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Secondary Serpentine Forests of Poland as a Refuge for Vascular Flora

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Abstract: The aim of present study was to determine the role of secondary, serpentine forests in Poland in the protection of rare vascular plant species. On the basis of 95 phytosociological relevés collected between 2009 and 2020, we identified the main types of serpentine forest communities and assessed their diversity indices. Ordination methods were used to determine the relationship between the degree of transformation of forest communities (reflected by the occurrence of alien and nitrophilic species) and the presence of endangered species in their undergrowth including the environmental background. We distinguished four types of communities: thermophilic and mesophilic pine plantations (both secondary in origin) as well as thermophilous oak forest and acidophilous oak–hornbeam forest (semi-natural and close to natural in character, respectively). Rare and endangered species were unevenly distributed and concentrated in oak forest (16 species) and thermophilic pine plantation (nine species). The endangered species mainly preferred sites at higher altitudes and with higher slope inclination, light availability, and soil reaction. We did not confirm that the presence of alien or nitrophilic species negatively influenced the ability of studied forests to preserve rare plants. As secondary forests can still harbor endangered species, they should fulfil complementary functions in the nature protection system.

Keywords: biodiversity; forest management; nature preservation; pine plantations; secondary habitats; Sudetes Foreland; ultramafic vegetation



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1. Introduction

Multi-species, deciduous forests of the temperate zone were the dominant type of vegetation in the Holocene over most of Central and Eastern Europe, except in marginal habitats and higher mountain altitudes [1]. As a result of thousands of years of human interference with the natural environment, forest communities of the temperate zone have been largely destroyed or transformed and primary forests are extremely rare today [2,3]. Increasing demand for timber, farmland, and pastures caused a significant proportion of forest communities to be cleared or converted into high-productivity silviculture [1]. On the other hand, recent, far-reaching impacts due to nitrogen deposition [4–6], management practices [7,8], and climate change [9,10] induce changes in species composition of the herb layer of temperate forests that are of natural or close to natural character. Moreover, these changes are strongly influenced by local factors, causing different forest communities to respond in different ways [11].

Ultramafic rocks and serpentine soils derived from them create one of the most specific habitats on which extraordinary flora and vegetation can be found [12–14]. Plants that occupy serpentine soils are forced to develop a number of adaptations due to the pressure of adverse metabolic factors such as high content of heavy metal ions (mainly nickel, cobalt, and chromium) and a disturbed ratio of calcium and magnesium, with the concentration

of the latter exceeding the toxicity threshold for some species [13,15,16]. However, other conditions associated with ultramafic substrates, such as low content of nutrients, limited water capacity, and susceptibility to drought stress due to the shallow soil profile mainly resulting from topographical features, appear to affect vegetation to a greater extent than heavy metal content [17,18].

In Poland, serpentinite substrates can be found only in the southwestern part of the country, extending over the area of approximately 100 km² [19], of which approximately 18 km² is forested. A specific forest community which develops on ultramafic soils are thermophilic oak forests (comm. *Galium verum-Quercus petraea*). They mainly consist of multi-stem forms of *Quercus petraea* (Matt.) Liebl., which usually occupy slopes with southern or southwestern exposure [20]. The outstanding species composition and physiognomy of these forests were largely shaped by cattle grazing and in the mid-19th century by their conversion into coppiced forests [21]. Presently, these phytocoenoses are highly endangered in the European Union (EU) and are disappearing throughout their range, similar to other types of coppiced forests [22–24]; hence, they have been included as a priority habitat 9110 Euro-Siberian steppic woods with *Quercus* spp. in Annex I of the Habitats Directive [25]. In the lower parts of the hills, on deeper soils, the oak–hornbeam forests *Tilio cordatae–Carpinetum betuli* Traczyk 1962 develop. They usually occur in the studied region on the western border of their range [26], gradually changing in some places into the acidophilic oak forests of the *Calamagrostio arundinaceae–Quercetum petraeae* (Hartmann 1934) Scamoni et Pass. 1959 [20]. Occasionally, we also meet here other forest communities, but they occupy extremely small areas and were therefore not included in this study.

Most of the forests communities originally found on Central European serpentinites have been converted into conifer monocultures, and less frequently into mixed forests with a still high proportion of coniferous species. The species commonly planted was *Pinus sylvestris* L. However, it should be emphasized that some anthropogenic pine forests on serpentine substrates are so specific that they were described as a separate association *Asplenio cuneifolii–Pinetum sylvestris* Pišta ex Husová in Husová et al., 2002 [27,28]. Other species introduced in serpentine habitats were *Picea abies* (L.) Karts. and North American taxa—*Pseudotsuga menziesii* (Mirbel) Franco [29], *Quercus rubra* L. [30], or *Robinia pseudoacacia* L. [31,32]. The latter species soon established themselves in Central European forests and became invasive, posing a serious threat to local biodiversity [33] reflected by its loss due to disappearance of species typical of deciduous forests [34].

In view of the progressive changes in the species composition of forest phytocoenoses, we in the present study had the main purpose of determining the role of secondary serpentine forests for the protection of rare vascular plant species. We hypothesized that (1) rare and endangered species are concentrated in particular types of forests, and (2) forest communities that host endangered species differ from others in respect of environmental characteristics.

2. Materials and Methods

2.1. Study Area

The research was conducted within forests occurring on ultramafic soils on the area of the Sudetes Mts and their foreland (Southwestern Poland, Figure 1). The study area, where the most of phytosociological relevés were collected, extends over the ranges of hills located in the southern and southwestern part of the Ślęza ophiolite massif (Oleszeńskie Hills, Kielczyńskie Hills) and in the Grochowa Massif located in the Pogórze Paczkowskie Plateau. Small patches of Scots pine forests on peridotite outcrops near Janowice Wielkie in the Rudawy Janowickie Mts were also included in the research. The altitude span of the studied phytocoenoses varies from 270 m.a.s.l. in Oleszeńskie Hills to 575 m.a.s.l. near the peak of Radunia Mt. The average annual rainfalls varies from 530 mm in the Sudetes Foreland (data for Sobótka) to 730 mm in the Rudawy Janowickie Mts (data for Kamienna Góra), with the highest rainfall during the summer time. The average annual temperature in the studied area for the last 30 years (1991–2020) varies from 9.7 °C on lowlands (data

for Wrocław) to 8 °C in the foothills (data for Jelenia Góra) (Institute of Meteorology and Water Management—National Research Institute, data were processed and rearranged, <https://meteomodel.pl/dane/> (accessed on 1 April 2021)).

Part of the study area is protected under EU legislation as the Sites of Community Importance (PLH020040 Masyw Ślęzy and PLH020021 Wzgórza Kiełczyńskie).

