

Research paper

# Diversity of *Pinus pumila*-dominated communities on the Kamchatka Peninsula

# Jaanus Paal<sup>1\*</sup>, Anton Pesterov<sup>2</sup> and Valentina Neshataeva<sup>2</sup>

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**Abstract.** On the Kamchatka Peninsula, Far East Russia, *Pinus pumila*-dominated communities occur from sea level up to 1200 m and geographically from the southern extremity of the peninsula up to the Kamchatka Isthmus and the Koryak Upland. Variation in species composition and abundance in *P. pumila* stands are determined mainly by the habitat's moisture, soil fertility (expressed as the litter-humus coefficient) and altitude. The fertility level of the habitats has a significant positive impact especially on the abundance of the herb layer species, and to a lesser extent on the cover of the shrub layer. The growth of dwarf-shrubs and lichens is inhibited in habitats with better fertility. In relation to the fertility gradient, the vertical structure of the communities is also changing explicitly; the thickness of snow cover and exposition has a modest effect on the vegetation of *P. pumila* stands on Kamchatka. The analysed set of 272 relevés were clustered into six community type groups: (i) pure dwarfpine communities, (ii) shrub-rich communities, (iii) dwarf-shrub-rich communities, (iv) herbgrass-rich communities, (v) moss-rich communities and (vi) lichen-rich communities; further 18 community types were established. They have a fairly good correspondence with most of the syntaxa described by previous scholars, but this is not always the case.

**Key words:** altitude, classification, elfin woods, gradient analysis, habitats fertility, moisture conditions, ordination, Siberian dwarf-pine.

**Authors' addresses:** <sup>1</sup>Institute of Ecology and Earth Sciences, University of Tartu, Lai 40, 51005 Tartu, Estonia; <sup>2</sup>Komarov Botanical Institute of the Russian Academy of Sciences, Professor Popov Str. 2, 197376, St. Petersburg, Russia; \*e-mail: jaanus.paal@ut.ee

# Introduction

The Siberian dwarf-pine (*Pinus pumila* (Pall.) Regel) has a peculiar form of growth that differs from trees or shrubs. The stems are prostrate, generally forming a network system buried in the thick litter of fallen needles. In the lowlands, the height of *P. pumila* stands is about 2.5–3.0 m, and in areas of their altitudinal limit only 40–50 cm, while the diameter of the stems is about

12–15 cm. The stems are resistant to low temperature and thick snow cover; they are lodging under the snow and can produce additional roots there. Due to its very wide ecological amplitude (Khomentovsky, 1995), *P. pumila* has a large geographical distribution and can grow in extremely severe climatic conditions. It occupies vast areas from the Lena River eastward to the coast of the Pacific Ocean, and extends northwards from the Korean Penin-

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sula, Honsu Island, Khingan, Sikhote-Alin and Tukuringra up to Southern Chukotka (Tikhomirov, 1949; Kabanov, 1977; Kharkevich, 1984, 1989). In Kamchatskiy Krai, including the Kamchatka Peninsula and northern Koryakia, the total area covered by *P. pumila* stands is about 8.6 million hectares (Grushin, 1961). In Japan, the vegetation belt dominated by *P. pumila* exists in most of the high mountains, being more pronounced on Hokkaido Island (Tatewaki, 1963; Kobayashi, 1967, 1971; Okitsu & Ito, 1984, 1989; Okitsu, 2002; Yasuda & Okitsu, 2012).

On the Kamchatka Peninsula, unlike Japan and easten Siberia, *P. pumila* occupies a very large altitudinal gradient that begins in some places from the sea coast and extends up to the alpine zone (Hultén, 1974; Khomentovsky, 1995; Neshatayeva, 2011); it often occupies dry and nutrient-poor sites, such as stony slopes and sandy deposits of so-called "dry rivers". The latter are temporary mudflows streaming down from the slopes of volcanoes. In the northern regions of Kamchatka and Koryakia, *P. pumila* stands predominate on plains.

The first aim of the present study was to characterize the main ecological gradients that determine the structure of the *P. pumila* stands on the Kamchatka Peninsula. Considering that the classification of these communities is in some aspects an open problem so far, the second aim was to establish the typology of these communities based on a representative data set and a multivariate approach, and to compare established syntaxa with the results of previous researchers.

The nomenclature for vascular plants follows Yakubov & Chernyagina (2004), for mosses it follows Czernyadjeva (2012), for liverworts Konstantinova *et al.* (1992), for lichens Santesson *et al.* (2004).

## Materials and Methods

#### Study area

The Kamchatka Peninsula occupies a huge area of 350000 km<sup>2</sup> from 50°52' to 60°52' north latitude and from 155°34' to 164°00' east longitude; the total length of the peninsula from north to south is 1200 km and the maximum width is 480 km. The peninsula has a folded volcanic topography with mountain ranges reaching 2500-3000 m a.s.l., separated by deep meridional depressions and lowlands. Nowadays, 30 active volcanoes are recorded on the peninsula, the highest of which is the Kluchevskaya Sopka - 4835 m a.s.l. Volcanic eruptions of low magnitude, with the ejection of 1-10 million m<sup>3</sup> of indigenous rock take place almost every year, producing a significant amount of volcanic ash, scoria and lava. Eruptions of high magnitude occur almost every 400 years, resulting in regional catastrophes (Braitseva et al., 1997; Gusev et al., 2003).

Kamchatka's climate is quite cold and humid; the sum of active temperatures above 10°C does not exceed 1200 and the duration of the vegetation period is about 100 days. The average temperature in July is +15°C, and in February it is -15–(-20)°C. The annual precipitation varies from 350 mm in the central valley to 1200 mm on the eastern coast. The average thickness of the snow cover is about 100 cm (Kondratyuk, 1974).

The soil cover of Kamchatka is mainly formed by specific types of volcanic soils (Andosols) (Sokolov, 1973; Zakharikhina & Litvinenko, 2011). They are characterized by several layers of volcanic tephra alternating with organic horizons.

# Field data

Field data were collected in all districts of the Kamchatka Peninsula (Figure 1) where *P. pumila* stands are present. Vegetation analyses were carried out in the course of 1974–2008, but always in the same vegetation period, from the second half of July to the end of August. In every sample area the sample plots of  $10 \times 10$  m were established along the downslope transects with an interval of 100 m through the whole *P. pumila* belt. In that way the sample plots covered all *P. pumila* communities presented in the considered sample area. The geographic coordinates and altitude were registered using a GPS device; exposition and inclinisation were estimated with a compass and declinometer.



Figure 1. Location of sample areas on the Kamchatka Peninsula.

The total cover percentage of *P. pumila* and all lower layers was estimated visually, as well as the cover of every species in the field and bottom layers.

Moisture conditions were evaluated according to Kachinsky (1970) and Mazirov *et al.* (2012) through the first four steps of their five-step scale: 1 – dry soil; brings forth dust, the hand does not feel coldness, no feeling when touching moisture, 2 – fresh soil; coldness in the hand, forms no dust, becomes a little lighter by drying, 3 – moist soil; moistens the filter paper, when drying it brightens remarkably, retains the shape given by the hand, moisture is clearly felt by touching, 4 – wet soil; when compressed it turns into a dough-like mass, wets hand but does not trickle between the fingers.

We used the ratio of the thickness of the humus horizon (A) to the thickness of the litter (O) or peaty litter (Oa) horizon as a proxy for soil fertility (Chertov, 1981); in the case of the absence of the humus horizon, value 1 was used in the calculation. In soil studies of the Russian Far East, this ratio is called as the "litter-humus coefficient" (Sapozhnikov, 1993). A consistent correlation between the soil real fertility and the value of the litter-humus coefficient was affirmed by statistical models (Chertov, 1981; Sapozhnikov, 1993; Komarova, 2004). According to the litter-humus coefficient, for oligotrophic soils the value of A/O or A/Oa is in limits of 0.00-0.10, for meso-oligotrophic soils 0.91-1.10 and for mesotrophic soils >1.10. Since there were no limestone outcrops (carbonate rocks) in Kamchatka, we also took into account the granulometric composition of the soils. The poorest (oligotrophic) soils are rocky, gravelly, or sandy; medium-rich soils (meso-oligotrophic and mesotrophic) are sandy loams or loamy sands; relatively richer (meso-eutrophic) soils are loams. Additionally, the presence of the peat horizon (H), indicating soil oligotrophy (due to the acid reaction of sphagnum peat) and the habitat drainage conditions were taken into account. The soil fertility was the lowest in dry habitats, as well as in poorly drained habitats; the soils in normally drained habitats were relatively rich.

The complete data set analysed in the current study included 272 relevés.

#### Data processing

To reduce the information noise in data processing, species that appear in the data fewer than three times were removed prior to multivariate analyses, except by calculating the average number of species and the evenness coefficients for community types. To assess the insolation effect, the exposition bearings (compass points) were transformed into continuous variables as follows: N – 0°, NW and NE – 45°, W and E – 90°, SW and SE – 135°, S – 180°, plain – 250°.

The mutual relationship of all environmental variables was evaluated by Spearman rank-order correlations (StatSoft Inc., 2005).

The main gradients of the species data were examined using the Detrended Correspondence Analysis DCA (Jongman et al., 1995) implemented in the PC-ORD software package ver. 7 (McCune & Mefford, 2016); the rescaling threshold was 0.1 and the number of segments was 26. The total cover of shrubs, herbs, dwarf-shrubs, mosses and lichens were also considered as environmental factors. The relationship between species abundance and environmental variables was depicted using ordination biplots. The strength of the environmental variables with ordination axes was evaluated by means of correlation coefficients between the axes scores and the variable values.

Multiple regression analyses were used to study the impact of environmental characteristics (predictor variables) variables to the variables of the vegetation structure; the models were built up by forward stepwise entry of variables (StatSoft Inc., 2005). The goal of the variables selection is to achieve a balance between simplicity (as few predictor variables as possible) and fit (as many predictors as needed) (Lancaster, 1999). The forward selection begins with an empty model and predictor variables are added one at a time beginning with the predictor with the highest correlation with the dependent variable. Variables of greater importance are entered first and the process is continued until no more predictor variables are admitted to the model and no more steps are repeated.

In cluster analysis, the chord distance and the flexible  $\beta$  algorithm ( $\beta$  = -0.6) were applied (McCune & Grace, 2002). Differences in the species composition between clusters were tested using a nonparametric multi-response permutation procedure (MRPP) (Mielke, 1984). To characterize the internal diversity of the clusters, the mean number of species and the evenness coefficient were used (Pielou, 1977).

The indicator values of the species in clusters were calculated using the Dufrêne and Legendre (1997) method included in the PC-ORD software package (McCune & Grace, 2002). The statistical significance of the obtained indicator values was evaluated by the Monte Carlo permutation test (4999 runs).

The difference between the mean values of the environmental variables in the established community types was tested by means of the univariate ANOVA and Fischer LSD post-hoc test; the difference in the median values for exposition, moisture and fertility estimations was verified by the Kruskal-Wallis ANOVA and Duncan's test (StatSoft Inc., 2005).

The classification of the geographical floristic elements (geoelements) of the vascular species proposed by Hultén (1968, 1974) and Hultén & Fries (1986) follows the adapted version for Far East elaborated by Qian *et al.* (2003) and Krestov (2003); the classification of vascular plant species according to their longitudinal and latitudinal areal types *sensu* Meusel *et al.* (1965) and Hundt (1985) follows Yurtsev (1994).

