



Research Article

Pinus heldreichii and *Pinus peuce* forests of the Pirin Mountains in Bulgaria*

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Abstract

We investigated the forest communities of *Pinus heldreichii* and *Pinus peuce* in the Pirin Mountains in Bulgaria. Both *Pinus* species are sensitive relicts with a very limited range, primarily in the Balkan Peninsula. Anthropogenic activities and global climate change pose serious challenges to their conservation. We have subjected 189 published and unpublished relevés from newly conducted field research to numerical analysis. Then we corroborated them by comparison with the previously identified and published syntaxa in neighbouring countries. The results indicated that the *Pinus heldreichii* communities form part of the *Festuco penzesii*-*Pinetum heldreichii* ass. nov. with two subassociations: *typicum* and *seslerietosum coerulantis* subass. nov. These communities are distinctly oromediterranean, characterised by their floristic composition and occurrence on marbles. In contrast, we classified the *Pinus peuce* communities in the Pirin Mts. at the community level as the *Festuca valida*-*Pinus peuce* community. These extrazonal boreomontane communities are also distributed at high elevations, but in contrast to the *Pinus heldreichii* communities, they occur on silicate terrains. *Pinus heldreichii* associations have a limited range, and due to their canopy openness and occurrence on marbles and serpentine terrains, they support many regional and even local endemics. Although *Pinus peuce* communities are also divided into geographically isolated groups, the high constancy of characteristic species of boreomontane forests calls this classification into question, suggesting that a comprehensive revision of *Pinus peuce* forests within their range is needed.

Keywords

Balkans, coniferous forests, endemic, high mountains, pines, *Pinion heldreichii*, *Pinion peuces*, phytosociology

Introduction

The genus *Pinus* and its associated communities are widespread across the globe, including both warm and boreal regions, however, its native range is limited to the Northern Hemisphere (Critchfield and Little 1966; Farjon 2017). Of particular interest are the communities of

some endemic species found in refugial areas during the Ice Age. These areas are located in the mountainous regions of southern Europe, particularly on the Balkan Peninsula. *Pinus peuce* Griseb. (Macedonian pine) and *Pinus heldreichii* Christ. (Bosnian pine) are Tertiary relicts. The former is endemic to the Balkan Peninsula, while the latter is also found, albeit to a limited extent, in the southern

* Topical Collection: "Vegetation classification: from classic to numeric approaches".

Apennines (Fukarek 1949a, 1949b; Stojanov 1950; Farjon 2017). Within their range, these two species form communities belonging to two alliances: *Pinion heldreichii* Horvat 1946 and *Pinion peuces* Horvat 1950 (Horvat et al. 1974). We report the latter as *Pinion peuces* Horvat 1950, according to the ICPN (p. 63), as the genitive of “*peuce*” is “*peuces*”. Both alliances are represented by open coniferous forests in the montane to subalpine belts. Despite developing on dry, relatively poor soils, *Pinion peuces* forests are generally more mesophilic and sciophytic than *Pinion heldreichii* forests, which are more heliophilous and resistant to summer drought. Another significant difference is that *Pinion peuces* forests generally develop on neutral or silicate substrates, whereas *Pinion heldreichii* forests develop on alkaline and serpentinite rocks (Preislerová et al. 2024).

These two species do not necessarily dominate forest communities everywhere within their range. Interestingly, the Pirin Mts. in Bulgaria are the only place in the eastern Balkan Peninsula where extensive communities of both species exist (Georgiev 1939; Stojanov 1941; Marinov and Naumov 1963; Penev et al. 1969). According to Panayotov et al. (2016), some of the best-preserved *Pinus peuce* forests are found in the Pirin Mts. They are located at the upper forest boundary, primarily between 1600–1700 m a.s.l. extending up to approximately 2250 m a.s.l. Notably in the Pirin Mts., there is a clear distinction between the communities dominated by the two species. In fact, *Pinus heldreichii* forests in the Pirin Mts. are found exclusively on shallow, basic soils on a marble rock base, while *Pinus peuce* forms communities mainly on poor soils on silicate rocks, mostly granites (Velchev and Vassilev 1984; Velchev and Russakova 1990; Vulchev 2000). However, *Pinus peuce* is relatively common as individual trees, or even as a secondary tree of *Pinus heldreichii* forests on limestones. In the Balkans, the forest communities of these two species have mostly been studied in the former Yugoslavia (Serbia, Kosovo, North Macedonia, Montenegro, and Bosnia and Herzegovina), where most of the information on their ecological characteristics and floristic structure originates (Janković 1958, 1960, 1965, 1971, 1975, 1990; Škorić 2006).

Velchev and Janković (1975) categorised the *Pinus heldreichii* communities in the Balkans as either Central-Balkan type (Bulgaria) or Western-Balkan type (Albania, Montenegro, Bosnia and Herzegovina, Kosovo, and Greece). *Pinus heldreichii* forests are ecologically more similar to *Pinus nigra* forests, but are found at the upper forest boundary, transitioning gradually into subalpine communities, becoming highly sparse and open forests, and forming complexes with alpine scrub and tufted grass communities. *Pinus peuce* forests are more similar to other boremontane forests, such as those of *Pinus sylvestris* and *Picea abies* (Horvat et al. 1974).

The communities of *Pinus heldreichii* in the Pirin Mts. have been phytocoenologically studied in two papers—with only one using the methodology of Braun-Blanquet (1964)—conducted at the very beginning of its

introduction in Bulgaria (Vulchev 2000). However, this publication does not contain complete phytocoenological relevés because many species occurring in only one relevé are listed separately but not assigned to the corresponding relevé. The published associations are invalid according to the ICPN (Theurillat et al. 2021) because holotypes were not designated (Art. 5), and also due to the misapplication of Art. 3f, particularly for the *Geranio-Pinetum heldreichii*, whose original diagnosis contains two species of *Geranium* but the name-giving taxon was not indicated. Vulchev (2000) also analysed the similarities and differences with previously described associations dominated by *Pinus heldreichii* in Kosovo, Montenegro, and Bosnia and Herzegovina. These associations are distributed in various mountains of the Dinaric Alps range and include both common species and endemics from the Western Balkans, some of which are also the type species of these associations (Dinić and Janković 2006a). The other phytocoenological publication on the *Pinus heldreichii* forests in the Pirin Mts. is by Velchev and Vassilev (1984), who conducted their research according to the Russian methodology based on dominant species (Sukachov et al. 1952), which was largely applied in Bulgaria at that time. In this methodology, the relevés are compiled in a similar way to those of Braun-Blanquet’s school, using the same scale of cover/abundance; however, the classification of communities is based on different criteria, mostly focusing on the dominant species in the different layers.

Most publications on *Pinus peuce* forests in Bulgaria focus on forestry, dendrology, or general ecological aspects (Penev 1966; Penev et al. 1969; Panayotov et al. 2016). Regarding the phytocoenology of *Pinus peuce* forests in the Pirin Mountains, there is only one study (Velchev and Russakova 1990), also conducted using the dominance method. However, Braun-Blanquet’s methodology has been applied to *Pinus peuce* forests in the Central Balkan National Park (Nikolov and Dimitrov 2015), which is the northernmost Balkan representation of this species, and the new association *Adenostylo alliariae-Pinetum peuces* was described in this area.

Our study aims to investigate the ecological characteristics and floristic composition of *Pinus heldreichii*- and *Pinus peuce*-dominated communities in the Pirin Mts., based on a numerical analysis of all relevés, both published and new. We are particularly interested in their current distribution in these mountains with respect to the Holocene vegetation development, and the main ecological factors and gradients shaping these communities.

Material and methods

Target species

The two target species are *Pinus peuce* and *Pinus heldreichii*. Despite belonging to the same genus, they are taxonomically very different. *Pinus peuce* is the only species of the subgenus *Cembra* in southern Europe (Farjon 2017).

The first representatives of this subgenus date back to the Eocene (Xu et al. 2015) and were mainly found in the temperate and boreal regions of Eurasia and North America. In contrast, *Pinus peuce* is a unique and endemic species found in the mountains of the Balkan Peninsula (Stojanov 1950; Horvat et al. 1974; Farjon 2017). *Pinus heldreichii* belongs to the subgenus *Pinus* subsection *Pinaster*, which includes Mediterranean pine species. Its occurrence in the Balkans is considered oromediterranean (Horvat et al. 1974; Velchev and Janković 1975; Farjon 2017).