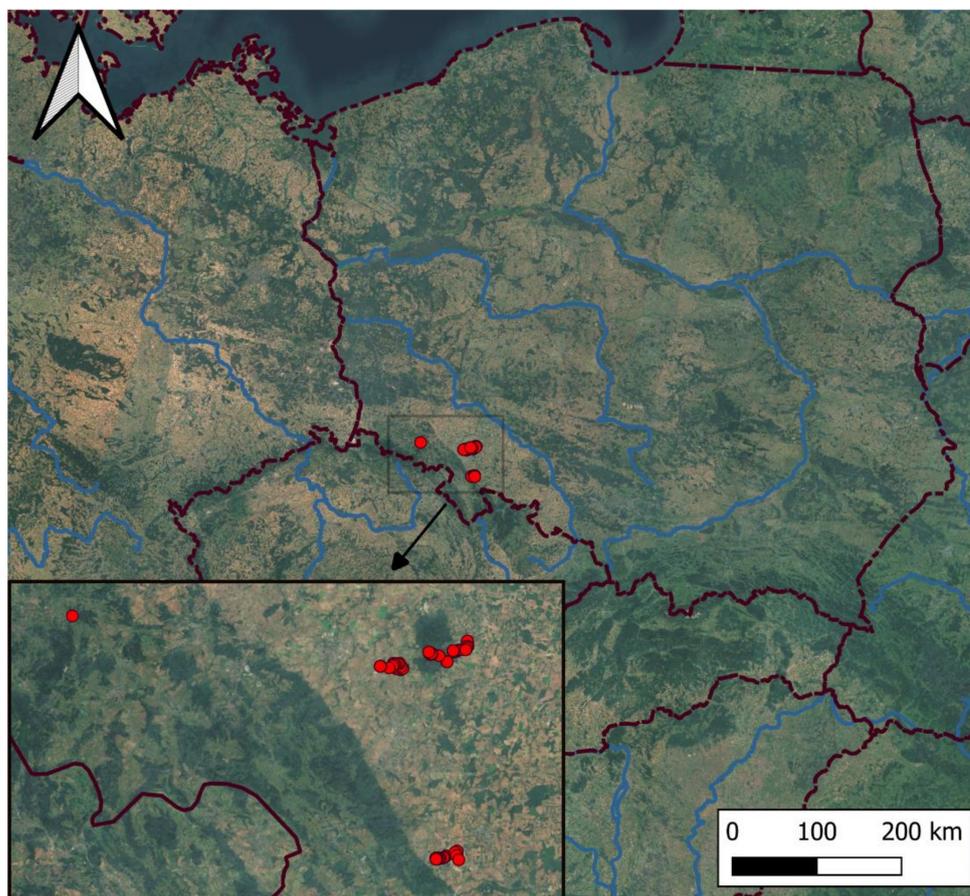


Figure 1. Area of investigation. Dots indicate the location of the relevés from serpentine forests in SW Poland analyzed in this study (©MapTiler ©OpenStreetMap contributors).

2.2. Field Sampling and Nomenclature

Data were collected within the following types of forests—deciduous (dominated by oak *Quercus petraea* and lime *Tilia cordata* Mill.) as well as coniferous (dominated by Scots pine *Pinus sylvestris*, Norway spruce *Picea abies*, or European larch *Larix decidua* Mill.) forests. Between 2009 and 2020 in randomly chosen stands, phytosociological relevés reflecting vegetation composition and structure were collected, according to the Braun–Blanquet approach using a 7-point scale for assessing species coverage [35]. The entire dataset used during analyses contained 95 relevés (6.3 vegetation plots per 1 square kilometer). The relevés’ area ranged from 100 square meters up to 400 square meters. The location of each relevé was recorded using Aventura TvoNav GPS with Sirf Star III chipset; slope was measured in the field with electronic compass, and altitude was taken from a topographical map based on field coordinates. All of the relevés were stored and maintained using TURBOVEG software [36], which enabled the creation of a database, which was then used for numerical and environmental analyses.

The nomenclature for vascular plants follows Euro+Med PlantBase [37] and Ochyra et.al. [38] for mosses. Species records of closely related species from *Rubus* genus, except *R. idaeus*, *R. caesius*, and *R. hirtus* agg. (*R. hirtus*, *R. pedemontanus*) were merged into

one aggregate *Rubus corylifolius* agg. The nomenclature of higher vegetation units in the rank of class, order, and alliance is in accordance with Mucina et al. [39].

2.3. Differentiation and Diversity Measures of Studied Communities

The vegetation types were identified using a modified TWINSpan algorithm [40] with Total Inertia measure of heterogeneity using JUICE software [41]. Species coverage was converted from the Braun–Blanquet scale into a percentage scale. 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 [42]. In order to determine diagnostic species, we used the Φ coefficient as a measure of fidelity for clusters of equalized size [43,44]. Species with $\Phi \geq (0.3 \times 100)$, constancy $\geq 20\%$, and constancy ratio higher than 1.5 were considered to be diagnostic for each cluster [45]. Constant species were defined as taxa with frequency $\geq 60\%$ in all relevés in a given cluster.

Three indices were used to estimate the level of vegetation diversity and species richness of the studied clusters. Shannon–Wiener Index, Simpson Index, and the mean number of species in relevés were calculated using JUICE software [41].

As there were no direct measurements of light and soil conditions, we used Ellenberg indicator values (EIVs) [46], corrected by datasets of Berg et al. [47] with reference to values of continentality. EIVs weighted by percentage species' cover were calculated for each relevé using the JUICE software [41] in order to enable passive projection of the variable into DCA diagram.

2.4. Analysis of Species of Interest Relationships

In order to determine the relationship between the degree of transformation of forest communities and the presence of valuable species of vascular flora in their undergrowth, we included only the groups of species of our interest, which were selected based on synthetic sources, in further analyses. We distinguished the following groups: species considered rare and endangered at national [48] and regional levels [49], alien species [33], and nitrophilic species for which the EIV for nutrients ≥ 7 [46]. The presence and abundance of alien and nitrophilic species is an unambiguous indicator of the distortion of ecosystems [50]—we were therefore particularly interested in those patches in which alien species, nitrophilic and threatened with extinction, coexisted side by side. In order to analyze their coexistence, we used two types of ordination methods. Unconstrained and constrained ordination were performed separately with the Canoco 5 software [51]. The structure of the dataset was analyzed with a detrended correspondence analysis (DCA). The gradient length for the first axis was found as 3.46 SD, which implied unimodal ordination methods. Scaling by segments and square-root transformation of species cover data were used in the DCA to compare distribution of the selected group of species. In the second stage, a canonical correspondence analysis (CCA) was performed to estimate the role of measured environmental variables (altitude, slope) in differentiation of selected groups of species occurring in the recognized clusters.

3. Results

3.1. Differentiation of Forest Communities

On the basis of numerical analyses, we distinguished four clusters significantly different in terms of origin, species composition, and habitat conditions (Figure 2). In the description of each cluster presented below, we focused on diagnostic and constant taxa. However, more detailed information on species composition of studied forest communities is included in Table S1.

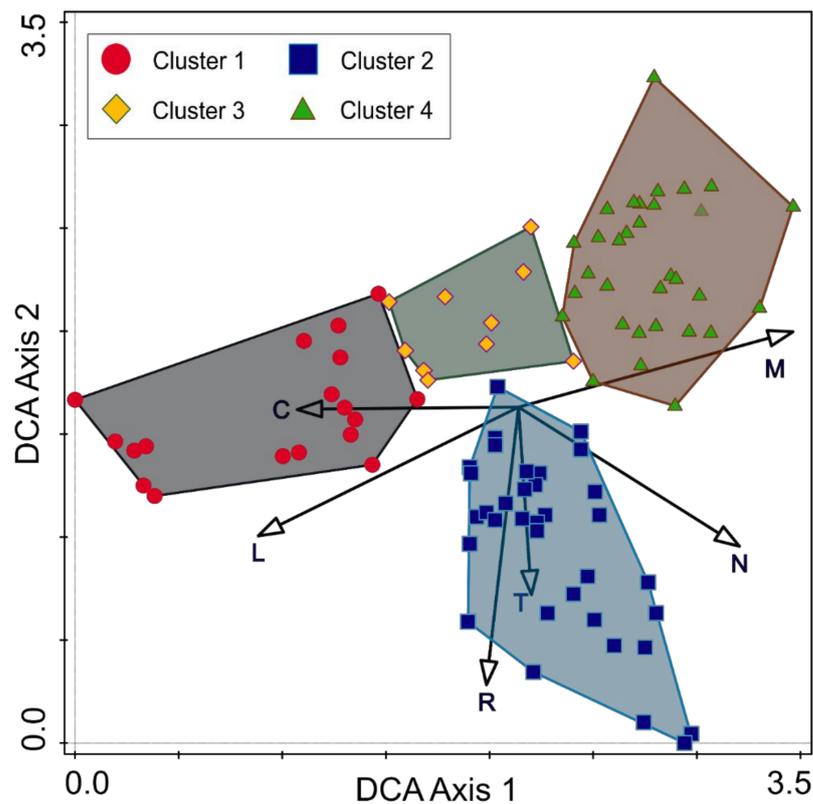


Figure 2. The passive projection of Ellenberg indicator values (EIVs) into the DCA ordination diagram of differentiation of forest communities on serpentinites of SW Poland. Gradient length = 3.46 SD units. Total variation was 5.81, supplementary variables accounted for 19.51% (adjusted explained variation was 13.03%). Explanation: cluster 1—Ass. *Asplenio cuneifolii*–*Pinetum*; cluster 2—comm. *Galium verum*–*Quercus petraea*; cluster 3—comm. *Pinus sylvestris*–*Molinia caerulea*; cluster 4—Ass. *Tilio cordatae*–*Carpinetum betuli*; C—EIV for continentality; T—EIV for temperature; L—EIV for light; M—EIV for moisture; R—EIV for soil reaction; N—EIV for nutrients.