# Results

The total number of vascular plant species identified in the current data set was 180, that of bryophytes was 56, and that of lichens was 78 (60 species of epiphytic lichens are not included in the current analysis). Phytogeographically, 130 of the 271 vascular plant species represented Euro-Siberian floristic elements (geoelements), of which 63 had circumpolar, 34 Eurasian, 21 continental Eurasian, 15 European and 7 subatlantic European distribution. The largest fraction of the species belonged to the mountain-tundra (58%) and forest (42%). Considering the temperature, the species of the mesothermal climate prevailed (65%), the proportion of microthermal species was remarkably lower (35%).

According to the longitudinal distribution of vascular plant species, the circumboreal species had the largest fraction (39%), followed by eastern Asiatic (29%), circumpolar (17%) and Asiatic-American (15%) species. The presence of Asiatic-American species in the subordinate layers is a regional peculiarity of the *P. pumila* stands of the Kamtchatka Peninsula and the Koryak Upland. According to the latitudinal distribution, the most important were the boreal (55%), arcto-alpine (25%) and hypoarctic species (9%).

Considering the moisture gradient, psychro-mesophytes (36%) and eu-mesophytes (33%) had the leading position, confirming in general a psychrophilic and subalpine character of *P. pumila* communities.

The variation of the content and abundance of species in *P. pumila* stands on the Kamchatka Peninsula is primarily determined by the habitat fertility level; its correlation coefficient with the first ordination axis is 0.605 (Figure 2 A,B, Table 1). The impact of the altitude and moisture level are remarkably weaker according to the ordination analysis: the correlation coefficient of the altidude with the first ordination axis is –0.346 and with the second axis 0.324; the moisture level has the highest correlation (–0.455) with the third ordination axis (Figure 2 A,B, Table 1).

Ordination biplots (Figure 2 A,B) also visualise the mutual relationships between the considered environmental and vegetation structure variables. A positive relationship between the habitat fertility level and the total cover of the herb layer is obvious; the total cover of the dwarf-shrubs and that of the lichen layer have a negative relation





Figure 2. Species and environmental variables ordination biplot by the DCA axes 1 and 2 (A), and axes 2 and 3 (B). Notations: Fert, Moist – habitat fertility and moisture level, Incl – habitat inclination, Alt – altitude, Exp – exposition; Shrub, Herb, DwShrub, Moss and Lichen – total cover of shrubs, herbs, dwarf-shrubs, mosses and lichens, respectively; Ppum – cover of *Pinus pumila*. The full names of the species are presented in Appendix 1.

with the habitat fertility level. The total cover of the moss layer increases, while the total cover of the lichen layer decreases along with the habitat moisture gradient. Dwarf-shrubs and lichens are modestly favoured at a higher altitude, but the herb layer is remarkably reduced.

Table 1.	Correlation of environmental variables with DCA ordination axes. Notations: $r - Pearson$ correlation coefficient, $\tau - Kendall rank order correlation coefficient; other notations as in Figure 2.$
	lii rigule 2.

Variable		Axis 1			Axis 2			Axis 3	
					Statistics				
	r	r²	τ	r	r²	τ	r	r²	τ
Moist	0.107	0.012	0.124	-0.223	0.050	-0.136	-0.455	0.207	-0.385
Fert	0.605	0.366	0.490	-0.067	0.004	-0.051	-0.294	0.087	-0.196
Exp	0.203	0.041	0.160	-0.013	0.000	0.005	-0.128	0.016	0.067
Incl	-0.188	0.035	-0.159	0.014	0.000	0.019	0.046	0.002	0.036
Alt	-0.346	0.119	-0.245	0.324	0.105	0.204	0.200	0.040	0.108
Shrub	0.218	0.047	0.187	0.649	0.421	0.405	-0.143	0.020	-0.122
DwShrub	0.593	0.352	0.423	-0.184	0.034	-0.146	-0.135	0.018	-0.131
Herb	-0.778	0.605	-0.663	-0.234	0055	-0.116	0.214	0.046	0.149
Moss	-0.306	0.094	-0.211	0.151	0.023	0.166	-0.708	0.501	-0.524
Lichen	-0.463	0.215	-0.461	0.084	0.007	0.004	0.470	0.221	0.207

The results of the ordination analysis were statistically specified by the multiple regression analyses. It appeared that the total number of species is suppressed by the increasing cover of *P. pumila* and shrub layer, as well as by the higher moisture level (Table 2); the higher fertility and altitude of habitats support the species diversity. Still, the regression model includes also squared terms of fertility and moisture, indicating a non-linear impact of these factors to the total number of species.

The total cover of the shrub layer (excluding *P. pumila*) is enhanced by the habitats' higher altitude and fertility but, again, the significance of squared fertility in the regression model refers to a non-linear relationship of that factor with the shrub layer total cover (Table 2). Somewhat surprisingly, we did not find any regressor having a significant influence on the *P. pumila* total cover.

The dwarf-shrubs are favoured on higher altitudes, but the higher fertility of habitats, similar to the higher cover of *P*. *pumila* and the shrub layer decreases their total cover (Table 2).

The herb layer has a higher cover on more fertile localities, a negative impact on which have the higher altitude and sharper inclination, the total cover of *P. pumila* and dwarf shrubs (Table 2).

The total cover of mosses is enhanced by the habitats' moisture, whereas the higher cover of herbs and habitats' exposition to southern directions or their location on plains has a negative impact on the moss layer development (Table 2).

The lichens have the highest cover in highlands, while in moist and relatively fertile habitats they are suppressed. Nevertheless, the significant terms of squared fertility and moisture in the regression model point on the non-linearity of these relationships. The regression model proves also the negative impact of *P. pumila* and the shrub layer cover on lichens.

The analysed set of 272 relevés was classified into six community type groups, quite distinctly separated on an ordination biplot (Figure 3), and further divided into 18 clusters, i.e. community types. In every community type, different species dominate (Appendix 1) and all types have their Table 2. Environmental variables affecting the total number of species and projective cover of different vegetation layers according to the multiple regression analyses by stepwise entry of variables. Notations:  $\beta$  – standardized regression coefficient, SE<sub> $\beta$ </sub> – its standard error, B – unstandardized regression coefficient (slope), SE<sub> $\beta$ </sub> – its standard error, t – value of t-criterion, p – significance level, Mu R<sup>2</sup> – multiple R<sup>2</sup>, Ad R<sup>2</sup> – adjusted R<sup>2</sup>, F – value of F-criterion. Other notations as in Figure 2.

Variable	ß	C E	D	C E	+	n		Summary	statistics	
variable	р	JL <sub>β</sub>		JLB	L	h	Mu R <sup>2</sup>	Ad R <sup>2</sup>	F	р
				Total nun	iber of sp	ecies				
Intercept			14.68	2.073	7.08	<0.001	0.156	0.134	7.23	<0.001
Ppum	-0.22	0.057	-0.06	0.014	-3.84	<0.001				
Moist <sup>2</sup>	1.29	0.370	1.42	0.407	3.50	0.001				
Shrub	-0.17	0.060	-0.04	0.013	-2.73	0.006				
Alt	0.14	0.062	0.01	0.001	2.21	0.025				
Moist	-1.22	0.382	-6.816	2.125	-3.22	0.002				
Fert	1.26	0.355	6.23	1.750	3.56	<0.001				
Fert <sup>2</sup>	-1.10	0.332	-1.11	0.337	-3.30	0.001				
		T	otal cover	ofshrubs	, square	root transf	ormed			
Intercept			-1.32	0.912	-1.44	0.150	0.136	0.126	14.55	<0.001
Alt	0.29	0.058	0.01	0.000	4.92	<0.001				
Fert	0.93	0.282	2.61	0.795	3.28	0.001				
Fert <sup>2</sup>	-0.74	0.284	-0.43	0.165	-2.59	0.010				
		Tota	l cover of	dwarfshr	ubs, squa	re root tra	nsformed			
Intercept			8.39	0.745	11.26	<0.001	0.344	0.335	36.38	<0.001
Fert	-0.35	0.051	-1.20	0.173	-6.93	0.001				
Ppum	-0.27	0.049	-0.05	0.009	-5.49	<0.001				
Shrub	-0.23	0.052	-0.04	0.017	-4.42	<0.001				
Alt	0.23	0.053	0.01	0.001	4.32	<0.001				
		1	otal cove	r of herbs,	. square r	oot transfo	ormed			
Intercept			3.32	0.663	5.00	<0.001	0.502	0.493	55.59	<0.001
Fert	0.44	0.047	1.28	0.137	9.32	<0.001				
Alt	-0.34	0.045	-0.01	0.000	-7.60	<0.001				
Ppum	-0.18	0.045	-0.03	0.007	-3.97	<0.001				
DwShrub	-0.16	0.049	-0.02	0.006	-3.22	0.001				
Incl	-0.10	0.044	-0.02	0.008	-2.38	0.018				
		Тс	otal cover	ofmosses	s, square	root transf	formed			
Intercept			2.55	0.625	4.08	<0.001	0.238	0.230	28.96	<0.001
Moist	0.41	0.053	1.70	0.222	7.67	<0.001				
Herb	-0.22	0.053	-0.04	0.008	-4.14	<0.001				
Exp	-0.15	0.053	-0.01	0.003	-2.87	0.004				

Variable	P	C E	D	S.E.	+	2		Summary	statistics	5
Variable	р	SE <sub>β</sub>	D	SE <sup>B</sup>	L	h	Mu R <sup>2</sup>	Ad R <sup>2</sup>	F	р
		То	otal cover	oflichen	s, square	root trans	formed			
Intercept			10.34	0.806	12.83	<0.001	0.504	0.492	39.81	<0.001
Fert	-0.79	0.272	-1.97	0.682	-2.89	0.004				
Moist	-1.27	0.294	-3.58	0.831	-4.31	<0.001				
Moist <sup>2</sup>	1.01	0.284	0.57	0.159	3.57	<0.001				
Ppum	-0.20	0.043	-0.03	0.006	-4.65	<0.001				
Alt	0.19	0.047	<0.01	0.000	4.08	<0.001				
Shrub	-0.16	0.047	-0.14	0.041	-3.44	0.001				
Fert <sup>2</sup>	0.56	0.255	0.29	0.131	2.18	0.030				

Table 2 continues

own significant indicator species (Appendix 2). The MRPP test confirmed the objectivity of community types: even taking into account the Bonferroni correction for multiple comparisons, all established types had a significantly different (p<0.001) species composition. In the following text, the established community types are labeled by their dominant and/or indicator species.

(i) Group of pure dwarf-pine communities: Among the communities belonging to this group, the other layers besides P. pumila are very poorly developed or completely absent. The average number of species in these communities is approximately 10 (Table 3). This group includes only the P. *pumila* pure type (1<sup>st</sup> cluster) with sparse and sporadic specimens of grasses, herbs and/or dwarf-shrubs (Appendix 1). The very low evenness of these communities is remarkable (Table 3), indicating a great disparity between the abundance of species (P. pumila versus other species). In these communities, only P. pumila is a significant indicator species (Appendix 2). These communities are situated on moderate slopes having medium moisture and fertility level (Table 3); they are distributed throughout the peninsula and can be encountered at different altitudes. By the floristic composition within this type, two subtypes could be distinguished: for the first subtype the occurrence of boreal low herbs - Linnaea



Figure 3. Community type centroids and environmental variables ordination biplot. Notations: group 1 – pure dwarf-pine communities, group 2 – shrub-rich communities, group 3 – dwarf-shrub-rich communities, group 4 – herb-grass-rich communities, group 5 – moss-rich communities, group 6 – lichen-rich communities; other notations as in Figure 2.

borealis, Trientalis europaea, Lycopodium annotinum, Maianthemum dilatatum, Equisetum sylvaticum and mesophytic mosses – Dicranum scoparium, D. majus, D. fuscescens are characteristic; in communities of the second subtype of dwarf-shrubs – Vaccinium minus, V. uliginosum, Ledum decumbens and Empetrum nigrum are present.

