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Analyzing Generalist Plant Species Using Topographic Characteristics of *Picea jezoensis* (Siebold & Zucc.) Carrière Forests in East Asia: From China (Mt. Changbai) to South Korea

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Abstract: *Picea jezoensis* (Siebold & Zucc.) Carrière forests are distributed in Korea and China and are crucial for phytogeographical research. Implementing conservation policies encompassing multiple species is necessary to conserve endangered species, particularly monitoring coexisting species and their interactions within an ecological network. Here, we identified plants within *P. jezoensis* forests in East Asia as generalist species to contribute foundational data for biodiversity conservation. We examined 91 standardized sites through the Braun-Blanquet method, while generalist indices were calculated using Levin's method. The top 5% of generalists in the *P. jezoensis* forests were *Acer komarovii* (0.7409), *Betula ermanii* (0.7214), *Asarum sieboldii* (0.7002), *Lepisorus ussuriensis* (0.6977), *Acer pseudosieboldianum* (0.6915), *Tripterygium regelii* (0.6876), *Thelypteris phegopteris* (0.6771), *Dryopteris expansa* (0.6745), *Sorbus commixta* (0.6642), and *Rhododendron schlippenbachii* (0.6625). Correlation analysis between ecological factors and generalist species revealed that the coverage of *Abies* spp., *Acer* spp., and *Rhododendron* spp. and the species diversity index were influenced by altitude. Convex hull analysis revealed that pteridophytes and broad-leaved plants regenerated through stump sprouts occupy ecological niche spaces, indicating diverse habitats within *P. jezoensis* forests. This study highlights the importance of the simultaneous monitoring of multiple species to conserve ecosystem health and offers broader implications for ecological understanding.

Keywords: *Picea jezoensis*; sub-alpine conifers; generalist species

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1. Introduction

An ecological niche refers to the physical space where an organism survives and lives, influencing its function and role as an organism in the ecosystem. It is closely associated with the distribution and scope of organisms [1,2] and serves as a shelter for plants, providing them with limited resources for their growth and survival. Various factors significantly influence the distribution of plant species in an ecosystem. Among these, topographic features play a crucial role in changing the complexity of the structure and function of vegetation [3].

Rapoport's rule is a representative hypothesis related to species distribution, which suggests that the species diversity and ecological niche increase when moving from the equator toward the poles [1]. This evidence suggests that physical distance, such as topographical differences among species, influences the availability of resources necessary for survival. Ecologists have thus shown interest in understanding the changes in ecological niche mechanisms associated with species' physical distance and topographic features' variations. For instance, environmental factors (such as soil physicochemical properties, air temperature, and relative humidity) differ depending on topographic features such as elevation and latitude), suggesting that these variations could influence species distribution [4,5]. Environmental changes also affect the composition of vegetation species in a particular area, leading to interspecific competition [6]. In topographies with diverse features, various species appear and are considered generalists owing to their wide range of available resources within a particular vegetation. They are defined as abundant species and well-adapted to environments owing to their wide range of tolerance limits and widespread distribution [7]. They also serve as indicator species within specific ecosystems and play a crucial role in maintaining the stability of ecosystem networks. Thus, the observation of generalists in specific ecosystems is important to assess and confirm the overall health of ecosystems.

Meanwhile, alpine conifer species are experiencing rapid declines in population and habitat due to the ongoing climate crisis. The alpine region has a harsh ecological environment for plant species, characterized by moisture stress, strong winds, and soil erosion [8–13].

Picea jezoensis (Siebold & Zucc.) Carrière, an endangered conifer species, is listed as Least Concern on the International Union for Conservation of Nature (IUCN) Red List. It is predominantly found in alpine areas above 1300 m above sea level [14,15]. *P. jezoensis* is the most widely distributed species in the sub-alpine forests of Northeast Asia, specifically in Korea, Manchuria, China, Russia, and Japan. Although it has recently maintained good populations in relatively cold habitats at high latitudes, populations are declining in low-latitude areas, such as Korea and the Changbai Mountain areas in China [14,16–20]. Therefore, identifying the ecosystem structures of *P. jezoensis* in South Korea and China (areas near Changbai Mountain) is crucial for observing the southern limit lines of this vegetation. On a global scale, changes in the distribution of *P. jezoensis* forests are observed in these areas, which are worthy of conservation from a phytogeographical perspective [12,20]. By formulating proactive national and international conservation strategies, the implementation of ecosystem management through the maintenance and enhancement of biodiversity should be prioritized [21].

Complex interrelationships exist between biotic and abiotic factors in ecosystems, and effective conservation of a particular species requires the simultaneous monitoring of neighboring species that share the same spatial extent. To conserve endangered species, it is necessary to implement conservation policies encompassing multiple species rather than a single species [22,23]. In short, active vegetation dynamics, facilitated by spatially flexible relationships, are crucial in maintaining healthy biodiversity within ecosystems. Thus, investigating the dynamics of co-occurring plant species in *P. jezoensis* communities is essential for conserving *P. jezoensis*, which first requires the selection of generalists based on species distribution.

This study aimed to select generalist plant species based on their ecological niche and analyze correlations between environmental factors and the topography. This study focused on the plants in Korea and parts of China that correspond to the southern limit line of the *P. jezoensis* forest in East Asia. The study results can provide basic data for conserving the *P. jezoensis* forest in East Asia.

2. Materials and Methods

2.1. Overview of the Target Site

This study investigated 91 standardized sites in five *P. jezoensis* habitats located in Gyebang (n = 28), Sobaek (n = 5), Deogyu (n = 8), and Jiri Mountains (n = 30) in South Korea, and Baekdu Mountain (n = 20) in China (Figure 1). Ninety-one circular sample plots, each covering an area of 400 m^2, were set up in standardized sites. The study targeted overstory and understory vegetation within a radius of 11.3 m.

The geographical distribution of the standardized survey plots is as follows: latitude 35°18′42″–42°30′6″ and longitude 127°33′53″–128°38′55″; the average elevation was 1492.5 ± 22.9 m and average slope was 24.0 ± 1.0°. Azimuth slopes were as follows: north at 27.6%, east at 18.4%, south at 14.9%, and west at 39.1%.

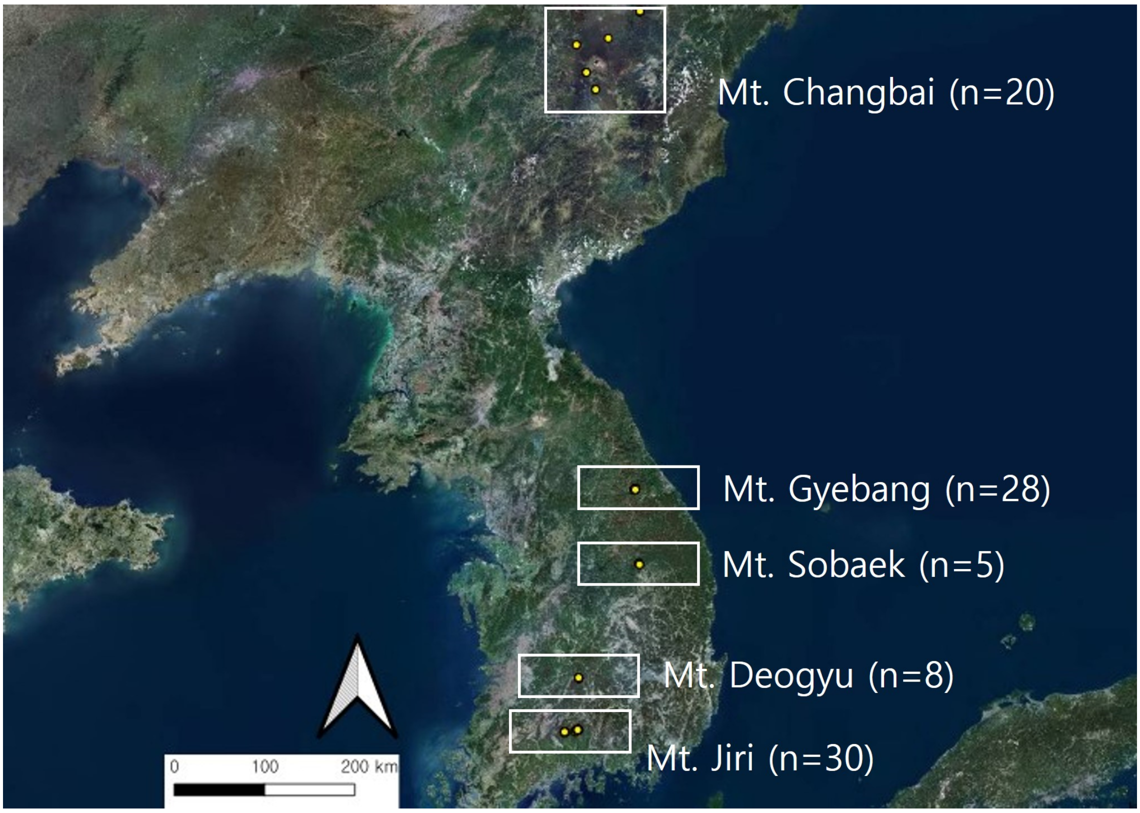

Figure 1. Survey plots of *Picea jezoensis* habitat in East Asia.