The distinguished forest communities differ among one another also in terms of biodiversity indices (Table 1). The *Asplenio*–*Pinetum* phytocoenoses show the highest values of both the average number of species per plot and the Shannon–Wiener Index, while the thermophilous oak forests are only slightly lower. Oak–hornbeam forests show the lowest values in all biodiversity indicators.

Table 1. Selected biodiversity indicators calculated for forest communities on serpentinites in SW Poland (Sudetes Foreland).

Forest Community	Mean No. of Species Per Plot	Simpson Index	Shannon–Wiener Index
Ass. <i>Asplenio cuneifolii</i> – <i>Quercetum petraeae</i>	33.3	0.87	2.73
Comm. <i>Galium verum</i> – <i>Quercus petraea</i>	32.8	0.83	2.62
Comm. <i>Pinus sylvestris</i> – <i>Molinia caerulea</i>	29.8	0.87	2.54
Ass. <i>Tilio cordatae</i> – <i>Carpinetum betuli</i>	23.0	0.77	2.14

Cluster 1. *Asplenio cuneifolii*–*Pinetum* Pišta ex Husová in Husová et al., 2002—thermophilous serpentine pine wood

Number of relevés: 18.

Diagnostic species: *Achillea millefolium*, *Asplenium cuneifolium*, *Calamagrostis epigejos*, *Campanula rotundifolia*, *Centaurea scabiosa*, *Centaurea stoebe*, *Danthonia decumbens*, *Dianthus carthusianorum*, *Euphorbia cyparissias*, *Festuca ovina*, *Filipendula vulgaris*, *Galium verum*, *Hieracium murorum*, *Hieracium pilosella*, *Koeleria macrantha*, *Phleum phleoides*, *Pimpinella saxifraga*,

Potentilla arenaria, *Prunus avium*, *Pyrus pyraister*, *Robinia pseudoacacia*, *Rumex acetosella*, *Thymus pulegioides*, *Viscaria vulgaris*.

Constant species: *Achillea millefolium*, *Calamagrostis epigejos*, *Campanula rotundifolia*, *Deschampsia flexuosa*, *Euphorbia cyparissias*, *Festuca ovina*, *Galium verum*, *Pimpinella saxifraga*, *Pinus sylvestris*, *Prunus avium*, *Quercus petraea*, *Rubus fruticosus* agg., *Silene vulgaris*, *Sorbus aucuparia*, *Viscaria vulgaris*.

The tree layer is anthropogenic in origin and dominated by *Pinus sylvestris*. However, within some patches, the admixture of *Larix decidua* and *Betula pendula* is present. The species that are a constant component of the herb layer of thermophilic serpentine pine forest mainly represent the *Festuco-Brometea* Br.-Bl. et Tx. ex Soo 1947 class and the *Quercion petraeae* Issler 1931 alliance. The most frequent occurrences here are *Viscaria vulgaris*, *Pimpinella saxifraga*, *Thymus pulegioides*, *Potentilla arenaria*, and *Asplenium cuneifolium*. A high proportion is presented also by graminoids such as *Festuca ovina*, *Calamagrostis arundinacea*, and *C. epigejos*. In some of the patches, bryophytes are also present, mainly *Pleurozium schreberi* and *Hypnum cupressiforme*.

The species richness of the *Asplenio cuneifolii*-*Pinetum* in the study area is marked by both the highest Shannon–Wiener (2.73) and Simpson (0.87) biodiversity indicators, as well as a very high average number of species in the relevés (33.3 specie per plot). The patches of the community usually occupy the southern and southwestern slopes with an inclination between 10° and 30°, at altitude from 320 m to 460 m.a.s.l.

Cluster 2. Community *Galium verum*-*Quercus petraea*—serpentine, thermophilous oak forest

Number of relevés: 37.

Diagnostic species: *Agropyron repens*, *Anthericum ramosum*, *Campanula persicifolia*, *Convallaria majalis*, *Dryopteris filix-mas*, *Euonymus europaea*, *Fallopia dumetorum*, *Galeopsis ladanum*, *Galium boreale*, *Galium schultesii*, *Genista tinctoria*, *Lathyrus niger*, *Lathyrus vernus*, *Lilium martagon*, *Linaria vulgaris*, *Melica nutans*, *Mercurialis perennis*, *Poa nemoralis*, *Polygonatum odoratum*, *Rhamnus catharticus*, *Sedum maximum*, *Serratula tinctoria*, *Urtica dioica*, *Vincetoxicum hirundinaria*.

Constant species: *Calamagrostis arundinacea*, *Convallaria majalis*, *Deschampsia flexuosa*, *Galium verum*, *Luzula luzuloides*, *Pinus sylvestris*, *Poa nemoralis*, *Polygonatum odoratum*, *Quercus petraea*, *Rubus idaeus*, *Silene vulgaris*, *Sorbus aucuparia*, *Vaccinium myrtillus*.

The tree layer mainly (in some patches even exclusively) consists of *Quercus petraea*, which may be occasionally accompanied by conifers such as *Pinus sylvestris* and *Pseudotsuga menziesii*. The species composition of the undergrowth includes numerous thermophilic species (*Euphorbia cyparissias*, *Polygonatum odoratum*, *Lathyrus niger*, *Anthericum ramosum*, *Galium verum*, *Silene vulgaris*); acidophytes (*Luzula luzuloides*, *Vaccinium myrtillus*); and the group of mesophilic, nemoral species (*Convallaria majalis*, *Calamagrostis arundinacea*, *Dryopteris filix-mas*, *Poa nemoralis*). Chasmophytic ferns of the genus *Asplenium* (*A. septentrionale*, *A. cuneifolium*, *A. adiantum-nigrum*) and other species rare in the region, such as *Galium pumilum*, *Allium montanum*, and *Festuca pallens*, occur in the serpentine outcrops and rubbles. The shrub layer is dominated by *Quercus petraea*. The moss layer is usually present but reaches here lower coverage in comparison to pine forest and its main component is *Hypnum cupressiforme*.

The species richness of the comm. *Galium verum*-*Quercus petraea* is comparable to the analogous habitats of anthropogenic pine forests. The mean number of species in the patch is similar (32.8 species per plot); Shannon–Wiener (2.62) and Simpson (0.83) indices are slightly lower. Within serpentine oak forests, a lower share and coverage in the patches is achieved by species of xerothermic grasslands, while the presence of mesophilic forest generalists is noticeable. This community usually occupies S-, SW-, and SE-facing slopes, with inclination between 5° and 30° at altitude from 260 m to 575 m.a.s.l.

Cluster 3. Community *Pinus sylvestris*-*Molinia caerulea*—mesophilous, secondary pine forest

Number of relevés: 12.