34	Table 3.	Median valı Ppum – <i>Pin</i> , chen-rich; S slopeness, l dwarf-shrut post-hoc te: univariate A	ues of expos us pumila pu 5 – average I humidity an 35, mosses a sts or simila (NOVA, p <sub>kw</sub> –	sition, moistu ure, Shrub – : number of sp id fertility, re and lichens ir ar medians ac · significance	irre and fertil shrub-rich, I ecies in com spectively; ' communiti, cording to tl level by the	lity, and a DwShrub – munities, CovShr, Co es. With u he Duncan Kruskal-W	verage valı dwarf-shr E – evenne vHerb, Cov ppercase lı 's post-hov allis post-h	ues of oth ub-rich, H sss coeffici vDwShr, C. etters are c tests (fo hoc media	ier enviror 1Grass – h ient; Alt, E ovMoss, C marked si r Expos, M n test.	nmental va erb- and g Expos, Sloj ovLich – a imilar aver loist and T	ririables of rass-rich, se, Moist, verage co age value rophy); p <sub>A</sub>	Communi Moss – mo Trophy – h ver of shru s accordin <sup>NOVA</sup> – signi	ty types. N ss-rich, Li abitats' ex abs, herbs g to the F ificance lev	lotations: chen – li- kposition, +grasses, isher LSD /el by the
	Commu-	Type						Variable	S					
	nity type	group	S	ш	Alt	Expos	Slope	Moist	Trophy	Cov Shr	Cov Herb	Cov DwShr	Cov Moss	Cov Lich
	1	Ppum	10 <sup>ab</sup>	0.382 <sup>a</sup>	359 <sup>bce</sup>	ш	8 <sup>ab</sup>	2 <sup>b</sup>	3efgh	6 <sup>ab</sup>	11 <sup>bc</sup>	2ª	6 <sup>a</sup>	0 <sup>a</sup>
	2	Shrub	$10^{abce}$	0.666 <sup>bcde</sup>	$536^{qtd}$	ш	$6^{\rm ab}$	2 <sup>bc</sup>	3 efghi	419	$17^{cd}$	6 <sup>ab</sup>	19 <sup>bcd</sup>	$3^{ab}$
	°	Shrub	$11^{\mathrm{abcde}}$	0.668 <sup>bcde</sup>	244 <sup>ab</sup>	ш	8 <sup>ab</sup>	2 <sup>bc</sup>	З <sup>јк</sup>	$22^{ef}$	43 <sup>e</sup>	0 <sup>a</sup>	8 <sup>abc</sup>	0ª
	4	Shrub	$13^{ m bcdefgh}$	0.727 <sup>def</sup>	$253^{abc}$	NE	9 <sup>abc</sup>	$2^{\mathrm{b}}$	3 <sup>hij</sup>	349	44°	2ª	55 <sup>f</sup>	0ª
	5	Shrub	11 <sup>abcdef</sup>	0.730 <sup>def</sup>	$564^{\text{defg}}$	ш	$11^{\rm abc}$	2 <sup>bc</sup>	2 cdef	31 <sup>fg</sup>	4 <sup>ab</sup>	9 <sup>abc</sup>	$77^{gh}$	$1^{ab}$
	6	Shrub	$10^{\rm abce}$	0.724 <sup>df</sup>	868 <sup>i</sup>	SW	17°	$2^{\mathrm{b}}$	2 cdef	48 <sup>h</sup>	3 <sup>a</sup>	$12^{\text{bc}}$	38°	$4^{\rm abc}$
	7	DShrub	16 <sup>i</sup>	0.707 <sup>cdef</sup>	754 <sup>hi</sup>	SW	8 <sup>ab</sup>	$2^{\mathrm{b}}$	2.5 <sup>efgh</sup>	$13^{de}$	$10^{\rm abc}$	41 <sup>e</sup>	20 <sup>cd</sup>	3 <sup>abc</sup>
	∞	DShrub	10 <sup>abc</sup>	0.633 <sup>bc</sup>	497 <sup>cdef</sup>	ш	$14^{\rm bc}$	$1^{a}$	$1^{\mathrm{ab}}$	$5^{\mathrm{abc}}$	2ª	37 <sup>e</sup>	$7^{ m abc}$	$8b^{c}$
	6	DShrub	$15^{hi}$	0.697 <sup>cdef</sup>	$558^{dfgh}$	SE	$6^{\rm ab}$	2 <sup>b</sup>	2 <sup>bcde</sup>	$6^{\rm abc}$	6 <sup>ab</sup>	$51^{f}$	$28^{de}$	10℃
	10	DShrub	12 <sup>cdef</sup>	0.653 <sup>bcd</sup>	393 <sup>bcde</sup>	NE	$10^{ab}$	2 <sup>bc</sup>	2 <sup>def</sup>	<b>9</b> abcd	8 <sup>ab</sup>	16 <sup>c</sup>	$55^{f}$	$4^{\rm abc}$
	11	HGrass	12 <sup>bcdefg</sup>	$0.616^{b}$	396 <sup>bcde</sup>	SW	$14^{\rm bc}$	$2^{\mathrm{b}}$	Ĺ	$5^{\mathrm{abc}}$	$22^{d}$	0 <sup>a</sup>	$17^{\rm abcd}$	5 abc
	12	HGrass	8ª	0.633 <sup>bc</sup>	$115^{a}$	NE	$6^{\rm ab}$	2 <sup>bc</sup>	4 <sup>k</sup>	13 <sup>bcde</sup>	42 <sup>e</sup>	0 <sup>a</sup>	6 <sup>abc</sup>	0 <sup>a</sup>
	13	HGrass	12 <sup>bcdefg</sup>	0.678 <sup>bcde</sup>	81 <sup>a</sup>	plain	4ª	2 <sup>bc</sup>	3 <sup>ghij</sup>	9 abcd	50 <sup>e</sup>	$6^{ab}$	$16^{\rm abd}$	0 <sup>a</sup>
	14	Moss	$13^{defghi}$	0.715 <sup>cdef</sup>	510 <sup>cdef</sup>	NE	10 <sup>ac</sup>	2 <sup>b</sup>	2 <sup>bcd</sup>	$16^{de}$	9 <sup>abc</sup>	$15^{\rm bc}$	60 <sup>fg</sup>	5 abc
	15	Moss	$11^{\mathrm{bcdef}}$	0.678 <sup>bcde</sup>	$671^{\rm fgh}$	NE	$6^{\rm ab}$	2 <sup>bc</sup>	3 <sup>fghi</sup>	<b>9</b> abcd	$11^{ m abc}$	9 <sup>abc</sup>	57 <sup>f</sup>	$1^{a}$
	16	Moss	15 <sup>ghi</sup>	0.660 <sup>bcde</sup>	450 <sup>bcde</sup>	SW	27 <sup>d</sup>	4 <sup>d</sup>	2 <sup>bc</sup>	6 <sup>ab</sup> cd	6 <sup>ab</sup>	26 <sup>d</sup>	86 <sup>h</sup>	$1^{ab}$
	17	Moss	$14^{\rm fghi}$	0.643 <sup>bce</sup>	$251^{ab}$	Μ	$12^{\rm abc}$	2c	2 <sup>efg</sup>	$5^{\mathrm{abc}}$	$4^{ab}$	45 <sup>ef</sup>	73 <sup>gh</sup>	$2^{ab}$
	18	Lichen	13 <sup>dfgh</sup>	0.769 <sup>f</sup>	737 <sup>ghi</sup>	SE/E	$13^{\rm bc}$	1ª	1ª	3ª	2ª	26 <sup>d</sup>	$11^{\rm abc}$	$51^d$
	PANOVA		<0.001	<0.001	<0.001		<0.001			<0.001	<0.002	<0.003	<0.004	<0.005
	p <sub>kw</sub>					0.741		<0.001	<0.001					

(ii) Group of shrub-rich communities: In these communities, besides *P. pumila*, shrubs such as *Spiraea beauverdiana*, *Sorbus sambucifolia* and/or *Rhododendron aureum* have a dominant position; the average number of species is 10–13 (Table 3). This group includes communities of five types:

*P. pumila–Spiraea beauverdiana–Calamagrostis langsdorffii* type (2<sup>nd</sup> cluster). These communities are characterized by the predominance of *Spiraea beauverdiana* in the shrub layer and the high abundance of *Calamagrostis langsdorffii* in the field layer. In the scarse bottom layer, *Plagiomnium cuspidatum* is the indicator species (Appendix 2), while *Dicranum scoparium, Polytrichum commune* and *Pleurozium schreberi* are admixed (Appendix 1). These communities develop on mesic mesotrophic sites in the upper-middle part of the subalpine zone, occurring throughout the peninsula.

*P. pumila–Sorbus sambucifolia–Maianthemum dilatatum* type (3<sup>rd</sup> cluster). For these communities low herbs (*Maianthemum dilatatum, Oxalis acetosella*) and quite abundant ferns (*Phegopteris connectilis, Dryopteris expansa*) are characteristic (Appendix 2). Sorbus sambucifolia prevails in the shrub layer. The bottom layer is tenuous, but *Brachythecium reflexum* and Sanionia uncinata are common (Appendix 1). These communities are located in rich mesic sites at low altitudes in the southern and south-eastern parts of the peninsula.

P. pumila–Sorbus sambucifolia-Gymnocarpium dryopteris type (4th cluster) is characterized by the relatively high cover of boreal low herbs: Linnaea borealis, Gymnocarpium dryopteris, Chamaepericlymenum suecicum and Lycopodium annotinum; Sorbus sambucifolia dominates in the shrub layer. In the bottom layer, Pleurozium schreberi is abundant, and Polytrichum commune, Dicranum majus, D. scoparium and Sanionia uncinata are also common (Appendix 1). These communities develop on rich mesic sites at low altitudes, occurring on maritime terraces of the Pacific coast of south-eastern Kamchatka.

In the communities of *P. pumila–Rhododendron aureum–Polytrichum commune* type (5<sup>th</sup> cluster), the predominance of *Rhododendron aureum* in the shrub layer and the high cover of *Polytrichum commune* in the bottom layer are specific (Appendix 1). Some other species of dwarf-shrubs (*Vaccinium vitis-idaea, Ledum palustre*) and mosses (*Pleurozium schreberi, Dicranum scoparium, Sphagnum girgensohnii*) are common. Communities occur in poor mesic sites in the upper-middle part of the subalpine zone; they are mainly distributed in eastern and central Kamchatka and on Karaginsky Island.

For the communities of P. pumila-Rhododendron aureum-Dicranum scoparium type (6<sup>th</sup> cluster), the low (40–50 cm) shrub layer formed by Rhododendron aureum, covering about 40% is characteristic. Instead of Polytrichum commune, Dicranum scoparium and Pleurozium schreberi prevailed in the bottom layer (Appendix 1). The communities were found in mesic mesotrophic sites at the upper limit of the subalpine belt, that is, 800-900 m a.s.l.. They occur in the eastern, central and south-eastern parts of Kamchatka. The average evenness coefficient of the latter three community types was relatively high (Table 3), denoting a rather equal abundance of species in the respective communities.