We analyzed meteorological data considering the 30-year climate characteristics (1991–2020) from the Korea Meteorological Administration for South Korea and the Changbai Mountain area in China. The data from the closest meteorological stations in the five regions per habitat were utilized: the data from the Hongcheon Meteorological Station for Gyebang Mountain, the Yeongju Meteorological Station for Sobaek Mountain, the Geochang Meteorological Station for Deogyu Mountain, the Sancheong Meteorological Station for Jiri Mountain, and the Samjiyeon Meteorological Station for Changbai Mountain [24]. South Korea is in a mid-latitude temperate climate zone characterized by four distinct seasons: sunny and dry in spring and fall, hot and humid in summer owing to the influence of the North Pacific anticyclone, and cold and dry in winter. The Changbai Mountain area in China has a cooler and drier continental climate than South Korea, with an annual temperature of approximately 36 °C. The average maximum monthly temperatures are as follows: 25.0 °C at Gyebang Mountain, 24.5 °C at Sobaek Mountain, 18.8 °C at Deogyu Mountain, 25.7 °C at Jiri Mountain, and 7.7 °C at Changbai Mountain. The average monthly temperatures are as follows: 11.5 °C at Gyebang Mountain, 11.8 °C at Sobaek Mountain, 12.2 °C at Deogyu Mountain, 13.3 °C at Jiri Mountain, and 10.0 °C at Changbai Mountain. The average monthly minimum temperatures are as follows: −0.8 °C at Gyebang Mountain, −0.2 °C at Sobaek Mountain, 6.5 °C at Deogyu Mountain, 2.0 °C at Jiri Mountain, and –5.3 °C at Changbai Mountain. Deogyu and Jiri Mountains show relatively mild temperatures. The annual precipitation is as follows: 1134.5 mm at Gyebang Mountain, 1274.7 mm at Sobaek Mountain, 1226.1 mm at Deogyu Mountain, 1551.7 mm at Jiri Mountain, and 950.8 mm at Changbai Mountain, and Jiri Mountain has the highest precipitation.

2.2. Field Survey Method

To conduct the vegetation survey in the target site, the layered structure of vegetation within the survey sites was classified into four distinct layers: tree layer, low-tree layer, shrub layer, and herbaceous layer. After identifying the plant species in each layer, we utilized the Braun-Blanquet phytosociological method [25] to assess the coverage and dominance. And we analyzed the median values of these classes as referenced below. The identification of plants was conducted based on the Colored Flora of Korea [26] for plant classification, and the identification of pteridophytes was conducted using the illustrated guide to Korean pteridophytes [27]. Scientific names and species names in Korean followed the Korean Plant Name Index [28], as the Korea National Arboretum and the Korean Society of Plant Taxonomists recommended. The survey was conducted from September 2019 to October 2022.

2.3. Statistical and Analytical Methods

Before analyzing the indicator species in this study, we examined species-area curves to confirm whether the appropriate number of standardized survey plots for the analysis was met [29]. We estimated the species number by randomly selecting the order of the cumulative survey sites in the species-area curves using a table of random sampling numbers, assigning serial numbers for 91 survey sites using the Chao1 estimator [30]. The ecological niche index was calculated using the following formula suggested by Levins [31]:

$$E = \frac{1}{S \times \sum_{k=1}^{S} {P_{ik}}^2}$$

where E is Levin's ecological niche breadth, P_{ik} is the relative species composition of a given species (i) to the whole gradient in realized gradient 'S', and S is the total number of gradients.

The environmental gradients used in the analysis were divided into vertical and horizontal distributions, and they were grouped as shown in Table 1, considering the minimum and maximum values of the topographical data.

Table 1. Environmental factors for analyzing ecological niche breadth.

Index	Environmental Factor (Number of Groups)	Remark
Vertical	Altitude (7)	~1300 m/1300–1400 m/ 1400–1500 m/1500–1600 m/1600–1700 m/1700–1800 m/1800~
Horizontal	Latitude (5)	35°/36°/37°/41°/42°
	Habitat (5)	JR/DG/SB/GB/BD
	Slope (5)	~15°/15°–20°/20°–25° /25°–30°/30°~
	Azimuth (8)	N/NE/NW/S SE/SW/W/E

The data used for relative species composition were analyzed based on two parameters: coverage and dominance. Moreover, topographic characteristics determined five environmental gradient factors: vertical distribution (elevation) and horizontal distribution (e.g., latitude, habitat, slope, and azimuth). According to the environmental gradient factor, the ecological niche index ranges between 0 and 1, and a value closer to 1 indicates a species widely distributed according to topographic characteristics.

We also conducted a non-metric multidimensional scaling (NMS) analysis to examine the environmental impact factors of generalist species and assess interspecific correlations. This approach is primarily applied to vegetation data, specifically ecosystem data, exhibiting a non-parametric pattern, and the interpretation can be made by representing correlations between biotic and abiotic factors in two dimensions [32]. We utilized the mean values of coverage and dominance of each plant species within the survey plots, and the Sørenson distance was used as the distance scale. Convex hull measurements were conducted to confirm the two-dimensional spatial range of each generalist according to species composition within the survey sites of the *P. jezoensis* forests. Convex hull can identify the correlations of ecological niches among species by visualizing measured values on spatial distribution after filtering out specific species' habitats within a community [33].

We used PC-ORD (ver. 7.0) as the analysis program [32]. The statistical analysis of topographical conditions was conducted using ANOVA, and post hoc testing was performed using Tukey's method. The topographical survey utilized a clinometer manufactured by Suunto (Tandem/360PC/360R DG CLINO/COMPASS) to measure the slope and azimuth. Rock exposure was assessed by investigating the rock ratio within a circular area with a radius of 11.3 m. Elevation was recorded using the numerical values from a GPS receiver (Table 2), the plant coverage values were determined using the Median Value according to the Braun-Blanquet method as presented in Table 3.

Table 2. Information on the *Picea jezoensis* forest survey areas from South Korea to China (a, b, and c indicate different delimiters in the ANOVA post hoc test (Tukey's post hoc), * $p < 0.05$).

Contents (Plots)	* Rock Exposure (%)	* Altitude (m)	* Slope (°)	Azimuth (%)			
				N	E	S	W
Mt. Gyebang (28)	40.8 ± 2.3^{ab}	1378.1 ± 13.8^{c}	28.4 ± 1.3^{ab}	20.0	36.0	20.0	24.4
Mt. Sobeak (5)	56.3 ± 3.7^{a}	1345.6 ± 10.8^{c}	37.8 ± 4.4^{a}	0.0	25.0	75.0	0.0
Mt. Deogyu (8)	35.6 ± 3.7^{ab}	1552.3 ± 10.0^{b}	22.4 ± 4.6^{b}	12.5	25.0	0.0	62.5
Mt. Jiri (30)	36.3 ± 1.9^{ab}	1731.7 ± 21.6^{a}	21.4 ± 1.4^{b}	6.7	10.0	33.3	50.0
Mt. Changbai (20)	24.3 ± 4.9^{c}	1282.3 ± 29.4^{c}	18.3 ± 2.1^{c}	30.0	5.0	25.0	40.0

Table 3. Braun-Blanquet cover-dominance scale.

Braun-Blanquet Scale	Range of Cover and Dominance (%)	Median Value
5	75–100	87.5
4	50–75	62.5
3	25–50	37.5
2	12.5–25	18.75
1	<12.5 numerous individuals	9.375
+	<5 few individuals	4.69
r	Species represented by a unique individual	1.01

3. Results

3.1. Species-Area Curves

To examine whether the appropriate quadrats were installed in the target sites, species-area curves were analyzed by estimating the number of species per level after dividing them into crown and understory vegetation (Figure 2). Consequently, based on the number of survey plots, the slope for species richness converged to 0, suggesting that an appropriate number of quadrats was installed for the vegetation analysis in the target site.

3.2. Selection of Generalist Species

The list of vascular plant species found in the 91 survey sites is presented in Table 4. In total, 202 taxa were identified, including 59 families, 127 genera, 171 species, 2 subspecies, 26 varieties, and 3 forms. The results of selecting generalist species of the *P. jezoensis* forests in East Asia are presented in Table 5. The identified generalists are the top 10 species in the ecological niche index, representing 5% of the plant species found. After calculating the ecological niche index for each species based on five topographic characteristics, we selected the final generalists based on their average values. The ecological niche index of *P. jezoensis*, the target species in this study, was 0.7411, and the top 10 generalists were as follows (Figure 3): *Acer komarovii* Pojark. (0.7409), *Betula ermanii* Cham. (0.7214), *Asarum sieboldii* Miq. (0.7002), *Lepisorus ussuriensis* (Regel & Maack) Ching (0.6977), *Acer pseudosieboldianum* (Pax) Kom. (0.6915), *Tripterygium regelii* Sprague & Takeda (0.6876), *Thelypteris phegopteris* (L.) Sloss.

(0.6771), *Dryopteris expansa* (C.Presl) Fraser-Jenk. & Jermy (0.6745), *Sorbus commixta* Hedl. (0.6642), and *Rhododendron schlippenbachii* Maxim. (0.6625).