Diagnostic species: *Betula pendula*, *Deschampsia flexuosa*, *Dryopteris carthusiana*, *Larix decidua*, *Pinus sylvestris*, *Pseudoscleropodium purum*, *Rubus hirtus* agg., *Senecio ovatus*, *Vicia cassubica*.

Constant species: *Calamagrostis arundinacea*, *Deschampsia flexuosa*, *Dryopteris carthusiana*, *Larix decidua*, *Luzula luzuloides*, *Pinus sylvestris*, *Quercus petraea*, *Rubus fruticosus* agg., *Sorbus aucuparia*, *Vaccinium myrtillus*.

Artificial stands dominated by *Pinus sylvestris*, *Larix decidua*, *Quercus petraea*, and frequent presence of *Betula pendula*, *Fagus sylvatica*, and *Picea abies*, of a submontane character (*Luzula luzuloides*, *Senecio ovatus* agg.). In the herb layer, acidophilic and mesophilic graminoids such as *Calamagrostis arundinacea*, *Luzula luzuloides*, *Deschampsia flexuosa*, and *Molinia caerulea* are the most abundant. This community is also characterized by a high contribution of other acidophytes (*Vaccinium myrtillus*, *Hieracium sabaudum*, *H. vulgatum*) and mesophytes (*Dryopteris carthusiana*, *Poa nemoralis*, *Maianthemum bifolium*). Occasionally, and with lower coverage, they are accompanied by representatives of thermophilic vegetation, mainly *Hypericum montanum*, *Silene vulgaris*, and *Galium verum*. Despite the anthropogenic origin of the community, geographically alien species have a small contribution here, which in turn does not apply to *Rubus fruticosus* agg. The shrub layer is scarcely developed and formed by *Quercus petraea*, less often by *Corylus avellana*. The moss layer reaches from 0% to 40% coverage, and their main components are *Pseudoscleropodium purum*, *Hypnum cupressiforme*, and *Polytrichastrum formosum*.

Phytocoenoses of the comm. *Pinus sylvestris*–*Molinia caerulea*, despite their anthropogenic origin, are only slightly behind the plots previously described in terms of mean number of taxa (29.8 species per plot), as well as Shannon–Wiener (2.54) and Simpson (0.87) indices. The community usually occupies northern and northwestern slopes with an inclination up to 20°, at altitude from 350 m to 415 m.a.s.l.

Cluster 4. Ass. *Tilio cordatae*–*Carpinetum betuli* Traczyk 1962—subcontinental oak-hornbeam forest

Number of relevés: 28.

Diagnostic species: *Atrichum undulatum*, *Dicranella heteromalla*, *Festuca altissima*, *Luzula luzuloides*, *Maianthemum bifolium*, *Tilia cordata*.

Constant species: *Calamagrostis arundinacea*, *Deschampsia flexuosa*, *Luzula luzuloides*, *Poa nemoralis*, *Quercus petraea*, *Rubus fruticosus* agg., *Sorbus aucuparia*, *Vaccinium myrtillus*.

Subcontinental oak-hornbeam forest with the tree layer formed mainly by *Quercus petraea*, sometimes with an admixture of *Tilia cordata*, *Acer pseudoplatanus*, and *Fagus sylvatica*. The shrub layer consists of *Quercus petraea* and *Tilia cordata*, while *Frangula alnus* and *Corylus avellana* are also relatively common. These phytocoenoses are characterized by a combination of acidophilic species (*Vaccinium myrtillus*, *Luzula luzuloides*, *Deschampsia flexuosa*, *Melampyrum pratense*); mesophilous forest generalists (*Maianthemum bifolium*, *Festuca altissima*, *Convallaria majalis*, *Pteridium aquilinum*, *Polygonatum verticillatum*); and eutrophic, deciduous forest species (*Polygonatum multiflorum*, *Milium effusum*). On the other hand, thermophilic species are almost completely absent. The degree of transformation of the patches of this association is evidenced by the large proportion of nitrophilic species such as *Galium aparine*, *Sambucus nigra*, and *Rubus fruticosus* agg., as well as the expansion of the invasive *Impatiens parviflora*. The moss layer is composed mainly of *Polytrichastrum formosum*, *Dicranella heteromalla*, and *Hypnum cupressiforme*, but in most plots, bryophytes do not reach a coverage higher than 10%.

Subcontinental oak–hornbeam forests are the poorest in species of all communities presented in this study. The value of the Shannon–Wiener and Simpson indices in their case were 2.14 and 0.77, respectively, while the average number of taxa was found to be 23 species per plot. The community occupies the N-, NW-, NE-, and W-facing slopes with an inclination up to 20° at altitudes from 275 m to 370 m.a.s.l.

3.2. Species of Interest in Studied Forest Communities

Within the 95 analyzed phytosociological relevés, 224 species of vascular plants and 13 species of bryophytes were found. The average number of species per one record within

the entire dataset was found to be 29.6, which indicates a significant species richness of communities associated with the serpentine substrates. Within the entire dataset, 20 species, considered to be rare or endangered at the country and/or region level, were found at 105 sites (Table 2).

Table 2. The list of rare and endangered species occurring within the study area, along with the extinction risk category based on the Red Lists of Plants for Poland [48] and Lower Silesia [49], as well as the confirmed number of sites in Lower Silesian serpentine forests.

Species Name—with Its Code ¹	Red List of Poland/Silesia Region	Total Number of Sites	Presence of Species in Recognized Cluster (Constancy in %)			
			1	2	3	4
<i>Asplenium cuneifolium</i> —AsplCune	EN/EN	12	50	8	-	-
<i>Cephalanthera longifolia</i> —CephLong	VU/VU	4	5	-	-	11
<i>Festuca heterophylla</i> —FestHetr	NT/VU	3	6	5	-	11
<i>Asplenium adiantum-nigrum</i> —AsplAdia	EN/CR	2	6	3	-	-
<i>Asplenium septentrionale</i> —AsplSept	VU/NT	3	-	8	-	-
<i>Asperula tinctoria</i> —AsprTinc	VU/EN	1	-	3	-	-
<i>Tanacetum corymbosum</i> —TancCorm	VU/VU	1	-	3	-	-
<i>Potentilla alba</i> —PotnAlba	-/NT	21	22	38	17	4
<i>Hypericum montanum</i> —HyprMont	-/NT	20	33	27	33	-
<i>Lilium martagon</i> —LiliMart	-/LC	11	-	30	-	-
<i>Potentilla cinerea</i> —PotnCirr	-/NT	9	44	-	-	-
<i>Bromus benekenii</i> —BromBenk	-/LC	5	11	-	-	4
<i>Festuca pallens</i> —FestPall	-/VU	3	-	8	-	-
<i>Allium montanum</i> —AlliMont	-/VU	2	-	5	-	-
<i>Galium pumilum</i> agg.—GaliPuml	-/LC	2	-	5	-	-
<i>Laserpitium latifolium</i> —LasrLatf	-/VU	2	-	5	-	-
<i>Chamaecytisus supinus</i> —ChamSupn	-/LC	1	-	3	-	-
<i>Thesium alpinum</i> —ThesAlpn	-/EN	1	11	-	-	-
<i>Geranium sanguineum</i> —GernSang	-/VU	1	-	3	-	-
<i>Peucedanum cervaria</i> —PeucCerv	-/NT	1	-	3	-	-
Total number of rare/endangered species			9	16	2	4

¹ Codes are the abbreviations of species names presented in ordination diagrams (DCA and CCA). Explanation: cluster 1—Ass. *Asplenio cuneifolii*-*Pinetum*; cluster 2—comm. *Galium verum*-*Quercus petraea*; cluster 3—comm. *Pinus sylvestris*-*Molinia caerulea*; cluster 4—Ass. *Tilio cordatae*-*Carpinetum betuli*.

