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Phytosociological Analysis of Natural and Artificial Pine Forests of the Class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939 in the Sudetes and Their Foreland (Bohemian Massif, Central Europe)

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Abstract: Research Highlights: Differentiation of Scots pine forests of the class *Vaccinio-Piceetea* in Poland has been the subject of numerous studies, including revisions. Despite that, the area of southwestern Poland was hitherto practically unexplored in this respect. Background and Objectives: The aim of this work was therefore (i) to present the diversity of the pine forests in the Sudetes and their foreland; (ii) to compare the ecology of studied communities. Materials and Methods: We analyzed 175 phytosociological relevés collected between 1991 and 2020 in natural and anthropogenic pine stands. To identify vegetation types, we used the modified TWINSpan algorithm; principal coordinate analysis, distance-based redundancy analysis and permutational tests were applied to identify the variation explained and the main environmental gradients shaping the studied plant communities. Results: Five associations were distinguished: thermophilous *Asplenio cuneifolii-Pinetum sylvestris* Pišta ex Husová in Husová et al. 2002, which develops on shallow soils over ultrabasic substrates, *Hieracio pallidi-Pinetum sylvestris* Stöcker 1965, which prefers outcrops of acidic rocks; *Betulo carpaticae-Pinetum sylvestris* Mikyška 1970, which is relict in origin and occurs on the upper Cretaceous sandstones, the peatland pine–birch forests of the *Vaccinio uliginosi-Betuletum pubescentis* Libbert 1933 and the *Vaccinio myrtilli-Pinetum sylvestris* Juraszek 1928. Moreover, community *Brachypodium sylvaticum-Pinus sylvestris* with the occurrence of many thermophilous and basiphilous species was also found on limestone substratum. The analysis of the species composition of pine plantations established on deciduous and mixed forests habitats revealed that these anthropogenic communities were marked by a random combination of species in which a certain group of common forest generalists participated. The distinguished communities differed clearly among each other also in habitat characteristics. Particularly important for their differentiation were soil reaction and nutrients, supported by differences in moisture, temperature and light availability. Apart from the edaphic factors, altitude and the bedrock type proved to be equally important. Conclusions: Our study provides new remarks to the typology and synecology of pine forest communities in SW Poland.

Keywords: *Pinus sylvestris*; forest plantations; *Dicrano-Pinion sylvestris*; *Vaccinio uliginosi-Pinion sylvestris*; vegetation classification; syntaxonomy; synecology



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1. Introduction

The history of research on pine forests in Poland dates back to the 1930s of the previous century [1]. However, more intensive investigations began at the turn of the 1950s and 1960s [2–4], and they continue today. Over the last seventy years, there have been several revisions on the national scale relating both to the phytosociological diversity of pine forests [5–8] and the main changes they undergo [9]. However, it should be emphasized

that the data underlying the abovementioned studies were mostly from lowland areas; therefore, they could not capture the full diversity of pine forest stands in the Sudetes mountains and their foreland. According to these studies [7,8], in the Sudetes and their foreland there are only three associations within pine forests of the *Dicrano-Pinion sylvestris* (Libbert 1933) W. Mat. 1962 alliance: mesic *Leucobryo-Pinetum* W. Mat. (1962) 1973, dry *Cladonio-Pinetum* Juraszek 1927 and moist *Molinio caeruleae-Pinetum* W. Mat. & J. Mat. 1973. The rocky *Betulo carpaticae-Pinetum* Mikyška 1970 association has also been described [10], but so far the concept of its distinction has not been accepted either in the Czech [11] or Polish phytosociological literature [7,8].

Although the first studies on phytosociological differentiation of the Sudetic pine forests date back to the late 1960s [12], over the next 60 years only 50 relevés were published from this area—including mixed pine forests and pine plantations [13–16]. Moreover, pine forest communities were distinguished only on a local scale, usually within nature reserves or at most a single microregion (i.e., a mountain range) and described syntaxa were adopted from national revisions without critical assessment. As the consequence, almost all phytosociological material from this area was included in the collective association *Leucobryo-Pinetum*, even when it represented monocultures and as such did not provide comprehensive information on the real range and diversity of these communities in the Sudetes mountains and their foreland.

The situation may have changed with both the emergence of new analytical tools based on numerical methods and the access to international databases allowing direct comparisons of communities from different geographical regions [17,18]. Consequently, traditional classification systems of forest communities in Central Europe have started to modify quickly, and many of the syntaxonomic units described from individual countries have been downgraded or renamed to synonyms, e.g., [19–22]. The final framework for the division into higher units (up to the level of alliance) is provided by the study of Mucina et al. [23], to which the national classification systems should be gradually adapted. This whole process created a space where the new approach could be implemented not only in the data analyses but also in the interpretation of the results from a broader—international—perspective.

Based on the current state of knowledge, it is obvious that the diversity of pine forests in SW Poland is insufficiently recognized. The aim of this work is therefore (i) to present the diversity of the *Vaccinio-Piceetea* pine forests in the Sudetes and their foreland; (ii) to compare the ecology of studied communities.

2. Materials and Methods

2.1. Study Area

Our research was conducted on the whole area of the Sudetes—mountain range in Southwestern Poland—and their foreland (Figure 1). The study area is the part of the Bohemian Massif—a geological unit covering a large part of the Czech Republic and parts of Austria, Germany and Poland. The massif is built of crystalline rocks—Paleozoic and Precambrian in origin which were deformed during the Variscan Orogeny and then covered by younger layers of Cretaceous sandstone with numerous remnants of Miocene volcanic activity. The part of the Bohemian Massif on the Polish side which embraces the Sudetes mountains and their foreland is characterized by varied geological structure and diverse relief forms [24]. It extends from the gentle hills in the north, which are covered by a thick layer of postglacial loess, through isolated hills of the Ślęza ophiolite massif up to the Sudetes mountains with steep slopes, isolated rocks and deep river valleys in the south. The altitude span varies from 120 m a.s.l. in the north to 1602 m. a.s.l. reaching the highest summit of the Sudetes mountains—Śnieżka Mt. It is worth mentioning here that pine forests occur up to 910 m a.s.l. Among the most common soil types connected with the studied communities are podzols, cambisols and rankers. The average annual temperature varies from 8.7 °C in the north to 0.6 °C for the top of Śnieżka Mt. The average annual

rainfall varies from ca 600 mm in the foreland up to 1370 mm in the highest parts of the mountains [24].

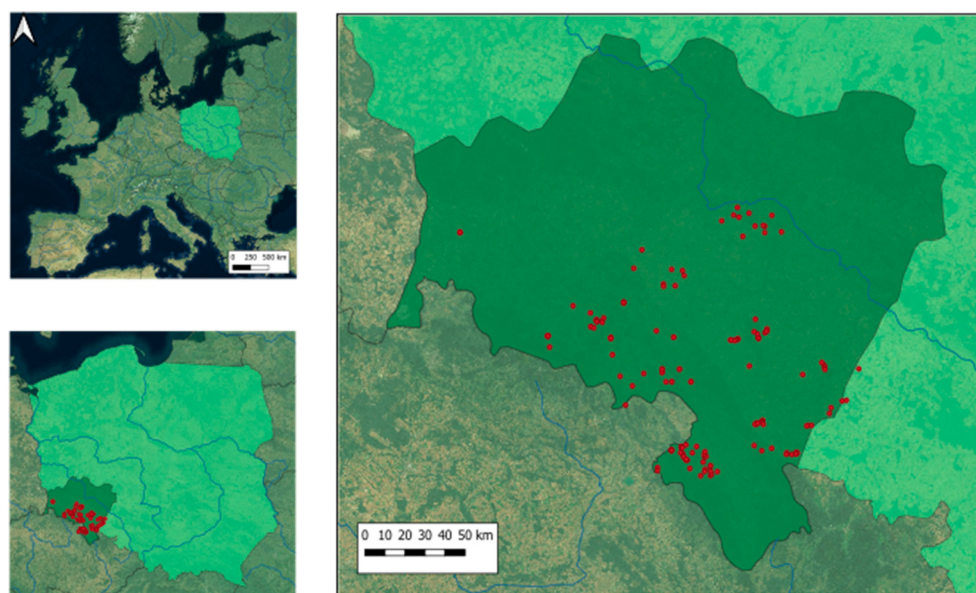


Figure 1. Area of investigation. Red dots represent analyzed relevés of the Scots pine forest in SW Poland.

2.2. Field Sampling

Vegetation composition was sampled by using phytosociological relevés according to the Braun-Blanquet approach [25]. Field sampling was conducted from 1991 to 2020. We focused on not only potentially natural pine forests (rock outcrops, peat bogs), but also anthropogenic stands. Collected data originated from the stands where Scots pine's cover reached more than 25% in the tree layer. The relevés area ranged from 25 square m up to 400 square m (on flat stands and within floristically homogenous plots). The inclusion of relevés of less than 100 square m to document the full variability of *Pinus sylvestris* L. communities was necessary because most of the sites within hard-to-reach places on rock ledges and pinnacle rocks have an area of 25–50 square meters. Excluding them from the analysis would mean omitting a key part of ecological and phytosociological diversity of the studied communities.

2.3. Environmental Variables

In order to identify ecological conditions of the pine forests within the study area, different environmental variables were analyzed. Altitude (measured in m a.s.l. and divided by 1000 to standardize value), heat load [26] and bedrock type were used as explanatory variables. The bedrock type at each site was obtained from a Detailed Geological Map of the Sudetes mountains. (Polish Geological Institute, National Research Institute, <http://sudety.pgi.gov.pl/>). Based on the criterion of mineral composition and major geological processes [27], nine categories of rocks were proposed as explanatory variables: Quaternary deposits (sands, clays and gravels), Quaternary peat bogs, serpentines, limestones, metamorphic rocks (gneisses, schists, mud- and claystones, greywackes, Paleozoic conglomerates), granitoids, trachytes and two kinds of sandstones—very different in terms of their properties. The first one labelled as Upper Jointed Sandstone of Late Turonian/Coniacian age [28] is subjected to very slow weathering processes; therefore, only initial podzols derive from it. The second one labelled as Lower Jointed Sandstone (Coenomanian/early Turonian) has got structures that are more prone to weathering; thus, deeper podzols and even cambisols derive from it. Heat load index (HL), is a direct measure of incident radiation calculated from slope inclination, aspect and latitude [26].

As there were no direct measurements of light and soil condition Ellenberg indicator values (EIVs) [29], corrected by datasets of Berg et al. [30] with reference to values of continentality were used. EIVs weighted by percentage species' cover were calculated for each relevé using the JUICE software [31].

2.4. Phytosociological Analysis

Occurrences of the same woody species in different vertical layers were merged using the procedure implemented in JUICE—under the assumption that the overlap of layers is random [31,32]. Plant nomenclature follows Euro+Med PlantBase [33] for vascular plants and Ochrya et al. [34] and Fałtynowicz [35] for bryophytes and lichens, respectively. The nomenclature of phytosociological alliances and classes is in accordance with Mucina et al. [23].