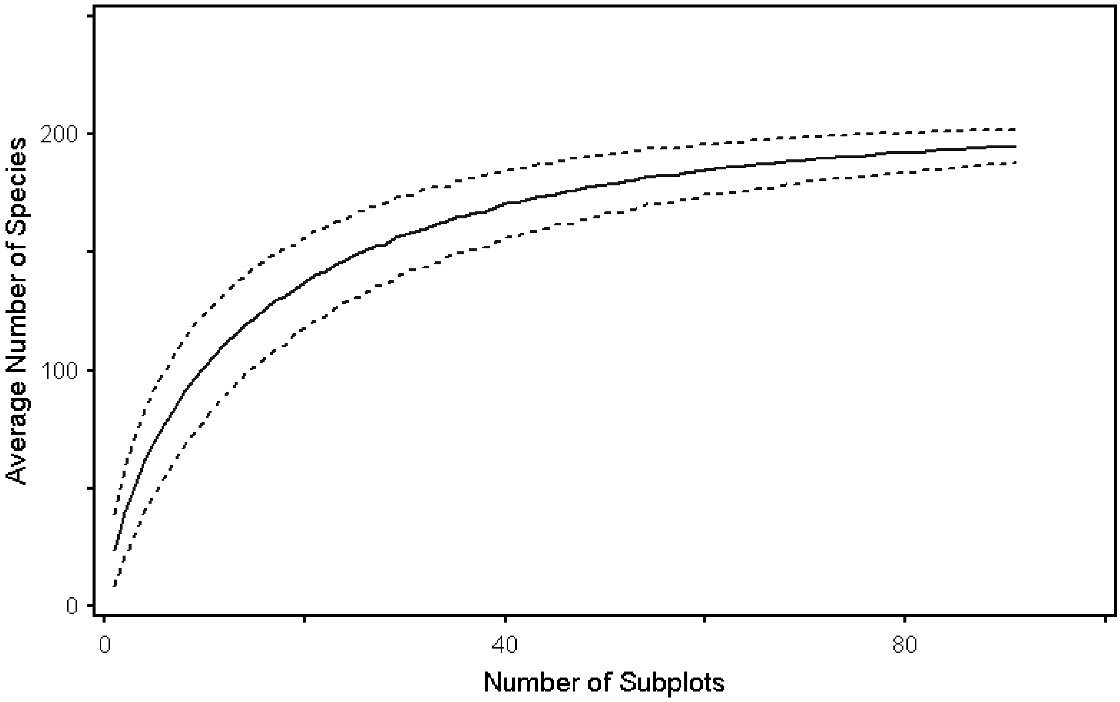

Figure 2. Species-area curves of forest layers by estimating species richness using the Chao1 estimator. Error bars indicate standard deviation.

Table 4. List of plant species in the *Picea jezoensis* forest.

Contents	Family	Genera	Species	Subspecies	Variety	Form	Total	Ratio (%)
Pteridophyte	7	11	17	0	1	0	18	8.9
Gymnosperm	3	6	7	0	1	0	8	4.0
Angiosperm	49	110	147	2	24	3	176	87.1
Dicotyledoneae	45	92	116	2	20	2	140	69.3
Monocotyledoneae	4	18	31	0	4	1	36	17.8
Total	59	127	171	2	26	3	202	100.0

Table 5. List of generalists in *Picea jezoensis* habitats in East Asia (above 5% in total species [202 taxa], ×1: altitude, ×2: latitude. ×3: habitat, ×4: slope, and ×5: azimuth, Refer to Appendix A for the niche breathe of plant species observed).

Scientific Name	×1	×2	×3	×4	×5	Mean	Generalist (G) Rank
Picea jezoensis (Siebold & Zucc.) Carrière	0.5357	0.7221	0.7366	0.8844	0.8267	0.7411	Target species (T)
Acer komarovii Pojark.	0.5506	0.6751	0.6935	0.9049	0.8802	0.7409	I
Betula ermanii Cham.	0.7720	0.4972	0.7275	0.8812	0.7288	0.7214	II
Asarum sieboldii Miq.	0.5411	0.5381	0.8826	0.8952	0.6440	0.7002	III
Lepisorus ussuriensis (Regel & Maack) Ching	0.5054	0.6760	0.8921	0.6043	0.8108	0.6977	IV
Acer pseudosieboldianum (Pax) Kom.	0.6544	0.4904	0.6903	0.9025	0.7197	0.6915	V
Tripterygium regelii Sprague & Takeda	0.7049	0.4501	0.5921	0.8652	0.8255	0.6876	VI
Thelypteris phegopteris (L.) Sloss.	0.6597	0.5766	0.5351	0.8358	0.7782	0.6771	VII
Dryopteris expansa (C.Presl) Fraser-Jenk. & Jermy	0.4433	0.6492	0.6102	0.8299	0.8398	0.6745	VIII
Sorbus commixta Hedl.	0.4706	0.5892	0.6250	0.8114	0.8250	0.6642	IX
Rhododendron schlippenbachii Maxim.	0.7110	0.3748	0.5172	0.9672	0.7425	0.6625	X

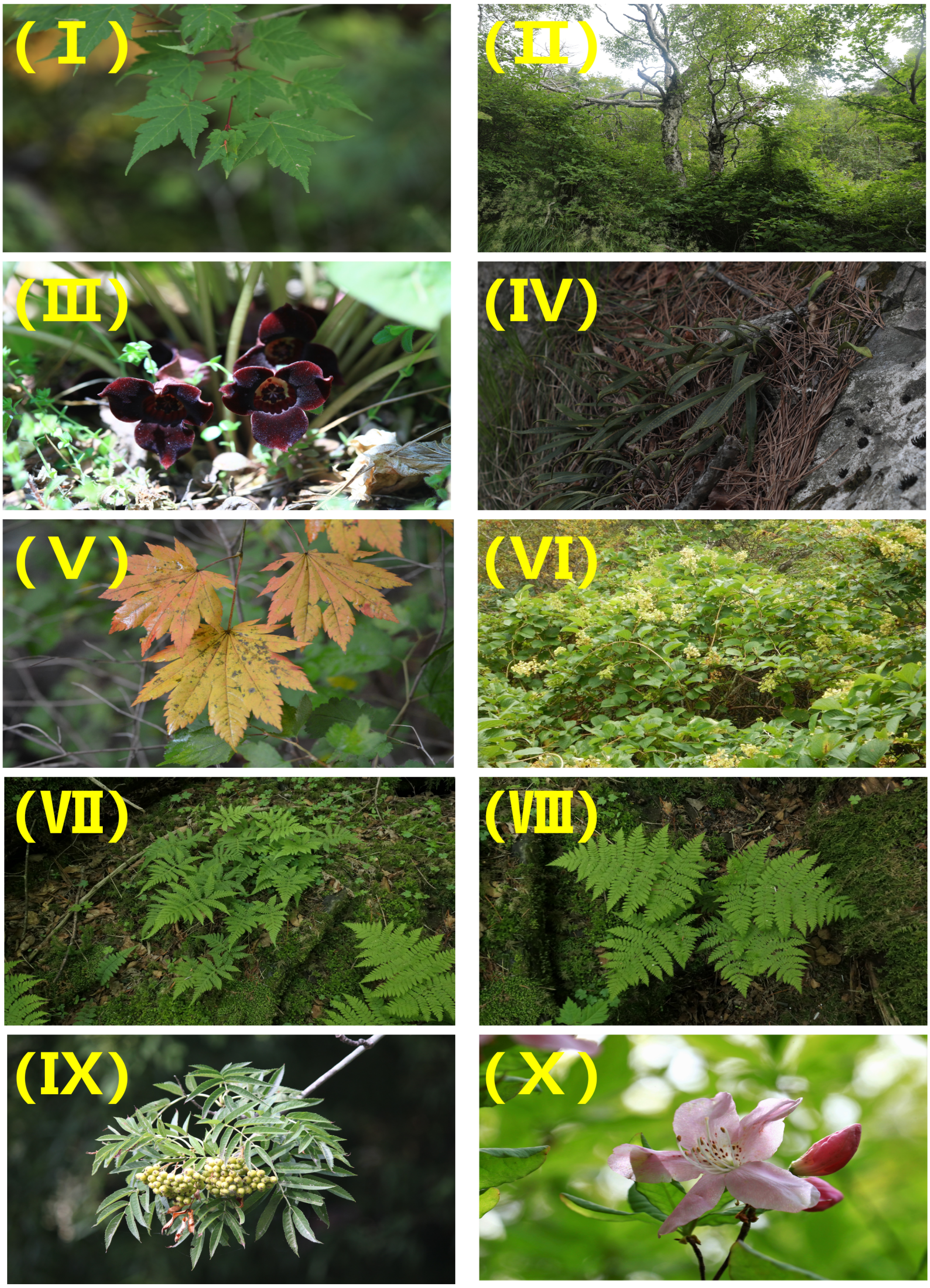

Figure 3. Pictures of generalists ((**I**) *Acer komarovii* Pojark; (**II**) *Betula ermanii* Cham; (**III**) *Asarum sieboldii* Miq; (**IV**) *Lepisorus ussuriensis* (Regel & Maack) Ching; (**V**) *Acer pseudosieboldianum* (Pax) Kom.; (**VI**) *Tripterygium regelii* Sprague & Takeda; (**VII**) *Thelypteris phegopteris* (L.) Sloss.; (**VIII**) *Dryopteris expansa* (C.Presl) Fraser-Jenk. & Jermy; (**IX**) *Sorbus commixta* Hedl.; (**X**) *Rhododendron schlippenbachii* Maxim.).

