	6	.	.
D.S. *Aremonio-Fagion*							
Mercurialis perennis	.	.	.	15	83 ^{72}	20	.
Cardamine trifolia	.	.	2	4	58 ^{56}	25	.
Carex digitata	.	.	2	22	50 ^{52}	.	.
Paris quadrifolia	.	.	2	15	62 ^{46}	40	12
Ranunculus platanifolius	.	.	2	11	50 ^{43}	30	4
Calamagrostis arundinacea	20	1	40	81 ^{24}	98 ^{38}	60	62
Daphne mezereum	.	.	.	26	35 ^{37}	.	4
Maianthemum bifolium	.	4	15	44	77 ^{35}	60	50
Euphorbia amygdaloides	.	.	.	.	12 ^{33}	.	.
Calamagrostis varia	7	.	2	26	33 ^{33}	.	.
Rosa pendulina	.	.	2	4	21 ^{32}	5	.
Thalictrum aquilegifolium	.	.	.	15	31 ^{32}	5	12
Lilium martagon	.	.	2	7	25 ^{32}	10	.
Carex ornithopoda	.	.	.	7	17 ^{30}	.	.
Actaea spicata	.	.	.	7	31 ^{29}	30	.
Galium schultesii	.	.	.	15	21 ^{29}	.	.
Orthilia secunda	7	.	2	11	23 ^{29}	.	.
Solidago virgaurea	7	1	13	41	44 ^{28}	5	12
Fraxinus excelsior	.	.	.	.	19 ^{27}	10	4
Hordelymus europaeus	.	.	.	.	8 ^{27}	.	.
Delphinium elatum	.	.	.	.	8 ^{27}	.	.
Athyrium filix-femina	.	.	35	41	73 ^{26}	70	69 ^{23}
Crepis paludosa	.	.	5	44	48 ^{26}	15	38
Gentiana asclepiadea	27	7	47	74	85 ^{26}	70	65
Ajuga reptans	.	.	.	7	17 ^{26}	5	.
Polystichum aculeatum	.	.	2	11	25 ^{25}	15	4

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Fortsetzung auf der Rückseite

No.	1	2	3	4	5	6	7
Syntaxon	*Pic exc (P. cembra)*	*Pic exc*	*Abi-Pic*	*Chry-Pic*	*Are-Fag*	*Fag syl* (mesic)	*Fag syl* (wet)
No. of relevés	15	67	62	27	48	20	26
D.S. *Fagion sylvaticae* (mesic forests of *Eu-Fagenion* and *Galio-Abietenion*)							
Viola reichenbachiana	.	.	.	.	21	55 [54]	8
Circaea alpina	.	.	3	.	6	55 [51]	27
Asarum europaeum	.	.	.	.	17	45 [41]	23
Galeobdolon luteum	.	.	10	48	69 [24]	85 [37]	69 [24]
Aegopodium podagraria	.	.	.	.	.	15 [36]	.
D.S. *Fagion sylvaticae* (hygrophilous fir forests of *Galio-Abietenion*)							
Leucanthemum waldsteinii	.	.	8	48 [22]	21	15	81 [53]
Caltha palustris agg.	.	.	3	.	.	.	23 [42]
Equisetum sylvaticum	.	.	2	.	.	15	31 [39]
Deschampsia cespitosa	.	4	13	37	15	15	58 [38]
Lysimachia nemorum	.	.	5	.	2	25	35 [35]
Myosotis palustris	.	.	2	.	.	.	15 [34]
Chaerophyllum hirsutum	.	.	8	59 [22]	56 [19]	40	73 [34]
Luzula luzulina	.	1	19	11	8	25	46 [34]
Myosoton aquaticum	.	.	2	.	.	5	15 [29]
Stellaria nemorum	7	.	18	.	2	30	35 [26]
D.S. for more than one vegetation type							
Vaccinium vitis-idaea	93 [52]	24	10	63 [26]	25	.	19
Fragaria vesca	.	1	5	93 [52]	71 [33]	30	31
Hieracium murorum	7	1	27	96 [51]	81 [38]	20	23
Phyteuma spicatum	.	.	6	74 [45]	79 [50]	10	12
Valeriana tripteris	.	1	8	74 [42]	92 [58]	10	12
Asplenium viride	13	.	5	56 [39]	50 [33]	5	.
Cirsium erisithales	.	.	.	41 [38]	38 [34]	.	.
Clematis alpina	.	.	2	56 [36]	73 [54]	.	12
Bellidiastrum michelii	7	.	.	37 [34]	33 [29]	.	.
Listera ovata	.	.	3	44 [34]	52 [43]	5	.