The vegetation types were identified using a modified TWINSpan algorithm [36] with Total Inertia measure of heterogeneity using JUICE software [37]. The obtained number of clusters coincided with the results of crispness analysis [38], suggesting the division of relevés into nine groups.

Diagnostic species were determined using the Φ coefficient as a measure of fidelity for clusters of equalized size [39–41]. Species with $\Phi \geq 20$ (0.10×100), constancy $\geq 20\%$, constancy ratio [42] higher than 1.5 and significant concentration in a particular cluster, tested by the Fisher's exact test ($p < 0.05$), were considered to be diagnostic. A species was considered diagnostic for more than one cluster with the $\Phi > 20$ (0.2×100) in at least two clusters, regardless of the constancy ratio. Species with constancy ratio < 1.5 and $\Phi > 20$ in only one cluster were not considered diagnostic. Constant species were defined as species with frequency of at least 60% in a cluster. Distribution maps of the recognized clusters were prepared using DMAP software [43].

2.5. Ecological Analysis

Principal coordinate analysis (PCoA) [44] was performed both to explore differentiation of recognized clusters and check the percentage of variation explained. Matrix of distance (175×175) was calculated using Sorensen distance and square-root species cover transformation. Distribution of the sample groups on PCoA diagram was visualized and interpreted.

To identify the statistical significance of correlations (using Spearman's coefficient) between the PCoA sample scores obtained from CANOCO and mean randomized EIVs for relevés a modified permutation test with 499 unrestricted permutations was conducted. The test was performed with *MoPeT_v1.2.r* script [45] in R software [46]. Permutational analysis of variance (one-way ANOVA on the mean randomized EIVs) and modified permutation test (with 499 unrestricted permutations) were also calculated using *MoPeT_v1.2.r* [45], to determine which EIVs differentiate the selected communities. Using permutation ANOVA is an alternative to other tests under non-normal conditions, because it does not operate under the assumption of normality and uses actual scores [47].

Distance-based redundancy analysis (db-RDA) embedded in CANOCO 5.0 [44], with Sorensen distance and square-root species transformation, was implemented to check the main ecological drivers affecting the diversity of distinct groups, and variation explained [48]. A standard Monte Carlo permutation test with 499 unrestricted permutations under the full model was conducted to identify the significance of the simple term and conditional effects of environmental variables (such as altitude, heat load and bedrock type) on the species composition of the analyzed samples [44]. The conditional effect expresses the variation explained by a single explanatory variable, whereas the others are used as covariables. The simple effect expresses the variation explained by the single explanatory variable without covariables.

3. Results

In the analyzed material we distinguished nine groups of Scots pine forests (both natural and semi-natural, and planted, Table 1, Figures 2 and 3), clearly different from each other in terms of the species composition and main ecological indicators (Tables 2 and 3, Figures 4 and 5).

3.1. Natural Or Semi-Natural Communities

Among the analyzed material, six groups (clusters) of the relevés represent natural or semi-natural phytocoenoses, possible for phytosociological identification, even if some of their patches are anthropogenic in character. The identified phytocoenoses can be arranged according to the following syntaxonomic classification.

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

Ordo *Pinetalia sylvestris* Oberd. 1957.

All. *Dicrano-Pinion sylvestris* (Libbert 1933) W. Matuszkiewicz 1962 nom. conserv. propos

1. Community *Brachypodium pinnatum*-*Pinus sylvestris* prov.
2. *Asplenio cuneifolii*-*Pinetum sylvestris* Pišta ex Husová in Husová et al. 2002.
3. *Hieracio pallidi*-*Pinetum sylvestris* Stöcker 1965.
4. *Vaccinio myrtilli*-*Pinetum sylvestris* Juraszek 1928.
5. *Betulo carpaticae*-*Pinetum sylvestris* Mikyška 1970.

Ordo *Vaccinio uliginosi*-*Pinetalia sylvestris* Passarge 1968.

All. *Vaccinio uliginosi*-*Pinion sylvestris* Passarge 1968.

6. *Vaccinio uliginosi*-*Betuletum pubescentis* Libbert 1933.

Non-hierarchical phytocenons (artificial forest) within *Pinetalia sylvestris* Oberd. 1957

7. Comm. *Pinus sylvestris*-*Impatiens parviflora*.
8. Comm. *Pinus sylvestris*-*Prunus serotina*.
9. Comm. *Pinus sylvestris*-*Molinia caerulea*.

Cluster 1—community *Brachypodium pinnatum*-*Pinus sylvestris* (non *Brachypodio pinnati*-*Pinus sylvestris* Michalko 1980)

Number of relevés: 5

Diagnostic species: *Anthyllis vulneraria*, *Brachypodium pinnatum*, *Campanula rotundifolia*, *Carlina vulgaris*, *Centaurea jacea*, *Ceratodon purpureus*, *Cornus sanguinea*, *Encalypta streptocarpa*, *Epipactis atrorubens*, *Euphorbia cyparissias*, *Fragaria viridis*, *Frangula alnus*, *Galium album*, *Hieracium murorum*, *H. vulgatum*, *Leontodon autumnalis*, *Leucanthemum vulgare*, *Lotus corniculatus*, *Origanum vulgare*, *Pimpinella saxifraga*, *Poa compressa*, *Potentilla tabernaemontani*, *Salix caprea*, *Sanguisorba minor*, *Scabiosa ochroleuca*, *Solidago virgaurea*, *Syntrichia ruralis*, *Thymus pulegioides*, *Viola hirta*.

Constant species: *Betula pendula*, *Brachypodium pinnatum*, *Campanula rotundifolia*, *Carlina vulgaris*, *Ceratodon purpureus*, *Cornus sanguinea*, *Encalypta streptocarpa*, *Euphorbia cyparissias*, *Frangula alnus*, *Galium album*, *Hieracium murorum*, *Lotus corniculatus*, *Origanum vulgare*, *Pimpinella saxifraga*, *Pinus sylvestris*, *Poa compressa*, *Potentilla tabernaemontani*, *Salix caprea*, *Sanguisorba minor*, *Scabiosa ochroleuca*, *Solidago virgaurea*, *Sorbus aucuparia*, *Thymus pulegioides*.

So far, the community has been known from only one site, where it develops on screes and steep, south-facing slopes, in an abandoned limestone quarry (artificial habitat) near the village of Rochowice (Kaczawskie mountains). The exploitation of limestone finished after the World War II, and since then the quarry has been subjected to gradual succession processes. Therefore, the afforestation of the slopes, even though it concerns an anthropogenic site, it is purely natural and the quarry itself is a local hotspot of rare and endangered calciphytic flora. The community has the character of an open forest with the dominance of low-growing pine and a high share of *Betula pendula* Roth. Early succession species such as *Sorbus aucuparia* L., *Frangula alnus* Mill. and *Salix caprea* L. are also common. The understory is composed of species typical of calcareous screes and thermophilic grasslands, while forest species of the *Vaccinio-Piceetea* class are almost

absent. With regard to the composition of species, we draw attention to the fact that the tree and shrub layers are composed of acidophilic species, while the undergrowth is rather basiphilous. Community is marked by high EIV for soil reaction, high EIV for temperature and low EIV for moisture (Figure 4). It is one of the richest in species Scots pine forest communities in the Sudetes—there are on average 26.6 plant species per relevé. The community develops at altitude 450–460 m a.s.l.

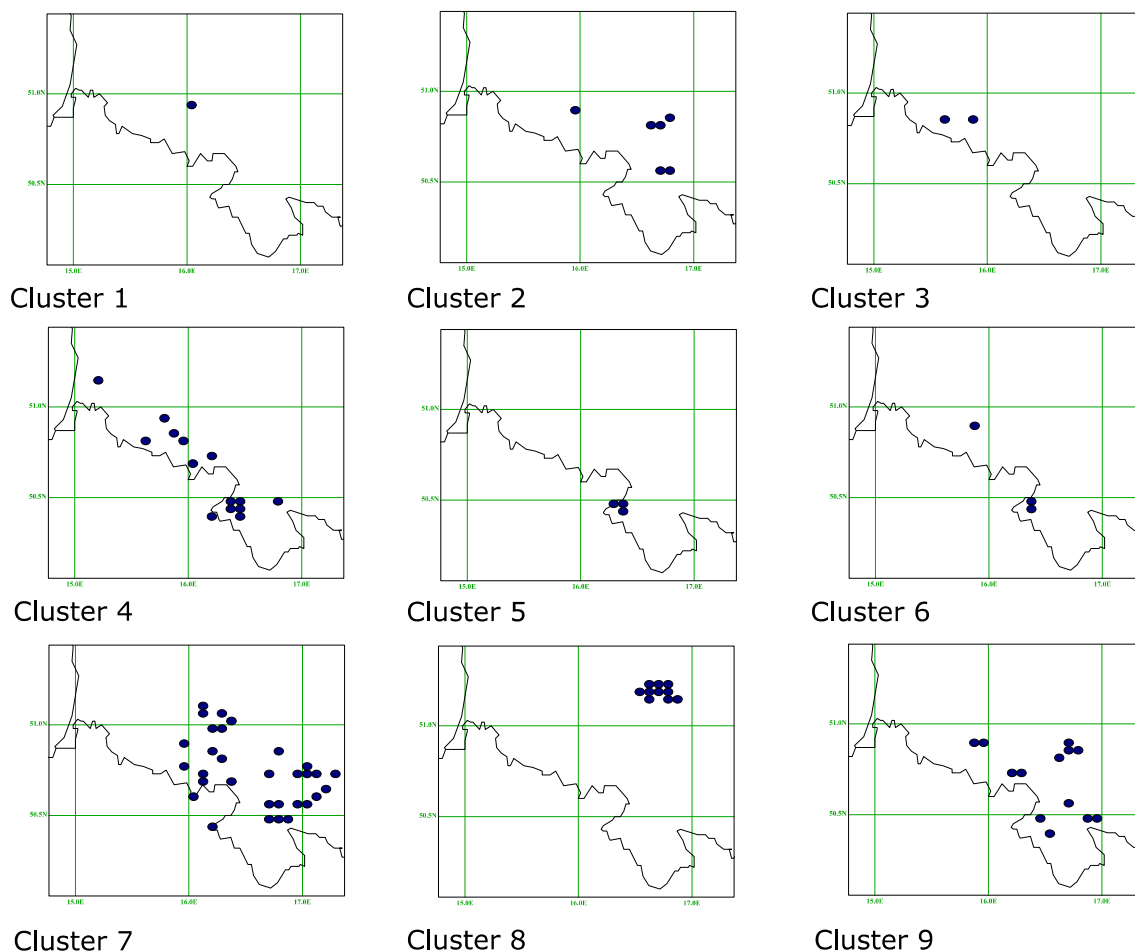


Figure 2. Distribution of relevés of Scots pine forests collected in the Sudetes mountains and their foreland and belonging to particular clusters. Explanation 1—comm. *Brachypodium pinnatum*-*Pinus sylvestris*; 2—*Asplenio cuneifolii*-*Pinetum sylvestris*; 3—*Hieracio pallidi*-*Pinetum sylvestris*; 4—*Vaccinio myrtilli*-*Pinetum sylvestris*; 5—*Betulo carpaticae*-*Pinetum sylvestris*; 6—*Vaccinio uliginosi*-*Betuletum pubescentis*; 7—comm. *Pinus sylvestris*-*Impatiens parviflora*; 8—comm. *Pinus sylvestris*-*Prunus serotina*; 9—comm. *Pinus sylvestris*-*Molinia caerulea*.