Study area

The Pirin Mountains are located in southwestern Bulgaria (Figure 1), stretching from northwest to southeast. They are the second-highest mountain range in Bulgaria after the Rila Mts. and the third-highest on the Balkan Peninsula after the Rila and Olympus Mts. Geomorphologically, the Pirin Mts. are divided into three parts: Northern, Central, and Southern Pirin. Tectonically, it is a horst, whose core is made up of five plutons of biotite granite

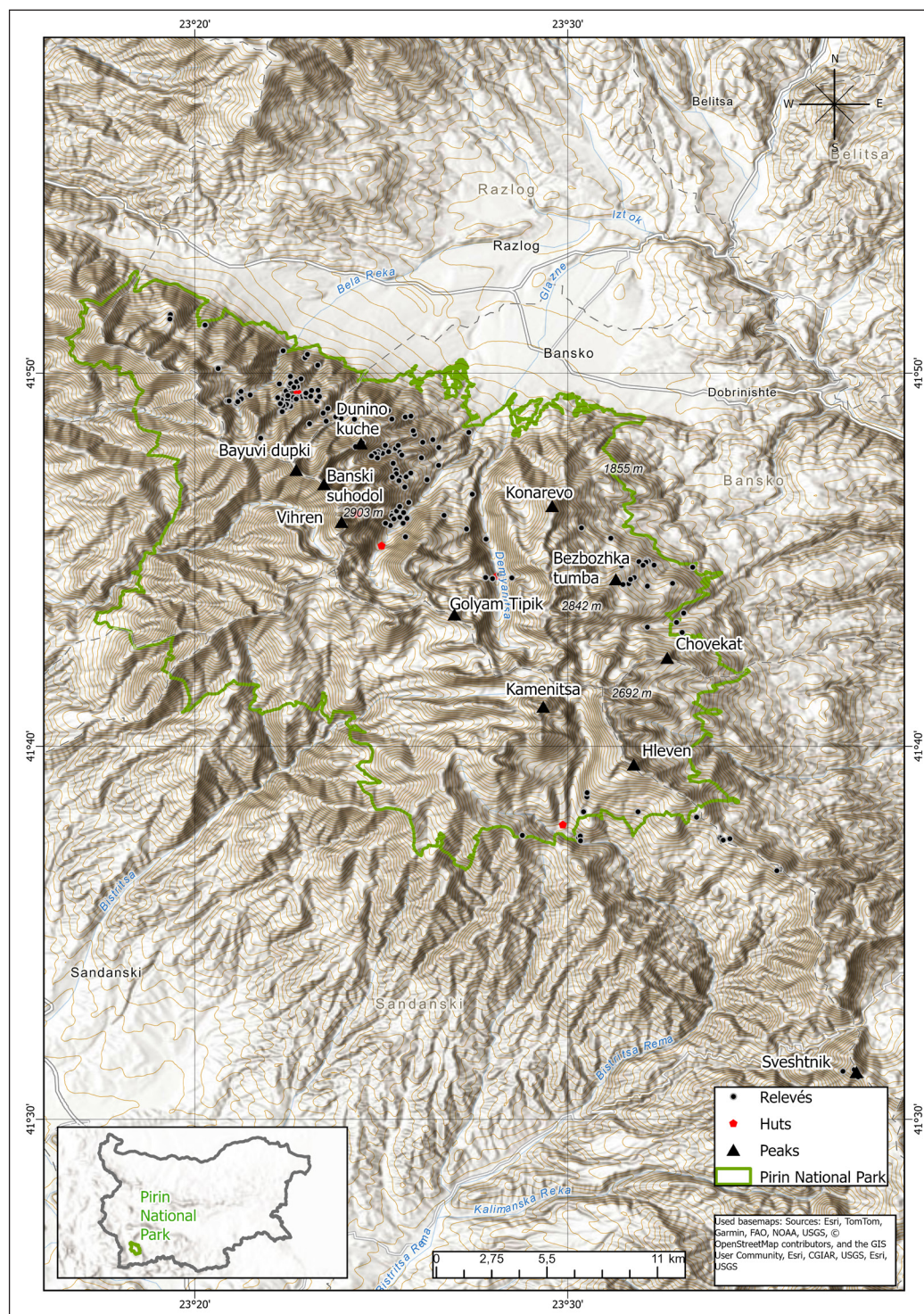


Figure 1. Map of the study area in the Pirin Mountains, southwestern Bulgaria.

and granitoid rock from the Cretaceous, Paleogene, and Paleozoic periods, which are visible in many places in the mountains. This core is covered by a fragmented mantle of diverse Precambrian metamorphic rocks belonging to two series: a lower series, consisting of granito-gneisses, and an upper series, consisting of amphibolite schists, mica schists, and marbles. In the Northern part of the mountain, where the highest peak Vihren (2914 m a.s.l.) is located, two types of rock are typically exposed: marbles and calcschists on the one hand, and biotite granites and granodiorites from the Central, Northern Pirin and Bezboz plutons on the other (Boyadjiev 1959; Zagorchev 1995). The formation of the modern relief of the Pirin Mts. began in the middle of the Tertiary period. Due to repeated uplifts, five denudation surfaces of different ages, heights, and ranges were formed. During the Quaternary period, the mountain was covered with glaciers at elevations over 2300 m a.s.l., which transformed the landscape into a typical glacial terrain of carlings, trough valleys and cirques (Vaptsarov et al. 1989; Georgiev 1991). The marble part of the mountain features the so-called glaciokarst, which has specific ecological and physicochemical characteristics (Gachev 2017) lacking in other Bulgarian mountains.

In terms of climatic zoning, the climate of the Pirin Mts. belongs to the Continental–Mediterranean climatic region of Bulgaria. Due to its southern position, the mountain experiences relatively easy penetration of Mediterranean influence along the valleys of the Struma and Mesta rivers, resulting in milder and drier climate moderation and xerophytisation. Compared to the Rila Mountains, which lie further north and run parallel to the Pirin Mts., the total amount of precipitation in the Pirin Mts. is lower, with maximum precipitation shifting toward autumn and winter, and with higher average annual temperature. In the highest summits, the climate is more typical of a mountain climate, although the effect of the Mediterranean climate is present. Average January temperatures range from -1 to -2 °C in the foothills and down to -5 °C at higher elevations. The mean annual temperature at Vihren Hut is 3.5 °C. Precipitation varies from 600–800 mm in the lower belts to 1400–1500 mm in the upper parts of the mountain (Georgiev 1991; Vaptsarov et al. 1989; Velev 2002).

Soil cover is dominated by acidic Dystric Cambisols and Humic Cambisols. Due to the widespread erosion, particularly in the higher parts, large areas are covered by shallow soils, including Rendzic Leptosols on marble bedrock and Umbric Leptosols on granite bedrock (Ninov 2002).

According to Bondev (2002), the Pirin district belongs to the Illyrian (Balkan) province of the European deciduous forest region geobotanical zone. The area has remarkably diverse vegetation. The alpine belt is dominated by calcicolous (*Sesleria korabensis*, *Festuca pirinica*, *Kobresia myosuroides*) and acidophilous (*Sesleria comosa*, *Agrostis rupestris*, *Carex curvula*) grasslands, as well as dwarf shrub communities (*Dryas octopetala*, *Salix reticulata*, *Salix herbacea*). The subalpine belt consists of *Pinus mugo* communities, which are often degraded and replaced by

secondary grasslands (*Nardus stricta*, *Festuca valida*) and dwarf shrubs communities (*Juniperus sibirica*, *Vaccinium* spp.). The coniferous forest belt consists of *Pinus sylvestris*, *Pinus nigra*, *Pinus peuce*, *Pinus heldreichii*, and *Picea abies*. In the lower, mainly southern parts of the mountains, there are also deciduous forests comprising *Fagus sylvatica*, *Quercus petraea*, and *Ostrya carpinifolia*. Around 84 Balkan endemics, including many local ones, are known to inhabit the mountain area.

Data collection and analysis

A total of 189 relevés were initially used in the present analysis, of which 54 were unpublished and came from newly conducted field research and 135 were previously published (Velchev and Vassilev 1984; Velchev and Ruskova 1990; Vulchev 2000). All of them were collected in the *Pinus heldreichii* and *Pinus peuce* forests in the Pirin Mts. between 1984 and 2024. Vegetation sampling followed the methods of the Zürich-Montpellier phytosociological school (Braun-Blanquet 1964; Kent 2012). The relevé sizes vary between 200 and 2000 m², with most of 400 m² (Suppl. material 1: table S1). A complete list of vascular taxa, bryophytes, and lichens, together with their cover-abundance values, was recorded for each sampling plot using the 9-degree modified Braun-Blanquet scale (van der Maarel 1979). Additional information on epiphytic lichens and allied fungi on *Pinus heldreichii* and *Pinus peuce* in the Pirin Mts. was used following Shivarov (2024). The complete set of relevés in the modified Braun-Blanquet scale is reported in Suppl. material 1: tables S1, S2, and are accessible through the CircumMed Vegetation Database (GIVD Code: EU-00026) (Bonari et al. 2019).

On the resulting dataset comprising 189 relevés and 572 taxa, a hierarchical cluster analysis was applied. The unweighted pair group method with arithmetic mean (UPGMA) was used as a classification method and the floristic similarity between relevés in the (dis)similarity matrix was calculated using Horn's index (Horn 1966). Prior to cluster analysis, cover-abundance data were transformed into ordinal numbers from 1 to 9 (van der Maarel 1979). The cluster analysis was performed using the SYN-TAX computer software (Podani 2001).

The cluster dendrogram initially contained 189 relevés (Figure 3), but nine were excluded because they represented different types of vegetation or vegetation complexes, rather than typical *Pinus peuce* and *Pinus heldreichii* forests. The resulting dataset of 180 relevés (135 published and 45 unpublished) and 500 taxa was used for further analysis. The diagnostic species of each of the obtained clusters were determined by calculating their fidelity (Chytrý et al. 2002) using the phi coefficient of association in JUICE.NET software based on presence/absence (Sokal and Rohlf 1995; Chytrý et al. 2002; Tichý 2002). The size of the target groups was fixed at 30% of the total dataset while maintaining the same percentage of species occurrences within and outside the target groups

(Tichý and Chytrý 2006). The threshold of the phi value for the diagnostic species was set at 0.30 (multiplied by 100 in the JUICE software) and a zero value was assigned to those species whose fidelity was not statistically significant ($p > 0.01$) in the Fisher's exact test. Each group was described based on its diagnostic, constant, and dominant species. Species were considered constant if their frequency exceeded 50% for the given community. Dominant species were defined as those with an average cover of more than 50% in at least 5% of the relevés within the group. The values of fidelity, frequency, and the percentage of relevés with cover greater than 50% are given in brackets for diagnostic, constant, and dominant species, respectively. The full lists of diagnostic species of the identified vegetation groups are indicated in the Suppl. material 1: table S2, and are not included in the main text of the results of the classification section, where only constant and dominant species are listed, except for the two holotypus relevés, where the complete relevé records are provided.