(iii) Group of dwarf-shrub-rich communities: In the communities of this group, the projective cover of *P. pumila* layer is comparatively low (about 50%), which promotes the growth of light-demanding dwarf-shrubs – *Vaccinium uliginosum, V. vitis-idaea, Empetrum sibiricum, Ledum palustre, Loiseleuria procumbens* and *Arctous alpine.* In the moss layer, *Pleurozium shreberi* is the most abundant species; among the lichens, *Cladonia rangiferina* and *C. gracilis* are common. This group includes communities of four types.

*P. pumila–Vaccinium uliginosum–Ceratodon purpureus* type (7<sup>th</sup> cluster) is characterized by the predominance of *Vaccinium uliginosum* and the presence of *Saussurea*  pseudo-tilesii, Pyrola incarnata, Atragene ochotensis and Carex koraginensis in the field layer. In the scattered shrub layer, Salix pulchra, S. hastata, Ribes triste and sometimes Rhododendron aureum can be come across (Appendix 1). In the bottom layer, the pioneer mosses Ceratodon purpureus, Racomitrium lanuginosum and Polytrichum juniperinum are indicative (Appendix 2). The average number of species in the communities is releatively high, at 16 (Table 3). These communities are distributed on the high mountain plateaus around active volcanoes in central and eastern Kamchatka, where they have developed on Andosols of dry mesotrophic sites in volcanic ash and scoria deposits. Communites of this type probably represent a successional stage of subalpine vegetation that recovers after damage caused by volcanic eruptions.

In the communities of P. pumila-Vac*cinium vitis-idaea–Stereocaulon paschale* type (8th cluster), Vaccinium vitis-idaea is prevalent in the dwarf-shrub layer, and Empetrum nigrum and Vaccinium uliginosum are also common (Appendix 1). In the bottom layer, there are numerous bryophytes, but with relatively low abundance; the most remarkable among them are *Poly*trichum commune and Dicranum fuscescens. Rather abundantly grow lichens Stereocaulon paschale and Cladonia rangiferina. These communities are located in relatively poor and dry sites on steep slopes at upper middle-altitudes (450-600 m a.s.l.) in the mountains of the Sredinny Range, Ganalsky Range, Valaginsky Range and in the northern part of the peninsula.

In the communities of *P. pumila–Empetrum nigrum–Cladonia gracilis* type (9<sup>th</sup> cluster), *Empetrum nigrum* and *Vaccinium uliginosum* predominate in the dwarf-shrub layer, and *Pleurozium schreberi* and *Cladon-ia gracilis* are frequent in the bottom layer (Appendix 1 and 2). The communities are comparatively rich in species, including about 15 species (Table 3). They develop in mesic and mesotrophic sites at an altitudinal range of 500–700 m, i.e. in the middle

part of the subalpine zone, and are widely distributed throughout the peninsula.

In the dwarf-shrub layer of P. pumila-Ledum palustre-Sphagnum lenense type communities (10<sup>th</sup> cluster), Ledum palustre is the most abundant species, but Vaccinium vitis-idaea and V. uliginosum are also present (Appendix 1). In the bottom layer, Pleurozium schreberi, Polytrichum commune and Sphagnum lenense are common, the latter being a significant indicator species (Appendix 2). These communities occupy relatively poor and wet sites. On Kamchatka peninsula, communities of this type are very rare, occurring only in the northern part of the peninsula, but they are very common on Cryosols of permafrost areas in the Koryak region and on Karaginsky Island.

(iv) Group of herb-grass-rich communities: This group comprises three community types:

*P. pumila–Lerchenfeldia flexuosa–Chamerion angustifolium* type (11<sup>th</sup> cluster) communities are characterized by a comparatively large number of herb species and abundant grasses (*Calamagrostis langsdorffii, Lerchenfeldia flexuosa* and *Deschampsia borealis*). The sedge *Carex pallida* and herbs, such as *Chamerion angustifolium, Thalictrum minus, Linnaea borealis*, etc. are also common; dwarf-shrubs are almost lacking. These communities are located in mesic and meso-eutrophic habitats in the middle part of the subalpine zone; their distribution is confined mainly to the humid coastal areas of the peninsula.

In the communities of *P. pumila–Calamagrostis langsdorffii–Rubus chamaemorus* type (12<sup>th</sup> cluster), *Calamagrostis langsdorffii* has the highest dominance (Appendix 1) and indicator value (Appendix 2). *Phegopteris connectilis* and *Rubus chamaemorus* are relatively abundant, as well. Dwarfshrubs and lichens are completely lacking, thus the average number of species in the communities is the lowest (8 species) among the established types (Table 2). In the sparse shrub layer, *Spiraea beauverdiana* 

is common. The communities have developed in the most nutrient-rich and rather wet habitats at the lower bound (50–200 m a.s.l.) of the *P. pumila* stands; they occur on Karaginsky Island and on the Kamchatka Isthmus.

In the communities of *P. pumila–Chamaepericlymenum suecicum–Equisetum sylvaticum* type (13<sup>th</sup> cluster), the title species are the most abundant in the field layer (Appendix 1), but also *Rubus chamaemorus*, *Carex globularis* and *Betula exilis* are significant indicator species (Appendix 2). Dwarf shrubs are presented, but with low abundance. These communities occupy mesotrophic moist sites at low altitudes; they occur on peaty permafrost soils (Cryosols) in the peripheral parts of raised bogs and palsas; their distribution is limited to the north and north-east of Kamchatka.

(v) Group of moss-rich communities: In these communities, the total cover of the moss layer can be as high as 80%. This group embraces communities of four types:

In the communities of *P. pumila–Dicranum* spp.–*Mnium thomsonii* type (14<sup>th</sup> cluster), a high abundance of *Dicranum* spp., *Pleurozium schreberi* and *Polytrichum commune* is inherent in the bottom layer; *Spiraea beauverdiana* occurs in the shrub layer, while *Vaccinium vitis-idaea* is quite abundant in the field layer (Appendix 1). The communities are situated in Leptosols of poor mesic sites on stony slopes of ancient lava flows and rocky outcrops where *Mnium thomsonii* is very common. They are distributed in the southern, central and eastern Kamchatka.

In communities of *P. pumila–Dicranum* spp.–*Polytrichum commune* type (15<sup>th</sup> cluster), *Polytrichum commune, Pleurozium schreberi, Sanionia uncinata* and some *Dicranum* species (*D. scoparium, D. majus,* and *D. flexicaule* are constant and abundant (Appendix 1); a significant indicator species is *D. flexicaule* (Appendix 2). Due to the high cover (80%) of *P. pumila,* there is virtually a lack of herbs and lichens. The respective communities are situated in the mesic and mesotrophic habitats at an altitudinal range of 600–700 m; they are widely distributed throughout the peninsula.

In communities of P. pumila-Ledum palustre-Sphagnum girgensohnii type (16th cluster), predominance of Sphagnum girgensohnii in the bottom layer is conspicuous, and among the dwarf-shrubs, Ledum palustre has the highest abundance (Appendix 1). In addition to the title species, several other species in communities of this type also appear to be significant indicators: Sphagnum fuscum, S. capillifolium, Oxycoccus microcarpus, etc. (Appendix 2). These communities are common in nutrient-poor moist habitats, usually on Histosols, but sometimes they develop on steep slopes where the subsoil flow takes place. In the northern districts of the peninsula, Sphagnum-rich communities are found on the Cryosols, but in the eastern and central parts of Kamchatka, they also appear on Histosols around the mires.

For communities of *P. pumila–Vaccinium uliginosum–Pleurozium schreberi* type (17<sup>th</sup> cluster), a very high cover of *Pleurozium schreberi* in the moss layer is outstanding. Scarse *Vaccinium uliginosum, V. vitis idaea, Ledum palustre* and *Empetrum nigrum* grow in the field layer. The communities are related to mesic and mesotrophic habitats at a low-altitude range of 200–300 m; they are frequent in eastern, southern and central Kamchatka.

(vi) Group of lichen-rich communities: In these communities, fruticose lichens, such as *Cladonia arbuscula*, *C. rangiferina*, *Cetraria islandica*, *Flavocetraria nivalis*, *Thamnolia vermicularis* and some others have a high cover. This group was presented only by the *P. pumila–Ledum palustre–Cladonia* spp. type (18<sup>th</sup> cluster). Among these communities, *P. pumila* layer has a cover of less than 50% and a height of no more than 1 m. Dwarf-shrubs (*Ledum palustre* and *Vaccinium uliginosum*) and some species of lichens (*Cladonia arbuscula*, *C. rangiferina*, *Cetraria islandica*, *Flavocetraria nivalis*, and *Thamno-* *lia vermicularis*) are constant and abundant. The communities are situated in the poorest and driest habitats at the upper limit of the subalpine zone on Leptosols of steep stony slopes and plateaus; they are widely distributed in all mountain ridges of the central, southern and eastern Kamchatka.

Although the species composition of several community types seems to be quite similar, the respective communities differ physiognomically well due to the proportions of species abundance. Certain differences can also be observed between the habitats' mean or median characteristics of community types (Table 3). For example, *Rhododendron*-rich communities (types 5 and 6) are often situated at comparatively high altitudes (800–900 m a.s.l.), whereas communities of *P. pumila–Calamagrostis langsdorffii–Rubus chamaemorus* type (12)

and *P. pumila–Chamaepericlymenum suecicum–Equisetum sylvatica* type (13) are usually found in lower habitats. At the same time, the fern-rich and *Calamagrostis*-dominated communities were developed in the most nutritious-rich habitats.

Through cross-tabulation (Table 4), we can obtain a firmer idea about the frequency of different communities on the slopes of various exposition. Thus, communities of *P. pumila* pure type are usually situated on plains or slopes of southern exposition and almost lacking on the east-exposed slopes; shrub-rich communities are favoured on plains, more modestly occurring on the north and south slopes and less on the east and west slopes; herb-grass-rich stands prefer plains and western slopes, whereas moss-rich and lichen-rich communities are mainly formed on north-facing slopes.

Community	Туре				Expos	sition				Plain	Total
type	group	Ν	NW	W	SW	S	SE	Е	NE		
1	P. pumila	2	3	4	8	3	2		1	21	44
2	Shrub		2	1		3	1	1	1	6	15
3	Shrub			5				3	2	15	25
4	Shrub	1		4	2	1		2	2	5	17
5	Shrub			1	1		1	1	1	2	7
6	Shrub	2					1	1		4	8
7	DwShrub			5	2		1	3	1	9	21
8	DwShrub	2	1	2		1	1	1	1	6	15
9	DwShrub	2			1	3		1		8	15
10	DwShrub	1	4	5	4	1	1	3	3	9	31
11	HGrass			7		1		3	1	2	14
12	HGrass	1	3		1	1			1	5	12
13	HGrass	1						2	1	1	5
14	Moss	4	2	1		1		1	3	1	13
15	Moss	1		1	1	1			1	9	14
16	Moss	4		1		1			1	1	8
17	Moss	1	2	2	2		1	1		1	10
18	Lichen	4	1						2	1	8
Total		26	18	39	22	17	9	23	22	106	282

Table 4. Exposition of habitats of different type communities. Type group notations as in Figure 3.