Cluster 2—*Asplenio cuneifolii*-*Pinetum sylvestris* Pišta ex Husová in Husová et al. 2002
Number of relevés: 22

Diagnostic species: *Achillea millefolium*, *Asplenium cuneifolium*, *Brachypodium pinnatum*, *Calamagrostis arundinacea*, *C. epigejos*, *Campanula rotundifolia*, *Centaurea stoebe*, *Danthonia decumbens*, *Euphorbia cyparissias*, *Fallopia dumetorum*, *Festuca ovina*, *Fragaria vesca*, *Galium rotundifolium*, *G. verum*, *Genista tinctoria*, *Hieracium pilosella*, *H. sabaudum*, *Hylotelephium maximum*, *Hypericum montanum*, *H. perforatum*, *Luzula luzuloides*, *Lychnis viscaria*, *Melica nutans*, *Moehringia trinervia*, *Phleum phleoides*, *Pimpinella saxifraga*, *Poa nemoralis*, *P. angustifolia*, *Polypodium vulgare*, *Potentilla alba*, *Prunus avium*, *Pyrus communis* agg., *Robinia pseudoacacia*, *Rosa canina*, *Rubus fruticosus* agg., *Rumex acetosella*, *Quercus petraea*, *Silene vulgaris*, *Thymus pulegioides*, *Viola canina*, *V. riviniana*.

Constant species: *Achillea millefolium*, *Avenella flexuosa*, *Calamagrostis epigejos*, *Campanula rotundifolia*, *Festuca ovina*, *Galium verum*, *Lychnis viscaria*, *Pimpinella saxifraga*, *Pinus sylvestris*, *Prunus avium*, *Quercus petraea*, *Rubus fruticosus* agg., *Silene vulgaris*, *Sorbus aucuparia*, *Vaccinium myrtillus*.

These are mostly open-canopy, managed and even-aged forests of *Pinus sylvestris* on shallow soils derived from serpentine or peridotite bedrock. However, there are some sites known with spontaneous Scots pine regeneration. On such localities the Scots pine trees are dwarf and looks malnourished, in contrast to young trees with straight trunks on intensively managed stands. Rich in species herb layer (mean 32 species per relevé) contains a differentiated composition of grasses, dwarf shrubs and thermophilic forbs, with many locally rare or endangered species. Community stands out from the other of Scots pine forests by the frequent occurrence of *Silene vulgaris* (Moench) Garcke, *Galium verum* L., *Asplenium cuneifolium* Viv. and *Potentilla alba* L., which locally prefers serpentine soils. This is rare community, known from four isolated localities in the Grochowa Massif (Pogórze Paczkowskie Plateau), Kielczyńskie and Oleszeńskie Hills (Ślęza ophiolite massif) and near Janowice (Rudawy Janowickie mountains). This community is characterized by high EIVs for nutrients and temperature, and low EIV for moisture (Figure 4). The community develops at altitude 320–460 m a.s.l.

On deeper soils derived from serpentine bedrock *Pinus*-dominated communities are developed usually as artificial forest, included in cluster 9, rarely 7 (see Figure 5), with dominance of mesophytic forest generalists and the absence of thermophilic species typical of open canopy forests.

Cluster 3—*Hieracio pallidi-Pinetum sylvestris* Stöcker 1965

Number of relevés: 10

Diagnostic species: *Calluna vulgaris*, *Ceratodon purpureus*, *Cladonia macilenta*, *C. uncialis*, *Grimmia pulvinata*, *Fagus sylvatica*, *Polytrichum piliferum*, *Vaccinium vitis-idaea*

Constant species: *Avenella flexuosa*, *Calluna vulgaris*, *Ceratodon purpureus*, *Cladonia macilenta*, *Fagus sylvatica*, *Picea abies*, *Pinus sylvestris*, *Sorbus aucuparia*, *Vaccinium myrtillus*, *V. vitis-idaea*.

Mixed, dwarf and open canopy Scots pine forests, usually with the share of *Fagus sylvatica* L., *Picea abies* (L.) H. Karst. and *Betula pendula* in the tree layer. Understory is very scarce and poor in species (mean 13.4 species per relevé), mainly dwarf ericoid shrubs, trees juveniles, thermophilic mosses and lichens occur here. Phytocoenoses belonging to this association are known from initial soils developed over granite rocks at altitudes from 480 m to 650 m a.s.l. They are probably of both natural and relict origin and have never been subjected to regular forest management. So far only three localities of this community have been known—all in the Western Sudetes—Chojnik Mt in the Karkonosze mountains, Witosza Mt and Krzyżna Mt near Jelenia Góra. However, it is still possible to find other, new sites. The community is marked by low EIVs for moisture, soil reaction and nutrients (Figure 4).

Cluster 4—*Vaccinio myrtilli-Pinetum sylvestris* Juraszek 1928 (incl. *Leucobryo-Pinetum* W. Matuszkiewicz 1962)

Number of relevés: 33

Diagnostic species: *Dicranella heteromalla*, *Dicranum polysetum*, *D. scoparium*, *Hylocomium splendens*, *Hypnum cupressiforme* agg., *Leucobryum glaucum*, *Pleurozium schreberi*, *Vaccinium vitis-idaea*.

Constant species: *Avenella flexuosa*, *Betula pendula*, *Dicranum scoparium*, *Hypnum cupressiforme* agg., *Picea abies*, *Pinus sylvestris*, *Vaccinium myrtillus*, *V. vitis-idaea*.

Table 1. Summarized synoptic table of the 175 relevés of Scots pine forest communities of the *Vaccinio-Piceetea* class in the Sudetes mountains and their foreland (SW Poland). The positive Φ coefficient values (multiplied by 100) are presented as superscripts. Diagnostic species ($\Phi > 20$ and constancy ratio > 1.5) are shaded in grey. Among accompanying species, only the most common ones are included in the table.

Cluster No. No. of relevés	Const. ratio	1 5	2 22	3 10	4 33	5 20	6 8	7 39	8 14	9 24
Comm. <i>Brachypodium pinnatum</i>-<i>Pinus sylvestris</i>										
<i>Sanguisorba minor</i>	100.0	100 ¹⁰⁰	.—	.—	.—	.—	.—	.—	.—	.—
<i>Scabiosa ochroleuca</i>	100.0	100 ¹⁰⁰	.—	.—	.—	.—	.—	.—	.—	.—
<i>Encalypta streptocarpa</i>	100.0	100 ¹⁰⁰	.—	.—	.—	.—	.—	.—	.—	.—
<i>Galium album</i>	17.6	80 ^{85.6}	5—	.—	.—	.—	.—	.—	.—	.—
<i>Poa compressa</i>	100.0	80 ^{88.4}	.—	.—	.—	.—	.—	.—	.—	.—
<i>Carlina vulgaris</i>	100.0	80 ^{88.4}	.—	.—	.—	.—	.—	.—	.—	.—
<i>Lotus corniculatus</i>	2.9	80 ^{73.1}	27 ^{16.2}	.—	.—	.—	.—	3—	.—	.—
<i>Cornus sanguinea</i>	7.8	60 ^{70.3}	.—	.—	.—	.—	.—	8—	.—	.—
<i>Solidago virgaurea</i>	11.7	60 ^{72.0}	.—	.—	.—	.—	.—	5—	.—	.—
<i>Salix caprea</i>	19.8	60 ^{73.4}	.—	.—	3—	.—	.—	.—	.—	.—
<i>Origanum vulgare</i>	100.0	60 ^{75.6}	.—	.—	.—	.—	.—	.—	.—	.—
<i>Potentilla tabernaemontani</i>	13.2	60 ^{72.4}	5—	.—	.—	.—	.—	.—	.—	.—
<i>Fragaria viridis</i>	100.0	40 ^{61.0}	.—	.—	.—	.—	.—	.—	.—	.—
<i>Syntrichia ruralis</i>	100.0	40 ^{61.0}	.—	.—	.—	.—	.—	.—	.—	.—
<i>Epipactis atrorubens</i>	100.0	40 ^{61.0}	.—	.—	.—	.—	.—	.—	.—	.—
<i>Hieracium vulgatum</i>	2.8	40 ^{39.2}	5—	10—	.—	.—	.—	5—	14—	4—
<i>Leucanthemum vulgare</i>	100.0	40 ^{61.0}	.—	.—	.—	.—	.—	.—	.—	.—
<i>Anthyllis vulneraria</i>	100.0	40 ^{61.0}	.—	.—	.—	.—	.—	.—	.—	.—
<i>Centaurea jacea</i>	100.0	40 ^{61.0}	.—	.—	.—	.—	.—	.—	.—	.—
<i>Leontodon autumnalis</i>	100.0	40 ^{61.0}	.—	.—	.—	.—	.—	.—	.—	.—
<i>Viola hirta</i>	100.0	40 ^{61.0}	.—	.—	.—	.—	.—	.—	.—	.—
<i>Asplenium cuneifolii</i>-<i>Pinetum sylvestris</i> Pišta ex Husová in Husová et al. 2002										
<i>Galium verum</i>	19.6	.—	82 ^{86.9}	.—	.—	.—	.—	.—	.—	4—
<i>Silene vulgaris</i>	30.1	.—	77 ^{85.1}	.—	.—	.—	.—	3—	.—	.—
<i>Achillea millefolium</i>	1.9	40—	77 ^{67.4}	.—	.—	.—	.—	.—	.—	.—
<i>Festuca ovina</i>	3.4	.—	73 ^{67.1}	.—	.—	.—	.—	3—	21—	8—
<i>Lychnis viscaria</i>	100.0	.—	73 ^{83.9}	.—	.—	.—	.—	.—	.—	.—
<i>Rosa canina</i>	7.1	.—	59 ^{64.8}	.—	.—	.—	.—	8—	.—	8—
<i>Galium rotundifolium</i>	4.4	.—	55 ^{60.5}	.—	.—	.—	.—	5—	.—	12—
<i>Hypericum montanum</i>	10.9	.—	45 ^{60.0}	.—	.—	.—	.—	3—	.—	4—
<i>Hypericum perforatum</i>	2.0	20—	41 ^{33.3}	.—	.—	.—	.—	13—	14—	12—
<i>Hieracium sabaudum</i>	4.9	.—	41 ^{51.7}	.—	.—	.—	.—	5—	.—	8—
<i>Robinia pseudoacacia</i>	5.1	.—	36 ^{50.1}	.—	.—	.—	.—	3—	7—	.—
<i>Hylotelephium maximum</i>	100.0	.—	36 ^{58.1}	.—	.—	.—	.—	.—	.—	.—
<i>Potentilla alba</i>	6.2	.—	32 ^{49.4}	.—	.—	.—	.—	5—	.—	.—
<i>Melica nutans</i>	1.6	20—	32 ^{38.2}	.—	.—	.—	.—	3—	.—	.—
<i>Viola riviniana</i>	2.5	.—	32 ^{37.1}	.—	.—	.—	.—	5—	7—	12—
<i>Hieracium pilosella</i>	100.0	.—	27 ^{50.0}	.—	.—	.—	.—	.—	.—	.—
<i>Asplenium cuneifolium</i>	100.0	.—	27 ^{50.0}	.—	.—	.—	.—	.—	.—	.—
<i>Genista tinctoria</i>	100.0	.—	27 ^{50.0}	.—	.—	.—	.—	.—	.—	.—
<i>Poa angustifolia</i>	3.2	.—	23 ^{35.1}	.—	.—	.—	.—	.—	7—	4—
<i>Viola canina</i>	100.0	.—	23 ^{45.5}	.—	.—	.—	.—	.—	.—	.—
<i>Danthonia decumbens</i>	100.0	.—	23 ^{45.5}	.—	.—	.—	.—	.—	.—	.—
<i>Phleum phleoides</i>	100.0	.—	23 ^{45.5}	.—	.—	.—	.—	.—	.—	.—
<i>Polypodium vulgare</i>	5.5	.—	23 ^{41.0}	.—	.—	.—	.—	.—	.—	4—
<i>Centaurea stoebe</i>	100.0	.—	23 ^{45.5}	.—	.—	.—	.—	.—	.—	.—
<i>Hieracio pallidi</i>-<i>Pinetum sylvestris</i> Stöcker 1965										
<i>Polytrichum piliferum</i>	23.1	.—	.—	70 ^{80.1}	3—	.—	.—	.—	.—	.—
<i>Cladonia uncialis</i>	100.0	.—	.—	30 ^{52.5}	.—	.—	.—	.—	.—	.—
<i>Grimmia pulvinata</i>	100.0	.—	.—	20 ^{42.7}	.—	.—	.—	.—	.—	.—