Digitalis grandiflora	.	.	.	37 [28]	50 [43]	5	4
Mycelis muralis	.	.	19	52 [27]	65 [40]	5	23
Fagus sylvatica	.	3	8	22	85 [49]	85 [49]	8
Sanicula europaea	.	.	5	22	71 [44]	55 [29]	19
Polygonatum verticillatum	7	.	21	63	88 [40]	75 [29]	27
Prenanthes purpurea	13	6	32	44	92 [38]	85 [33]	42
Acer pseudoplatanus	.	1	11	56	83 [37]	90 [43]	31
Abies alba	.	7	21	7	81 [35]	95 [46]	65
Dentaria glandulosa	.	.	3	19	67 [34]	80 [46]	35
Dryopteris filix-mas	.	.	8	30	56 [31]	55 [30]	19
Phegopteris connectilis	.	9	29	11	25	65 [32]	65 [33]
Other species							
Picea abies	100	100	100	100	100	100	100
Sorbus aucuparia	93	82	90	89	96	70	92
Vaccinium myrtillus	100	97	97	85	79	70	92
Oxalis acetosella	53	64	90	85	92	95	92
Senecio nemorensis agg.	.	3	48	67	69 [17]	75	77 [23]
Rubus idaeus	47	10	77 [15]	74	60	70	77
Dryopteris dilatata agg.	80	85 [19]	74	37	44	45	73
Homogyne alpina	73	75	84	81	75	60	73
Petasites albus	7	.	8	19	52 [23]	55	50
Gymnocarpium dryopteris	7	.	24	41	42	50	46
Luzula sylvatica	33	40	71 [17]	78	54	35	42
Carex sylvatica	.	.	3	11	38 [21]	35	38
Dryopteris carthusiana	13	15	34	11	38	55	38
Calamagrostis villosa	60	52 [19]	40	4	6	20	35
Lonicera nigra	7	.	18	33	46 [21]	30	35
Athyrium distentifolium	60	36	48 [18]	7	4	20	27
Salix silesiaca	27	3	8	26	21	.	23
Cardamine flexuosa	.	.	.	15	10	15	19
Geum rivale	.	.	.	22	8	5	19
Urtica dioica	.	1	10	15	12	15	15
Veronica officinalis	.	.	8	26	19	25	15
Sambucus racemosa	.	.	24	22	21	40	15
Doronicum austriacum	.	.	.	4	6	5	12
Agrostis capillaris	.	1	5	4	.	.	12
Impatiens noli-tangere	.	.	2	.	2	15	12
Chrysosplenium alternifolium	.	.	3	4	4	5	12
Alnus incana	.	.	.	4	.	.	12
Epilobium montanum	.	.	16	30	25	25	12
Senecio subalpinus	.	.	5	22	4	.	12
Galium saxatile	.	3	11	.	.	.	12
Ranunculus repens	.	.	3	7	.	20	12
Juncus effusus	.	1	.	.	.	10	8
Cicerbita alpina	.	.	3	4	8	15	8
Veratrum lobelianum	7	.	.	4	25 [21]	25	8
Cirsium palustre	.	.	2	7	10	.	4
Neottia nidus-avis	.	.	.	4	10	5	4
Dentaria bulbifera	.	.	.	.	10	20	4
Aruncus sylvestris	.	.	.	4	23 [25]	20	4
Geranium robertianum	.	.	.	4	19 [18]	25	4
Galeopsis tetrahit	.	.	3	4	.	20	4
Galium rotundifolium	.	.	3	4	8	15	4
Hieracium lachenalii agg.	.	.	10	11	2	10	4
Larix decidua	.	1	.	.	2	10	4
Sedum fabaria	.	.	2	7	8	10	4
Laserpitium latifolium	.	.	.	11	2	.	.
Potentilla erecta	.	.	.	15	8	.	.
Solidago virgaurea subsp. alpestris	13	.	.	4	4	.	.
Tussilago farfara	.	.	2	11	8	.	.
Melampyrum sylvaticum	7	.	.	.	12 [24]	.	.
Cystopteris fragilis	7	1	.	15	10	.	.
Empetrum hermaphroditum	13	.	.	.	.	.	.
Anemone nemorosa	.	.	.	.	4	10	.
Luzula pilosa	.	.	2	.	.	10	.
Veronica montana	.	.	.	.	4	10	.
Ribes alpinum	.	.	3	7	10	10	.
Juniperus communis ssp. nana	13	1	.	.	.	.	.
Galium odoratum	.	.	2	.	12 [25]	5	.
Cystopteris montana	.	.	.	11	6	5	.
Potentilla aurea	.	1	5	15	.	.	.
Selaginella selaginoides	.	.	2	11	.	.	.
Betula pubescens ssp. carpatica	13	.	2	4	.	.	.