The vast majority of rare and endangered species was recorded from one to three sites, only four species occurred in more than 10 sites, and the most frequent *Potentilla alba* was the component of the herb layer in 21 relevés. The highest risk categories in the region were assigned to *Asplenium adiantum-nigrum* (CR), *A. cuneifolium*, *Asperula tinctoria*, and *Thesium alpinum* (EN). Among threatened taxa, the most numerous was the group comprising species typical of rocky vegetation of the class *Asplenieta trichomanis* (Br.-Bl. in Meier et Br.-Bl. 1934) Oberd. 1977 (seven species) and xerophilous grasslands of the *Festuco-Brometea* class (eight species). The remaining five taxa were typical of thermophilous oak woods (*Lilium martagon*, *Potentilla alba*) and mesophilous deciduous forests (*Bromus benekenii*, *Festuca heterophylla*, *Cephalanthera longifolia*). The highest share of rare and endangered species was recorded in thermophilous oak forests (16 species—cluster 2) and anthropogenic thermophilous pine stands *Asplenio cuneifolii*-*Pinetum sylvestris* (nine species—cluster 1). In the other two clusters, they occurred sporadically.

In the entire dataset, 7 geographically alien species in 60 locations were found, four of which considered to be invasive taxa that pose a threat to the native flora (Table 3). A higher share of alien species was found in anthropogenic pine communities (4–5 species), while in deciduous forests there were only two taxa. *Impatiens parviflora* occurred in all types of studied communities but only in *Asplenio cuneifolii*-*Pinetum* phytocoenoses was it sporadically recorded; in other types of forests, its frequency achieved at least 25%.

Table 3. The list of alien (including invasive) and nitrophilic species (EIVs for nutrients ≥ 7) recorded in forest communities on serpentinites in SW Poland (Sudetes Foreland). For each species, the total number of sites and the percentage share in a given cluster are presented.

Species Name—with Its Code ¹	Total Number of Sites	Presence of Species in Recognized Cluster (Constancy in %)			
		1	2	3	4
Alien species					
<i>Impatiens parviflora</i> *—ImptParv	27	6	35	25	36
<i>Robinia pseudoacacia</i> *—RobnPseu	9	50	-	-	-
<i>Pseudotsuga menziesii</i> *—PseuMenz	7	-	3	8	-
<i>Quercus rubra</i> *—QuerRubr	6	17	-	17	4
<i>Vicia hirsuta</i> —ViciHirs	2	11	-	-	-
<i>Sarothamnus scoparius</i> —SartScop	1	-	-	8	-
<i>Amelanchier lamarckii</i>	1	-	-	8	-
Total number of alien species		4	2	5	2
Nitrophilic species					
<i>Stellaria media</i> —StellMedi	28	11	46	25	21
<i>Fallopia dumetorum</i> —FallDumt	25	22	54	8	-
<i>Agropyron repens</i> —AgrpRepn	20	17	41	-	7
<i>Galium aparine</i> —GaliApar	17	-	27	8	21
<i>Geranium robertianum</i> —GernRobr	15	6	30	17	4
<i>Urtica dioica</i> —UrtcDioi	12	-	24	-	11
<i>Taraxacum sect.</i>					
<i>Ruderalia</i> —TarSecRd	12	17	24	-	-
<i>Arrhenatherum elatius</i> —ArrhElat	7	17	8	8	-
<i>Sambucus nigra</i> —SambNigr	6	-	8	8	7
<i>Senecio ovatus</i> —SencOvat	6	6	3	25	4
<i>Geum urbanum</i> —GeumUrbn	5	6	8	-	4
<i>Chenopodium album</i> —ChenAlbm	1	6	-	-	-
<i>Chaerophyllum bulbosum</i> —ChaeBulb	1	-	3	-	-
<i>Rubus caesius</i> —RubsCaes	1	6	-	-	-
<i>Verbascum nigrum</i> —VerbNigr	1	-	9	-	-
<i>Verbascum thapsus</i> —VerbThap	1	6	-	-	-
<i>Alliaria petiolata</i>	1	-	3	-	-
<i>Anthriscus sylvestris</i>	1	-	3	-	-
<i>Tanacetum vulgare</i>	1	-	-	-	4
Total number of nitrophilic species		11	15	7	9

¹ Codes are the abbreviations of species names presented in ordination diagrams (DCA and CCA). Explanation: cluster 1—Ass. *Asplenio cuneifolii*–Pinetum; cluster 2—comm. *Galium verum*–*Quercus petraea*; cluster 3—comm. *Pinus sylvestris*–*Molinia caerulea*; cluster 4—Ass. *Tilio cordatae*–*Carpinetum betuli*. * (asterisk)—invasive alien species.

A reverse relationship was found for nitrophilic species (18 species), where the largest number was found in the *Galium verum*–*Quercus petraea* community (15 species). In the remaining communities—both in oak–hornbeam forests and in two types of anthropogenic pine stands—from 7 to 11 species from this group were recorded. *Stellaria media*, *Geranium robertianum*, and *Senecio ovatus* occurred in all clusters, while *Fallopia dumetorum*, *Agropyron repens*, *Galium aparine*, *Sambucus nigra*, and *Geum urbanum* were recorded in three types of studied ultramafic forests.

3.3. Main Environmental Gradients

The diversified species composition of the studied phytocoenoses, showing different preferences in relation to habitat and topographic factors, allowed for the identification of the main environmental gradients that caused the variability in the presence of the analyzed groups of species, i.e., rare and endangered, nitrophilic, and alien taxa. In the analysis of the coexistence of rare and endangered and alien species (Figure 3), the first and second DCA axes were responsible for 9.03% and 8.07% of the observed variability, respectively. The passive projection of the EIVs into the DCA diagram suggested that some of the geographically alien species were associated with moist and more nutrient-rich

habitats (*Impatiens parviflora*, *Quercus rubra*), as well as with a higher continentalism index (*Robinia pseudoacacia*) or light availability (*Vicia hirsuta*).

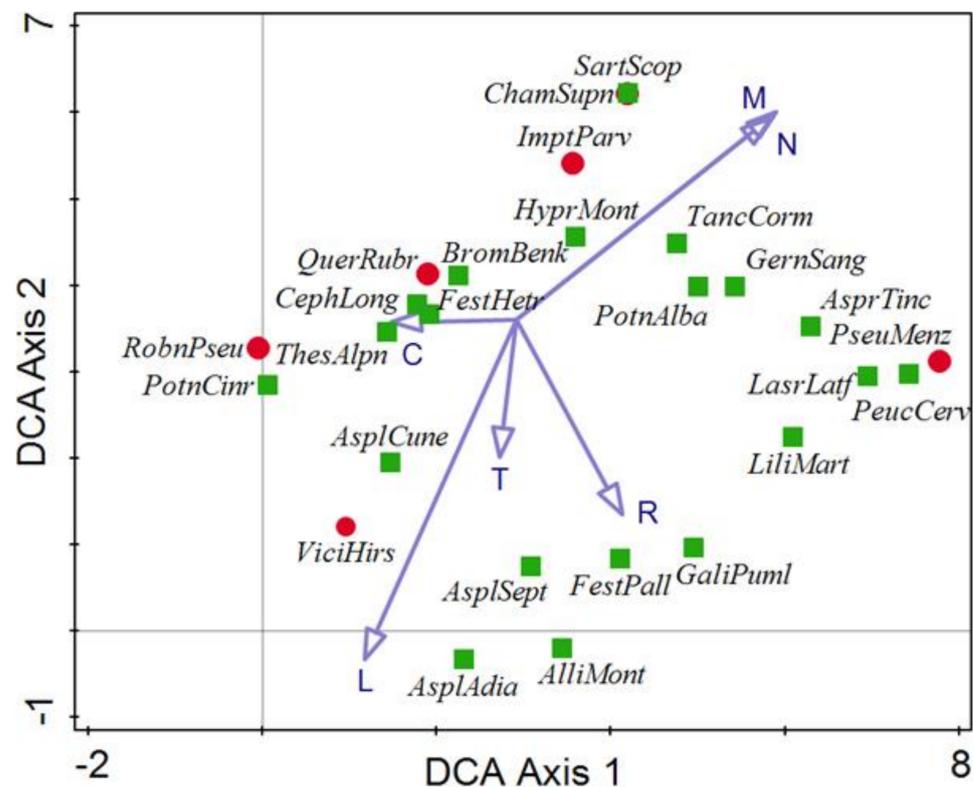


Figure 3. The passive projection of Ellenberg indicator values (EIVs) into DCA distribution diagram of alien (red circles) and rare/endangered species (green squares) recorded in serpentine forest communities in SW Poland. Species scores limit to 26 by weight. Abbreviations of species names are in accordance with these presented in Tables 2 and 3. Explanation: C—EIV for continentalism; T—EIV for temperature; L—EIV for light; M—EIV for moisture; R—EIV for soil reaction; N—EIV for nutrients.