Table 1. Cont.

Vaccinio myrtilli-Pinetum sylvestris Juraszek 1928										
<i>Dicranum polysetum</i>	3.3	.—	5—	10—	33 ^{38.1}	.—	.—	.—	7—	4—
<i>Leucobryum glaucum</i>	3.0	.—	5—	10—	30 ^{34.2}	5—	.—	.—	.—	8—
<i>Hylocomium splendens</i>	3.6	.—	.—	.—	30 ^{45.3}	.—	.—	.—	.—	8—
<i>Dicranella heteromalla</i>	1.7	.—	.—	10—	21 ^{21.7}	.—	.—	13—	.—	12—
Betulo carpaticae-Pinetum sylvestris Mikyška 1970										
<i>Betula pubescens</i> var. <i>glabrata</i>	100.0	.—	.—	.—	.—	90 ^{94.3}	.—	.—	.—	.—
<i>Empetrum nigrum</i> subsp. <i>nigrum</i>	100.0	.—	.—	.—	.—	40 ^{61.0}	.—	.—	.—	.—
<i>Vaccinium uliginosum</i>	100.0	.—	.—	.—	.—	40 ^{61.0}	.—	.—	.—	.—
<i>Pinus x rhaetica</i>	100.0	.—	.—	.—	.—	35 ^{56.9}	.—	.—	.—	.—
<i>Cetraria islandica</i>	3.5	.—	.—	10—	.—	35 ^{48.6}	.—	.—	.—	.—
Vaccinio uliginosi-Betuletum pubescentis Libbert 1933										
<i>Sphagnum fallax</i>	100.0	.—	.—	.—	.—	.—	100 ¹⁰⁰	.—	.—	.—
<i>Betula pubescens</i> var. <i>pubescens</i>	2.5	.—	.—	40 ^{17.5}	15—	.—	100 ^{70.3}	.—	21—	4—
<i>Polytrichum commune</i>	100.0	.—	.—	.—	.—	.—	88 ^{92.8}	.—	.—	.—
<i>Molinia caerulea</i> subsp. <i>arundinacea</i>	6.4	.—	14—	.—	9—	.—	88 ^{80.0}	3—	.—	.—
<i>Carex rostrata</i>	100.0	.—	.—	.—	.—	.—	75 ^{85.3}	.—	.—	.—
<i>Juncus effusus</i>	9.8	.—	.—	.—	3—	.—	75 ^{73.1}	8—	7—	4—
<i>Eriophorum vaginatum</i>	100.0	.—	.—	.—	.—	.—	62 ^{77.3}	.—	.—	.—
<i>Salix aurita</i>	100.0	.—	.—	.—	.—	.—	50 ^{68.6}	.—	.—	.—
<i>Sphagnum palustre</i>	100.0	.—	.—	.—	.—	.—	50 ^{68.6}	.—	.—	.—
<i>Carex acutiformis</i>	100.0	.—	.—	.—	.—	.—	25 ^{47.8}	.—	.—	.—
<i>Trientalis europaea</i>	3.0	.—	.—	.—	3—	.—	25 ^{37.6}	.—	.—	8—
<i>Carex leporina</i>	2.0	.—	.—	.—	.—	.—	25 ^{35.2}	3—	.—	12 ^{13.8}
<i>Carex nigra</i>	100.0	.—	.—	.—	.—	.—	25 ^{47.8}	.—	.—	.—
<i>Carex panicea</i>	100.0	.—	.—	.—	.—	.—	25 ^{47.8}	.—	.—	.—
<i>Eriophorum angustifolium</i>	100.0	.—	.—	.—	.—	.—	25 ^{47.8}	.—	.—	.—
Comm. Pinus sylvestris-Impatiens parviflora (Artificial Forest)										
<i>Impatiens parviflora</i>	2.2	.—	18—	.—	.—	.—	.—	79 ^{60.6}	36—	12—
<i>Dryopteris filix-mas</i>	2.8	.—	18—	.—	.—	.—	.—	59 ^{52.8}	21—	4—
<i>Urtica dioica</i>	11.3	.—	5—	.—	.—	.—	.—	51 ^{66.1}	.—	.—
<i>Acer platanoides</i>	2.4	20—	14—	.—	.—	.—	.—	49 ^{41.6}	7—	12—
<i>Sambucus nigra</i>	3.1	.—	.—	.—	.—	.—	.—	38 ^{50.1}	.—	12—
<i>Crataegus monogyna</i>	1.8	20—	5—	.—	.—	.—	.—	36 ^{33.8}	14—	4—
<i>Galeopsis pubescens</i>	2.2	.—	.—	.—	.—	.—	.—	31 ^{41.7}	14—	.—
<i>Brachypodium sylvaticum</i>	2.8	.—	9—	.—	.—	.—	.—	26 ^{34.5}	.—	8—
<i>Drymochloa sylvatica</i>	1.6	.—	.—	.—	.—	.—	.—	21 ^{31.6}	.—	12—
Comm. Pinus sylvestris-Prunus serotina (Artificial Forest)										
<i>Prunus serotina</i>	8.4	.—	.—	.—	.—	.—	.—	10—	86 ^{85.9}	.—
<i>Viscum album</i>	100.0	.—	.—	.—	.—	.—	.—	.—	71 ^{83.1}	.—
<i>Convallaria majalis</i>	2.8	.—	18—	.—	3—	.—	.—	10—	50 ^{50.4}	.—
<i>Holcus mollis</i>	4.3	.—	.—	.—	.—	.—	.—	3—	36 ^{48.7}	8—
<i>Atrichum undulatum</i>	2.8	.—	.—	.—	3—	.—	.—	8—	21 ^{34.0}	.—
<i>Hedera helix</i>	1.7	.—	.—	.—	.—	.—	.—	13 ^{13.4}	21 ^{27.7}	8—
Comm. Pinus sylvestris-Molinia caerulea (Artificial Forest)										
<i>Maianthemum bifolium</i>	3.0	.—	.—	.—	3—	.—	12—	18—	14—	54 ^{47.7}
<i>Molinia caerulea</i> subsp. <i>caerulea</i>	2.5	.—	5—	.—	6—	.—	.—	5—	21—	54 ^{51.4}
<i>Athyrium filix-femina</i>	4.5	.—	.—	.—	.—	.—	.—	10—	.—	46 ^{57.9}
<i>Rubus hirtus</i> agg.	2.3	.—	.—	.—	.—	.—	.—	18—	.—	42 ^{49.8}
<i>Luzula pilosa</i>	2.4	.—	5—	.—	9—	.—	.—	10—	.—	25 ^{30.5}
<i>Pteridium aquilinum</i>	1.7	.—	.—	.—	15—	.—	.—	10—	.—	25 ^{29.8}
<i>Pseudoscleropodium purum</i>	1.7	.—	5—	.—	12—	.—	.—	3—	7—	21 ^{24.7}
<i>Polytrichastrum formosum</i>	1.6	.—	18—	.—	42—	10—	12—	33—	29—	67 ^{35.8}

Table 1. Cont.