3.3. Correlations between Environmental Factors

The results of the correlation analysis between environmental factors of generalist plant species within the *P. jezoensis* forests are presented in Figure 4. The explanatory power of the NMS ordination was 0.417 and 0.202 for the first and second axes, respectively, resulting in a total explanatory power of 0.619. The correlation factors were elevation, *Rhododendron* spp. coverage, *Abies* spp. coverage, *Acer* spp. coverage, and the species diversity index. The correlation between *Abies* spp. coverage and *Acer* spp. coverage was heterogeneous. The generalist species correlated with the coverage of the genus of *Abies* were *Acer komarovii* Pojark., *Thelypteris phegopteris* (L.) Sloss., and *P. jezoensis*. The one species that showed correlations with *Acer* spp. coverage and species diversity index was *Lepisorus ussuriensis* (Regel & Maack) Ching. The species that were correlated with elevation and *Rhododendron* spp. were *Rhododendron schlippenbachii* Maxim., *Acer pseudosieboldianum* (Pax) Kom., *Asarum sieboldii* Miq., and *Tripterygium regelii* Sprague & Takeda.

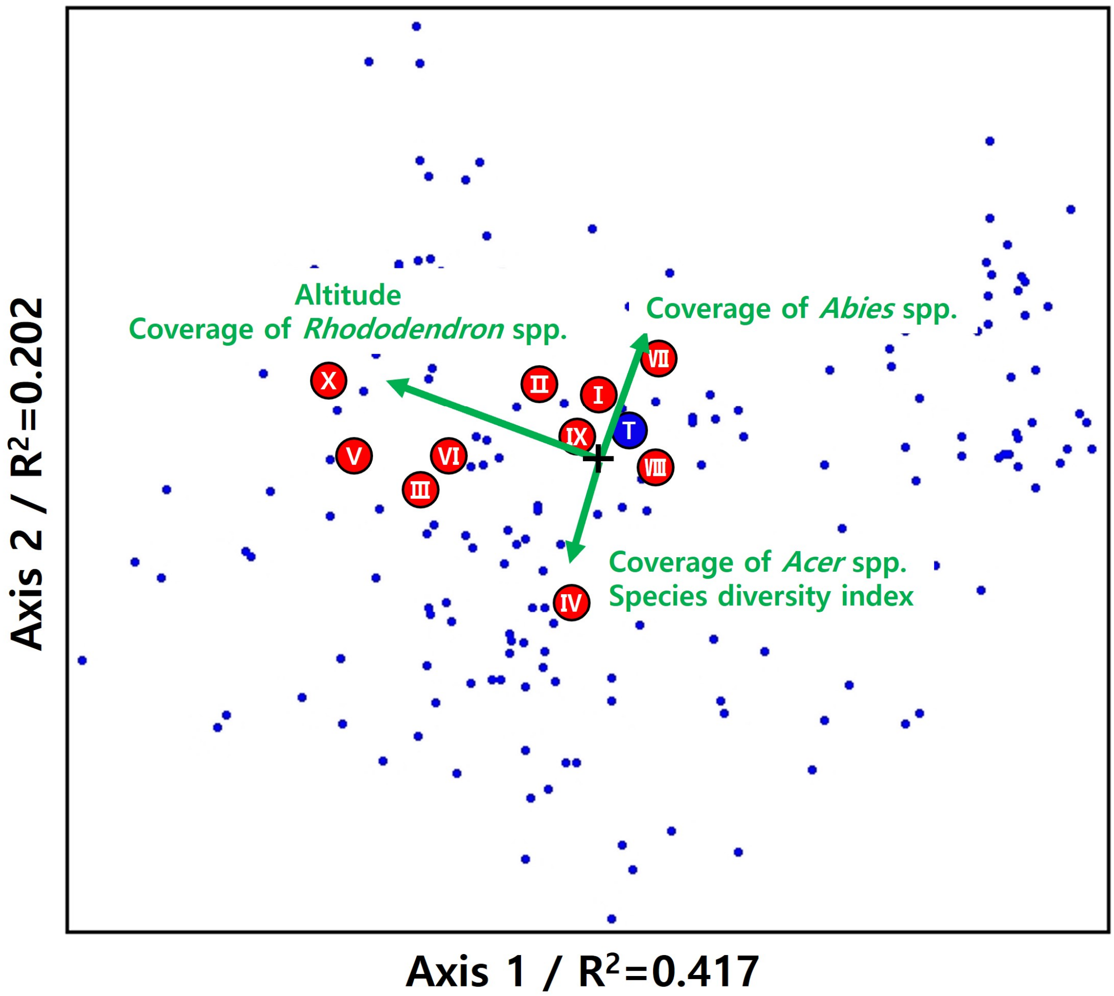

Figure 4. The distribution of the 10 generalists in two-dimensional space and correlation with environmental factors (NMS ordination was used, Total R2 = 0.619, cut off = 0.3). Blue dots represent the two-dimensional spatial distribution of emerging species (I, *Acer komarovii* Pojark; II, *Betula ermanii* Cham; III, *Asarum sieboldii* Miq; IV, *Lepisorus ussuriensis* (Regel & Maack) Ching; V, *Acer pseudosieboldianum* (Pax) Kom.; VI, *Tripterygium regelii* Sprague & Takeda; VII, *Thelypteris phegopteris* (L.) Sloss.; VIII, *Dryopteris expansa* (C.Presl) Fraser-Jenk. & Jermy; IX, *Sorbus commixta* Hedl.; X, *Rhododendron schlippenbachii* Maxim.).

The habitat of *P. jezoensis* in Korea reportedly has the same habitat status as that of subalpine conifers, such as *Abies nephrolepis* (Trautv. Ex Maxim.) Maxim. and *Abies koreana* E. H. Wilson [12,13]; our study yielded the same results. Notably, *Rhododendron schlippenbachii* Maxim. is a species that typically thrives at high altitudes, frequently appearing in habitats where the *Rhododendron* spp. is prevalent [12].

3.4. Convex Hull

A two-dimensional representation of the ecological niche range of generalists as determined through convex hull analysis is shown in Figure 5. The area shown in the convex hull result indicates the diversity of species composition and complexity of vegetation structure in the survey plot to which the generalist belongs. *Rhododendron schlippenbachii* Maxim. was found in various vegetation structure types. In addition, *Acer komarovii* Pojark., *Betula ermanii* Cham., *Asarum sieboldii* Miq., *Lepisorus ussuriensis* (Regel & Maack) Ching, *Acer pseudosieboldianum* (Pax) Kom., *Tripterygium regelii* Sprague & Takeda, and *Sorbus commixta* Hedl. were identified with ecological niches distributed within similar species composition structures. Meanwhile, pteridophytes or epiphytes such as *Thelypteris phegopteris* (L.) Sloss., *Dryopteris expansa* (C.Presl) Fraser-Jenk. & Jermy, and *Lepisorus ussuriensis* (Regel & Maack) Ching exhibited a heterogeneous spatial distribution.