## Discussion

By virtue of a very long south-north reach, mountainous topography, volcanic activities and marine impact, several gradients of habitat conditions accruing from these phenomena are distinctly expressed on the Kamchatka Peninsula. Due to the extremely wide ecological tolerance, P. pumila stands are found here in a very large scope of habitats, thus distinguishing a substantial variation of their communities. According to Khomentovsky (1995), the main environmental factors that determine the diversity of P. pumila stands on the Kamchatka Peninsula are habitat moisture, soil fertility and light conditions. Our results confirm at least a significant impact of the first two factors; the lightness of the habitat was not directly measured in the current study, but only as a potential insolation in terms of habitat exposition. Based on these assessments, lightness/insolation has no considerable effect on species richness or the cover of vegetation layers.

In Japan (Okitsu & Ito, 1984, 1989; Okitsu, 1998; Kolbek et al., 2003) and in the mountains of Sikhote-Alin (Grishin et al., 1996), P. pumila stands form a distinct vegetation belt (zone) above the forest limit. The same has been observed on the altitudinal distribution of the Pinus mugo communitites in Europe (Ellenberg, 1996; Šibik et al., 2010). On the Island of Hokkaido, P. *pumila* often occupies the deforested areas in the boreal subalpine zone that is generally intrazonal, and the altitudinal ranges of P. pumila belt vary from 200 to 500 m, being independent at the top of the mountains (Okitsu & Ito, 1989). Locally, they replace the Betula ermanii forests at the altitudinal forest limit and can reach the altitude of up to 1850 m (Okitsu, 2003); at the sites, *P*. pumila is also an undergrowth element of Larix gmelinii (= L. cajanderi) forests (Okitsu & Ito, 1989; Okitsu, 1998).

In Hokkaido, the development of *P*. *pumila* thickets is associated with peculiar environmentally restricted regions where

the thermal regime potentially permits the forest growth, but due to strong winds, heavy snowfall in winter and exposure of a rocky substrate, the forest development is hindered (Okitsu, 2002, 2003). For this reason, in the Taihetsu mountain range in central Hokkaido, P. pumila occurs mainly on gentle slopes in sheltered depressions on mountain tops and on deep leeward slopes that descend from the edge of a plateau; its height and cover declines with increasing wind exposure and reduced snow depth (Okitsu & Ito, 1984, Okitsu 2002). The thermal conditions in the growing season of the P. pumila zone in Hokkaido do not coincide with any specific value of the warmth index (Okitsu & Ito, 1984, 1989). Okitsu (1984) observed that the altitudinal difference between the ridge top and the forest limit tends to be wider on the northand west-facing slopes, which are windward sides to the prevailing winds in winter, and narrower in south- and east-facing leeward slopes.

On Mt. Vysokaya, the Central Sikhote-Alin, Grishin et al. (1996) pointed out that *P. pumila* forms a narrow but clear strip that is about a few tens of meters wide. The structure of these communities varies greatly depending upon the position on the slope and the shape of the terrain. There, the heterogeneity of dwarf pine communities is mainly determinated by the habitat's moisture, insolation and distribution of snow cover. The authors also emphasized on the importance of fires, which have had a strong impact on the structure of subalpine vegetation for a long time. The same can be observed in large areas in regions of active volcanism in Central, Eastern and Southern Kamchatka (Neshatayeva, 2011).

On the Kamchatka Peninsula, the altitude of the subalpine zone occupied by *P. pumila* stands is altered by variation in different regions of the peninsula. In some areas, mainly in southern Kamchatka, the *P. pumila* belt has developed almost from sea level, whereas on Sredinnyi mountain range, Malkinskiy range, on the watershed between Yurtovaya river and Ozernaya Kamchatka river, it ascends to the altitude range of 1100-1200 m. In eastern Kamchatka (in the Kronotsky Nature Reserve), communities of Pineta pumilae hylocomiosa and P. p. herbosa occurring on steep smooth rocks, predominate in the altitude range of 700–900 m, but sometimes occur up to 1000-1100 m a.s.l.. On the Kronotsky Peninsula extending far into the ocean, P. pumila belt including communities of P. p. fruticulosa and P. p. lichenosa is located much lower, at an altitudinal range of 150–300 m, locally reaching 400 m a.s.l.. On the eastern macroslope of the Sredinnyi mountain range (in the vicinity of Esso village), P. pumila belt has developed again at an altitudinal range of 700-900 m, but on the eastern slopes of the Klyuchevskaya group of volcanos, it is found in the limits of 900-1200 m.

Unlike Japan, where *P. pumila* stands grow only in the subalpine belt/zone (Suzuki, 1964; Kobayashi, 1971; Okitsu, 2003), on the Kamchatka Peninsula, due to the considerably wide scope of environmental conditions, the habitat gradients for P. pumila are much longer; on Kamchatka, these communities occur attitudinally from sea level to high mountains and geographically from the southern extremity of the peninsula to the Kamchatka Isthmus and the Koryak Upland. Thus, herein, P. pumila also grows in climatic conditions corresponding to the northern-boreal and subarctic zones lacking in Japan. While in the southern and northern parts of the peninsula only two vegetation belts (subalpine and mountain tundra) are represented, in the Central Valley four vegetation belts can be clearly distinguished: dominated by coniferous forests (mountain-taiga), B. ermanii forests, P. pumila stands and mountain-tundra (Neshatayeva, 2009, 2011). Therefore, the typological diversity of *P*. *pumila* stands on the Kamchatka Peninsula is remarkably higher than in Japan or in the continental regions of Eastern Siberia and the Russian Far East. As community site types are changing along the nutrition and moisture gradients, *P. pumila* stands vary from xeric lichen-dominated communities to wet *Sphagnum*-rich stands, and from nutrient-poor dwarf-shrub and lichen-rich communities to meso-eutrophic herb and fern-rich communities. The latter already represent a syntaxonomical continuum towards *Alnus fruticosa* var. *kamtshatica* communities.

According to the results of multiple regression analysis carried out in the present study, the cover of *P. pumila* is not significantly dependent on altitude. Still, a certain negative trend is observable - together with the cover, its height decreases and more light reaches the lower layers of vegetation. This will promote a higher diversity of dwarf-shrub, herb, and especially lichen species. It should be noted that, in some places on Kamchatka, a similar relation can also be followed between the cover of P. pumila and the lower layers at almost on the same altitudinal level. Consequently, the cover of *P. pumila* creates an amazingly expressed gradient for the lower layers: if its projective cover exceeds 90%, the vegetation of the lower layers may be totally lacking; although the P. pumila stand is sparse (cover less than 50%), the lichens, mosses and dwarf-shrub species that tolerate/prefer more light will considerably increase their species richness. Moreover, in addition to *P. pumila*, the shrub layer has a negative effect to the underlaying dwarfshrubs and lichens cover, while the herb layer adversely affects the development of the moss layer. In the Taihetsu mountains, Okitsu (2002) observed that in areas of a shallow snow cover P. pumila increases the accumulation of snow around the shrubs and thus encourages the spread of the stand.

In conformity with the altitudinal gradient, the change in the species composition of the communities is clearly expressed. At high altitudes, *P. pumila* occurs on steep slopes of ridges and/or in places too rocky for *Alnus fruticosa* var. *kamtschatica* thickets. At higher altitudes, dwarf-shrubs, such as Vaccinium vitis-idaea, V. uliginosum, Empetrum nigrum, Ledum decumbens and several fruticose lichens (Cladonia arbuscula, C. rangiferina, C. stellaris, Cetraria islandica, Flavocetraria nivalis, and Thamnolia vermicularis) are dominating. In lower altitudinal level, the cover of the herb layer is higher and mesic boreal herb-rich assemblages of species, such as Maianthemum dilatatum, Trientalis europaea, Linnaea borealis, Lycopodium annotinum, and Oxalis acetosella, are typical. On the sea shore level along the eastern coast of Kamchatka, small patches of P. pumila are also found in the Betula ermanii forests. Among these patches, the forest species (Maianthemum dilatatum, Gymnocarpium dryopteris, Trientalis europaea, Solidago spiraeifolia, Chamerion angustifolium and some others) occasionally occur, especially in less dense thickets of dwarf-pine where light can reach the field and bottom layers. Similarly, in the P. pumila patches occurring among the Alnus fruticosa thickets, some herbs and ferns belonging to the undergrowth of the dwarf-alder communities can be found: Cirsium kamtschaticum, Veratrum oxysepalum, Cacalia kamtschatica, Dryopteris expansa, Athyrium filix-femina, Phegopteris connectilis, etc.

Attempting to extrapolate the dependence of the distribution of *P. pumila* communities on altitude, it can be said that:

(i) At lower altitudes (150–400 m) generally, the herb-grass-rich communities dominated in the field layer by *Calamagrostis purpurea* ssp. *Langsdorffii, Lerchenfeldia flexuosa, Maianthemum dilatatum, Trientalis europaea, Lycopodium annotinum,* etc. have developed;

(ii) At medium altitudes (450–600 m), shrub-rich communities dominated by *Spiraea beauverdiana* and/or *Sorbus sambucifolia* are typical;

(iii) To some extent higher (600–700 m), moss-rich communities with the abundant cover of *Pleurozium schreberi*, *Polytrichum commune*, *Dicranum scoparium* are widely distributed; (iv) At an altitude from 750 to 1000 m, the psychrophilic communities with *Rho-dodendron aureum* appear;

(v) The uppermost position at an altitude from 700 to 1100 m is usually occupied by the dwarf-shrub-rich and/or lichen-rich *P. pumila* stands.

The fertility level of habitats has a significantly positive impact in the first place on the abundance of herb layer species, to a lesser extent on the cover of the shrub layer; at the same time, the growth of dwarfshubs and lichens is inhibited in relatively rich habitats well supplied with nutrients. In relation to the fertility gradient, the vertical structure of the communities is also changing explicitly: in lichen and/or moss-rich communities, only two layers are present; in habitats where the fertility level is higher, more complicated herb and shrub-rich communities with three layers develop.

On Mt. Ebeko, Paramushir Island, Okitsu et al. (2001) recorded a reduction in the total number of species from 50 at lower altitudes to 20 in communities at higher elevations. According to their explanation, many sporadic species grow at lower altitudes and non-volcanic mountains with a frequency below 10%, while at higher altitudes almost all recorded species were common ones. The decreasing number of species towards a higher altitude may be partly related to the effect of repeated volcanism, wherein the plant communities remain, hence at an earlier stage of succession. Another issue associated with the effect of volcanic activity on plant communities is an admixture of species from different habitats, for the reason that repeated volcanism effectively aborts any development of habitat segregation, whereas at lower altitudes, many species only occur there. The insufficient time for maturation of plant communities under the impact of volcanoes causes some species to occur only sporadically without a clear altitudinal tendency. In a recent study, we did not analyse changes in the number of species of *P. pumila* stands along the altitudinal gradient of individual mountains; therefore, the statements above were not verified. Based on the average number of species in the communities, it can be said that some types of herb-grass-rich and shrub-rich communities, but generally species-poor communities are found from the lowest to medium altitudes, while communities having the highest average number of species (some types of dwarf-shrub-rich and moss-rich communities) occur at medium altitudes. Here, it must also be noted that, whilst instead of lichen-rich communities, the highest average location on Kamchatka have the communities of P. pumila-Rhododendron aureum-Dicranum scoparium type and P. pumila-Vaccinium uliginosum-Ceratodon purpureus type, the linear consecution of altitudinal belts of vegetation is often disturbed by several local factors, mainly by volcanic activities.