Species diagnostic for at least two clusters										
<i>Hieracium murorum</i>	2.8	100 ^{69.7}	36 ^{14.0}	20 —	9 —	—	—	18 —	—	—
<i>Campanula rotundifolia</i>	7.6	100 ^{71.9}	64 ^{39.4}	—	—	—	—	3 —	—	8 —
<i>Brachypodium pinnatum</i>	16.0	80 ^{68.0}	41 ^{27.8}	—	—	—	—	3 —	—	—
<i>Thymus pulegioides</i>	100.0	60 ^{58.1}	32 ^{25.2}	—	—	—	—	—	—	—
<i>Pimpinella saxifraga</i>	100.0	60 ^{47.4}	64 ^{51.1}	—	—	—	—	—	—	—
<i>Euphorbia cyparissias</i>	21.3	60 ^{49.3}	55 ^{43.5}	—	—	—	—	3 —	—	—
<i>Ceratodon purpureus</i>	5.0	80 ^{58.2}	5 —	50 ^{30.3}	—	10 —	—	5 —	7 —	—
<i>Frangula alnus</i>	1.5	80 ^{29.4}	36 —	—	9 —	—	50 —	23 —	100 ^{43.9}	54 ^{10.8}
<i>Quercus petraea</i>	0.9	—	100 ^{43.3}	30 —	42 —	—	75 —	26 —	14 —	71 ^{22.3}
<i>Calamagrostis epigejos</i>	5.0	—	64 ^{43.1}	—	—	—	—	13 —	71 ^{50.3}	8 —
<i>Poa nemoralis</i>	2.3	20 —	45 ^{29.0}	—	—	—	—	51 ^{34.6}	7 —	17 —
<i>Fragaria vesca</i>	100.0	—	27 ^{32.1}	—	—	—	—	26 ^{29.6}	—	—
<i>Prunus avium</i>	1.7	—	64 ^{41.1}	—	—	—	12 —	49 ^{27.5}	29 —	12 —
<i>Luzula luzuloides</i>	1.9	—	41 ^{33.8}	10 —	3 —	—	—	15 —	—	29 ^{20.6}
<i>Moehringia trinervia</i>	2.2	—	36 ^{21.9}	—	—	—	—	13 —	64 ^{50.0}	17 —
<i>Pyrus communis</i> agg.	100.0	—	27 ^{30.8}	—	—	—	—	—	29 ^{32.7}	—
<i>Fallopia dumetorum</i>	100.0	—	27 ^{34.1}	—	—	—	—	—	21 ^{25.0}	—
<i>Rumex acetosella</i>	2.7	—	27 ^{24.9}	10 —	—	—	—	3 —	29 ^{26.6}	4 —
<i>Calamagrostis arundinacea</i>	1.4	—	45 ^{26.1}	10 —	9 —	—	—	33 —	—	58 ^{38.1}
<i>Cladonia macilenta</i>	6.6	—	—	70 ^{53.2}	9 —	60 ^{43.4}	—	—	—	—
<i>Calluna vulgaris</i>	1.7	—	18 —	80 ^{43.8}	48 ^{18.4}	80 ^{43.8}	—	—	—	4 —
<i>Vaccinium vitis-idaea</i>	4.4	—	14 —	60 ^{26.2}	61 ^{26.7}	100 ^{58.0}	—	—	—	8 —
<i>Dicranum scoparium</i>	1.5	—	9 —	40 —	61 ^{31.5}	60 ^{31.0}	12 —	8 —	—	17 —
<i>Fagus sylvatica</i>	1.4	20 —	14 —	80 ^{34.1}	48 —	—	25 —	38 —	14 —	67 ^{24.2}
<i>Pleurozium schreberi</i>	2.5	—	18 —	—	45 ^{25.7}	5 —	12 —	5 —	64 ^{43.1}	8 —
<i>Hypnum cupressiforme</i> agg.	1.2	—	50 —	50 —	61 ^{24.5}	—	—	59 ^{23.2}	—	42 —
<i>Lysimachia vulgaris</i>	3.7	—	—	—	—	—	38 ^{30.5}	10 —	7 —	42 ^{35.2}
<i>Corylus avellana</i>	1.2	—	32 —	—	—	—	—	49 ^{33.9}	14 —	38 ^{22.7}
<i>Acer pseudoplatanus</i>	1.9	—	23 —	—	6 —	—	—	77 ^{48.5}	29 —	54 ^{28.8}
<i>Oxalis acetosella</i>	100.0	—	—	—	—	—	—	33 ^{31.9}	—	42 ^{42.5}
<i>Stellaria media</i>	1.8	—	18 —	—	—	—	—	33 ^{22.7}	50 ^{40.7}	8 —
<i>Quercus robur</i>	1.9	—	5 —	—	27 —	—	—	64 ^{32.2}	93 ^{55.7}	33 —
<i>Quercus rubra</i>	2.2	—	9 —	—	—	—	—	15 —	43 ^{35.4}	33 ^{24.8}
<i>Carex pilulifera</i>	3.8	—	—	—	—	—	—	8 —	43 ^{42.2}	29 ^{25.2}
<i>Dryopteris carthusiana</i>	2.8	—	14 —	10 —	12 —	—	25 —	69 ^{25.9}	100 ^{48.7}	79 ^{33.2}
<i>Rubus fruticosus</i> agg.	3.0	—	77 ^{25.8}	—	6 —	—	25 —	87 ^{32.9}	100 ^{42.1}	75 ^{24.2}
The most common accompanying species										
<i>Pinus sylvestris</i>		100 —	100 —	100 —	100 —	100 —	75 —	100 —	100 —	100 —
<i>Betula pendula</i>		80 —	32 —	60 —	76 ^{19.3}	30 —	38 —	28 —	50 —	42 —
<i>Sorbus aucuparia</i>	1.2	60 —	95 ^{23.0}	60 —	61 —	25 —	12 —	79 —	93 ^{21.1}	92 ^{20.2}
<i>Picea abies</i>	1.0	40 —	5 —	90 ^{23.5}	82 ^{17.7}	65 —	88 —	36 —	29 —	79 ^{15.8}
<i>Avenella flexuosa</i>	1.1	—	73 —	80 —	94 ^{28.5}	20 —	12 —	23 —	93 ^{27.7}	88 ^{23.9}
<i>Vaccinium myrtillus</i>	1.1	—	64 —	90 —	97 ^{24.8}	90 ^{19.8}	88 —	26 —	29 —	83 ^{14.9}

This is the most common association in the study area. It occurs on rocky outcrops on steep slopes in the areas of acidic bedrocks (granites, gneisses); on deep soils resulting from weathering serpentinites; on other neutral rocks; and on weathered and blown sands and the podzolic soils derived from them. In most cases, its phytocoenoses are of anthropogenic origin. However, in some localities in the Sudetes they may be close to natural in character, as evidenced by the natural habit of trees, which is not the result of forest management pressure. Herb layer is extremely poor (13 species per relevé) and consists of the common species of acidophilic grasses and ericoid dwarf shrubs; acidophilic bryophytes often dominate or co-dominate here. The community is marked by low EIVs for moisture, soil reaction and nutrients (Figure 4), and develops at altitudes from 220 m to 735 m a.s.l.

Cluster 5—*Betulo carpaticae-Pinetum sylvestris* Mikyška 1970**Number of relevés: 20**

Diagnostic species: *Betula pubescens* var. *glabrata*, *Calluna vulgaris*, *Cetraria islandica*, *Cladonia macilenta*, *Dicranum scoparium*, *Empetrum nigrum* subsp. *nigrum*, *Pinus x rhaetica*, *Vaccinium uliginosum*, *V. vitis-idaea*.

Constant species: *Betula pubescens* var. *glabrata*, *Calluna vulgaris*, *Cladonia macilenta*, *Dicranum scoparium*, *Picea abies*, *Pinus sylvestris*, *Vaccinium myrtillus*, *V. vitis-idaea*.

The community occurs only in the highest parts of the Stołowe mountains (from 760 m up to 905 m a.s.l.), on the initial soils derived from sandstone. The best-developed patches occupy the flat tops of sandstone monoliths (Szczeliniec Wielki and Mały Mt., Błędne Skały nature reserve), they are also found on ledges on steep slopes and on the tops of rock monoliths along their edges (Narożnik Mt., Ptak Mt and Skalniak Mt). The community is extremely species-poor (on average only 9.25 species per relevé), however, it is composed of unique set of species rare in the Sudetes. Although it is often found on almost solid rock, it is distinguished by the presence of species typical for peat bogs, such as *Vaccinium uliginosum* L. or *Pinus x rhaetica* Brügger. A special feature is the presence of high-mountain forms of *Betula pubescens* Ehrh. similar to var. *glabrata* and relict, postglacial populations of *Pinus sylvestris*. The community is marked by the lowest EIVs for temperature, soil reaction and nutrients of all the syntaxa described in this study (Figure 4).

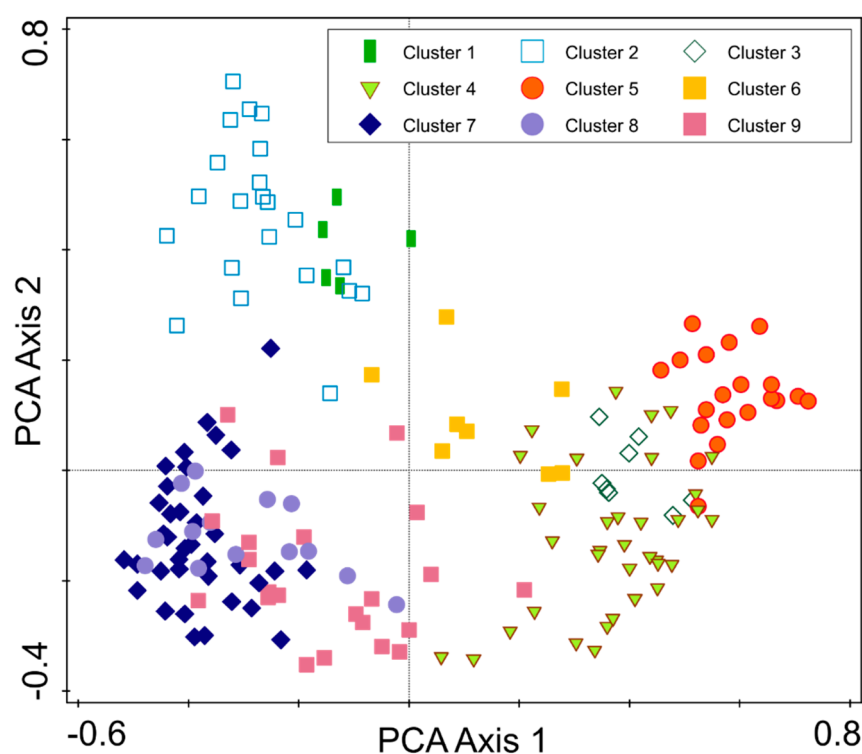


Figure 3. PCoA diagram for the 175 vegetation plots of the Scots pine forests in the Sudetes mountains and their foreland (SW Poland). The numbers of centroids are compatible with Figure 2. Groups 1 and 2 refer to thermophilic forests on basic and ultrabasic substrata; group 3 and 4 represent acidophilic stands (extremely dry and moderately moist) and clusters from 7 to 9 are anthropogenic pine plantations. Isolated positions of 5 (oligothermic *Betulo carpaticae-Pinetum sylvestris*) and 6 (bog woodland of *Betulo pubescensis-Vaccinietum uliginosi*) associations are clearly discernible.

All. *Vaccinio uliginosi-Pinion sylvestris* Passarge 1968—bog woodlands**Cluster 6—*Vaccinio uliginosi-Betuletum pubescentis* Libbert 1933****Number of relevés: 8**

Diagnostic species: *Betula pubescens* var. *pubescens*, *Carex acutiformis*, *C. leporina*, *C. nigra*, *C. panicea*, *C. rostrata*, *Eriophorum angustifolium*, *E. vaginatum*, *Juncus effusus*, *Lysimachia*

vulgaris, *Molinia caerulea* subsp. *arundinacea*, *Polytrichum commune*, *Salix aurita*, *Sphagnum fallax*, *S. palustre*, *Trientalis europaea*.

Constant species: *Betula pubescens* var. *pubescens*, *Carex rostrata*, *Eriophorum vaginatum*, *Juncus effusus*, *Molinia caerulea* subsp. *arundinacea*, *Picea abies*, *Pinus sylvestris*, *Polytrichum commune*, *Quercus petraea*, *Sphagnum fallax*, *S. palustre*, *Vaccinium myrtillus*.

This very rare community has been known so far from only three localities—one in the Trzcińskie Mokradła peat-bog (Kotlina Jeleniogórska) and two in the Stołowe mountains, where it develops on drained moors on sandstone plateau. The phytocoenoses are loose; the cover of the tree layer reaches 40%–50%; however, in contrast to the remaining natural or semi-natural forests, the shrub layer is well developed, and the undergrowth is abundant, with coverage close to 90%–100%. Depending on their location, apart from Scots pine, they are co-dominated by *Betula pubescens* var. *pubescens* Ehrh. or *Picea abies*. In the shrub layer, the presence of *Salix aurita* L., *S. cinerea* L. and *Frangula alnus* is significant. The understory may be dominated by graminoids (such as *Molinia caerulea* (L.) Moench, *Eriophorum* sp., *Carex* sp., *Juncus* sp.), dwarf shrubs (mainly *Vaccinium myrtillus* L.) and bryophytes (numerous species of the genus *Sphagnum* sp. and *Polytrichum* sp.). In these phytocoenoses on average occur 17 plant species in the relevé. The community is marked by the highest EIV for moisture from all the recorded syntaxa (Figure 4). The community develops at altitudes from 400 m to 720 m a.s.l.