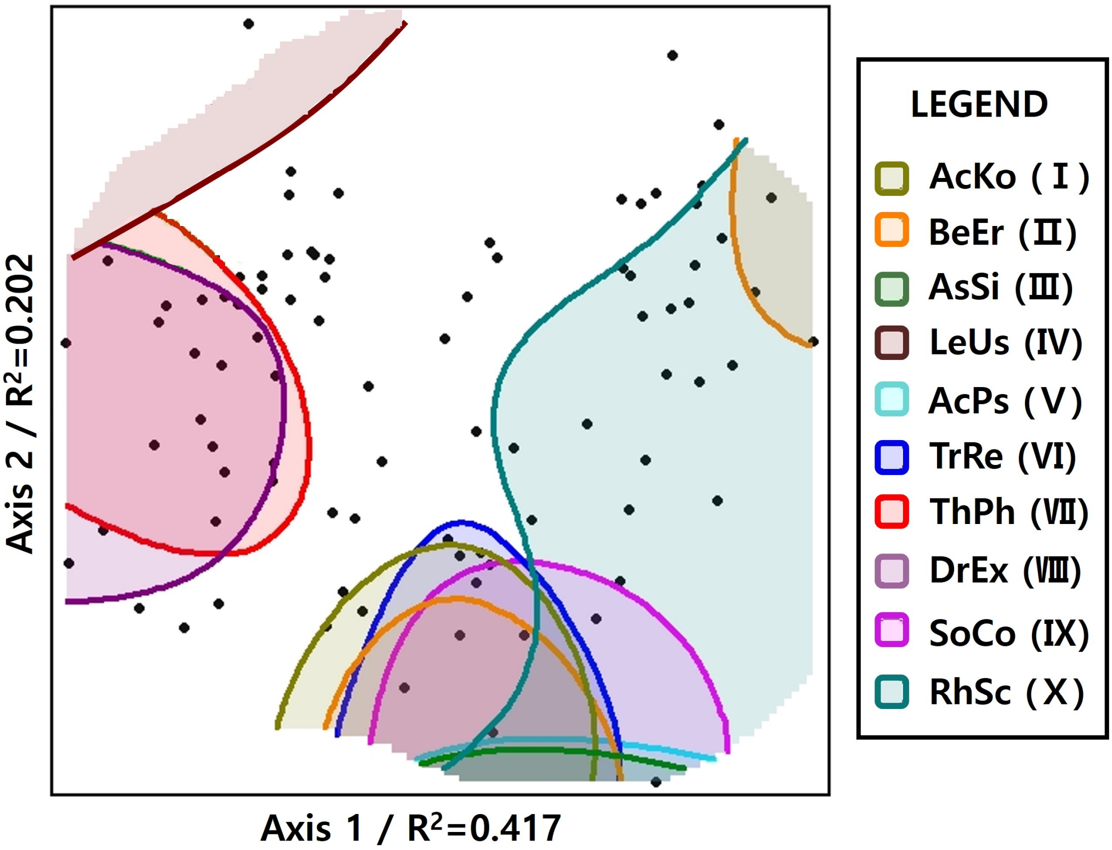

Figure 5. The convex hull graph shows the ecological niche of 10 generalists in the *Picea jezoensis* habitat from South Korea to China (black dots represent survey plots by calculating the species composition value on a two-dimensional axis, AcKo (I), *Acer komarovii* Pojark; BeEr (II), *Betula ermanii* Cham.; AsSi (III), *Asarum sieboldii* Miq.; LeUs (IV), *Lepisorus ussuriensis* (Regel & Maack) Ching; AcPs (V), *Acer pseudosieboldianum* (Pax) Kom.; TrRe (VI), *Tripterygium regelii* Sprague & Takeda; Th Ph (VII), *Thelypteris phegopteris* (L.) Sloss.; DrEx (VIII), *Dryopteris expansa* (C.Presl) Fraser-Jenk. & Jermy; SoCo (IX), *Sorbus commixta* Hedl.; RhSc (X), *Rhododendron schlippenbachii* Maxim).

4. Discussion

4.1. Ecological Characteristics of Generalist Species

The generalists along the southern limit line of *P. jezoensis* were identified as the genus *Acer* and the genus *Betula*, which are widely distributed plant species. The species of *Acer* or *Betula* are noticeable as they are woody plants with the potential to evolve into woody species in sub-alpine ecosystems in the future [20]. These species are widely distributed in sub-alpine coniferous forest zones, including *Abies nephrolepis* (Trautv. ex Maxim.) Maxim.

and *Abies koreana* E. H. Wilson in Korea. *Betula ermanii* Cham. was analyzed as a generalist species with the highest vertical range.

P. jezoensis forests in Korea and China are characterized by highly complex and diverse vegetation structures owing to secondary forests. The generalists that exhibit such characteristics are *Acer* spp. and *Tripterygium regelii* Sprague & Takeda. In Korea, *Acer* spp. maintain their ecological niche through sprout regeneration; as the *Acer* spp. is highly affected by pests in seeds within natural forests, approximately 30% of the seeds produced by an individual are perforated by pests. Approximately 70% of the seeds undergo advanced seed decay, making it difficult to naturally regenerate through seeds [34]. Therefore, most grow by branching out from the root-sucker, forming populations. These growth patterns of broad-leaved species are characteristic of the typical vegetation structure of a secondary forest in Korea. Secondary forests occur in frequent disturbances, leading to the predominant regeneration of vegetation primarily through stump saplings for broad-leaved trees; this forest structure is predominantly found in sub-alpine coniferous forests in Korea [20].

Meanwhile, *Tripterygium regelii* Sprague & Takeda vigorously reproduces after the occurrence of a forest gap, making it a major species for confirming disturbance frequencies within forest stands [13,20]. After the occurrence of forest gaps, secondary forests undergo dynamic transitions, experiencing frequent disturbances until the crown layer within the forest become stable [35]. Regarding *Betula ermanii* Cham., *Asarum sieboldii* Miq., *Acer pseudosieboldianum* (Pax) Kom., *Tripterygium regelii* Sprague & Takeda, and *Sorbus commixta* Hedl., multiple generalists have the same ecological niche ranges, indicating that they are simultaneously found in similar vegetation structures. This phenomenon is speculated to be the result of a highly dynamic response to changes in vegetation structure caused by frequent disturbances, particularly forest gaps; these disturbances, involving the repeated opening and closing of canopies, affect species richness within the vegetation, contributing to the complexity in vegetation structure [20,36,37]. This is assumed to result from natural disturbances driven by conditions such as wind damage and moisture deficit in the sub-alpine zone of the *P. jezoensis* forests [8,9,11,12].

In addition, pteridophyte species, such as *Thelypteris phegopteris* (L.) Sloss. and *Dryopteris expansa* (C.Presl) Fraser-Jenk. & Jermy, and the epiphyte *Lepisorus ussuriensis* (Regel & Maack) Ching, exhibited spatial arrangements different from those of other generalists. Epiphytes are plant species that generally thrive in areas with poorly developed soils; they show a unique ecological life history by growing on the surface of other plants and absorbing water and nutrients from the atmosphere and soil through their roots. Furthermore, epiphytes exhibit adaptability to various habitats, including rainforests, deserts, and alpine areas, indicating their ability to survive in diverse environments without being significantly influenced by host specificity [38–40]. Our study also revealed their ability to survive in barren environments, such as the habitat for *P. jezoensis,* indicating adaptation to various stresses.

Pteridophytes, such as *Dryopteris expansa* (C.Presl) Fraser-Jenk. & Jermy and *Thelypteris phegopteris* (L.) Sloss., thrive in environments with abundant moisture in the air and soil and grow in shaded areas or rocky crevices within forests. Pteridophytes also exhibit ecological features, including reproduction via spores and the ability of individuals to thrive in habitats with low moisture stress [41–44]. Undisturbed areas in the *P. jezoensis* forests within the southern limit line are expected to have high aerial humidity, and it is assumed that the *P. jezoensis* forests, where these pteridophytes thrive, have not experienced significant and frequent disturbances. In the future, if natural disturbances occur, forest gaps will form, and the resultant drop in atmospheric humidity can provide a dry environment in the forest, contributing to a decline in pteridophytes; considering this, these species are considered indicator plants that provide insights into disturbance levels.

Rhododendron schlippenbachii Maxim. belongs to the *Rhododendron* spp., a shrubby tree species and a plant species with a wide vertical range that can grow above the tree line. The *Rhododendron* spp., which grows in sub-alpine regions, is widely distributed in East Asia, including Korea and China, and is considered the genus representing the vegetation in Korea [45]. The *Rhododendron* spp. is an important indicator plant for monitoring, which confirms the shrinkage and expansion of sub-alpine ecosystems in response to global environmental changes [46]. In an analysis of indicator species based on elevation in East Asia, the *Rhododendron* spp. was identified as an indicator species at high elevations [46]; in this study, the species was the second highest generalist species in terms of elevation, demonstrating a broad vertical range and highlighting its adaptability across diverse elevations.

The selection of generalists within coniferous forests is crucial for predicting future changes in vegetation structures driven by long-term transitions, and such plant species evolve owing to the interrelations among them [47]. The findings of this study will provide a basis for understanding the vegetation structure of climax forests during the transition from coniferous to broadleaf forests.

4.2. Correlations between Generalist Species and Ecological Niche Distribution

Generalist species with equivalent ecological niches demonstrate the same environmental adaptability in the ecosystem [48]. Variations in the ecological niches of plant species within vegetation ultimately reflect differences in their habitats, and plant species with overlapped ecological niches have similar habitats [49].

Examining the ten generalist species in *P. jezoensis* forests in East Asia found that each species does not have the same habitat type. This study categorized the ecological niche range into two groups: woody broad-leaved species and pteridophytes. This result suggests that the same woody community can consist of different habitats. The most significant difference between the two groups lies in the moisture environment within the vegetation. The broad-leaved tree species group is characterized by irregularities due to frequent disturbances, whereas the pteridophyte group is considered relatively stable. As the broadly distributed pteridophyte group is more sensitive to other environmental factors and occupies a smaller habitat than the woody plant species [50], it is identified as a vegetation structure that should be intensively monitored within *P. jezoensis* forests.

Seasonal winds are a crucial factor influencing East Asia's diverse vegetation structure of sub-alpine coniferous forests. The climatic requirement in East Asia is monsoonal winds, vital in determining the vegetation structure. Monsoonal winds are dry and create diverse vegetation types along the vertical range within mountains [51]. This complexity causes diverse habitats, and *Picea* forests, forming part of the remnant population, are predominantly found in small numbers in areas with frequent disturbances, such as cliffs and rocky terrain [52–55]. The analysis identified broad-leaved species, such as *Acer* spp. or *Betula* spp., as generalists, favoring regeneration through sprouts within secondary forests after frequent disturbance; this observation aligns with the complexity of sub-alpine ecosystems observed in previous studies. The diverse distribution of ecological niches of generalists in *P. jezoensis* forests at the southern limit line in East Asia, as revealed through convex hull analysis, can be considered an indirect example of the dynamics and diversity of habitats [46].