To explore the general patterns of these forests and to visualise the differences in species composition between clusters, we performed an indirect ordination analysis. We used the data matrix of 180 sample plots and 500 taxa, with original percentage values from the new unpublished relevés and mid-percentage values from the published ones. An initial detrended correspondence analysis (DCA) revealed a gradient length along the first axis greater than 3 standard deviation (SD) units, enabling the application of DCA as an unconstrained unimodal ordination (Šmilauer and Lepš 2014). The cover values of taxa were transformed using the square root method, and rare species were downweighted. To assist with interpreting main gradients within the species composition variation, species ecological indicator values (EIVs) for temperature, light, moisture, soil reaction, and available nutrients for 80% of the species (Tichý et al. 2023) were used as explanatory variables. Unweighted average EIVs were calculated for all relevés, and these, together with elevation, slope, and total vegetation cover, which had been directly measured during fieldwork, were passively projected onto the ordination space. Prior to the ordination, Spearman's test was used to check for correlations between environmental variables. Correlations were considered statistically significant at $p < 0.05$, and correlation strength was interpreted based on the absolute value of Spearman's coefficient as weak (< 0.30), moderate ($0.30-0.70$), or strong (> 0.70). We detected significant correlations among several EIVs as well as between selected environmental variables, while no significant correlations were found for vegetation cover and for several EIV-topographic variables combinations. DCA was performed in CANOCO 5 software (Šmilauer and Lepš 2014). We also calculated proportions of categories of chorological spectra and plant life form spectra for the vegetation units (clusters). The chorotypes of the species follow Assyov et al. (2012) and Stoyanov et al. (2021).

The nomenclature of the vascular plants follows the Euro+Med online database (Euro+Med 2006+: <https://europlusmed.org/>), except for the genus *Campanula*, for which reference is made to Anchev and Kovanda (2012).

The nomenclature of mosses follows Hill et al. (2006) and Gospodinov and Natcheva (2022), while for lichens we followed Denchev et al. (2022). For epiphytic lichen taxa published after 2022 on *Pinus heldreichii* and *Pinus peuce* forests in the Pirin Mts., we followed Shivarov (2024). New syntaxa are named according to the rules of the International Code of Phytosociological Nomenclature (Theurillat et al. 2021). The higher syntaxa above the association level are according to Mucina et al. (2016) and consistent with FloraVeg.EU (Chytrý et al. 2024).

Results

Classification

The results of the cluster analysis are presented in the dendrogram (Figure 2), where the main groups are outlined in colour-coded rectangles.

The results of the classification are summarised in Table 1, in which the diagnostic species are ranked in order of decreasing frequency. All complete relevés and the header data (geographical distribution and main environmental parameters) of these clusters within the study area are provided in Suppl. material 1: tables S1, S2. The syntaxonomic scheme of the pine forests analysed is as follows:

Class *Erico-Pinetea* Horvat 1959

Order *Erico-Pinetalia* Horvat 1959

Alliance *Pinion heldreichii* Horvat 1946

Association *Festuco penzesii-Pinetum heldreichii* Vulchev ex Nacheva, Bonari, Pachedjieva, Vulchev, Gussev, Shivarov, Ganeva et Tzonev ass. nov. (Cluster 1)

subassociation *typicum*

subassociation *seslerietosum coerulantis*
Nacheva, Bonari, Pachedjieva, Vulchev, Gussev, Shivarov, Ganeva et Tzonev subass. nov. (Cluster 2)

Class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939

Order *Piceetalia excelsae* Pawłowski et al. 1928

Alliance *Pinion peuces* Horvat 1950

Festuca valida-*Pinus peuce* community (Cluster 3)

***Pinus heldreichii* forests**

We describe the three pine forest communities (Suppl. material 4: figure S2) and provide information on holotype for the two newly described communities, diagnostic species, structure, ecology, dynamics, and chorology. The numerical analysis identified the existence of a large polymorphic association dominated by *Pinus heldreichii*, structured in two groups of relevés (Clusters 1 and 2), which were recognised at the subassociation level. The

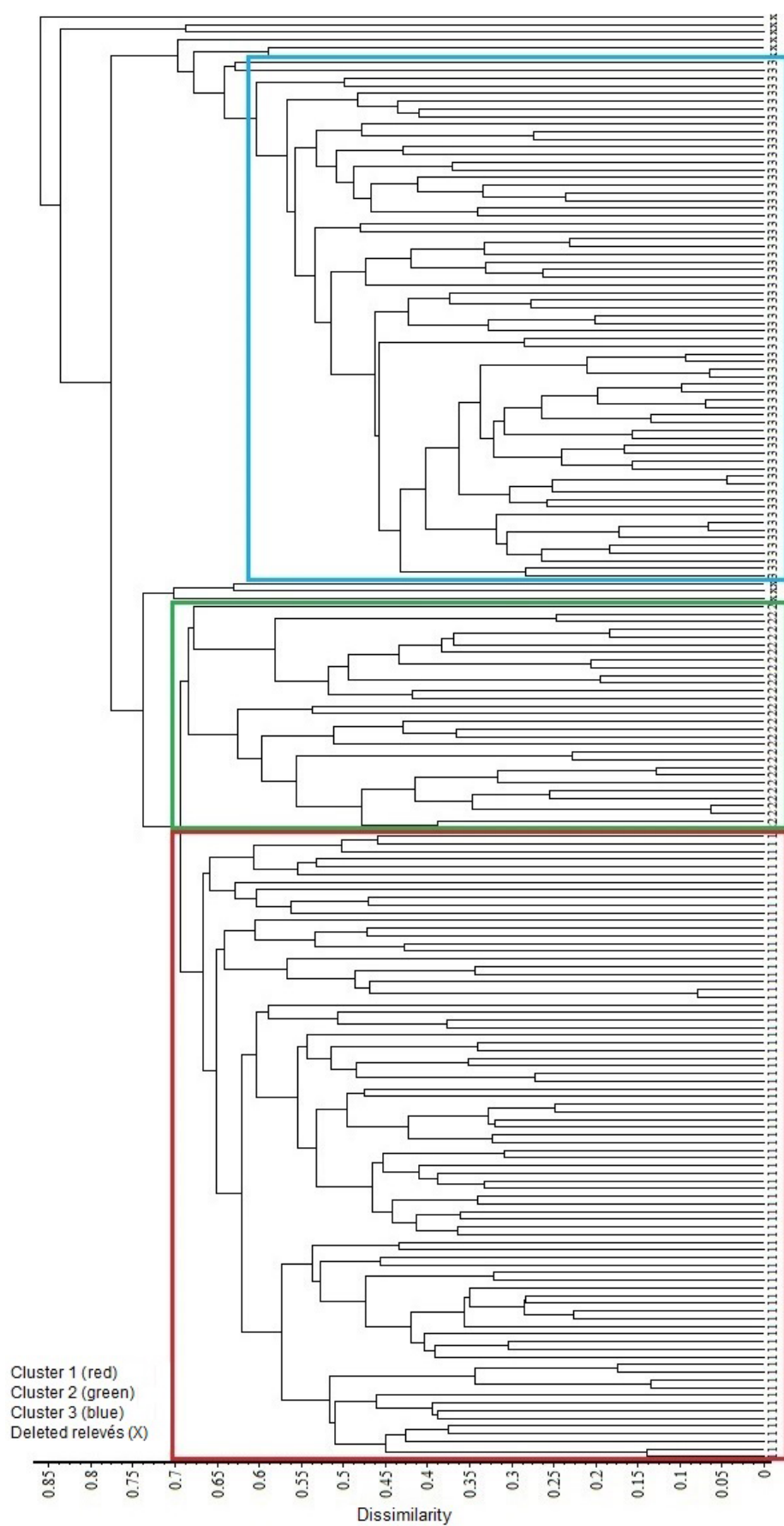


Figure 2. Cluster dendrogram with the three main clusters and the deleted relevés (X). Cluster 1 is indicated in red, cluster 2 in green, and cluster 3 in blue.

Table 1. Synoptic table of the clusters resulting from the hierarchical cluster analysis. Values are percentage constancies. Diagnostic taxa, those with values of phi-coefficient exceeding 0.3, have shaded background. Companion taxa with constancy values equal to or less than 20% in the entire dataset were omitted. The complete table with all species is in the Suppl. material 1: table S2.