The thickness of the snow cover and exposition has only a modest effect on the vegetation of P. pumila stands on Kamchatka. Due to the impact of the cold-water seas (Sea of Okhotsk, Bering Sea and the northern part of the Pacific Ocean) that surround the pensinsula, the climate is humid and rather cold, and the thickness of the snow cover is usually more than 1 m everywhere. In the eastern coastal regions, the average snow thickness is even more than 2.5 m (Kondratyuk, 1974). Regarding the exposition, it seemed in our study that on the slopes that had exposition towards the northern rumbs, only the cover of the moss layer was significantly promoted; whereas for the cover of dwarf-shrubs and herbs, the exposition was included in the regression models, but as a non-significant factor.

The most widely distributed *P. pumila* communities were dominated by dwarf-shrubs and mosses in the lower layers, and occupied the middle part of the moisture and fertility gradients of the habitats (Ne-shatayeva, 2011), which were also confirmed by the ordination analysis results

in the present paper. Generalizing the facts about habitat conditions, which are related to those geographical distributions and of *P. pumila* stands on Kamchatka, we can conclude that:

(i) In eastern Kamcahtka, the *P. pumila* stands form a major vegetation type at an altitudinal range of 700–900 m, and its communities occupy ledges and gentle slopes of volcanic upland, in which they can locally spread to 1000–1100 m, growing there on volcanic plateaus (P. pumila communities with dwarf-shrubs and lichens). On the Kronotsky Pensinsula, the vegetation belts are situated at a lower position due to the oceanic climate and permafrost, and the *P. pumila* stands start there from the coast up to 400-450 m upwards, being more pronounced at an altitudinal range of 150-300 m. A similar inversion is characteristic to the flat depressions between the mountain ranges and the river valleys, where the cold air masses that descend from the mountains are standstill. There, the P. pumila stands are intermixed with the thickets of Alnus fruticosa covering the deeper slopes. Around the Kronotsky Lake, P. pumila stands occur at an altitudinal range of 900 m and higher, being replaced by tundra communities.

(ii) Alnus fruticosa thickets dominate on the southeastern coast of the Kamchatka Peninsula, and *P. pumila* communities are represented within them as comparatively small patches located on drier and nutrient-poor slopes of the northern and western exposition. In the southern part of the Central Valley, the P. pumila stands (with Rhododendron aureum, dwarf-shrubs and/ or lichens) are typical at an altitudinal range of 900-1200 m. On the eastern slope of the Sredinnyi Mt. Range, in the vicinity of Esso village, at an altitudinal range of 700-900 m, almost all the community type groups of P. pumila appear. On the western slopes of the volcanic plateau of the Kluchevskaya group of volcanoes, the *P. pumila* belt is situated at an altitudinal range of 850–1200 m. There the stands in vast areas are damaged by contemporary volcano eruptions.

(iii) On the western coast of the peninsula, the *P. pumila* stands cover relatively small areas, usually on slopes, hillocks and periphery of mire (paludified) habitats.

(iv) In southern Kamchatka, the communities of *P. pumila* can be found on the western (Sea of Okhotsk) coast; on the southeastern (Pacific) coast, they occur relatively seldom, only on the rocky capes; however, in the Southern Kamchatka Nature Reserve, a large variety of them grow on the slopes of the volcanic plateaus.

(v) On Karaginsky Island, *P. pumila* stands cover about 35% of the territory, occupying mainly the mountain slopes, but also the Bering Sea coast. The stands cover the watershed areas and terraces with relic peat deposits up to an altitudinal range of 500–600 m. Here, pure stands of *P. pumila* and/or those with *Spiraea beauverdiana* or *Sorbus sambucifolia* are common.

The first brief floristical overview of P. pumila stands on Kamchatka Peninsula was published by Komarov (1912, 1927) and the first typological characterization of its communities in southern Kamchatka was published by Hultén (1927), who described three community types (associations): (i) Spiraea-moss-rich, (ii) Spiraea-Sphagnum-rich and, (iii) Rhododendronmoss-rich. Based on studies in Central Kamchatka, Lipshits & Liverovskii (1937) supplemented this list ten years later with tree associations: Pinetum pumilae purum, P. pumilae spiraeosum and P. pumilae rhododendrosum. Later, numerous scientists described some other associations of the *P*. pumila stands in the Russian Far East and north-eastern Siberia, but these classifications were based on various methodological approaches and were therefore often poorly comparable.

The first classification of *P. pumila* stands for northern Japan (Hokkaido Island) was elaborated by Tatewaki (1963). Based on dominant species of different layers, he distinguished between six associations: 1) P. pumila-Rhododendron aureum-Empetrum nigrum var. japonicum; 2) P. pumila-Arctous alpina var. japonica-Vaccinium uliginosum; 3) P. pumila-Ledum palustre; 4) P. pumila-Sorbus matsumurana; 5) P. pumila-Sasa kurilensis; 6) P. pumila without lower layers. Suzuki (1964) and Suzuki & Umezu (1965), following the principles of the Braun-Blanquet classification approach, estimated in Central Japan (Honshu mountains) only one association: Vaccinio-Pinetum pumilae, alliance Vaccinio-Pinion pumilae (Suzuki, 1964).

Kobayashi (1967), using the same methodological approach, studied the P. pumila communities on the Taisetsu and Hidaka Ranges (Hokkaido). He described three associations there: 1) Sorbeto-Pinetum pumilae, 2) Rubeto-Pinetum pumilae, and 3) Ledeto-Pinetum pumilae. The first of them is close to the association P. pumila-Sorbus matsu*murana* and the last one to the association P. pumila-Ledum palustre distinguished by Tatewaki (1963). Later, Kobayashi (1971) developed the classification of P. pumila communities for the whole of Japan. Within the alliance Vaccinio-Pinion pumilae Suzuki (1964) distinguished between and characterized four broad associations: 1) Ledo-Pinetum pumilae, 2) Cetrario-Pinetum *pumilae*, 3) *Rhodoro-Pinetum pumilae*, and 4) Rubo-Pinetum pumilae. These associations were further divided into 16 sub-associations.

In Hokkaido, Okitsu & Ito (1984) distinguished between four types of dwarf-pine communities: 1) *Empetrum–Rhododendron* type, best represented on leeward slopes, which are somewhat protected from strong winds and where the cover of *P. pumila* is high, 2) lichen type, occurring in more severe habitats, 3) *Empetrum–Loiseleuria procumbens–Diapensia lapponica* type and, 4) *Empetrum–Loiseleuria–Diapensia* sparse type (differentiated by the open canopy of *P. pumila*). Communities of the last two types occupied more exposed positions, the latter being presented in the most extreme conditions. Types 1, 2 and 3 are analogous to Kamchatka subalpine *P. pumila* schrubs (*Pinetum pumilae rododendrosum*, *Pinetum pumilae lichenosum* and *Pinetum pumilae fruticulosum*).

Neshatayeva (2011) published a detailed synopsis about *P. pumila* stands on the entire Kamchatka Peninsula. The empirical classification based on 379 relevés was elaborated using the dominant-determinant species and classification approach of the Russian geobotanical school (Neshatayeva, 2004). Based on soil moisture and fertility, nine habitat site types and 15 associations were established, along with four sub-associations and 32 variants.

When comparing these results with community types established on the basis of multivariate analysis in the present study, in most cases, we can find a fairly good correspondence between them, but not always:

(i) The first variant of *P. pumila* pure type (1<sup>st</sup> cluster) corresponds to the association *Pinetum pumilae oligoherbosum* subass. *typicum*, and subass. *oligofruticulosum*.

(ii) The *P. pumila–Spiraea beauverdiana– Calamagrostis langsdorffii* type (2<sup>nd</sup> cluster) corresponds to the association *Pinetum pumilae spiraeosum beauverdianae*.

(iii) The *P. pumila–Sorbus sambucifolia–Maianthemum dilatatum* type (3<sup>rd</sup> cluster) corresponds to the association *Pinetum pumilae sorbosum sambucifoliae*.

(iv) The *P. pumila–Sorbus sambucifolia–Gymnocarpium dryopteris* type (4<sup>th</sup> cluster) corresponds to *Pinetum pumilae sorbosum sambucifoliae* var. *hylocomiosum*.

(v) The *P. pumila–Rhododendron aureum– Polytrichum commune* type (5<sup>th</sup> cluster) and

(vi) the *P. pumila–Rhododendron aureum– Dicranum scoparium* type (6<sup>th</sup> cluster) correspond to the association *Pinetum pumilae rhododendrosum aurei*.

(vii) The *P. pumila–Vaccinium uligino*sum–Ceratodon purpureus type (7<sup>th</sup> cluster) corresponds to the association *Pinetum* pumilae hylocomioso-fruticulosum subass. typicum var. laricetosum.

(viii) The P. pumila-Vaccinium vi-

*tis-idaea–Stereocaulon paschale* type (8<sup>th</sup> cluster) coincides best with the association *Pin-etum pumilae herboso-fruticulosum*.

(ix) The *P. pumila–Empetrum nigrum–Cladonia gracilis* type (9<sup>th</sup> cluster) corresponds to *Pinetum pumilae hylocomioso-fruticulosum.* 

(x) The *P. pumila–Ledum palustre–Sphagnum lenense* type communities (10<sup>th</sup> cluster) corresponds to the association *Pinetum pumilae herboso-fruticulosum* var. *calamagrostidosum*.

(xi) The *P. pumila–Lerchenfeldia flexuosa– Chamerion angustifolium* type (11<sup>th</sup> cluster) and

(xii) P. pumila-Calamagrostis langsdorffii-Rubus chamaemorus type (12<sup>th</sup> cluster) correspond best to the association Pinetum pumilae calamagrostidosum var. lerchenfeldiosum and associations of the Pineta pumilae pteridosa group, i.e. the associations Pinetum pumilae phegopteridosum and Pinetum pumilae dryopteridosum.

(xiii) The *P. pumila–Chamaepericlyme*num suecicum–Equisetum sylvaticum type (13<sup>th</sup> cluster) corresponds to the association *Pinetum pumilae chamaemori-rubosum* var. chamaepericlymenosum.

(xiv) The *P. pumila–Dicranum* spp.–*Mni-um thomsonii* type (14<sup>th</sup> cluster) corresponds to the association *Pinetum pumilae hylocomiosum* var. *oligoherbosum*.

(xv) The *P. pumila–Dicranum* spp.–*Pol-ytrichum commune* type (15<sup>th</sup> cluster) corresponds to the association *Pinetum pumilae hylocomiosum* var. *typicum*.

(xvi) The *P. pumila–Ledum palustre–Sphagnum girgensohni* type (16<sup>th</sup> cluster) corresponds to the association *Pinetum pumilae sphagnosum girgensohnii.* 

(xvii) The *P. pumila–Vaccinium uligino*sum–Pleurozium schreberi type (17<sup>th</sup> cluster) corresponds to the association *Pinetum pumilae hylocomiosum* var. *oligofruticulosum*.

(xviii) The *P. pumila–Ledum palustre– Cladonia* spp. type (18<sup>th</sup> cluster) corresponds to the association *Pinetum pumilae cladinosum*.