As the fluctuations in bioclimatic factors increase, the residual community species experiencing unstable climate conditions gradually decline [51]. Therefore, the stability of climatic factors is a prerequisite for protecting specific plant species, and long-term, stable remnant populations, characterized by rich gene pools and species diversity, have the potential for new speciation over time [56–60].

For the sub-alpine remnant populations, unstable climatic requirements disadvantage the in situ survival of specific species. Within forest ecosystems, the complex habitat mosaic suggests that *P. jezoensis* forests persist as remnant populations within sub-alpine vegetation owing to rising temperatures, with the high dynamics of forest ecosystems rendering it difficult to maintain a stable ecosystem structure [12,14].

5. Conclusions

This study aimed to obtain scientific evidence for conservation policy recommendations to maintain and enhance biodiversity by selecting generalist plant species in

P. jezoensis forests in Korea and China. Identifying generalist plant species influenced by topographic features is crucial in formulating effective conservation strategies. However, this study has limitations in quantitative analysis based on short-term vegetation survey data. Thus, it is necessary to clarify changes and patterns through continuous and long-term monitoring of *P. jezoensis* forests in Northeast Asia, including Korea.

Remnant populations in sub-alpine ecosystems face considerable challenges in directly collecting data on environmental factors owing to the harsh and barren nature of the ecosystems. Therefore, co-occurring species refer to species that naturally appear together with a specific organism or in a particular habitat. These species coexist in a specific environment and can influence or interact with each other. From a conservation perspective, investigating and understanding co-occurring species is essential for comprehending the ecosystem of a specific habitat and designing conservation strategies. Conservation efforts for a particular species require understanding not only the environment in which the species exists but also the roles of other organisms coexisting in that environment. This understanding can provide insights into inter-species interactions and the stability of the habitat ecosystem. This is the ultimate purpose of this study, and the results can provide essential foundational data that can be instrumental in formulating ecosystem conservation policies in the future.

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Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

List of niche breadth for plants on *P. jezoensis* habitats (×1: altitude, ×2: latitude, ×3: habitat, ×4: slope, ×5: azimuth).

Scientific Name	×1	×2	×3	×4	×5	Mean
Abies koreana Wilson	0.3210	0.2000	0.2467	0.9516	0.5379	0.4514
Abies nephrolepis (Trautv.) Maxim.	0.2409	0.6784	0.4601	0.7196	0.8919	0.5982
Acer barbinerve Maxim.	0.3842	0.7315	0.6249	0.4055	0.4471	0.5186
Acer komarovii Pojark.	0.5506	0.6751	0.6935	0.9049	0.8802	0.7409
Acer mandshuricum Maxim.	0.1825	0.2000	0.2000	0.3702	0.3497	0.2605

Scientific Name	×1	×2	×3	×4	×5	Mean
Acer pictum subsp. *mono* (Maxim.) Ohashi	0.5180	0.5519	0.5901	0.6604	0.5332	0.5707
Acer pseudosieboldianum (Pax) Kom.	0.6544	0.4904	0.6903	0.9025	0.7197	0.6915
Acer tegmentosum Maxim.	0.2722	0.4916	0.4916	0.7416	0.7063	0.5406
Acer ukurunduense Trautv. & C.A.Mey.	0.2805	0.4640	0.4600	0.5489	0.9036	0.5314
Aconitum jaluense Kom.	0.3542	0.4565	0.4565	0.7059	0.5415	0.5029
Aconitum pseudolaeve Nakai	0.1429	0.3291	0.2533	0.2953	0.2524	0.2546
Actaea asiatica H. Hara	0.1920	0.2000	0.2000	0.3456	0.4253	0.2726
Actinidia arguta (Siebold & Zucc.) Planch. ex Miq.	0.3094	0.2443	0.2443	0.6333	0.5115	0.3885
Actinidia polygama (Siebold & Zucc.) Planch. ex Maxim.	0.1429	0.3812	0.2000	0.3812	0.2383	0.2687
Adenophora remotiflora (Siebold & Zucc.) Miq.	0.2593	0.2649	0.2649	0.4667	0.4712	0.3454
Agastache rugosa (Fisch. & Mey.) Kuntze	0.2857	0.4000	0.4000	0.8000	0.5000	0.4771
Agrimonia pilosa Ledeb.	0.2857	0.4000	0.4000	0.4000	0.2500	0.3471
Ainsliaea acerifolia Sch.Bip.	0.5001	0.3253	0.3645	0.8053	0.6956	0.5382
Angelica amurensis Schischk.	0.4244	0.2477	0.4701	0.6709	0.4193	0.4465
Angelica gigas Nakai	0.3295	0.2535	0.2559	0.6213	0.7163	0.4353
Anthriscus sylvestris (L.) Hoffm.	0.1429	0.2000	0.2000	0.3171	0.2359	0.2192
Aralia elata (Miq.) Seem.	0.4947	0.4241	0.6421	0.6679	0.3174	0.5092
Arisaema amurense Maxim.	0.2062	0.2000	0.2000	0.4000	0.3700	0.2752
Arisaema peninsulae Nakai	0.2339	0.2000	0.2000	0.3274	0.3456	0.2614
Aruncus dioicus var. *kamtschaticus* (Maxim.) H. Hara	0.6377	0.6558	0.5829	0.5185	0.4685	0.5727
Asarum sieboldii Miq.	0.5411	0.5381	0.8826	0.8952	0.6440	0.7002
Asplenium yokoscense (Franch. & Sav.) H.Christ	0.4049	0.2115	0.3624	0.8239	0.6195	0.4844
Aster scaber Thunb.	0.5762	0.4822	0.6155	0.6368	0.3750	0.5371
Astilbe rubra Hook.f. & Thomson	0.5751	0.5410	0.5410	0.7512	0.7401	0.6297
Athyrium brevifrons Kodama ex Nakai	0.2404	0.8458	0.6476	0.4577	0.6951	0.5773
Athyrium niponicum (Mett.) Hance	0.3673	0.4000	0.4000	0.7200	0.3750	0.4525
Berberis amurensis var. *brevifolia* Nakai	0.3737	0.4000	0.4000	0.5232	0.2400	0.3874
Betula costata Trautv.	0.2822	0.3951	0.2000	0.3340	0.2088	0.2840
Betula davurica Pall.	0.2125	0.2974	0.2974	0.5324	0.3328	0.3345
Betula ermanii Cham.	0.7720	0.4972	0.7275	0.8812	0.7288	0.7214
Betula platyphylla var. *japonica* (Miq.) H. Hara	0.1429	0.2000	0.2000	0.3028	0.3012	0.2294
Betula schmidtii Regel	0.1429	0.2830	0.2830	0.2830	0.1769	0.2338
Bistorta manshuriensis (Petrov ex Kom.) Kom.	0.2407	0.2000	0.2000	0.3370	0.2106	0.2377
Calamagrostis arundinacea (L.) Roth	0.5561	0.4203	0.4645	0.8610	0.8218	0.6247
Cardamine komarovii Nakai	0.1429	0.5556	0.5556	0.7143	0.2404	0.4417
Cardamine leucantha (Tausch) O.E.Schulz	0.1429	0.2000	0.2000	0.4000	0.2500	0.2386
Carex biwensis Franch.	0.1429	0.2000	0.2000	0.4000	0.2500	0.2386