Cluster number	1	2	3	Cluster number	1	2	3
Number of relevés	82	30	68	Number of relevés	82	30	68
<i>Festuco penzesii-Pinetum heldreichii</i> subass. <i>typicum</i>				<i>Festuca valida-Pinus peuce</i> community			
<i>Pinus heldreichii</i>	100	100	1	<i>Campanula persicifolia</i>	1	17	.
<i>Hieracium murorum</i>	80	37	41	<i>Cyanus achartarovii</i>	2	17	.
<i>Daphne mezereum</i>	71	47	19	<i>Poa macedonica</i>	.	13	.
<i>Fragaria vesca</i>	65	20	40	<i>Helianthemum canum</i>	.	13	.
<i>Cytisus eriocarpus</i>	62	37	21	<i>Polygala forojulensis</i> subsp. <i>carniolica</i>	.	13	.
<i>Aremonia agrimonoides</i>	60	17	18	<i>Festuca valida-Pinus peuce</i> community			
<i>Cruciata glabra</i>	48	.	10	<i>Pinus peuce</i>	54	23	100
<i>Cicerbita muralis</i>	45	3	18	<i>Vaccinium myrtillus</i>	48	17	99
<i>Polystichum lonchitis</i>	40	13	4	<i>Luzula luzuloides</i>	18	27	81
<i>Viola canina</i>	39	.	.	<i>Avenella flexuosa</i>	4	7	76
<i>Brachypodium sylvaticum</i>	39	3	.	<i>Melampyrum sylvaticum</i>	46	7	62
<i>Euphorbia cyparissias</i>	37	20	.	<i>Veronica officinalis</i>	17	7	50
<i>Cephalanthera rubra</i>	35	3	.	<i>Pinus mugo</i>	10	23	50
<i>Clinopodium alpinum</i> subsp. <i>alpinum</i>	33	13	3	<i>Oxalis acetosella</i>	12	.	44
<i>Geranium macrorrhizum</i>	30	3	10	<i>Dryopteris filix-mas</i>	17	.	44
<i>Dactylis glomerata</i>	27	7	.	<i>Crocus veluchensis</i>	.	.	40
<i>Symphytum tuberosum</i>	27	.	6	<i>Dicranum scoparium</i>	7	.	29
<i>Clinopodium vulgare</i>	23	3	.	<i>Anemone nemorosa</i>	4	.	28
<i>Valeriana tripteris</i>	23	.	3	<i>Prenanthes purpurea</i>	.	.	26
<i>Gentiana asclepiadea</i>	23	3	1	<i>Homogyne alpina</i>	4	.	22
<i>Anemone ranunculoides</i>	21	.	.	<i>Lamium maculatum</i>	.	.	18
<i>Carduus kernerii</i> subsp. <i>scardicus</i>	21	.	.	<i>Hypericum maculatum</i>	1	.	18
<i>Ajuga reptans</i>	21	.	3	<i>Vaccinium vitis-idaea</i>	1	.	15
<i>Myosotis alpestris</i>	20	.	.	<i>Galium odoratum</i>	1	.	15
<i>Heracleum sphondylium</i> subsp. <i>sibiricum</i>	16	.	.	<i>Festuca valida</i>	.	.	13
<i>Senecio rupestris</i>	13	.	.	Other taxa			
<i>Festuco penzesii-Pinetum heldreichii</i> subass. <i>seslerietosum coerulantis</i>				<i>Euphorbia amygdaloides</i>	93	90	66
<i>Festuca penzesii</i>	59	77	4	<i>Calamagrostis arundinacea</i>	78	77	69
<i>Carum graecum</i>	38	83	1	<i>Picea abies</i>	73	20	66
<i>Sesleria coerulans</i>	20	57	3	<i>Moehringia pendula</i>	70	10	65
<i>Linum capitatum</i>	38	57	.	<i>Juniperus sibirica</i>	59	47	56
<i>Campanula rapunculoides</i>	32	50	1	<i>Luzula sylvatica</i>	61	13	57
<i>Scabiosa ochroleuca</i>	15	47	3	<i>Pinus sylvestris</i>	48	47	37
<i>Hieracium olympicum</i>	1	40	.	<i>Poa nemoralis</i>	46	27	41
<i>Bromopsis riparia</i>	13	40	.	<i>Veronica chamaedrys</i>	50	17	25
<i>Origanum vulgare</i>	15	37	.	<i>Abies alba</i>	46	40	19
<i>Securigera varia</i>	17	33	.	<i>Fagus sylvatica</i>	28	30	25
<i>Pinus nigra</i>	.	33	3	<i>Galium sylvaticum</i> subsp. <i>laconicum</i>	34	20	21
<i>Geranium sanguineum</i>	7	33	.	<i>Campanula sparsa</i>	37	7	21
<i>Juniperus communis</i>	7	30	1	<i>Rubus idaeus</i>	24	.	38
<i>Brachypodium pinnatum</i>	4	27	.	<i>Daphne oleoides</i>	38	47	.
<i>Thymus pulegioides</i>	2	23	.	<i>Trifolium medium</i>	43	30	1
<i>Genista subcapitata</i>	2	20	.	<i>Senecio nemorensis</i>	17	7	37

associations of Vulchev (2000) were not confirmed, except for *Festuco penzesii-Pinetum heldreichii*, which is validated here. However, its scope was expanded to include practically all relevés of this forest type. At the subassociation level, the typical association *Festuco penzesii-Pinetum heldreichii* encompasses the largest number of relevés (82). It is represented by forests dominated by *Pinus*

heldreichii or codominated by other tree species, such as *Picea abies*, *Pinus sylvestris*, and *Pinus peuce*. They have a rich floristic composition, which distinguishes them from the second subassociation. It also includes poorer communities, most often found in extreme habitats. The second cluster comprises 30 relevés and has been recognised as the subassociation *seslerietosum coerulantis*.

Festuco penzesii*-*Pinetum heldreichii* Vulchev ex Nacheva, Bonari, Pachedjieva, Vulchev, Gushev, Shivarov, Ganeva et Tzonev 2026 ass. nov. subass. *typicum
(for diagnostic species see Suppl. material 1: table S2)

Constant species: *Euphorbia amygdaloides* (93), *Calamagrostis arundinacea* (78), *Picea abies* (73), *Moehringia pendula* (70), *Luzula sylvatica* (61), *Juniperus sibirica* (59), *Festuca penzesii* (59), *Pinus peuce* (54), *Veronica chamaedrys* (50), *Vaccinium myrtillus* (48), *Pinus sylvestris* (48), *Poa nemoralis* (46), *Melampyrum sylvaticum* (46), *Abies alba* (46), *Trifolium medium* (43), *Linum capitatum* (38), *Daphne oleoides* (38), *Carum graecum* (38), *Campanula sparsa* (37), *Galium sylvaticum* subsp. *laconicum* (34), *Hieracium pannosum* (33), *Lilium martagon* (32), *Campanula rapunculoides* (32), *Silene vulgaris* (30), *Polygala major* (30).

Dominant species: *Pinus heldreichii* (90); *Brachypodium sylvaticum* (10).

Holotypus: Relevé number (Online Suppl. material 1: tables S1, S2): 45; Relevé area: 400 m²; Elevation: 2200 m a.s.l.; Slope: 45–50°; Exposition: South; Cover: tree layer: 60%; herbaceous layer: 50%; Latitude, Longitude: 41.835461°N, 23.343766°E; Locality: South slope of Dautov peak; Date: 24. 07. 1997; Author: V. Vulchev. Complete relevé record: Tree layer: *Pinus heldreichii* 5, *Pinus peuce* +, *Picea abies* +, *Abies alba* +. Shrub layer: *Juniperus sibirica* 2b, *Pinus mugo* 2a, *Cytisus eriocarpus* +, *Daphne mezereum* +. Herbaceous layer: *Festuca penzesii* 4, *Moehringia pendula* 2a, *Sesleria coerulans* 1, *Cerastium decalvans* 1, *Cerastium pumilum* 1, *Doronicum austriacum* 1, *Helianthemum nummularium* 1, *Galium pseudoaristatum* 1, *Minuartia verna* 1, *Moneses uniflora* 1, *Poa media* 1, *Sedum album* 1, *Thymus willdenowii* 1, *Anemone ranunculoides* +, *Arabis sudetica* +, *Aremonia agrimonoides* +, *Campanula sparsa* +, *Carduus kernerii* subsp. *scardicus* +, *Cicerbita muralis* +, *Clinopodium alpinum* subsp. *alpinum* +, *Cruciata glabra* +, *Euphorbia amygdaloides* +, *Dianthus petraeus* +, *Fragaria vesca* +, *Galium sylvaticum* subsp. *laconicum* +, *Galium verum* +, *Hieracium murorum* +, *Isopyrum thalictroides* +, *Lamium purpureum* +, *Luzula luzuloides* +, *Luzula sylvatica* +, *Myosotis alpestris* +, *Poa nemoralis* +, *Polygala major* +, *Polystichum lonchitis* +, *Senecio rupestris* +, *Silene vulgaris* +, *Veronica chamaedrys* +.

Structure: *Pinus heldreichii* forests are typically old-growth, with many trees that are one or more centuries old. Almost everywhere in these forests, *Pinus heldreichii* is the dominant species, although *Picea abies*, *Pinus nigra*, and *Pinus sylvestris* are also well represented, and *Pinus peuce* often participates. This indicates that *Pinus peuce* is a less demanding species, both in terms of substrate pH and habitat conditions in general (like light, competitive relationships with other tree species). However, under these drier conditions, it is clearly less competitive than *Pinus heldreichii*, as some former studies (Janković 1960; Janković et al. 1987) ratify. There is no shrub layer. Only *Juniperus sibirica*, *Daphne mezereum*, *Daphne oleoides*, and *Cytisus eriocarpus* are usually represented by single individuals or small groups. The herbaceous layer is represented by both widespread species and typical, even regional endemics. The group of regional endemics is represented by species

such as *Erysimum pirinicum*, *Festuca pirinica*, *Verbascum davidoffi*, *Rhinanthus javorkae*, and *Potentilla apennina* subsp. *stojanovii*. The group of widespread species includes *Calamagrostis arundinacea*, *Brachypodium sylvaticum*, *Dactylis glomerata*, *Geranium macrorrhizum* (forming a variant in wetter places and in depressions between the rocky blocks), *Hieracium murorum*, *Euphorbia amygdaloides*, and *Luzula sylvatica*. Balkan endemics here are *Festuca penzesii*, *Carum graecum*, *Linum capitatum*, and *Galium laconicum*.

Ecology: The communities of the typical subassociation of *Pinus heldreichii* in the Pirin Mts. are found at an elevation between 1700 and 2200 m, but most often between 1800 and 1900 m. Despite this high elevation, their habitats are influenced by the Mediterranean climate, which significantly moderates the harsh local mountain climate (Velchev and Vassilev 1984), and affects their floristic composition. The predominant aspects are east and south. Slopes are most often between 30 and 50 degrees, although sometimes less steep. In the typical subassociation, rendzinas are the main type of soil on which the communities develop (humus-carbonated soils). These soils are characterised by an alkaline or neutral reaction, good drainage and aeration, and a medium to low moisture content. In most cases, they are shallow, with a high skeletal content, well-drained and relatively poor in organic matter as the bedrock is predominantly carbonate, mainly marble. However, relatively thick, rich, and moderately moist rendzinas are not uncommon. At lower elevations and on more favourable terrain, these communities also develop on dark brown forest soils (Mollic Cambisols), which are richer and better moisturised. These communities develop in relatively favourable conditions for forest vegetation, which is why they have a relatively high floristic diversity. The number of species (including mosses and lichens) ranges from 13 to 74, with an average of about 39.