In the present study, we did not find

a satisfactory correspondence for associations *Pinetum pumilae nanoherbosum* and *Pinetum pumilae equsietosum sylvatici;* through multivariate analysis, the communities of the former association are merged with the 11<sup>th</sup> or 12<sup>th</sup> cluster, and the communities of the latter association with the 13<sup>th</sup> cluster.

The empirical classification focuses more on certain indicator species, which may lead to an overestimation of their importance and sometimes distinguishing subordinated units in order to emphasize some peculiarities or the individual features of communities (e.g. the height of P. pumila shrubs, the density of layers, the presence of some forest or tundra species, the altitudinal limits, etc.). The numerical classification is much more formal and rigorous; if there are no special procedures involved, the abundance of all species is objectively considered without subjectively aggravating any species. Moreover, the very rare communities, having a peculiar structure and subjectively awakening special interest, could be ignored by numerical classification as outliers or statistically unreliable objects due to infrequent occurences. Therefore, we cannot conclude here which of the compared classifications is better: it depends on which characteristics are considered more informative or correspond better with the aim of the classification.

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Appendix 1. Centroids of community types.

Notations: Ppum - Pinus pumila, N - number of communities, S - mean number of species, E - evenness corefficient, SD - standard deviation. Only species with a mean cover of >0.3% at least in communities of one type and significant indicator species are presented.

_		_																							
	Lichen- rich		18		∞	13	4	0.77	0.07		47.9	I	I		I	I	I	I	I	1.8	ı	I	ı	I	I
			17		15	14	7	0.64	0.05		54.4	0.6	I		I	0.6	2.2	0.7	I	0.2	I	I	I	I	I
	rich		16		£	15	3	0.66	0.10		68.3	I	5.0		1.7	I	I	I	I	I	I	I	I	I	I
	Moss-		15		13	11	2	0.68	0.07		80.7	I	0.4		I	I	I	I	I	2.5	ı	I	I	I	I
			14		12	13	3	0.72	0.07		69.0	I	0.5		I	ı	<0.1	I	1.1	4.3	ı	I	ı	I	I
	ich		13		12	12	ŝ	0.68	0.06		58.7	I	ı		ı	ı	2.4	0.2	I	I	ı	ı	ı	ı	I
	-grass-r		12		30	∞	2	0.63	0.09		69.0	I	ı		ı	0.1	ı	1.0	I	I	1	I	ı	I	I
ypes	Herb		11		14	12	5	0.62	0.12		63.8	0.8	0.4		0.8	I	I	2.8	<0.1	I	1	1	1	I	I
munity t		ty types	10	tics	6	16	4	0.77	0.05		70.9	0.3	0.8		0.1	0.4	0.4	0.3	I	1.4	1	1	<0.1	I	I
s of com	ub-rich	ommuni	6	Statis	14	15	4	0.70	0.08		52.9	I	1.4		0.4	I	0.3	I	I	2.0	1	0.1	1.7	0.8	I
Groups	warf-shr	Ŭ	8		10	10	4	0.63	0.10	Trees	65.0	I	1	Shrubs	0.8	0.7	0.4	I	I	2.4	1	1	1.3	I	I
	D		7		14	16	4	0.71	0.05		61.4	I	2.1		0.4	ı	0.9	0.6	I	6.1	1.1	0.9	1.6	2.6	I
			9		15	10	4	0.72	0.11		57.0	I	1		0.9	I	I	I	I	41.7	1	1	0.4	I	0.4
			5		15	11	4	0.73	0.11		55.7	I	1		I	0.7	I	0.1	I	22.9	1	1	ı	I	I
	rub-rich		4		7	13	3	0.73	0.12		62.5	I	1		I	I	I	0.6	1.9	0.1	1	1	ı	I	I
	Sh		3		23	11	4	0.67	0.07		64.7	0.3	1		I	1	I	I	I	0.7	1	1	1	I	I
			2		14	10	4	0.67	0.10		68.0	I	1		I	1	I	0.8	I	2.7	1	1	ı	I	I
	Ppum pure		1		42	10	3	0.38	0.14		81.3	I	0.1		0.2	0.1	0.7	0.3	<0.1	1.0	1	1	<0.1	I	I
	Species				Z	S	SDs	ш	SD <sub>F</sub>		Pinus pumila	Betula ermanii	Larix cajanderi		Alnus fruticosa	Betula divaricata	Betula exilis	Lonicera caerulea	Lonicera chamissoi	Rhododendron aureum	Ribes triste	Salix hastata	Salix arctica	Salix pulchra	Salix caprea

								Group	s of com	munity	spes							
Species	Ppum pure		S	hrub-ric	Ļ		D	warf-sh	rub-rich		Herb	)-grass-i	ich		Moss-r	rich		-ichen- rich
								C	ommun	ty types								
	1	2	3	4	5	9	7	8	6	10	11	12	13	14	15	16	17	18
Salix crassijulis	I	Ι	Ι	I	I	I	I	I	I	I	I	I	I	1.0	I	I	I	I
Sorbus sambucifolia	1.1	1.7	15.7	25.1	2.1	1.7	I	I	I	1.3	I	2.1	<0.1	<0.1	0.7	1.7	0.6	0.1
Juniperus sibirica	<0.1	I	I	I	I	I	I	I	<0.1	<0.1	0.8	I	I	I	I	ı	1.1	I
Spiraea beauverdiana	2.8	37.3	5.7	6.3	5.5	5.8	3.1	0.4	1.4	5.3	1.3	9.5	7.2	10.8	6.3	5.2	1.9	0.7
							Dw	arf shru	bs									
Aconogon tripterocarpum	<0.1	<0.1	I	I	I	I	<0.1	<0.1	0.5	<0.1	I	I	I	0.3	0.2	I	0.1	0.7
Arctous alpina	I	<0.1	Ι	I	I	0.9	1.4	1.9	1.0	0.1	I	I	I	I	I	I	0.2	2.0
Empetrum nigrum	0.6	0.8	I	<0.1	Ι	0.2	5.1	4.9	32.1	0.8	I	I	3.8	2.7	1.4	2.4	6.9	I
Ledum palustre	0.3	0.7	Ι	I	2.3	2.3	7.9	1.8	4.4	7.6	<0.1	I	0.8	4.0	1.3	15.7	13.6	14.4
Loiseleuria procumbens	I	I	I	I	I	I	0.9	0.4	<0.1	I	I	I	I	I	I	I	I	I
Phyllodoce caerulea	I	0.7	I	I	I	0.9	1.1	I	I	I	I	I	I	I	I	I	I	I
Vaccinium vitis-idaea	0.6	0.8	Ι	1.5	5.1	5.8	4.5	22.1	4.5	4.6	<0.1	I	0.8	6.6	2.7	2.6	9.7	4.4
Vaccinium uliginosum	0.4	2.5	I	I	1.4	1.7	20.0	5.5	9.4	3.1	<0.1	I	1.1	1.4	3.7	5.6	14.6	5.4
							Herbs	and gra	asses									
Aconogonon tripterocarpum	<0.1	<0.1	I	I	I	I	<0.1	<0.1	0.5	<0.1	I	I	I	0.3	0.2	I	0.1	0.7
Artemisia arctica	I	I	Ι	I	I	I	0.4	<0.1	<0.1	I	<0.1	I	I	I	I	I	1	I
Artemisia opulenta	I	I	0.3	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Aruncus kamtschaticus	I	I	0.3	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Atragene ochotensis	I	I	Ι	I	I	I	<0.1	I	<0.1	I	I	I	I	I	I	I	I	I
Bromopsis pumpelliana	<0.1	I	I	I	I	I	0.7	<0.1	I	I	I	I	I	I	I	I	I	I
Calamagrostis purpurea	1.9	9.7	11.3	1.5	0.9	0.5	0.4	0.5	<0.1	1.1	8.5	31.5	8.3	0.6	2.4	2.3	I	<0.1
Carex globularis	<0.1	I	I	I	I	I	I	I	<0.1	0.9	I	I	2.6	I	ı	I	0.4	I

							Group	s of com	munity t	ypes							2 2 2 - -
		S	hrub-ricl	_			warf-sh	rub-rich		Herb	-grass-r	ich		Moss-I	rich		Lichen- rich
		[					0	ommuni	ty types								
2 3	m		4	5	9	7	∞	6	10	11	12	13	14	15	16	17	18
	I		I	I	I	0.1	I	I	I	I	I	I	I	I	I	I	I
	1		I	I	ı	1.5	<0.1	0.2	0.2	1.5	ı	ı	ı	<0.1	I	ı	I
1	I		I	I	I	I	I	I	I	I	I	0.3	0.1	I	I	I	I
	1		10.0	I	I	<0.1	I	1.1	0.1	1.2	0.2	18.0	0.7	I	I	I	I
<0.1 0.3	0	~	0.2	I	I	0.5	<0.1	<0.1	<0.1	1.9	1.3	0.5	0.7	I	I	0.6	I
1	I		I	I	I	I	I	I	I	I	I	I	I	I	I	I	0.7
- 0.3	0.3		I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
- 0.3	0.3		I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
-   9.(	9.0		I	I	ı	ı	ı	I	I	ı	<0.1	<0.1	ı	I	I	1	I
1	1		I	I	ı	I	I	I	I	1.9	I	ı	I	I	I	I	I
-	°.	_	<0.1	<0.1	I	<0.1	I	I	I	0.2	0.1	1.1	0.1	0.7	<0.1	1.3	I
0.7 –	I		1.3	0.6	I	1.1	0.4	1.5	1.5	0.6	1.1	10.2	I	2.9	I	0.1	I
-	Ŷ		I	I	I	I	I	I	I	I	0.5	I	I	I	I	ı	I
<0.1 5.1	5.1		13.8	0.4	I	I	I	I	0.2	I	I	I	<0.1	I	I	I	I
1	I		I	I	I	0.5	I	I	I	I	I	I	I	I	I	ı	0.5
- 0.	0	3	0.3	I	I	I	I	<0.1	0.2	5.0	I	0.1	0.7	I	I	I	I
0.8 1.	-i	5	12.5	0.7	0.8	1.4	I	1.2	1.1	1.3	<0.1	0.2	1.7	1.2	1.5	0.2	1.0
3.1 2.	2.	0	1.6	1.3	<0.1	I	I	0.2	0.5	0.8	I	I	1.5	<0.1	1.2	I	I
0.7	'		I	I	0.1	I	I	I	<0.1	I	I	I	0.5	1.4	I	I	I
1.0 9.6	9.6		4.6	<0.1	0.1	I	I	<0.1	0.1	0.5	0.3	I	0.2	0.2	0.3	0.2	I