3.2. Artificial Scots Pine Forests

Among the analyzed material, we also distinguished three groups of fully artificial forests dominated by *Pinus sylvestris*, differing in floristic composition, fertility of the habitat and soil reaction. All these communities, due to domination of Scots pine in the tree layer may be conditionally included in the *Pinetalia sylvestris* order as non-hierarchical phytocoenoses. A characteristic feature that distinguishes them from natural or semi-natural communities (except for *Vaccinio myrtilli-Pinetum*, whose patches are also partially anthropogenic) is low light availability (Figure 4).

Cluster 7—Comm. *Pinus sylvestris*-*Impatiens parviflora*

Number of relevés: 39

Diagnostic species: *Acer platanoides*, *A. pseudoplatanus*, *Brachypodium sylvaticum*, *Corylus avellana*, *Crataegus monogyna*, *Dryopteris carthusiana*, *D. filix-mas*, *Drymochloa sylvatica*, *Fragaria vesca*, *Galeopsis pubescens*, *Hypnum cupressiforme* agg., *Impatiens parviflora*, *Oxalis acetosella*, *Poa nemoralis*, *Prunus avium*, *Quercus robur*, *Rubus fruticosus* agg., *Sambucus nigra*, *Stellaria media*, *Urtica dioica*.

Constant species: *Acer pseudoplatanus*, *Dryopteris carthusiana*, *Impatiens parviflora*, *Pinus sylvestris*, *Quercus robur*, *Rubus fruticosus* agg., *Sorbus aucuparia*.

The most common recorded community with the dominance of *Pinus sylvestris*, but with a constant and high proportion of nemoral species. The undergrowth includes common forest species of the *Carpino-Fagetea sylvaticae* Jakucs ex Passarge 1968 class (e.g., *Acer platanoides* L., *Corylus avellana* L., *Brachypodium sylvaticum* (Huds.) P. Beauv., *Dryopteris filix-mas* (L.) Schott, *Drymochloa sylvatica* (Pollich) Holub), along with nitrophilous (*Urtica dioica* L., *Rubus fruticosus* agg., *R. idaeus* L.) and alien species (*Impatiens parviflora* L.) is particularly common in this cluster). Among plantation forests, this community has the highest EIVs for soil reaction and nutrients, which indicates that pine was planted here on fertile habitats of deciduous forests of the *Carpino-Fagetea sylvaticae* class, most often in sub-mountainous locations (*Carpinion betuli* Issler 1931 alliance), less often in nutrient-rich beech forest habitats of the *Fagetalia sylvaticae* Pawł. in Pawł., Sokoł. et Wall. 1928. However, the identified combination of species indicates important transformation of the ecosystem, in which native forest species play a weak role in relation to non-forest species. The mean number of species per relevé is quite high (23.6).

Cluster 8—Comm. *Pinus sylvestris*-*Prunus serotina*

Number of relevés: 14

Diagnostic species: *Atrichum undulatum*, *Calamagrostis epigejos*, *Carex pilulifera*, *Convallaria majalis*, *Dryopteris carthusiana*, *Fallopia dumetorum*, *Frangula alnus*, *Hedera helix*, *Holcus mollis*, *Moehringia trinervia*, *Pleurozium schreberi*, *Prunus serotina*, *Pyrus communis* agg., *Quercus robur*, *Q. rubra*, *Rubus fruticosus* agg., *Rumex acetosella*, *Stellaria media*, *Viscum album*.

Constant species: *Avenella flexuosa*, *Calamagrostis epigejos*, *Dryopteris carthusiana*, *Frangula alnus*, *Moehringia trinervia*, *Pinus sylvestris*, *Pleurozium schreberi*, *Prunus serotina*, *Quercus robur*, *Rubus fruticosus* agg., *Sorbus aucuparia*, *Viscum album*.

A lowland community characterized by a high share of mesophilous forest generalists (*Dryopteris carthusiana* (Vill.) H. P. Fuchs, *Frangula alnus*, *Sorbus aucuparia*), species of the forest clearings (*Calamagrostis epigejos* (L.) Roth, *Rubus fruticosus* agg.) and invasive alien species (*Prunus serotina* Ehrh., *Quercus rubra* L., *Impatiens parviflora* L.). Among plantation forests, these phytocoenoses are marked by intermediate values of EIVs for soil reaction and nutrients, which indicates that pine was planted here in the habitats of mesotrophic deciduous and mixed forests (poor forms of oak-hornbeam forests *Tilio-Carpinetum* Traczyk 1962, acidophilic oak forests of the *Quercetea robori-petraeae* Br.-Bl. et Tüxen ex Oberdorfer 1957 class). However, the identified combination of species indicates a complete transformation of the ecosystem, in which native forest species play a marginal role in relation to non-forest's ones. The mean number of species per relevé is quite high (21.4). The community develops at altitudes between 120 and 320 m a.s.l.

Cluster 9—Comm. *Pinus sylvestris*-*Molinia caerulea*

Number of relevés: 24

Diagnostic species: *Acer pseudoplatanus*, *Athyrium filix-femina*, *Calamagrostis arundinacea*, *Carex pilulifera*, *Corylus avellana*, *Dryopteris carthusiana*, *Fagus sylvatica*, *Luzula luzuloides*, *L. pilosa*, *Lysimachia vulgaris*, *Maianthemum bifolium*, *Molinia caerulea* subsp. *caerulea*, *Oxalis acetosella*, *Polytrichastrum formosum*, *Pseudoscleropodium purum*, *Pteridium aquilinum*, *Quercus rubra*, *Q. petraea*, *Rubus fruticosus* agg., *R. hirtus* agg.

Constant species: *Avenella flexuosa*, *Dryopteris carthusiana*, *Fagus sylvatica*, *Picea abies*, *Pinus sylvestris*, *Polytrichastrum formosum*, *Quercus petraea*, *Rubus fruticosus* agg., *Sorbus aucuparia*, *Vaccinium myrtillus*.

Submountain community (as evidenced by the constant share of *Luzula luzuloides* (Lam.) Dandy & Wilmott or *Fagus sylvatica*), similarly to the previous one in terms of high share of mesophilous general forest species but with higher requirements as to the soil moisture (*Athyrium filix-femina* (L.) Roth, *Maianthemum bifolium* (L.) F. W. Schmidt, *Luzula pilosa* (L.) Willd., *Molinia caerulea*). The share of alien species is much lower here than in the two previous groups (only *Quercus rubra* seems to be common). Among plantation forests, this community has the lowest EIVs for soil reaction and nutrients, but a constant share of forest species (e.g., *Corylus avellana*, *Acer pseudoplatanus* L.) suggests that pine was planted here on mesotrophic deciduous and mixed forests' habitats (submountain forms of the *Tilio-Carpinetum* and beech forests of the *Luzulo-Fagion sylvaticae* Lohmeyer et Tüxen in Tüxen 1954 alliance). Among artificial forest, this community retained its character most closely to the natural. The mean number of species per relevé is 21.4.

3.3. Ecological Differentiation

PCoA ordination diagram (Figure 3) shows a species compositional pattern within all distinguished associations and communities. The PCoA results derived from CANOCO revealed that the first and the second PCoA axes explained 13.64% and 5.92% of compositional variability of studied communities, respectively. The first PCoA axis was significantly correlated with the EIVs for soil reaction and nutrients (both $p < 0.01$) and for temperature ($p < 0.05$). The second PCoA axis was significantly correlated ($p < 0.01$) with the EIV for light (Table 2).

Table 2. Significance of Spearman's rank correlation of mean EIVs with two main PCoA axes within the Scots pine forests in the Sudetes and their foreland using a modified permutation test.

	Axis 1		Axis 2	
	<i>rho</i> ¹	<i>p</i> ²	<i>rho</i>	<i>p</i>
EIV_Light	0.54	0.164	−0.65	0.004 **
EIV_Temperature	−0.68	0.044 *	−0.35	0.112
EIV_Continentality	0.63	0.064	0.13	0.52
EIV_Moisture	−0.19	0.712	0.34	0.176
EIV_Soil Reaction	−0.86	0.004 **	−0.04	0.772
EIV_Nutrients	−0.91	0.004 **	0.32	0.18

¹ Spearman's rho estimate; ² modified, **— $p < 0.01$; *— $p < 0.05$.

The obtained results suggest that the studied communities are arranged along the first axis from those developing on nutrient-rich substrates with higher pH and favorable thermal conditions towards poor, acidic and oligothermic sites. The second axis determines a gradient along which studied forests are distributed from shaded ones to those with loose structure and higher light availability.

ANOVA of the six EIVs for the nine relevé groups suggested that most of the analyzed factors (except for continentality index) played a significant role in shaping the diversity of the studied vegetation types (Figure 4), as reflected by $p < 0.01$ for soil reaction, moisture and nutrients and $p < 0.05$ for light and temperature.

The db-RDA revealed that the explanatory variables used in the analysis accounted for 27.26% (adjusted explained variation was 22.76%) of variation in species composition. Figure 5 presents the db-RDA diagram of studied samples and main environmental gradients derived from: altitude, heat load index and the main types of bedrock. However, their contribution to the explained variability varies depending on whether we consider simple term effects or conditional effects (Table 3).

Table 3. The simple terms and conditional effects of the environmental variables analyzed on the species compositions of the distinguished pine forest communities identified using dbRDA and Monte Carlo permutation test. Lambda—variance explained by the environmental variable (in %).

Environmental Variable	Simple Term Effects			Conditional Effects		
	Lambda	Pseudo-F	<i>p</i>	Lambda	Pseudo-F	<i>p</i>
Altitude	9.2	17.4	0.002	9.2	17.4	0.002
Upper sandstone	6.7	12.3	0.002	2.8	5.8	0.002
Serpentine	5.3	9.6	0.002	4.6	9.0	0.002
Lower sandstone	3.1	5.5	0.002	2.1	4.6	0.002
Quaternary deposits	3.0	5.3	0.002	0.7	1.5	0.022
Limestone	2.5	4.4	0.002	2.7	5.6	0.002
Quaternary peat bogs	2.4	4.3	0.002	2.6	5.5	0.002
Metamorphic	1.9	3.3	0.002	1.4	3.1	0.002
Granitoids	1.3	2.2	0.002	0.5	1.2	0.232
Heat load index	0.9	1.6	0.014	0.7	1.5	0.008

The most important variable (both in simple and conditional effects) is altitude, but the effect of some bedrock types (especially two different kinds of sandstones, postglacial formations, limestones and serpentinites) is also significant.