Dynamics: These forests are primary with a comparatively well-preserved structure. They are often located in areas with limited accessibility, most within the boundaries of Pirin National Park. However, in the past, their existence has been associated with human disturbances by burning and logging, which in many places has thinned the tree layer, increasing sunlight exposure and, in turn, the number of light-demanding grass and shrub species, such as *Cytisus eriocarpus*.

Chorology: In the marble part of the Pirin Mts.: circuses of Banski Suhodol, Razlozhki Suhodol, Bayuvi Dupki, Kutelo, Kazana, above Banderitsa hut and Demyanitsa hut, Okadenski Ridge, Byala River, Shiligarnika and Kutechkoto areas.

***Festuco penzesii*-*Pinetum heldreichii* Vulchev ex Nacheva, Bonari, Pachedjieva, Vulchev, Gushev, Shivarov, Ganeva et Tzonev 2026 subass. *seslerietosum coerulantis* subass. nov**

(for diagnostic species see Suppl. material 1: table S2)

Constant species: *Euphorbia amygdaloides* (90), *Calamagrostis arundinacea* (77), *Pinus sylvestris* (47), *Juniperus sibirica* (47), *Daphne oleoides* (47), *Daphne mezereum* (47),

Abies alba (40), *Hieracium murorum* (37), *Dianthus petraeus* (37), *Cytisus eriocarpus* (37), *Helianthemum nummularium* (33).

Dominant species: *Pinus heldreichii* (87), *Pinus nigra* (10), *Festuca penzesii* (10), *Fagus sylvatica* (7).

Holotypus: Relevé number (On-line Suppl. material 1: tables S1, S2): 34, Relevé area: 400 m²; Elevation: 1840 m a.s.l.; Slope: 35°; Exposition: southeast; Cover: tree layer: 30%; shrub layer: 3%; herbaceous layer: 30%; Latitude, Longitude: 41.7737532°N, 23.424854°E; Locality: cirque Kazana; Date: 1984; Authors: V. Velchev and P. Vassilev. Complete relevé record: Tree layer: *Pinus heldreichii* 5. Shrub layer: *Juniperus sibirica* 2a, *Daphne oleoides* 1, *Genista subcapitata* 1. Herbaceous layer: *Festuca penzesii* 4, *Carex kitaibeliana* 3, *Sesleria coerulans* 2b, *Bromopsis riparia* 2a, *Helianthemum canum* 2a, *Alyssoides utriculata* 1, *Aster alpinus* 1, *Brassica jordanoffii* 1, *Calamagrostis arundinacea* 1, *Cyanus acharovii* 1, *Dianthus petraeus* 1, *Drymocallis regisborisii* 1, *Euphorbia seguieriana* 1, *Genista subcapitata* 1, *Globularia cordifolia* 1, *Hieracium olympicum* 1, *Hieracium pannosum* 1, *Jurinea mollis* 1, *Leontopodium nivale* subsp. *nivale* 1, *Linum capitatum* 1, *Onobrychis montana* subsp. *scardica* 1, *Poa macedonica* 1, *Saxifraga ferdinandi-coburgi* 1, *Sedum sediforme* 1, *Silene fabarioides* 1, *Sorbus aria* 1, *Verbascum davidoffii* 1.

Structure: The communities of this syntaxon are often found in the vicinity of the communities of the subassociation *typicum*. However, the main distinguishing feature of these two *Pinus heldreichii* syntaxa is that the communities discussed here have a poorer floristic composition, with an average of about 27 species. Due to the more pronounced xerophytisation, the predominant species are various xerophytic herbaceous plants (including many endemics), which grow in both the sparsely populated forests and in the open rocky and stony areas in the subalpine belt of the Pirin Mts. Such species include *Sesleria coerulans*, *Sesleria acharovii*, *Carum graecum*, *Hieracium olympicum*, *Genista subcapitata*, *Dianthus petraeus*, *Linum capitatum*, and *Festuca penzesii*. There is also no developed shrub layer, although some low shrubs such as *Daphne oleoides*, *Daphne mezereum*, *Juniperus communis*, and *Juniperus sibirica* can be found. Among the trees, *Abies alba* is relatively common, and in some of the communities, *Pinus nigra* may even be dominant. The communities of this subassociation most often transition into the subalpine belt, where they are dominated by old-growth *Pinus heldreichii* trees, some of which are several centuries old or even more. These trees grow either individually or in groups and have a low, highly branched crown.

Ecology: These forests occur at different elevations, but almost half of the relevés are above 1900 metres. The predominant exposure is south and west, on slopes of 30 degrees and more. This indicates that the habitats are less favourable for tree vegetation, with greater rock outcrops, and represent extreme conditions for this type of forest. The soil is poor, with large areas of marble outcrops.

Dynamics: These communities are found in even more inaccessible terrain than the previous ones. Here, the conditions for the development of forest vegetation

are extreme. At their upper elevational limit, they form mixed communities with *Pinus mugo*, which replaces the *Pinus heldreichii* trees when these are destroyed. In lower areas, they can be replaced by *Pinus nigra* forests, which are also drought-resistant but slightly more heat-tolerant than *Pinus heldreichii*.

Chorology: These forests are distributed in the same places as the previous subassociation. However, they are more often found in places with a higher elevation and on steeper and rockier terrain.

Pinus peuce forests

Pinus peuce communities proved to be more uniform in terms of their floristic composition than *Pinus heldreichii* communities. Like *Pinus heldreichii*, *Pinus peuce* is also found on extreme, often rocky terrain; however, its forests are typically boreomontane and very similar in their floristic composition to those of *Pinus sylvestris* and *Picea abies* (see also Horvat et al. 1974). Although the communities in the Pirin Mts. differ floristically and ecologically from those in the Central Balkan Mountains, currently we prefer classifying them at a community level rather than assigning them to any existing association or describing a new association.

Festuca valida-*Pinus peuce* community

(for diagnostic species see Suppl. material 1: table S2)

Constant species: *Calamagrostis arundinacea* (69), *Picea abies* (66), *Euphorbia amygdaloides* (66), *Moehringia pendula* (65), *Luzula sylvatica* (57), *Juniperus sibirica* (56), *Poa nemoralis* (41), *Hieracium murorum* (41), *Fragaria vesca* (40), *Rubus idaeus* (38), *Senecio nemorensis* (37), *Pinus sylvestris* (37).

Dominant species: *Pinus peuce* (90), *Vaccinium myrtillus* (19).

Structure: *Pinus peuce* forests are usually old-growth (above 250 and up to 1000 yr) (Rangelova and Panayotov 2013), with a tree layer reaching heights of around 20–30 metres. The floristic composition of the *Pinus peuce* forests is very similar to that of other boreomontane forests in Bulgaria, such as spruce forests. While this composition can be rich and diverse, it is generally poorer than that of *Pinus heldreichii* forests. The average number of species found in the relevés is 22. *Pinus sylvestris* and *Picea abies* can be found even as co-dominants in the tree layer. In the highest and most thinned areas, *Pinus mugo* may also penetrate from the neighbouring subalpine communities. A developed tall shrub layer is lacking, but *Juniperus sibirica* and *Daphne mezereum* may occur sporadically. The low shrub layer is often dominated by *Vaccinium myrtillus*, particularly in places where there are fewer outcrops of the bedrock. The herbaceous layer is dominated by species that are widespread in this type of mountain coniferous forests, such as *Luzula luzuloides*, *Calamagrostis arundinacea*, *Hieracium murorum*, *Senecio nemorensis*, *Festuca valida*, and *Moehringia pendula*. In more shaded areas, it is also dominated by *Oxalis acetosella* and *Luzula sylvatica*. Several moss and lichen species are also present, particularly in communities with high air humidity.

Ecology: *Pinus peuce* forests in the Pirin Mts. form a separate sub-belt (1800 to 2100 m a.s.l.) within the coniferous belt similar to those in the Rila Mts. (see also Velchev and Russakova 1990). They are ecologically very similar to those of *Pinus sylvestris* and *Picea abies*, but unlike them, they are more adaptable and able to occupy areas with poorer soils and rocky terrain. Barely 10 out of the 68 relevés analysed are located below 1800 m. Most are above 1900 m and just over 2100 m. Terrains are steep, with a predominant slope of 30–45 degrees, and very few slopes below 20 degrees. The predominant exposure is north or east, and to a lesser extent west. Substrates are silicate rocks (granites, granitoids, and gneisses) and the soils are usually shallow Cambic Umbrisols, or Leptic Cambisols in places at lower elevation. In some areas, the soil is relatively well developed and moist. Depending on the exposure, air humidity is relatively high, though it can be low in rare cases, for example in southern exposures.

Dynamics: These forests are indigenous and many of them are over 120 years old. According to Panayotov et al. (2016), there are many trees over 400 years old and some even over 600 years old. In some places they have been replaced by secondary forests of *Betula pendula* and *Populus tremula*.

Chorology: These forests are widespread in the silicate parts of the Pirin Mts., including the area below Bezboğ Peak, the valleys of the Demyanitsa River, Three Rivers, Dessilitza, Kamenititsa Peak, Debeli Ridge area, Yavorov Hut, and Kremenski Chal.

The spatial distribution of the clusters from all three communities is provided in the supplementary material (Suppl. material 2: figure S1).