In the analysis of the coexistence of groups of rare and nitrophilic species, the first DCA axis accounted for 8.48% and the second axis for 6.91% of the observed variability (Figure 4). Passive projection of the EIVs suggested that nitrophilic species occurred mainly in habitats with higher soil moisture and nutrient availability. In such conditions, however, they were accompanied by a number of rare species, such as *Potentilla alba*, *Hypericum montanum*, *Lilium martagon*, *Laserpitium latifolium*, or *Asperula tinctoria*. Occasionally, nitrophilic species may also appear in habitats with lower nutrients content (e.g., *Chenopodium album*).

The comparison of the distribution of rare and alien species in relation to environmental variables showed that the first CCA axis was related to altitude (pseudo-F 4.6, $p_{(adj.)} < 0.006$), while the second was related to slope inclination (pseudo-F 2.9, $p_{(adj.)} < 0.006$) (Figure 5). Moreover, the first and second axes accounted for 6.74% and 3.95% of variance, respectively. The distribution of alien species did not show a clear relationship with environmental variables, suggesting that they were reluctant to occupy higher locations (except *Pseudotsuga menziesii*) and steep slopes. The rise in the contribution of rare and endangered species was accompanied by the increase in altitude and slope inclination. A group of *Festuca pallens*, *Allium montanum*, *Asplenium adiantum-nigrum*, *A. septentrionale*, *Galium pumilum*, and *Tanacetum corymbosum*, for which no coexistence with alien species has been reported, was particularly distinguished.

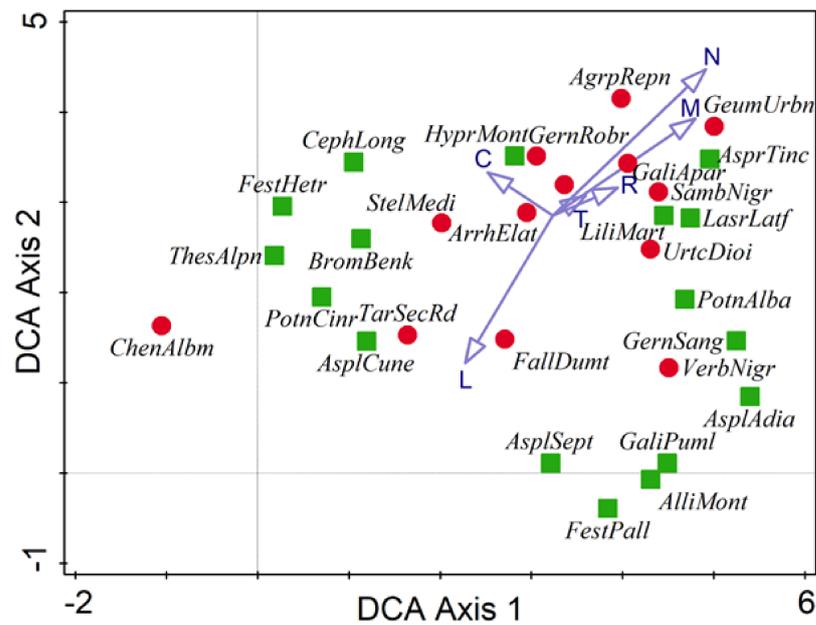


Figure 4. The passive projection of Ellenberg indicator values (EIVs) into DCA distribution diagram of nitrophilic (red circles) and rare/endangered species (green squares) recorded in serpentine forest communities in SW Poland. Species scores limit to 30 by weight. Abbreviations of species names are in accordance with these presented in Tables 2 and 3. Explanation: C—EIV for continentiality; T—EIV for temperature; L—EIV for light; M—EIV for moisture; R—EIV for soil reaction; N—EIV for nutrients.

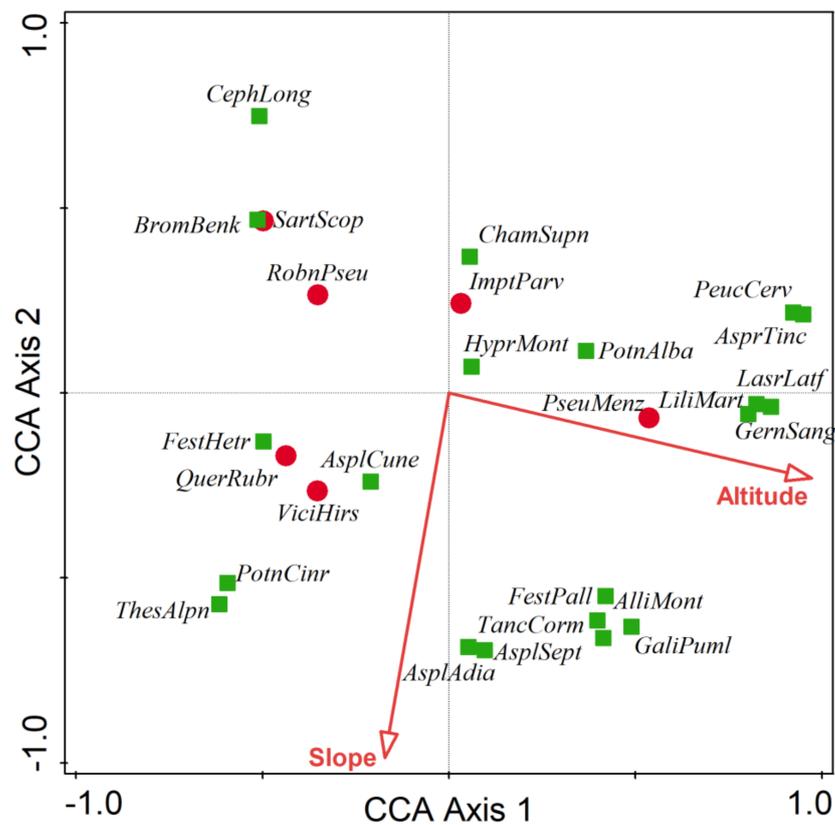


Figure 5. CCA distribution diagram of alien (red circles) and rare/endangered species (green squares) recorded in serpentine forest communities in SW Poland. Species scores limit to 26 by weight. Abbreviations of species names are in accordance with these presented in Tables 2 and 3.

The analysis of the coexistence of nitrophilic and rare species (Figure 6) also did not reveal that these two groups were clearly separated in terms of habitat preferences. The first and second CCA axes explained 5.93% and 2.82% of the observed variance, respectively. Only the group of rock and xerothermic species, as in the case of alien species, showed no coexistence with nitrophilic species. Forward selection results revealed that altitude (pseudo-F 3.5, $p_{(adj.)} < 0.006$) and slope inclination (pseudo-F 2.9, $p_{(adj.)} < 0.006$) explained 4.8% and 3.9% of variation, respectively.