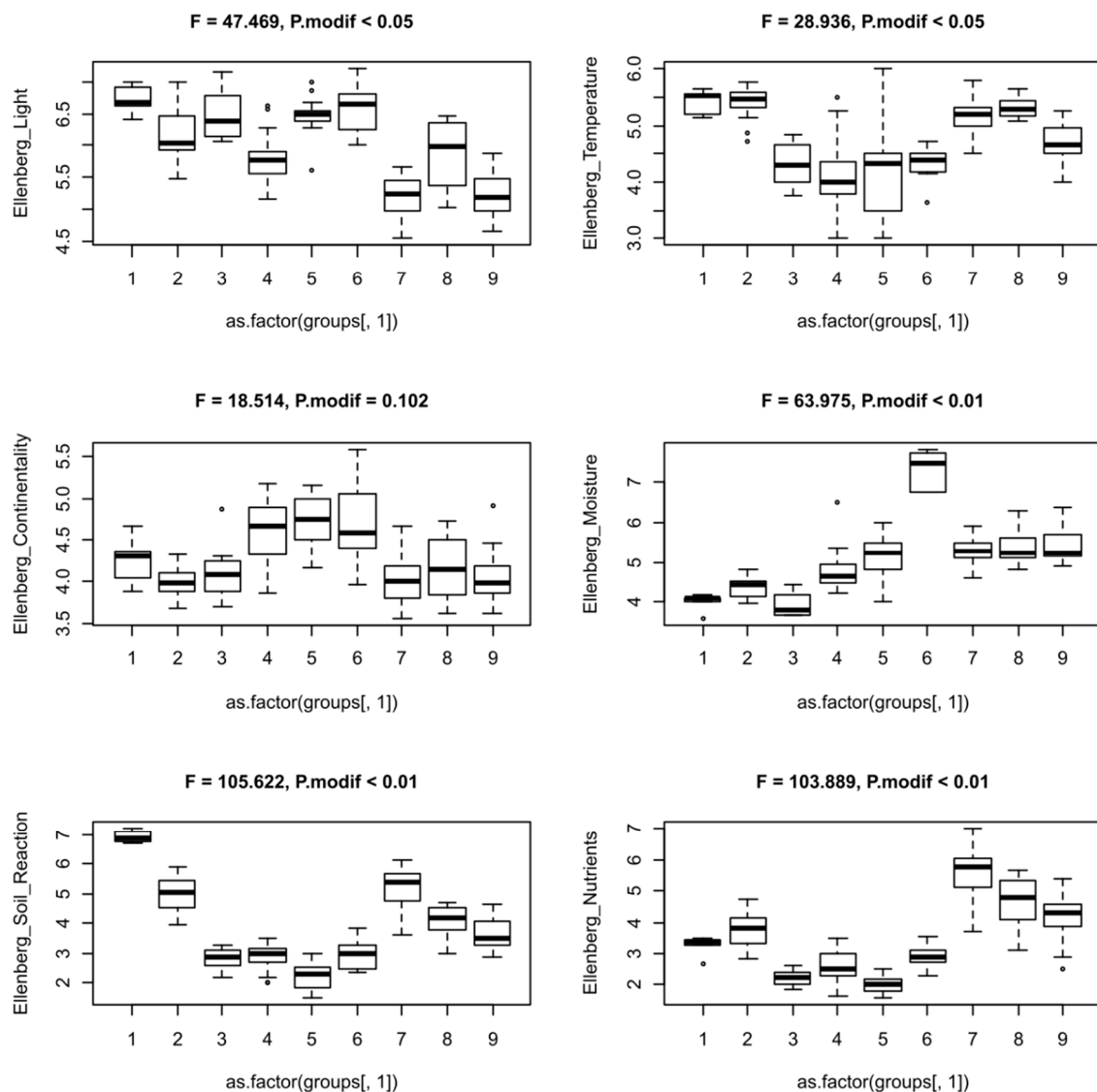


Figure 4. Summary box-and-whisker plots of mean Ellenberg's indicator values (EIVs) for clusters recognized within Scots pine forests of the Sudetes and their foreland (SW Poland) produced by one-way ANOVA. The central line of each box indicates the median value; box boundaries the lower (25%) and upper (75%) quartiles; and whiskers the range of values. P.modif was calculated using a modified permutation test of significance for analysis of mean Ellenberg indicator values (EIVs); F—test statistic. Numbers of clusters are the same as in Figure 2.

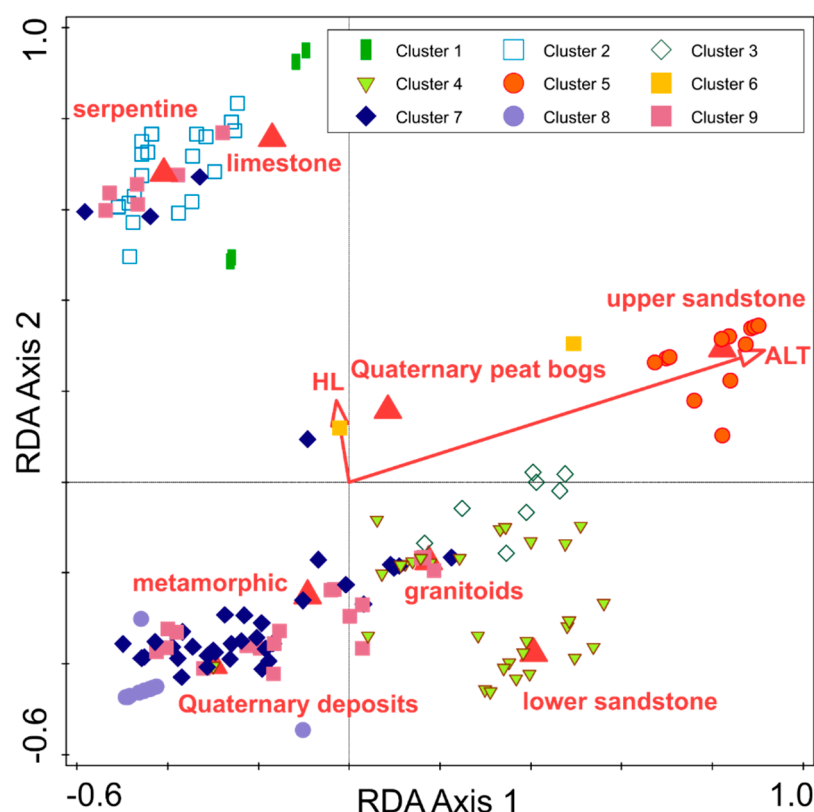


Figure 5. Db-RDA plot of samples of the Scots pine forest communities overlaid with environmental variables. Numbers of groups (clusters) are compatible with Figure 2. Explanation: ALT—altitude, HL—heat load.

4. Discussion

The present study suggests that pine forests of the Sudetes mountains and their foreland are more differentiated than previously reported in phytosociological literature. Instead of three associations of pine forests known so far, five (and one community) were distinguished, and their distinctiveness was confirmed both by the differences in species combinations and ecological conditions under which they develop.

Cluster 1 embraces phytocoenoses of pine forest communities developing on limestone substrate and classified as the community *Brachypodium pinnatum*-*Pinus sylvestris*, resembling more the *Festuco-Pinion sylvestris* alliance phytocoenoses than typical *Dicrano-Pinion* forest. These basiphilous, species-rich pine forests have been found so far neither in the Sudetes, nor in Poland at all (except for *Erico-Pinetea* Horvat 1959 relic Carpathian forest). They are reported in the north-western part of the Czech Republic [49] and Slovakia [50]. Communities described from Slovakia as *Brachypodio pinnati*-*Pinus sylvestris* Michalko 1980 are very different from the Sudeten phytocoenoses, in terms of the occurrence of Carpathian and sub-Mediterranean species, such as *Calamagrostis varia* (Schr.) Host, *Pulsatilla helleri* subsp. *slavica* (G. Reuss) Zámelis, *Tanacetum corymbosum* subsp. *subcorymbosum* (Schur) Pawł., *Aster amellus* L., *Cotoneaster melanocarpus* (Bunge) Loudon, *Aegonychon purpureoaceruleum* (L.) Holub and *Euphorbia epithymoides* L. The species composition of our community is almost identical with Czech basiphilous Scots pine forests [49], which are, however, probably erroneously identified with thermophilic, but acidophilous *Festuco ovinae*-*Pinetum* Kobendza 1930 association, described from rather acidic dunes in Central Poland [8]. The other type of subcontinental pine forests with the occurrence of thermophilous species (ass. *Peucedano-Pinetum* W.Mat. (1962) 1973 subass. *pulsatilletosum* and ass. *Serratulo-Pinetum* J.Mat 1981) is recorded from the central and north-western part of Poland and belongs to the *Dicrano-Pinion* alliance. These forests prefer poor in nutrients podzolic soils derived from Quaternary postglacial formations [7]. According to the Central

European classification, the alliance *Festuco-Pinion sylvestris* is included in the separate class *Pyrolo-Pinetea sylvestris* Korneck 1974 embracing Euro-Siberian (sub)continental psammophilous (sub)thermophilous steppic pine forests [23]. Therefore, for the time being, we kept the classification of comm. *Brachypodium pinnatum*-*Pinus sylvestris* within the *Dicrano-Pinion* alliance. Certainly, this community requires further research based on wider phytosociological material from southern Poland.

Cluster 2 includes xerothermic pine forests developing on shallow soils formed on ultra-metamorphic bedrock, included in the Czech Republic in the *Asplenio cuneifolii-Pinetum sylvestris* Pišta ex Husová in Husová et al. 2002 [51]. The differences between phytocoenoses described from the Czech Republic and Poland are insignificant—in the Czech Republic, *Erica carnea* L., which is not present in Poland, is one of the diagnostic species, and *Larix decidua* Mill., which is a symptom of phytocoenoses deformations due to forest management, was also more frequent in the Czech stands. Other species, such as *Asplenium cuneifolium*, *Silene vulgaris* and *Festuca ovina* L., are diagnostic for the association in both countries. However, analogous serpentine communities in Austria (*Festuco eggleri-Pinetum* Eggler 1954 corr Wallnofer 1993) already differ significantly in terms of floristic composition [52,53]. The *Asplenio cuneifolii-Pinetum sylvestris* association has not been recorded in Poland so far.

Cluster 3 includes rocky, thermophilic pine forests of the *Hieracio pallidi-Pinetum sylvestris* Stöcker 1965 association, found so far on three sites on the peaks of granite hills in the Kotlina Jeleniogórska and its surroundings (Chojnik Mt., Witosza Mt. and Krzyżna Góra Mt.). The phytocoenoses known from Chojnik were originally described by Matuszkiewicz A. and W. [12,13] as *Leucobryo-Pinetum*, then by Świerkosz [54] as *Betulo carpaticae-Pinetum*; the other sites have no published phytosociological documentation. Of the diagnostic species [55], the most important ones are bryophytes (*Polytrichum piliferum* Hedw., *Ceratodon purpureus* (Hedw.) Brid), although one of the plots on Chojnik Mt. also recorded another important species for the diagnosis of the association, *Hieracium schmidtii* Tausch [54] (Table 1, erroneously as “*Hieracium glaucinum*”). The phytocoenoses of rocky pine forests in the Sudetes are severely impoverished, probably due to their presence on the northern border of the range and a small number of typical species’ sites. They are also exposed to the invasion of alien species, especially *Pseudotsuga menziesii* (Mirb.) Franco. These communities require further research, especially on the associated lichen flora and the origin of the pine trees. This association has not been recorded in Poland so far, but is found in the close vicinity of its borders in the Czech Republic [55] and Germany [56].