Multivariate analysis of species composition, plant life forms, and chorotypes

Floristic differentiation between the three clusters was also confirmed by the ordination analysis (Figure 3). The total variation in DCA was equal to 3.97. Along the first DCA axis, which has an eigenvalue of 0.47 and explained variation of 11.8%, the relevés of *Pinus heldreichii* (clusters 1 and 2) are clearly differentiated from the *Pinus peuce* relevés (cluster 3). The EIVs themselves were correlated to varying degrees (Suppl. material 3: table S3). The high values of Spearman's coefficient between soil reaction, temperature, and moisture are a consequence of an underlying intrinsic correlation between these environmental factors. Elevation, slope, and total vegetation cover were not correlated with each other. Taking into account the passively projected environmental variables (Figure 3B) and the differentiation of the classified clusters, the first DCA axis represents a pH gradient that negatively correlates with moisture. The two groups of relevés of the calciphilous *Pinus heldreichii* forests are positioned along the first half of the axis. Cluster 2 (*Festuco penzesii*-*Pinetum heldreichii* subass. *seslerietosum coeruleantis*) is distinguished from the typical subassociation (Cluster 1) by the presence of slightly higher light levels and warmer conditions. This is also confirmed by the occurrence of more light- and heat-tolerant species, such as *Bromopsis riparia*, *Geranium sanguineum*, and *Juniperus communis*. These species are positioned at the very beginning of the first DCA axis (Figure 3B). The relevés of cluster 3 (*Festuca valida*-*Pinus peuce* community) form a more compact group positioned on the right-hand side of the first DCA axis. In terms of the pH and moisture

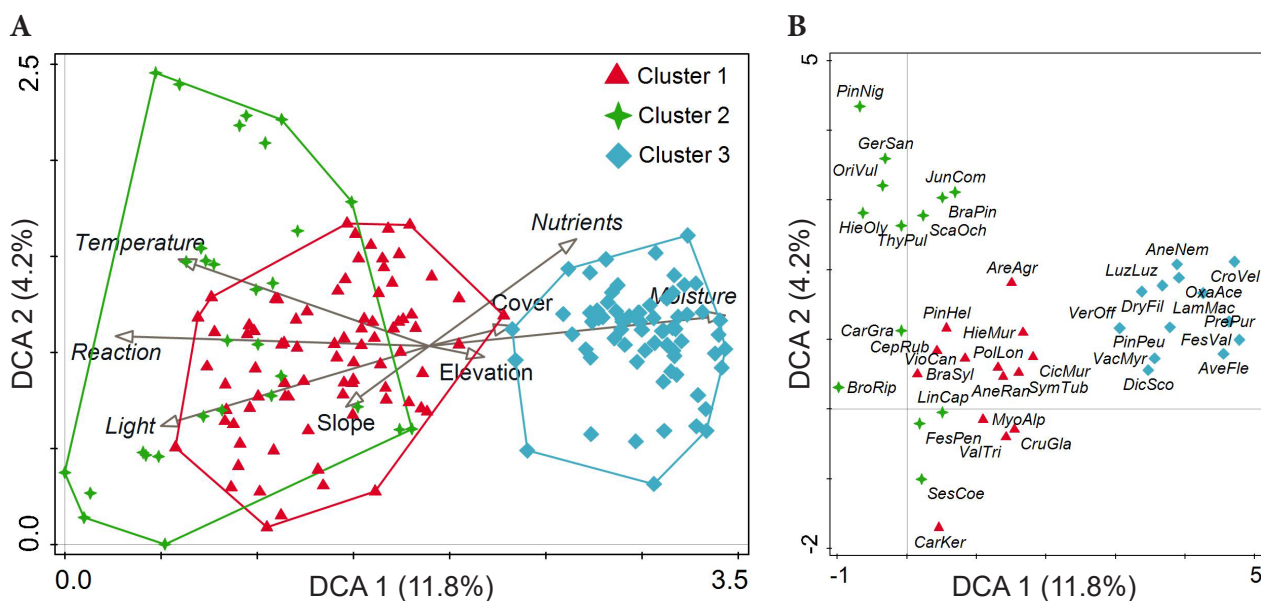


Figure 3. DCA ordination diagrams of clusters (A) and associated diagnostic species (B). Environmental variables are passively projected onto the ordination space. Variables calculated through ecological indicator values are indicated in italics. Only species with fidelity higher than 0.35 are shown on the species scattergram (B). Diagnostic taxa are abbreviated with the first three letters of the genus and species epithets, respectively. Cluster 1: *Festuco penzesii*-*Pinetum heldreichii* subass. *typicum*; Cluster 2: *Festuco penzesii*-*Pinetum heldreichii* subass. *seslerietosum coeruleantis*; Cluster 3: *Festuca valida*-*Pinus peuce* community.

gradients, *Pinus peuce* forests in the Pirin Mts. prefer acidic, moist soils. The diagnostic species of this cluster are also positioned on the right-hand side of the axis and occur under acidic, mesic, and shaded conditions (e.g. *Avenella flexuosa*, *Oxalis acetosella*, *Luzula luzuloides*, *Vaccinium myrtillus*). Both types of forest occur at similar elevations, forming the upper forest belt in the Pirin Mts., as it is evident from the short length of the elevation gradient (Figure 3A).

Relevés and species are scattered along the second DCA axis (with an eigenvalue of 0.167 and a cumulative explained variation of 16.3% together with the first axis), particularly those of *Pinus heldreichii* (clusters 1 and 2). Considering the ordering of species and the passively projected environmental variables, oriented horizontally, it seems that the second axis also represents an ecological gradient related in part to light intensity.

The ecological and phytogeographical specifics of the communities dominated by the two pine species

are well demonstrated by the spectra of plant life forms (Figure 4A) and chorotypes (Figure 4B).

The biological spectra of the studied communities are typical of the coniferous forests in the high mountain regions. Hemicryptophytes are predominant and distributed relatively evenly across the three communities. However, chamaephytes and therophytes are more abundant in the two *Pinus heldreichii* syntaxa, showing that they develop under a more pronounced oromediterranean influence. Conversely, the presence of more phanerophytes and geophytes in the *Pinus peuce* communities reflects their development in a more extreme mountain climate and boreomontane conditions.

Geographically, the Mediterranean and Palearctic geoelements prevail in the two *Pinus heldreichii* communities, while alpine species are most abundant in the second subassociation of *Pinus heldreichii*. In the *Pinus peuce* communities, boreomontane, cosmopolitan, and European species are more prevalent. Interestingly, the

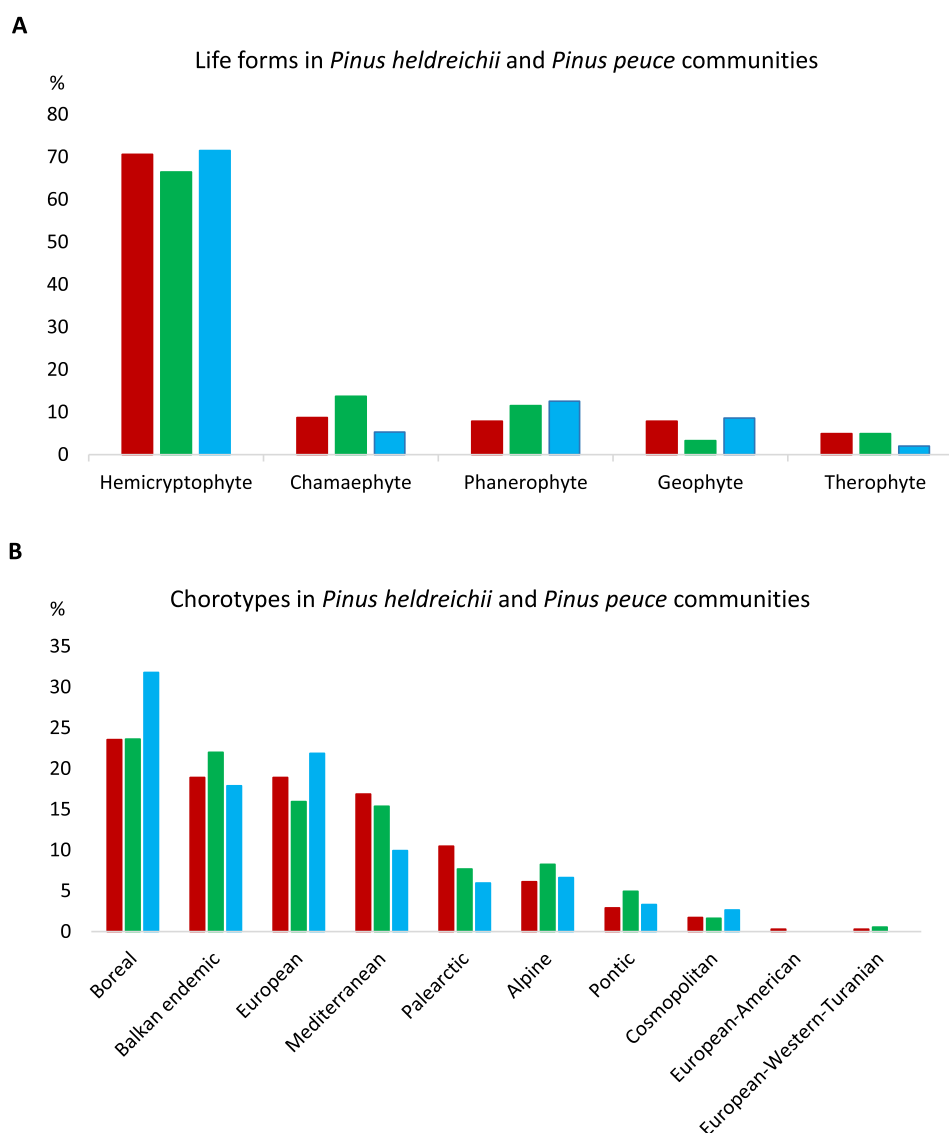


Figure 4. Plant life forms (A) and chorotypes (B) of *Pinus heldreichii* and *Pinus peuce* communities: *Festuco penzesii*-*Pinetum heldreichii* subass. *typicum* (red), *Festuco penzesii*-*Pinetum heldreichii* subass. *seslerietosum coerulantis* (green), *Festuca valida*-*Pinus peuce* community (blue).

presence of Balkan endemics and subendemics is relatively equal in both community types, but those in *Pinus heldreichii* forests are predominantly regional and local endemics, whereas those in *Pinus peuce* forests are mainly subendemics.