Scientific Name	×1	×2	×3	×4	×5	Mean
Carex erythrobasis H.Lév. & Vaniot	0.3136	0.5651	0.2915	0.5525	0.5679	0.4581
Carex glabrescens Ohwi	0.1429	0.2000	0.2000	0.2000	0.1250	0.1736
Carex hakonensis Franch. & Sav.	0.5190	0.5685	0.5685	0.5310	0.3566	0.5087
Carex humilis var. *nana* (H.Lév. & Vaniot) Ohwi	0.5708	0.4575	0.7294	0.4922	0.5746	0.5649
Carex lanceolata Boott	0.5135	0.3155	0.5780	0.8294	0.2812	0.5035
Carex okamotoi Ohwi	0.2056	0.2000	0.2000	0.6939	0.3745	0.3348
Carex siderosticta Hance	0.2676	0.3567	0.3625	0.6276	0.6413	0.4511
Caulophyllum robustum Maxim.	0.2857	0.2000	0.2000	0.4000	0.2500	0.2671
Chrysosplenium flagelliferum F.Schmidt	0.1429	0.2000	0.2000	0.2000	0.3621	0.2210
Cimicifuga dahurica (Turcz. ex Fisch. & C.A.Mey.) Maxim.	0.3155	0.2000	0.2000	0.6055	0.6106	0.3863
Cimicifuga simplex (DC.) Turcz.	0.1429	0.3340	0.2000	0.2000	0.1250	0.2004
Circaea alpina L.	0.1429	0.2000	0.2000	0.5155	0.3222	0.2761
Clematis fusca var. *violacea* Maxim.	0.3452	0.3951	0.3951	0.3951	0.2469	0.3555
Clematis koreana Kom.	0.1977	0.2000	0.2000	0.5686	0.4820	0.3296
Clintonia udensis Trautv. & C.A.Mey.	0.3632	0.5168	0.4404	0.7506	0.6750	0.5492
Cornus controversa Hemsl.	0.1429	0.3514	0.3514	0.5070	0.2394	0.3184
Corylus heterophylla Fisch. ex Trautv.	0.2163	0.4820	0.4820	0.4820	0.1892	0.3703
Corylus sieboldiana var. *mandshurica* (Maxim. & Rupr.)	0.2657	0.2000	0.2000	0.3797	0.5552	0.3201
Cymopterus melanotilingia (H.Boissieu) C.Y.Yoon	0.5352	0.3951	0.5686	0.8695	0.5091	0.5755
Deutzia glabrata Kom.	0.2740	0.2883	0.2883	0.5640	0.6025	0.4034
Deutzia parviflora Bunge	0.2723	0.2000	0.3812	0.3812	0.2383	0.2946
Diarrhena fauriei (Hack.) Ohwi	0.2723	0.3812	0.3812	0.3812	0.2383	0.3308
Diarrhena mandshurica Maxim.	0.1429	0.2000	0.2000	0.5684	0.2088	0.2640
Disporum smilacinum A.Gray	0.4861	0.3836	0.5893	0.4836	0.4253	0.4736
Disporum viridescens (Maxim.) Nakai	0.2857	0.4000	0.4000	0.4000	0.2500	0.3471
Dryopteris chinensis (Baker) Koidz.	0.4060	0.3951	0.5685	0.2000	0.2469	0.3633
Dryopteris crassirhizoma Nakai	0.4039	0.5375	0.5402	0.6442	0.8201	0.5892
Dryopteris expansa (C.Presl) Fraser-Jenk. & Jermy	0.4433	0.6492	0.6102	0.8299	0.8398	0.6745
Eleutherococcus senticosus (Rupr. & Maxim.) Maxim.	0.2820	0.2621	0.2000	0.4077	0.2956	0.2895
Epilobium angustifolium L.	0.1429	0.2000	0.2000	0.2000	0.1250	0.1736
Equisetum hyemale L.	0.2336	0.2000	0.2000	0.4891	0.5294	0.3304
Euonymus macropterus Rupr.	0.6096	0.6037	0.6617	0.5648	0.7545	0.6389
Euonymus oxyphyllus Miq.	0.3333	0.3379	0.3379	0.3920	0.3224	0.3447
Euonymus pauciflorus Maxim.	0.1429	0.2000	0.2000	0.3774	0.3621	0.2565
Euonymus sachalinensis (F.Schmidt) Maxim.	0.2682	0.4977	0.5555	0.4468	0.3472	0.4231
Filipendula glaberrima Nakai	0.4622	0.5253	0.5253	0.5285	0.5873	0.5257
Fraxinus rhynchophylla Hance	0.3774	0.5440	0.5440	0.5173	0.4327	0.4831

Scientific Name	×1	×2	×3	×4	×5	Mean
Fraxinus sieboldiana Blume	0.4412	0.2000	0.2600	0.7338	0.6768	0.4624
Galium kamtschaticum Steller ex (Roem. & Schult.)	0.1429	0.4000	0.2000	0.2000	0.2500	0.2386
Gentiana triflora var. *japonica* (Kusn.) H. Hara	0.2286	0.3200	0.3200	0.3200	0.5000	0.3377
Geranium koreanum Kom.	0.2857	0.4000	0.4000	0.4000	0.2500	0.3471
Hemerocallis hakuunensis Nakai	0.1429	0.2000	0.2000	0.2826	0.2613	0.2173
Hosta capitata (Koidz.) Nakai	0.3507	0.2000	0.3951	0.4910	0.2470	0.3368
Hosta plantaginea (Lam.) Asch.	0.1429	0.3340	0.2000	0.3340	0.3553	0.2732
Hydrangea serrata f. *acuminata* (Siebold & Zucc.) E.H.Wilson	0.3280	0.3995	0.4592	0.2352	0.3512	0.3546
Hydrocotyle sibthorpioides Lam.	0.1429	0.2000	0.2000	0.3812	0.2382	0.2325
Hypericum ascyron L.	0.2857	0.2000	0.2000	0.4000	0.2500	0.2671
Impatiens nolitangere L.	0.2101	0.2000	0.2000	0.3600	0.4767	0.2894
Isodon excisus (Maxim.) Kudo	0.3321	0.2231	0.2231	0.7402	0.6529	0.4343
Juglans mandshurica Maxim.	0.1429	0.4000	0.4000	0.2000	0.1250	0.2536
Kalopanax septemlobus (Thunb.) Koidz.	0.1429	0.2000	0.2000	0.4000	0.2500	0.2386
Larix olgensis var. *koreana* (Nakai) Nakai	0.2723	0.3812	0.2000	0.2000	0.2382	0.2583
Lepisorus ussuriensis (Regel & Maack) Ching	0.5054	0.6760	0.8921	0.6043	0.8108	0.6977
Ligularia fischeri (Ledeb.) Turcz.	0.5812	0.5502	0.6168	0.6845	0.5974	0.6060
Lilium distichum Nakai ex Kamib.	0.4083	0.3802	0.3802	0.5716	0.3573	0.4195
Lilium tsingtauense Gilg	0.2339	0.3274	0.3274	0.5529	0.1250	0.3133
Lonicera caerulea var. *edulis* Turcz. ex Herder	0.1429	0.3456	0.2000	0.3456	0.2160	0.2500
Lonicera chrysantha Turcz.	0.3982	0.2999	0.2999	0.6506	0.7263	0.4750
Lonicera maackii (Rupr.) Maxim.	0.2463	0.2000	0.2000	0.2000	0.2155	0.2124
Lonicera sachalinensis (F.Schmidt) Nakai	0.2302	0.3223	0.3223	0.3486	0.5614	0.3570
Lonicera tatarinowii var. *leptantha* (Rehder) Nakai	0.1429	0.2912	0.2000	0.2722	0.4045	0.2622
Lychnis cognata Maxim.	0.4286	0.2000	0.2000	0.3600	0.3750	0.3127
Lycopodium chinense H.Christ	0.2368	0.4954	0.2972	0.5843	0.5630	0.4353
Lycopodium obscurum L.	0.2021	0.3618	0.2829	0.5528	0.4579	0.3715
Lycopodium serratum Thunb.	0.2923	0.6467	0.7273	0.6845	0.6056	0.5913
Magnolia sieboldii K.Koch	0.3708	0.3328	0.3382	0.5491	0.5104	0.4202
Maianthemum bifolium (L.) F.W.Schmidt	0.2482	0.3474	0.3474	0.3474	0.4765	0.3534
Maianthemum dilatatum (Wood) A.Nelson & J.F.Macbr.	0.1637	0.3969	0.2000	0.5218	0.5680	0.3701
Malus baccata (L.) Borkh.	0.2723	0.3812	0.3812	0.3812	0.2382	0.3308
Meehania urticifolia (Miq.) Makino	0.2740	0.4657	0.4657	0.7925	0.7707	0.5537
Oplopanax elatus (Nakai) Nakai	0.2405	0.3367	0.3367	0.7484	0.4458	0.4216
Osmunda cinnamomea var. *forkiensis* Copel.	0.2772	0.3881	0.2000	0.2000	0.3371	0.2805