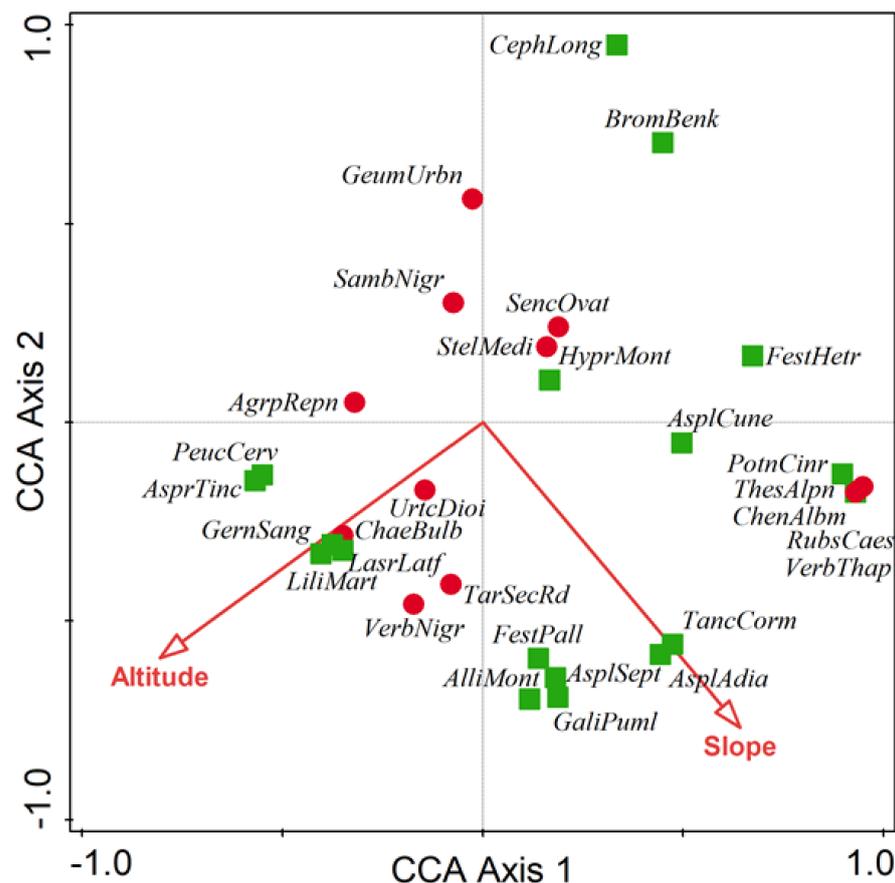


Figure 6. CCA distribution diagram of nitrophilic (red circles) and rare/endangered species (green squares) recorded in serpentine forest communities in SW Poland. Species scores limit to 30 by weight. Abbreviations of species names are in accordance with these presented in Tables 2 and 3.

4. Discussion

The conducted analyses allowed us to determine the relationship between the studied groups of species and the main types of forest communities developing on the serpentinites of Southwestern Poland. Rare and endangered species belong here to three ecological groups. The first is related to the shallow serpentine outcrops (*Asplenium* sp. div., *Allium montanum*, *Festuca pallens*, *Asperula tinctoria*, and *Galium pumilum*). The second group consists of species typical of xerothermic grasslands as well as thermophilous fringes and thermophilous oak forests of the *Quercion petraeae* alliance, including *Hypericum montanum*, *Potentilla cinerea*, and *Geranium sanguineum*. In the third group, there are species typical of mesic, deciduous, and mixed forests of the *Carpino-Fagetea* Jakucs ex Passarge 1968 class: *Festuca heterophylla*, *Lilium martagon*, *Bromus benekenii*, and *Cephalanthera longifolia*. Therefore, their occurrence in individual distinguished clusters corresponds to the ecological variability of studied communities. In thermophilous pine forests of *Asplenio cuneifolii-Pinetum* [27,28], there are mainly species of xerothermic and rocky grasslands; in thermophilous oak forests of *Galium verum-Quercus petraea* [20], species connected with

forest communities of the *Quercion petraeae* alliance occur more frequently; while in mesic pine stands and oak–hornbeam forests, there are more forest specialists.

Although most of the rare species occur in semi-natural thermophilic oak forests on serpentinite (16 species), secondary forests of *Asplenio cuneifolii–Pinetum sylvestris* association also show the ability to maintain a significant proportion of them (nine species—twice as many as in the close to natural subcontinental oak–hornbeam forest).

Therefore, it is not the stand origin itself that seems to be of key importance, but the habitat conditions typical of the community. The most important are topoclimatic factors that promote the occurrence of thermophilic species in habitats with high sun exposure and heat, which is favored by the southern or south-western exposure of the slope.

In such conditions, geographically alien species are much less common, and the DCA analysis (Figure 3) suggests that at least some of them (e.g., *Impatiens parviflora*, *Quercus rubra*) are associated with moist and more nutrient-rich habitats. Similar relationships, although on a larger scale and in relation to general climatic factors, have already been found. For example, Carboni et al. [52] examined Mediterranean coastal sand dunes on the Italian Tyrrhenian coast and found that alien species richness was strongly related to climatic factors, and more aliens occurred in areas with high precipitation. A significant influence of the climatic factors on alien species richness was also found in the small Mediterranean islands of Sardinia [53]. Although the cited studies did not refer directly to topoclimatic factors, the convergence of the results suggests that alien and endangered species often occupy sites with divergent habitat conditions.

Moreover, the specific habit of oak and pine trees overgrowing ultramafic sites provides more light into the forest floor (high EIV for light), while the presence of serpentine outcrops and rubble determines higher EIV for soil reaction. Under such conditions, the accumulation of rare species is much higher than in stands with high crown density and lower EIVs for light and temperatures values and higher soil moisture. These results are similar to those obtained by Roleček et al. [54], who analyzed the distribution of rare species within coppiced forests in Dúbrava (Hodonín, Czech Republic), confirming their irregular distribution in space and the relationship with the presence of well-lit gaps within subcontinental oak forests on relatively base-rich soils. A wider analysis covering the entire Czech Republic shows that previously coppiced old-growth oak forests are important refugia for threatened plant species [55]. Similar results are provided by the synthesis of data on endangered species in the forests of Sweden [56], where the majority of endangered vascular plant species occupies open (25%) or semi-shady (52%) habitats.

As shown in this study, thermophilic Scots pine artificial stands on serpentinites are a specific type of community that ensures the development of many light-demanding species. Equally rich in rare species are secondary Scots pine forests of loose structure, developing on polymetallic outcrops in central Poland [57], or spontaneous mixed forests with *Pinus sylvestris* on limestone screes in abandoned quarries [28]. The orchid *Goodyera repens*, rare in Poland, has also shown expansion in the latter type of community in recent years [58]. However, the increase in shading and deposition of pine litter causes a rapid loss of natural value in Scot pine stands and the disappearance of related species [59]. Such relationships are also reported from various types of forest communities in the Czech Republic [54] or Italy [17,60], which practically excludes the Scots pine forest plantation with dense canopy as an important habitat for rare vascular plant species. Our research also shows that in the shaded phytocoenoses of the comm. *Pinus sylvestris–Molinia caerulea*, the presence of rare and endangered species is limited. Similar phenomena also occur in these types of forest communities where the coppicing management ceased [61]. It is worth noting that the lowest abundance of rare species, as in the study by Roleček et al. [54], were recorded in phytocoenoses of close to natural, subcontinental oak–hornbeam forests, which was undoubtedly associated with the high density of the crowns and lower light availability near the forest floor. On the other hand, most forest species in the southwestern part of Poland are still so frequent that only a few are assigned regional or supra-regional risk categories. In the discussed communities, we can also observe various forms of their