Discussion

The communities of both *Pinus heldreichii* and *Pinus peuce* have been studied across their entire geographic range, with the possible exception of Albania. According to Kalajnxhiu et al. (2011), the mixed *Pinus heldreichii* forests identified in Central Albania are syntaxonomically closer to *Fagetalia* than to *Pinion heldreichii*.

Several *Pinus heldreichii* forest associations have been described from the Western Balkans, including Kosovo, Montenegro, and Bosnia and Herzegovina, reflecting the specific ecological and floristic characteristics of these forests and the authors' tendency to describe numerous small-range associations isolated in different mountain ranges and even within them. Dinić and Janković (2006a) provided a comprehensive overview of the existing associations for both Serbia and Kosovo. They are primarily found in the Metohian sector of the Prokletije Mountains. The primary association is *Pinetum heldreichii* Janković 1958 (Janković 1958; Blečić 1959), characterised by a well-developed shrub layer, comprising species that are absent from the Pirin Mts., such as *Rhamnus alpinus* subsp. *fallax*, *Cotoneaster integerrimus*, and *Lonicera alpigena*. There are also differences in the herbaceous layer due to the lower elevation and a more pronounced Mediterranean climatic influence in the Prokletije Mountains compared to the Pirin Mts. In addition to the *Pinetum heldreichii*, other forest associations of this species with restricted distributions have been described from the mountains of Kosovo and Metohija: *Helleboro purpurascens-Pinetum heldreichii* Janković 1958; *Thalictrum aquilegifolium-Pinetum heldreichii* Janković 1958; *Genista radiata-Pinetum heldreichii* Janković 1958; *Rhamnus fallacis-Pinetum heldreichii* Janković et D. Pavlović-Muratpahić 2003; *Sesleria autumnalis-Pinetum heldreichii* Jank. et R. Bog. 1962; and *Fago moesiaca-Pinetum heldreichii* Janković 1958. One association, *Junipero oxycedri-Pinetum heldreichii* Blečić et Tatić 1960, was described from serpentinite outcrops on Mt. Ostrovica (Blečić and Tatić 1960) and is floristically distinguished by acidophilic species such as *Bruckenthalia spiculifolia*, *Avenella flexuosa*, *Luzula sylvatica*, as well as serpentinophytes, such as *Bornmuellera dieckii*. Dinić and Janković's (2006a) attempts to revise some of these associations have proven unsuccessful, as these associations were once again not typified in accordance with the rules of the ICPN (Theurillat et al. 2021). In addition, *Pinetum heldreichii mediterraneo-montanum* and *Pinetum heldreichii continentale* reported for the Sitovo and Bjelasica Mountains in Montenegro (Blečić and Lakušić 1969) were named with illegitimate epithets (Art. 34). Nevertheless, their floris-

tic composition differs markedly from that of the Pirin Mts stands. Several other associations from the Western Balkans are: *Fritillario-Pinetum heldreichii* and *Peucedano-Pinetum heldreichii* from Bosnia and Herzegovina (Janković 1965, 1967), and *Amphoricarpo-Pinetum leucodermis*, *Pinetum nigro-heldreichii*, *Senecioni-Pinetum leucodermis*, and *Mugheto-Pinetum leucodermis* from the Prenj Mts. in Montenegro (Fukarek 1966). All these communities are characterised by their occurrence at lower elevations (1500–1700 m) and their strong exposure to the influence of the Mediterranean climate. Consequently, their flora contains many thermophilic calcicolous species, some of which are regional endemics to the Western Balkans (Dinaric Alps range). The nomenclatural validity of many of these associations is questionable.

Pinus heldreichii is also distributed across Greece, particularly in the northern Pindus Mountain range, the Olympus Mts., Orvilos, Vermio, and Vourino Mts. (Fukarek 1949b; Caudullo et al. 2017). Its communities have been studied in the Pindus and Olympus mountains (Barbero and Quézel 1976; Habeck and Reif 1994; Xystrakis et al. 2006), where *Pinus heldreichii* often occurs as scattered individuals, groups of old trees, or low, creeping krummholz-like forms within shrub and grassland communities. These individuals most commonly occur in subalpine communities with *Buxus sempervirens*, *Bornmuellera tymphaea*, and *Genista radiata*, which may locally develop into small *Pinus heldreichii* forest stands. On Mt Olympus, Habeck and Reif (1994) assigned some *Pinus heldreichii* communities to *Fagetalia* and others to *Pinion peuces*, although the occurrence of subalpine species such as *Sesleria korabensis* complicates their syntaxonomic interpretation. Similarly, Barbero and Quézel (1976) noted the presence of many *Vaccinio-Piceetea* species in the Pindus communities; nevertheless, the oromediterranean *Pinus heldreichii* communities in Greece differ markedly, both ecologically and floristically, from those in the Pirin Mts.

Finally, *Pinus heldreichii* communities in the Apennines are restricted to Monte Pollino and adjacent areas. Two associations have been described: *Pino leucodermis-Juniperetum alpinae* Stanisci 1997, representing shrub communities and assigned to *Daphno oleoidis-Juniperion alpinae* Stanisci 1997 (Stanisci 1997), and *Sorbo graecae-Pinetum leucodermis* Maiorca et Spampinato 1999, a forest association occurring on rocky terrains at 1000–1600 m a.s.l. (Maiorca and Spampinato 1999). Although the latter was originally placed in *Daphno oleoidis-Juniperion alpinae*, recent studies assign it to *Pinion heldreichii* (Preislerová et al. 2024).

As previously mentioned, the distribution of *Pinus peuce* communities is more limited in the Balkans, with occurrences documented in Montenegro, Kosovo, North Macedonia, and Albania. A review of the available literature reveals the absence of phytosociological information from Albania, except for the unpublished doctoral dissertation of Vangjeli (1982), cited by Ruci et al. (2001). Therefore, the association *Pinetum peuco-leucodermis* Vangjeli 1982 has not been effectively published.

In Bulgaria, the association *Adenostylo alliariae*-*Pinetum peuces* Nikolov et Dimitrov 2015 has been described in the Central Stara Planina Mountains. Many of its species are common to *Pinus peuce* forests in the Pirin and Rila Mountains. A notable feature, however, is the presence of a core of more moisture-demanding species, such as *Adenostyles alliariae*, *Cirsium appendiculatum*, *Heraclium verticillatum*, *Veronica beccabunga*, *Stellaria nemorum*, *Gymnocarpium dryopteris*, and *Dryopteris dilatata*. These species suggest that these communities develop under more mesophilic conditions on the northern slopes of the mountains, likely in the presence of small streams and springs. Additionally, the Central Stara Planina Mountains represent the northeasternmost extent of the *Pinus peuce* range, where the influence of the Mediterranean climate is absent. The disturbance in these relatively young communities is more pronounced due to past human activity.

In the western Balkan region, the syntaxonomic treatment of *Pinus peuce* followed an approach similar to that applied to *Pinus heldreichii*. Several associations have been documented as limited to certain mountain ranges or parts of them (Dinić and Janković 2006b). These include the associations: *Wulfenio carinthiacae*-*Pinetum peuces* Blečić et Tatić 1957, which is actually described as *Pinetum peucis montenegrinum* (Blečić and Tatić 1957) in the Montenegrin part of the Prokletije Mts.; *Pinetum peucis typicum* Janković 1959 (Janković 1960) in Metohija; and *Ajugo pyramidalis*-*Pinetum peuces* and *Rhododendro ferruginei*-*Pinetum peuces*, both found in the Šar Mts. (Janković and Bogojević 1962). Two additional associations, *Gentiano luteae*-*Pinetum peuces* Em 1962 and *Digitali viridiflorae*-*Pinetum peuces* Em 1962, were described from the Pelister Mts. in North Macedonia, although both were published only with synoptic tables (Em 1962; Em and Džekov 1970). Finally, *Pinetum heldreichii-peuces scardicum* Stevanović et al. 1994 was reported from the Gine Vode area of the Šar Mts. as a *Pinus peuce* association with substantial participation of *Pinus heldreichii*, occurring on serpentinite bedrock with carbonate inclusions (Stevanović et al. 1994). Despite the presence of several neutrophilous species, including endemics such as *Sesleria latifolia* and *Linum capitatum*, the floristic composition is dominated by widely distributed acidophilous taxa characteristic of *Pinus peuce* associations.

The aforementioned *Pinus peuce* associations are differentiated by certain diagnostic species which in part are widespread Balkan endemics. Examples include *Wulfenia carinthiaca*, *Geum montanum*, *Ajuga pyramidalis*, *Briza media*, *Platanthera bifolia*, *Rhododendron ferrugineum*, *Gentiana punctata*, *Gentiana lutea*, *Lilium albanicum*, *Lilium carnioolicum*, *Saxifraga rotundifolia*, *Sorbus aucuparia*, *Digitalis viridiflora*, and *Helleborus cyclophyllus*. However, the most widespread and even dominant species belong to a group typical to the boreomontane coniferous forests of the Balkans, including *Vaccinium myrtillus*, *Picea abies*, *Daphne mezereum*, *Juniperus sibirica*, *Arenaria agrimonoides*, *Anemone nemorosa*, *Euphorbia amygdaloides*, *Hieracium murorum*, *Veronica chamaedrys*,

Veronica officinalis, *Galium rotundifolium*, *Homogyne alpina*, *Oxalis acetosella*, *Symphytum tuberosum*, *Crocus veluchensis*, *Luzula luzuloides*, *Luzula sylvatica*, *Senecio nemorensis*, and *Prenanthes purpurea*. These taxa are also found in *Pinus peuce* communities in Bulgaria, including those in the Rila, Pirin, and Stara Planina Mts. This suggests that, despite the presence of certain differential species, all *Pinus peuce* communities throughout the Balkans are generally highly homogeneous, particularly regarding their dominant and constant taxa. Therefore, the syntaxonomic independence of many of these associations is debatable, and for this reason we prefer to consider the *Pinus peuce* forests of the Pirin Mts. at the broader vegetation-type level. A comprehensive future review of all previously described associations in the Balkans is necessary to determine their syntaxonomic status. Based on current knowledge, these forests are more likely to represent a single broadly defined association, probably including several subassociations distributed across different mountain ranges of the Balkans.