Cluster 4 embraces a typical forms of mesic pine forests which are of both anthropogenic and probably natural origin, belonging to the association *Vaccinio myrtylli-Pinetum* with the typical species composition of vascular plants and bryophytes [7,11]. The part of the phytocoenoses reported in the past from the Karkonosze mountains [12,13], the Ślęza Massif and Oleszeńskie Hills [14] and the Grochowa Massif [15] under the name *Leucobryo-Pinetum* (earlier synonym) in fact represent *Vaccinio myrtylli-Pinetum*. The association is frequent throughout Central Europe [7,11,50,52,53,57].

The relict, rocky pine forests on the sandstones of lower mountain zone (cluster 5), occurring on both sides of the Polish-Czech border. They were first described as *Betulo carpaticae-Pinetum* by Mikyška [10] and then reported by Passarge [58] from the Zittau mountains (Zittauer Gebirge) on the Czech-German border. This is how they were treated in some synthetic studies from the Bohemian Massif [59], and even suggested that they form an endemic association of this structural unit [60]. This concept has not yet been adopted and the name is now treated as a synonym for the *Vaccinio myrtylli-Pinetum* [11], while the association’s distinctiveness is supported by many specific floral and ecological characteristics. Pine trees occurring here are a postglacial relicts as shown by Bobowicz [61] and Krzakowa, Lisowska [62] and differ significantly from the lowland populations in Poland. The closest to them, in biochemical term, populations of pine are found in Finland [62]. The species composition of phytocoenoses from SW Poland includes both *Betula pubescens* specimens with distinct features of subalpine *B. pubescens* var. *glabrata* [63,64]

and hybrids with *Betula pubescens* var. *pubescens* [65]. Another species recorded in these phytocoenoses is subalpine *Pinus mugo* Turra and its hybrids with *P. sylvestris*—*P. x rhaetica* (= *P. uliginosa* Neumann) [66,67]. The herb layer is composed of rare in the study area species of boreocontinental range type (*Empetrum nigrum* L., *Vaccinium uliginosum*). The similarities of these phytocoenoses to subarctic ones are so clear that Kački et al. [68] proposed their inclusion in the *Betuletum pubescentis* var. *glabratae* Lohmeyer and Bohn 1962 from the class *Betuletea pendulo-pubescentis* Julve 2016 (now as *Vaccinio myrtilli-Betuleta pubescentis* Mucina et Willner ined.) [23], embracing European boreo-subarctic and orotemperate birch woods and krummholz on nutrient-poor podzolic soils. Regardless of the final solution adopted at a higher syntaxonomic level, it seems that this community should be given the status of an independent unit in the rank of an association.

Equally intriguing as the previous one is cluster 6, which includes bog pine–birch forests with the participation of *Betula pubescens* var. *pubescens* (communities with *Pinus sylvestris* belonging to the class *Oxycoco-Sphagnetes* Br.-Bl. et Tüxen ex Westhoff et al. 1946 were not the subject of present study). The species composition of phytocoenoses included here clearly indicates their affiliation with the *Vaccinio uliginosi-Betuletum pubescentis* Libbert 1933 (e.g., through the presence of *Salix aurita* and some bog species of *Cyperaceae* and the lack of *Rhododendron tomentosum* Harmaja); in the Polish phytosociological literature this name refers to communities in the north-western part of Poland occurring in the sub-Atlantic climate range [7,8]. It is not known where this limitation comes from, since the association is also recorded in the southern part of Germany [57]; in the Czech Republic [69], Austria [52] and Slovakia a similar *Eriophoro vaginati-Betuletum pubescentis* (Hueck 1931) Passarge et Hoffmann 1968 [50,70] was recorded. However, in Slovakia this community is more continental in character, and is classified within the *Alnetea glutinosae* Br.-Bl. et R. Tx. ex Westhoff et al. 1946 or the *Molinio-Betuletea pubescentis* Passarge et Hofmann 1968 classes [38].

In present study we also distinguished three different communities of anthropogenic pine forests established by planting *Pinus sylvestris* in deciduous and mixed forest habitats. Most of these patches represent anthropogenic ecosystems with random combinations of species, in which a group of common forest generalists also participates. Only the communities on nutrient-poor substrates (comm. *Pinus sylvestris-Molinia caerulea*) refer to the floristic composition of the native communities within the *Luzulo-Fagion sylvaticae* alliance.

A distinct feature of these anthropogenic and artificial forest ecosystems is the presence of non-forest species which find here optimal conditions and benefit from changes caused by forest management and other anthropogenic processes of global character—eutrophication [71,72], invasions of geographically alien species [73,74] and thermophilization—all connected with climate change and enhanced by direct human impact on forests [75,76]. These processes favor the entry of species which have not been present in native forest ecosystems so far, and their impact is particularly noticeable in the group of secondary (artificial) communities. The same refers to neophyte species whose presence is particularly pronounced in the discussed communities of anthropogenic character (Table 4).

Among the neophytes, the most common are *Impatiens parviflora*, *Quercus rubra* and *Robinia pseudoacacia* L. for which artificial pine forests are favorable habitats, especially when compared with pine communities of natural character. Among the latter ones, neophytes were encountered only occasionally (clusters 3 and 4) or were not recorded at all (clusters 5 and 6). This suggests that anthropogenically altered forests, heavily overexposed and with a disturbed undergrowth structure, may be a kind of gateway through which alien species enter the local pool of forest communities. Such a mechanism is known and well documented from both forests [77–79] and other types of ecosystems worldwide [80]. Research conducted in both tropical [81] and temperate forests [82] indicates that tree felling creating large gaps, combined with wide roads for transporting timber, enhances the penetration of alien species into native communities. The share of neophytes in the undergrowth increases as the crown density decreases [82]. Although many attempts of invasion fail and alien species disappear as the forest regenerates and

light availability declines [81], some of them become invasive. They start to modify the structure of ecosystems significantly, e.g., by limiting the growth of seedlings [83], directly competing with native species and changing the physical, chemical and biotic properties of environment [83,84]. Among the species considered highly invasive in Europe [83], and reported also during present study, at least five (*Impatiens parviflora*, *Solidago gigantea*, *Quercus rubra*, *Robinia pseudoacacia* and *Prunus serotina*) fully meet the definition of “transformers”—species which change the structures of ecosystems [85]. Their high share in forest plantations creates a serious risk of transition to native forest communities in the closest vicinity, as previously reported from many forests of tropical [81] and subtropical zones [84].

Table 4. The percentage frequency of neophytes in a given cluster, selected from the full synthetic table of the Scots pine forests, recorded in the Sudetes mountains and their foreland.

Cluster No.	1	2	3	4	5	6	7	8	9
<i>Impatiens parviflora</i>	-	18	-	-	-	-	79	36	13
<i>Quercus rubra</i>	-	9	-	-	-	-	15	43	33
<i>Robinia pseudoacacia</i>	-	36	-	-	-	-	3	7	-
<i>Solidago gigantea</i>	-	5	-	-	-	-	3	7	-
<i>Prunus serotina</i>	-	-	-	-	-	-	10	86	-
<i>Pseudotsuga menziesii</i>	-	-	25	6	-	-	-	-	-
<i>Amelanchier spicata</i>	-	-	-	-	-	-	3	7	-
<i>Oxalis corniculata</i>	-	-	-	-	-	-	5	-	-
<i>Symphoricarpos albus</i>	-	-	-	-	-	-	5	-	-
<i>Pinus strobus</i>	-	-	-	-	-	-	3	-	-
<i>Parthenocissus inserta</i>	-	-	-	-	-	-	-	7	-

A similar relationship was observed for nitrophilous species ($EIV \leq 7$)—*Rubus fruticosus* agg., *Sambucus nigra* L., *S. racemosa* L., *Senecio ovatus* (G. Gaertn. & al.) Hoppe, *Stellaria media* (L.) Cirillo, *Galium aparine* L., *Urtica dioica* L., *Geum urbanum* L., *Elytrigia repens* (L.) Nevski, *Alliaria petiolata* (M. Bieb.) Cavara & Grande, *Geranium robertianum* L., *Aegopodium podagraria* L., *Chaerophyllum temulum* L., *Chelidonium majus* L. and *Ranunculus repens* L. were found only in secondary pine forests (comm. *Impatiens parviflora*-*Pinus sylvestris*, comm. *Prunus serotina*-*Pinus sylvestris*, comm. *Molinia caerulea*-*Pinus sylvestris* and ass. *Asplenio cuneifolii*-*Pinus sylvestris*). This may indicate the role that secondary forests play in the general decline of native forest biodiversity in Europe [72,86]. It should be emphasized that the majority of the analyzed patches are located within larger forest complexes, and the Polish rules of forest management do not require additional fertilization of plantations established in such areas. Therefore, the presence of alien and nitrophilous species can be associated with the direct impact of the management itself, i.e., the harvesting of wood and then the renewal of the area by natural or artificial pine planting.

5. Conclusions

In this study we distinguished five associations: thermophilous *Asplenio cuneifolii*-*Pinetum sylvestris*, which develops on shallow soils over ultrabasic substrates, *Hieracio pallidi*-*Pinetum sylvestris*, which prefers outcrops of acidic rocks; *Betulo carpaticae*-*Pinetum sylvestris*, which is relict in origin and occurs on the upper Cretaceous sandstones; the peatland pine–birch forests of the *Vaccinio uliginosi*-*Betuletum pubescentis* and the *Vaccinio myrtilli*-*Pinetum sylvestris* previously described as the *Leucobryo*-*Pinetum*. Moreover, community *Brachypodium sylvaticum*-*Pinus sylvestris* with the occurrence of many thermophilous and basiphilous species was also found on limestone substratum. Three of the abovementioned syntaxonomical units are new for Poland. The obtained results also indicate that the anthropogenic pine plantations established in deciduous and mixed forests habitats are marked by a random combination of species in which a certain group of common forest generalists participated. The distinguished syntaxonomical units differ clearly among each other in habitat characteristics as well. Particularly important for their differentiation are

edaphic conditions reflected by soil reaction and nutrients. Studied communities show their distinctiveness also in terms of moisture, temperature, light availability, altitude and bedrock type.

Aliens, including invasive species and nitrophilous, non-forest species were recorded within secondary forest communities (comm. *Impatiens parviflora*-*Pinus sylvestris*, comm. *Prunus serotina*-*Pinus sylvestris*, comm. *Molinia caerulea*-*Pinus sylvestris*, ass. *Asplenio cuneifolii*-*Pinus sylvestris*) almost exclusively. This may indicate the general role of such secondary forests in the decreasing of native forest biodiversity not only on a local, but also on a European scale.

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