degeneration manifested in the presence of geographically alien and nitrophilic species. The largest number of alien species occurs in both types of anthropogenic pine stands (both thermophilic and mesophilic), and the largest number of nitrophilic species (including as many as seven recorded in at least 24% of the relevés) in thermophilic oak forests. In both cases, it obviously causes an increase in the species diversity indicators, and therefore the data from Table 1 should be interpreted with great caution. However, the presence of alien or nitrophilic species does not seem to have a negative impact on the ability of the analyzed forest phytocoenoses to preserve rare species. This is confirmed by the analyses of the coexistence of distinguished groups of species (Figures 3–6), which show that most of them coexist with each other in similar habitat conditions and space. Particularly rare species such as *Potentilla alba*, *Hypericum montanum*, *Bromus benekenii*, *Festuca heterophylla*, or *Cephalanthera longifolia* coexist with both alien and nitrophilic species in various types of phytocoenoses—natural or anthropogenic in character, as already demonstrated for other endangered species, for example various European orchids [62]. This phenomenon confirms the suggestions, already appearing in the literature, for development of a new pathway in secondary succession where native and alien species could coexist [63–65]. Many studies show that the presence of alien species is rarely the direct cause of species extinctions, although they tend to reduce species diversity in habitats where they are abundant [66]. The displacement of native species by aliens is strongly dependent on the scale on which we observe this relationship [67]; on the characteristics of the functional traits that enable invasion; and on other, often distant, interactions within the ecosystem [68]. However, as stated by Powell et al. [66], “We also show that non-neutral species extirpations are due to a proportionately larger effect of invaders on common species, suggesting that rare species are buffered against extinction”. It seems that the results obtained by us confirm this thesis.

On the other hand, such ecosystems are often no longer able to maintain appropriate conditions for the occurrence of, e.g., forest specialists [69] or other species with specific habitat requirements, sometimes even posing a threat to their survival [17,60]. Moreover, in the analyzed material, we distinguished a group of five rare species (*Festuca pallens*, *Allium montanum*, *Asplenium adiantum-nigrum*, *A. septentrionale*, and *Galium pumilum*) that do not coexist with species that indicate phytocoenosis distortions. This suggests that they may be particularly vulnerable to changes in forest communities caused by eutrophication or invasion of geographically alien species.

Due to the progressive degradation and declining acreage of natural forests around the world [70], secondary forests are becoming increasingly important in the protection of natural resources. Obviously, these communities do not match the species richness of primary forests [71], but they can fulfil complementary functions in the nature protection system. Many plant species are associated with secondary communities because they find favorable habitat conditions in them—the same as in the forests we studied. Such habitats are associated with the occurrence of critically endangered species such as *Gleditsia amorphoides* [72], *Tigridiopalma magnifica* [73], *Camellia changii* [74], or *Magnolia stellata* [75].

It should be emphasized that many secondary coniferous forests in the world show high floristic values. In the undergrowth of artificial pine forests on the Italian peninsula [76] there are numerous psammophilous species typical of both coastal dunes (*Pinus helepis* stands) or thermophilic mixed forests (*Pinus pinea* stands). These communities are one of the types requiring protection in Europe as * 2270 habitat Wooded dunes with *Pinus pinea* and/or *Pinus pinaster*, which emphasizes the natural values of their long-established stands, even in the case of their artificial origin [25]. Mixed forests with *Pinus roxburghii* and *Pinus wallichiana* in the Central Himalayas gather a number of rare species typical of the native forests of the lower parts of this mountain range [77]. Moreover, older stands of *Pinus radiata* plantations in New Zealand allow for the establishment of a mostly indigenous forest understory community with considerable similarities to indigenous forests located nearby [78].

Many other secondary scrub and forest ecosystems play an important role in the preservation of entire groups of endangered and sometimes even endemic species. This applies to such different habitat types as Chinese ancient tea gardens [79], secondary succession on abandoned fields [80] and hedgerows [81] in Europe, secondary subtropical dry forest in Puerto Rico [82], and mountain and seasonal rainforest in China [83,84]. The great number of endemic and the highly endangered species has been found also in *Zamio debilis*–*Metopietum toxiferi* secondary forest in the Dominican Republic, developing on coral limestones [85].

Secondary forest can play an important role not only in the protection of plants, but also of many groups of animals, as demonstrated by many studies conducted in tropical and subtropical zones. For example, out of 15 species of amphibians found in the primary forest in Sri Lanka, as many as 12 (including eight threatened with extinction) occurred in the neighboring secondary habitats [63], while in Borneo it was found that secondary forests retained a large proportion of amphibian species known from lowland primary rainforests [86]. In the case of birds, an important role in their protection is assigned to secondary forest communities both for individual species, such as *Neospiza concolor* in São Tomé and Príncipe (Africa) [87], and their entire assemblages, e.g., in Sulawesi, where the richness of Wallacean endemics was similar in primary and disturbed secondary forest [88], or in the Ecuadorian Andes, where more rare bird species use the secondary forest, even in highly disturbed areas where surrounding pristine forest constitutes less than 10% of local forest cover [89]. Secondary forest can also be an important habitat for mammals. Pinotti et al. [90] found that the Atlantic forests may be valuable for conservation of small mammal assemblages, at least where habitat loss and fragmentation are not high and old-growth forest is available. Other studies have also reported value for larger mammals such as the lowland tapir *Tapirus terrestris* in South America [91] or Hainan gibbon *Nomascus hainanus* in China [92].

These conclusions are confirmed by the meta-analyses carried out on the basis of partial studies, devoted to various groups of the animal world, e.g., [93–95], in which it is also emphasized that the conservation value of secondary forest communities is high but still limited due to slow recovery of species compositional similarity; forest specialists; and many functional groups, e.g., insectivorous or canopy frugivorous birds [96]. This reservation also results from botanical studies showing a very slow recolonization rate of secondary communities by old-forest species, e.g., [69,71,84]. Nevertheless, with the increasingly shrinking area of primary and natural forests, paying attention to the natural values that we can maintain within the secondary forest becomes a key issue.

5. Conclusions

We distinguished four types of communities: thermophilic ass. *Asplenio cuneifolii*–*Pinetum sylvestris*, mesophilic *Pinus sylvestris*–*Molinia caerulea* community, thermophilic oak forest (comm. *Galium verum*–*Quercus petraea*), and acidophilous oak–hornbeam forest (ass. *Tilio cordatae*–*Carpinetum*). The first two are pine plantations that are secondary in origin; the latter two are semi-natural and close to natural in character. Our results revealed that rare and endangered species were unevenly distributed between studied forests and concentrated mainly in thermophilic oak forest (16 species), and secondary, thermophilic pine forests (nine species—twice as many as in the close to natural oak–hornbeam forest). The latter also showed the highest values of both the average number of species per plot and the Shannon–Wiener index, while the thermophilous oak forests were only slightly lower. Subcontinental oak–hornbeam high forests were characterized by the lowest values in all analyzed biodiversity indicators. The largest number of alien species occurred in both types of anthropogenic pine stands, while the largest number of nitrophilic species occurred in thermophilic oak forests.

The obtained results also confirmed that the endangered species mainly preferred sites at higher altitudes and with higher slope inclination, light availability, and soil reaction.

Surprisingly, we did not confirm that the presence of alien or nitrophilic species negatively influenced the ability of studied forests to preserve rare species.

Therefore, we can conclude that this is not the origin of the stand itself seems to be of key importance, but topoclimatic factors that may favor rare, thermophilic, and light-loving species. Moreover, since secondary forests can still harbor a number of endangered species, they should fulfil complementary functions in the nature protection system as a refuge of these taxa for the future.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/d13050201/s1>, Table S1: Summarized synoptic table derived from 95 relevés of serpentine forest communities from Poland.

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