Consequently, it can be concluded that *Pinus heldreichii* forests exhibit greater diversity due to their more open structure, particularly within the higher mountain belt. This enables the entry of various representatives of subalpine and alpine flora, particularly on limestone substrates, which are characterised by a higher concentration of endemic species. In contrast, *Pinus peuce* forests are distinguished by a more homogeneous floristic composition, with most of the species exhibiting a broad distribution in the boreomontane forests, such as those dominated by *Picea abies* and *Pinus sylvestris*. Despite the differences, these two types of communities have some significant similarities. In parts of the southwestern Balkan Mountain belt (Šar, Prokletije, Korab, and adjacent Albanian mountains), both species co-occur and may form mixed communities, although the available studies indicate that most of their stands are clearly delineated (Fukarek 1949a, 1949b; Stevanović et al. 1994; Dinić and Janković 2006a, 2006b). A similar pattern is observed in the Pirin Mts., where the two species co-occur only in the eastern part of their distributional overlap. However, as previous studies have shown (Dinić and Janković 2006a, 2006b; Velchev and Vassilev 1984; Velchev and Russakova 1990), and what we also revealed in the present study, *Pinus peuce* is more frequently found in *Pinus heldreichii* dominated forests than vice versa. The differentiation of their communities is primarily driven by their position along distinct ecological gradients. As Janković (1960) emphasised, their dependence on soil pH is conditional. Although *Pinus peuce* communities are associated with silicate substrates, whereas *Pinus heldreichii* forests occur on carbonate and serpentinite substrates, this pattern appears to reflect rock physical properties related to soil structure and composition, rather than chemical composition alone. Calcareous and serpentinite substrates are significantly drier, whereas silicate substrates are more humid, due to their capacity to retain water over longer periods. Both species can establish on different substrates. *Pinus peuce* occurs in

some stands on carbonates and can even form independent communities. However, its floristic structure differs from that of communities on silicate terrains (Janković 1960; Mandžukovski et al. 2022). According to Janković et al. (1987), *Pinus heldreichii* transpires at a rate 2.5 times lower than *Pinus peuce* (0.898 versus 2.547 mg/g/min). The water content of the needles is also lower (55% versus 58%), and the osmotic pressure is significantly higher (20–22 bars versus 12–15 bars). Thus, *Pinus heldreichii* has an advantage in dry, sunny stands, while *Pinus peuce* has an advantage in more humid and shaded habitats. *Pinus heldreichii* is clearly more heliophilous than *Pinus peuce* (Janković 1960) and therefore regenerates poorly on silicate terrains, especially on northern slopes, where the low shrubs and grasses develop more rapidly due to higher humidity. A dendrochronological study from Bulgaria (Ivanova et al. 2013) show that over the same period, *Pinus heldreichii* produces more wood cells than *Pinus peuce*, particularly during warmer winters.

Indirect evidence from paleobotany and palynology may help clarify the origin and formation of *Pinus heldreichii* and *Pinus peuce* communities in the Pirin Mts. *Pinus peuce* has been present in Bulgaria since the Middle Miocene (Bozukov et al. 2018). Prior to the last glacial period, this species was more widespread across Europe, particularly during interglacial periods. Fossil female cones and seeds, approximately 780,000 years old, have been found in the Pianico basin in the Italian Pre-Alps (Pini et al. 2014). The Holocene history of *Pinus peuce* in the Pirin Mts. is relatively well studied (Tonkov 2021, 2024). Its pollen belongs to the so-called *Pinus haploxylon* type, which can be clearly distinguished from the *Pinus diploxylon* type, which encompasses all other representatives of the genus in Bulgaria, including *Pinus heldreichii*, and their pollen is practically indistinguishable (Beug 2004). Palynological evidence summarised by Tonkov (2021, 2024) suggests that both *Pinus peuce* and probably *Pinus heldreichii* persisted in lower elevation refugia in the Pirin Mts. after the last glacial period and were subsequently shaped by long-term Holocene forest dynamics (their increase started after 7800 cal. yr BP) and later anthropogenic disturbance. The history of forest vegetation in the Pirin Mts. suggests that *Pinus peuce* and *Pinus heldreichii* repeatedly contracted and expanded their ranges in parallel in response to climatic changes, while occupying different ecological niches without clear evidence of direct competition. Similar range dynamics probably also occurred in other Balkan mountain ranges, where both species had coexisted since before the Ice Age. Based on the studies cited above, competitive interactions appear to be stronger between *Pinus peuce* and *Picea abies* (Kolev and Dimitrov 2022), and between *Pinus heldreichii* and *Pinus nigra*, than between *Pinus peuce* and *Pinus heldreichii*, despite their partial ecological overlaps.

The role of *Pinus heldreichii* as a community-forming species has been questioned because its stands are generally open and frequently form vegetation complexes with surrounding shrublands and grasslands (Fukarek 1966;

Barbero and Quézel 1976; Xystrakis et al. 2006). However, *Pinus* species are commonly regarded as community-forming trees and can support well-defined plant communities even under open-canopy conditions (Bonari et al. 2021; Ciaramella et al. 2024; Costa et al. 2025). They even emphasise that it is more likely to be found in high-mountain shrub and grassland habitats than to form its own communities. Forests dominated by this species appear to lack good diagnostic species largely because of the predominance of herbaceous plants and low shrubs that are typical of the rocky, subalpine, and alpine grassland and low-shrub communities in the vicinity. This interpretation may be applicable within certain parts of the species' range, particularly where *Pinus heldreichii* behaves as a pioneer species. However, the floristic composition and ecological characteristics of the communities, and the Holocene dynamics of the species indicate that it forms communities at the upper forest boundary, which are therefore highly transitional in some areas. Still, both *Pinus peuce* and *Pinus heldreichii* possess sufficient characteristics to be regarded as dominant species in forest communities with their own floristic composition, ecology and history, although this dominance is not uniform everywhere throughout the forests.

Conclusions

Based on data on the ecological characteristics, floristic structure, and evolutionary history of *Pinus peuce* and *Pinus heldreichii* forests in the Balkans, it can be concluded that their communities represent forest vegetation with a high degree of uniqueness. Both types of communities develop under harsh conditions, at the upper forest boundary. However, the differences between them are significant enough to place them in separate vegetation classes: *Vaccinio-Piceetea* and *Erico-Pinetea*, respectively. The *Pinus heldreichii* communities essentially represent more thermophilous forest vegetation on limestone rock in a mild mountain climate. In contrast, the *Pinus peuce* communities are located at the upper limit of the boreo-montane vegetation, but on moist, more nutrient-rich soils on silicate rock. The *Pinus heldreichii* and *Pinus peuce* communities in the Pirin Mts. have a very high conservation value. In the past, however, these forests have often been degraded due to anthropogenic and natural disturbances, such as avalanches and several large-scale fires, to which *Pinus heldreichii* is more resistant thanks to its thick bark. While *Pinus peuce* stands were mainly subject to natural disturbances, those of *Pinus heldreichii* were subject to large-scale logging after 1912. To protect them, part of these communities was included in the established Bayuvi Dupki Natural Reserve back in 1934, which later became the basis for the establishment of Pirin National Park. Currently, the most representative forest communities of *Pinus peuce* and *Pinus heldreichii* lie within the boundaries of Pirin National Park and the Bayuvi Dupki-Dzhindzhirtsitsa Natural Reserve.

They are also protected as a natural habitat (95A0 High oro-Mediterranean pine forests) within the Natura 2000 site BG0000209 Pirin. Nevertheless, their location at the upper forest boundary, an area that is highly sensitive to climate change, and their unique ecology, pose a scientific and practical challenge to their future conservation.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

The Editor-in-Chief, a co-author of this manuscript, was excluded from all editorial handling and decision-making related to this submission.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.

No AI tools were used in the preparation of this manuscript.

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Author contributions

VN, RTz, VV, and KP designed and conducted the survey; RTz, ChG, VV, AG, and VSh identified the vascular plant, moss and liverwort and lichen specimens; VN, RTz, GB, and KP wrote the manuscript. All authors contributed to the manuscript and approved the final submission.

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Data availability

The data used in this article are accessible through the CircumMed Vegetation Database (GIVD Code: EU-00026).

Supplementary material 1

Suppl. tables S1, S2

Authors: Veradina Nacheva

Data type: xlsx

Explanation note: **table S1**: Header data of relevés used in the study and **table S2**: Complete relevé records.

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Link: <https://doi.org/10.3897/ved.199011.suppl1>

Supplementary material 2

Suppl. figure S1

Authors: Veradina Nacheva

Data type: docx

Explanation note: Map of the study area in the Pirin Mts. with indicated clusters.

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Link: <https://doi.org/10.3897/ved.199011.suppl2>

Supplementary material 3

Suppl. table S3

Authors: Kalina Pachedjieva

Data type: docx

Explanation note: Spearman correlation coefficients between ecological indicator values (EIVs) and elevation, slope, and total vegetation cover.

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Supplementary material 4

Suppl. figure S2

Authors: Veradina Nacheva

Data type: docx

Explanation note: Photographs of *Festuco penzesii*-*Pinetum heldreichii* subass. *typicum* (A), *Festuco penzesii*-*Pinetum heldreichii* subass. *seslerietosum coerulantis* (B) and *Festuca valida*-*Pinus peuce* community (C) forests in Pirin Mts.

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