Scientific Name	×1	×2	×3	×4	×5	Mean
Ostericum grosseserratum (Maxim.) Kitag.	0.1429	0.2000	0.2000	0.5104	0.4301	0.2967
Oxalis acetosella L.	0.2175	0.7986	0.4526	0.5912	0.6992	0.5518
Oxalis corniculata L.	0.1429	0.3812	0.2000	0.2000	0.2383	0.2325
Paeonia japonica (Makino) Miyabe & Takeda	0.2571	0.3600	0.3600	0.3600	0.3750	0.3424
Parasenecio adenostyloides (Franch. & Sav. ex Maxim.) H.Koyama	0.1798	0.3513	0.2456	0.5639	0.4906	0.3663
Parasenecio auriculata var. *kamtschatica* (Maxim.) H.Koyama	0.2608	0.4296	0.4296	0.4391	0.5727	0.4263
Parasenecio auriculata var. *matsumurana* Nakai	0.3567	0.3858	0.4486	0.5101	0.3188	0.4040
Paris verticillata M.Bieb.	0.4595	0.3701	0.3701	0.7476	0.5360	0.4966
Patrinia saniculaefolia Hemsl.	0.1429	0.2000	0.2000	0.4000	0.2500	0.2386
Pedicularis resupinata L.	0.6221	0.4593	0.4995	0.6834	0.7320	0.5993
Philadelphus tenuifolius Rupr. & Maxim.	0.3506	0.4194	0.4194	0.9324	0.4525	0.5149
Picea jezoensis (Siebold & Zucc.) Carrière	0.5357	0.7221	0.7366	0.8844	0.8267	0.7411
Pilea mongolica Wedd.	0.2857	0.4000	0.4000	0.4000	0.2500	0.3471
Pinus densiflora Siebold & Zucc.	0.2265	0.3171	0.3171	0.3171	0.1982	0.2752
Pinus koraiensis Siebold & Zucc.	0.4197	0.4702	0.5293	0.8479	0.8306	0.6195
Polygonatum odoratum var. *pluriflorum* (Miq.) Ohwi	0.2131	0.2983	0.2983	0.2983	0.4611	0.3138
Polystichum braunii (Spenn.) Fee	0.1429	0.2601	0.2601	0.3982	0.3388	0.2800
Polystichum tripteron (Kunze) C.Presl	0.3690	0.4297	0.4497	0.7268	0.7183	0.5387
Populus maximowiczii A.Henry	0.2857	0.4000	0.4000	0.4000	0.2500	0.3471
Potentilla fragarioides var. *major* Maxim.	0.1429	0.3449	0.3449	0.3449	0.2155	0.2786
Primula jesoana Miq.	0.1429	0.2000	0.2000	0.2000	0.1250	0.1736
Prunus maximowiczii Rupr.	0.2844	0.2000	0.2000	0.3982	0.3451	0.2856
Prunus padus L.	0.2524	0.2490	0.2490	0.6954	0.8644	0.4620
Prunus sargentii Rehder	0.2266	0.3172	0.3172	0.3172	0.1982	0.2753
Pseudostellaria heterophylla (Miq.) Pax ex Pax & Hoffm.	0.1429	0.2000	0.2000	0.2000	0.1250	0.1736
Pseudostellaria palibiniana (Takeda) Ohwi	0.2725	0.3048	0.3048	0.6185	0.5527	0.4106
Pseudostellaria setulosa Ohwi	0.3092	0.3821	0.3821	0.5302	0.4278	0.4063
Pyrola renifolia Maxim.	0.1429	0.2000	0.2000	0.4910	0.3069	0.2681
Quercus mongolica Fisch. ex Ledeb.	0.4982	0.5348	0.7782	0.8367	0.5108	0.6317
Rhododendron mucronulatum var. *ciliatum* Nakai	0.5280	0.2886	0.3532	0.9478	0.6356	0.5506
Rhododendron schlippenbachii Maxim.	0.7110	0.3748	0.5172	0.9672	0.7425	0.6625
Rhododendron tschonoskii Maxim.	0.4209	0.2000	0.3664	0.4504	0.3246	0.3525

Scientific Name	×1	×2	×3	×4	×5	Mean
Ribes mandshuricum (Maxim.) Kom.	0.4083	0.3802	0.3802	0.3802	0.3573	0.3812
Ribes maximowiczianum Kom.	0.5241	0.4558	0.5432	0.5498	0.5126	0.5171
Rodgersia podophylla A.Gray	0.3456	0.2000	0.2000	0.6989	0.3943	0.3678
Rosa davurica Pall.	0.2766	0.3990	0.3990	0.2517	0.2494	0.3151
Rosa suavis Willd.	0.3412	0.4040	0.3675	0.8889	0.7396	0.5482
Rubia akane Nakai	0.2920	0.3662	0.3662	0.5598	0.2555	0.3680
Rubia chinensis Regel & Maack	0.2206	0.2000	0.2000	0.2000	0.1930	0.2027
Rubia cordifolia var. *pratensis* Maxim.	0.1429	0.2000	0.2000	0.2000	0.1250	0.1736
Rubus crataegifolius Bunge	0.2857	0.4000	0.4000	0.4000	0.2500	0.3471
Rubus idaeus var. *microphyllus* Turcz.	0.1429	0.3028	0.2000	0.4820	0.4747	0.3205
Salix caprea L.	0.5149	0.3581	0.5453	0.5453	0.2531	0.4433
Sambucus sieboldiana var. *miquelii* (Nakai) Hara	0.1429	0.2000	0.2000	0.3812	0.2383	0.2325
Sambucus williamsii var. *coreana* (Nakai) Nakai	0.6465	0.4043	0.6774	0.6108	0.4971	0.5672
Sasa borealis (Hack.) Makino	0.2206	0.2000	0.2363	0.3989	0.2432	0.2598
Saussurea gracilis Maxim.	0.4791	0.2324	0.2324	0.7460	0.4339	0.4248
Saussurea grandifolia Maxim.	0.4591	0.6427	0.5334	0.5334	0.3334	0.5004
Saxifraga fortunei var. *incisolobata* (Engl. & Irmsch.) Nakai	0.2986	0.5322	0.5322	0.2826	0.2612	0.3814
Saxifraga oblongifolia Nakai	0.1429	0.2000	0.2000	0.4000	0.1250	0.2136
Saxifraga octopetala Nakai	0.1429	0.2000	0.2000	0.4000	0.2500	0.2386
Schisandra chinensis (Turcz.) Baill.	0.3810	0.3200	0.3200	0.4000	0.3333	0.3509
Sedum polytrichoides Hemsl.	0.2857	0.4000	0.4000	0.2000	0.2500	0.3071
Smilacina japonica A.Gray	0.2774	0.5764	0.5764	0.5007	0.3966	0.4655
Solidago virgaurea subsp. *asiatica* Kitam. ex Hara	0.7979	0.3458	0.4939	0.8644	0.7344	0.6473
Sorbus alnifolia (Siebold & Zucc.) K.Koch	0.1429	0.2000	0.2000	0.3600	0.1250	0.2056
Sorbus commixta Hedl.	0.4706	0.5892	0.6250	0.8114	0.8250	0.6642
Spiraea chamaedryfolia L.	0.2286	0.3200	0.3200	0.3200	0.5000	0.3377
Spiraea fritschiana C.K.Schneid.	0.2131	0.2983	0.2983	0.3891	0.2355	0.2868
Spodipogon cotulifer (Thunb.) Hack.	0.2286	0.2000	0.3200	0.3200	0.5000	0.3137
Streptopus amplexifolius var. *papillatus* Ohwi	0.1429	0.3340	0.2000	0.2000	0.2088	0.2171
Streptopus koreanus (Kom.) Ohwi	0.1429	0.3787	0.2000	0.2000	0.4479	0.2739
Streptopus ovalis (Ohwi) F.T.Wang & Y.C.Tang	0.2571	0.2000	0.2000	0.6000	0.3750	0.3264
Symplocos chinensis f. *pilosa* (Nakai) Ohwi	0.3902	0.3999	0.4704	0.7879	0.4843	0.5065
Synurus deltoides (Aiton) Nakai	0.5387	0.2689	0.2689	0.6805	0.5690	0.4652
Syringa patula (Palib.) Nakai	0.3301	0.2638	0.2638	0.3359	0.2249	0.2837
Taxus cuspidata Siebold & Zucc.	0.4287	0.3665	0.3824	0.7177	0.7628	0.5316
Thalictrum aquilegifolium var. *sibiricum* Regel & Tiling	0.2183	0.3057	0.3057	0.3057	0.1911	0.2653

Scientific Name	×1	×2	×3	×4	×5	Mean
Thalictrum filamentosum var. *tenerum* (Huth) Ohwi	0.1978	0.3948	0.3255	0.3255	0.2868	0.3061
Thelypteris japonica (Baker) Ching	0.2857	0.4000	0.4000	0.4000	0.3333	0.3638
Thelypteris phegopteris (L.) Sloss.	0.6597	0.5766	0.5351	0.8358	0.7782	0.6771
Thuja koraiensis Nakai	0.1947	0.2726	0.2726	0.3554	0.3136	0.2818
Tilia amurensis Rupr.	0.2034	0.5254	0.4835	0.6196	0.5732	0.4810
Trillium kamtschaticum Pall. ex Pursh	0.1429	0.4996	0.4996	0.5331	0.4579	0.4266
Trillium tschonoskii Maxim.	0.1429	0.2000	0.2000	0.2000	0.2332	0.1952
Tripterygium regelii Sprague & Takeda	0.7049	0.4501	0.5921	0.8652	0.8255	0.6876
Ulmus laciniata (Trautv.) Mayr	0.2445	0.2000	0.2000	0.3689	0.1590	0.2345
Vaccinium hirtum var. *koreanum* (Nakai) Kitam.	0.4794	0.5267	0.5267	0.4585	0.3246	0.4632
Veratrum maackii var. *japonicum* (Baker) T.Schmizu	0.1429	0.4000	0.4000	0.4000	0.1250	0.2936
Veratrum oxysepalum Turcz.	0.2822	0.3951	0.3951	0.5685	0.3553	0.3992
Viburnum opulus var. *calvescens* (Rehder) H. Hara	0.1997	0.2795	0.2795	0.2795	0.1747	0.2426
Viola selkirkii Pursh ex Goldie	0.3487	0.5919	0.5919	0.5222	0.3264	0.4762
Viola verecunda A.Gray	0.1429	0.2000	0.2000	0.2000	0.2500	0.1986
Weigela florida (Bunge) A.DC.	0.7171	0.4287	0.5220	0.6481	0.6917	0.6015
Woodsia polystichoides D.C.Eaton	0.3810	0.2000	0.3200	0.5333	0.3333	0.3535

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