	Lichen- rich		18	I	I	I	I	I	I	I	I	<0.1	I	I	I	I		I	I	I	I	I	I	I	I
			17	I	I	I	I	0.2	I	I	0.7	I	I	I	I	<0.1		0.6	I	I	I	I	I	0.6	I
	rich		16	I	0.1	I	I	0.7	0.1	I	I	I	Ι	I	I	I		I	I	I	I	I	I	I	0.7
	Moss-		15	I	I	I	ı	I	I	I	I	1.2	0.1	I	ı	<0.1		I	I	0.4	ı	I	I	2.5	0.4
			14	I	I	I	I	0.1	I	I	I	1.5	I	I	I	<0.1		I	I	<0.1	I	I	I	I	I
	ich		13	I	I	I	0.7	ı	I	I	8.1	<0.1	I	I	ı	<0.1		I	2.1	I	I	I	I	I	I
	-grass-r		12	0.1	I	3.0	ı	I	I	I	4.8	0.2	I	I	ı	0.3		I	1.0	0.3	I	I	I	I	0.2
ypes	Herb		11	I	I	I	ı	ı	I	I	0.1	0.9	0.5	1.5	ı	0.5		I	<0.1	0.4	I	I	0.4	I	0.8
nunity t		ty types	10	I	I	I	ı	0.1	1	I	1.1	<0.1	I	I	ı	0.6		0.3	0.1	I	I	0.6	1.1	0.1	0.3
of com	ub-rich	ommuni	6	ı	I	I	ı	<0.1	I	0.4	0.5	I	<0.1	I	ı	<0.1		I	I	<0.1	1.1	<0.1	0.4	ı	<0.1
Groups	varf-shr	ŭ	8	ı	I	I	<0.1	<0.1	1	ı	0.8	I	<0.1	I	ı	ı	/ophyte:	<0.1	<0.1	I	ı	I	<0.1	ı	I
	D		7	ı	I	I	0.8	ı	1	0.4	I	I	1.2	I	I	ı	Bry	0.7	I	I	7.9	1.1	I	I	I
			6	I	I	I	1	ı	I	ı	1.4	I	I	I	ı	<0.1		I	I	I	ı	I	ı	ı	I
			5	I	I	I	I	1	I	I	0.4	I	I	I	I	0.1		I	I	I	I	I	I	1.3	I
	rub-rich		4	<0.1	I	I	I	I	1	I	I	I	I	I	I	1.0		I	I	I	I	I	I	I	I
	Sh		3	0.5	I	5.0	1	1	1	I	I	1	<0.1	<0.1	0.3	1.2		I	I	1.1	1	I	1	I	0.1
			2	I	I	<0.1	1	1	1	I	0.7	<0.1	<0.1	I	I	1.1		I	I	I	I	I	I	I	I
	Ppum pure		1	0.1	I	1	1	1	I	0.1	1.8	0.2	<0.1	I	I	0.5		<0.1	<0.1	<0.1	0.2	I	1	0.3	I
	Species			Oxalis acetosella	<i>Oxycoccus</i> <i>microcarpus</i>	Phegopteris connectilis	Poa malacantha	Poa platyantha	Poa pratensis	Pyrola incarnata	Rubus chamaemorus	Rubus arcticus	Saussurea pseudo- tilesii	Thalictrum minus	Trisetum sibiricum	Trientalis europaea		Aulacomnium turgidum	Brachythecium oedipodium	Brachythecium reflexum	Ceratodon purpureus	Dicranum bergeri	Dicranum elongatum	Dicranum flexicaule	Dicranum fragilifolium

							Group:	s of com	munity t	Spes							-
m Shrub-rich	Shrub-rich	ırub-rich	_			Ō	warf-shi	rub-rich		Herb	-grass-r	ich		Moss-1	rich		Licheı rich
							J	ommuni	ty types								
2 3 4 5	3 4 5	4 5	5		9	7	∞	6	10	11	12	13	14	15	16	17	18
1	1	1	I		I	0.7	I	<0.1	I	I	I	I	I	I	I	I	I
- 0.7	0.7	1	I		0.2	I	1.7	I	0.1	1.2	0.6	I	I	I	I	<0.1	1.6
- 0.6 8.1 1.9	0.6 8.1 1.9	8.1 1.9	1.9		0.6	I	I	0.4	0.4	1.4	0.2	I	I	3.6	0.9	I	0.4
2 4.7 0.2 6.9 3.6	0.2 6.9 3.6	6.9 3.6	3.6		11.5	0.4	0.4	1.4	2.9	0.5	0.7	6.2	ı	7.9	I	3.1	1.8
     	1 1 1	1	I		I	I	I	I	I	I	0.3	I	I	I	ı	I	I
7 0.7 0.4 - 0.4	0.4 - 0.4	- 0.4	0.4	_	0.7	I	0.8	1.6	1.2	1.3	I	0.3	28.5	0.4	ı	1.1	I
0.1	0.1	- 0.1	0.1		0.9	<0.1	I	1.4	I	<0.1	I	I	I	I	<0.1	I	I
1	1		I	<u> </u>	I	I	ı	I	I	I	I	I	0.5	I	I	I	I
0.1	0.1	- 0.1	0.1		1.3	I	I	I	I	<0.1	I	I	I	I	0.9	I	I
1 1 1	1	1	I		I	I	I	I	I	I	I	I	0.5	I	I	I	I
   	1 1 1	1	I		I	I	I	0.4	I	I	I	I	3.5	I	I	I	I
0.5	1	1	I		I	I	I	I	<0.1	I	I	I	I	I	I	I	I
1 1 1	1 1 1	1	I		I	I	ı	I	I	I	I	I	I	I	0.4	I	I
•         8.3         1.1         25.6         16.4	1.1 25.6 16.4	25.6 16.4	16.4		14.6	5.4	0.4	14.6	39.9	6.9	1.0	3.2	17.1	12.1	10.5	65.6	4.3
1 1 1	1	1	I		I	I	I	0.4	I	<0.1	I	I	I	I	I	I	ı
- <0.1	<0.1	1	I		I	0.9	ı	2.5	I	I	I	I	I	ı	I	I	I
1	1	1	I		I	1.1	0.4	<0.1	1.1	I	I	I	0.1	I	I	I	I
   	1	1	I		I	I	0.4	I	0.2	<0.1	I	I	I	I	I	I	1.2
3 4.3 1.0 10.0 50.0	1.0 10.0 50.0	10.0 50.0	50.0		3.4	0.4	2.5	3.1	4.5	2.4	1.3	4.3	9.5	23.6	5.4	2.0	1.6
I I I	1	1	I		I	I	I	<0.1	<0.1	0.1	I	I	0.1	0.7	0.3	I	I
1 1 1	1	I	I		I	0.8	<0.1	<0.1	I	I	I	I	I	I	I	I	I

								Group	s of com	munity t	Spes							
Species	Ppum pure		S	hrub-ric	ų		D	warf-sh	rub-rich		Herb	-grass-r	ich		Moss-1	rich		Lichen- rich
								C	ommuni	ity types								
	1	2	3	4	5	9	7	8	6	10	11	12	13	14	15	16	17	18
Rhytidium rugosum	I	I	Ι	I	I	I	I	<0.1	I	I	1	I	ı	I	I	I	1.1	I
Sanionia uncinata	0.5	Ι	3.3	4.6	I	3.5	1.2	0.4	<0.1	0.3	0.1	I	1	I	4.4	0.7	I	1.1
Sphagnum capillifolium	I	I	I	I	I	I	I	I	I	I	<0.1	I	I	I	I	4.6	I	I
Sphagnum fuscum	I	I	Ι	Ι	I	I	I	I	I	I	1	1	1	1	ı	3.3	ı	I
Sphagnum girgensohnii	I	I	I	I	2.9	1.0	I	I	0.4	0.5	1.5	I	0.3	0.5	0.7	60.8	0.6	I
Sphagnum lenense	I	I	Ι	I	I	I	I	I	I	1.8	1	1	1	1	ı	ı	ı	I
Sphagnum fimbriatum	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	4.4	I
							-	Lichens										
Cetraria islandica	ı	I	I	I	I	0.3	I	I	0.2	<0.1	I	1	ı	1	ı	ı	I	2.2
Cladonia gonecha	I	I	I	I	I	I	I	I	I	I	I	I	1	I	I	0.1	I	I
Cladonia gracilis	Ι	<0.1	Ι	Ι	Ι	Ι	<0.1	I	1.2	I	I	I	1	I	I	I	<0.1	I
Cladonia grisea	I	I	I	Ι	I	I	I	I	I	0.2	I	I	I	I	I	I	I	I
Cladonia rangiferina	<0.1	0.7	Ι	Ι	0.4	1.3	1.7	2.4	2.8	1.8	1.2	1	1	1.5	0.4	0.5	0.4	13.9
Cladonia stellaris	I	I	I	I	I	I	I	<0.1	<0.1	0.3	3.5	I	I	0.5	I	I	ı	6.1
Cladonia arbuscula	<0.1	1.7	I	I	0.4	1.5	0.6	1.1	2.3	1.4	1.8	I	I	1.0	0.1	0.4	0.7	18.2
Cladonia ecmocyna	I	I	I	I	I	I	0.4	I	<0.1	0.3	<0.1	I	1	I	0.2	<0.1	0.3	0.1
Cladonia uncialis	I	I	<0.1	I	I	I	<0.1	0.1	I	<0.1	I	I	I	1.1	I	I	0.1	0.2
Cynodontium strumiferum	I	I	I	I	I	I	<0.1	I	I	I	I	I	I	1.0	I	I	I	I
Flavocetraria nivalis	I	I	I	Ι	I	0.7	0.6	0.7	I	<0.1	<0.1	I	I	I	I	I	I	2.5
Nephroma arcticum	I	I	I	I	I	I	I	I	0.4	I	I	I	I	I	I	I	ı	1.1
Stereocaulon alpinum	I	I	I	I	I	<0.1	I	0.4	2.9	I	I	I	I	I	I	I	I	1.9
Stereocaulon paschale	I	<0.1	I	I	<0.1	I	I	3.3	<0.1	0.4	<0.1	I	I	1.1	I	I	I	0.7
Thamnolia vermicularis	I	0.3	Ι	I	I	<0.1	I	<0.1	0.3	<0.1	<0.1	I	I	<0.1	I	I	<0.1	3.4

community types.

Appendix 2. Significant indicator species and their indicator value for established

$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	Max	d								ē	mmun	itv tvi	) e							
$\begin{array}{ c c c c c c c c c c c c c c c c c c c$			-	2	m	4	5	9	2	∞	6	10	11	12	13	14	15	16	17	18
$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	1	0.001	7	9	9	ъ	2	5	ъ	9	5	9	9	9	ъ	9	~	9	ъ	4
$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	2	<0.001	2	32	m	4	m	2	5	0	-	с		9	9	7	5	4		0
$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	2	0.029	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3 $0.004$ 2         0         22         0	m	<0.001	2	m	37	0	18	0	0	0	0	0		0	0	0	0	0	0	0
$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	m	0.004	2	0	22	0	0	0	0	0	0	0	0		0	0	0	0	0	0
3 $0.017$ 0         0         13         0	m	0.009	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	m	0.017	0	0	13	0	0	0	0	0	0	0			0	0		0	0	0
$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	с	0.028	0	0	12	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0
$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	4	<0.001	0	-	0	38	9	-	0	0	-	2		0	2	9	18	m		
$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	5	<0.001	-	-	27	-	47		0	0	0		0		0	0	0		0	0
$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	5	<0.001	0	0	10	0	35	0	0	0	0	0	0	0	0	0	0	0	0	0
$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	5	0.001	2	-	2		27		2	0	2		2	0	0	m	2	4	0	
$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	5	0.002	0	0	0	0	23	0	0	0	0	0	0	0	0	0	0	0	0	0
$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	5	0.003	0	0	0	0	23	0	0	0	0	0	0	0	0	7	0	0	0	0
	5	0.010	0	0	1	с	17	0	0	0	0	0	2	0	0	0	10	2	0	0
6         <0.001         0         1         0         11         0         47         2         1           6         0.026         1         4         0         3         6         12         0	5	0.022	-	0	7	0	14	m	2	0	0	0	0	0	0	0	11		0	2
6         0.026         1         4         0         3         6         12         0         0           7         <0.001	9	<0.001	0	-	0	11	0	47	2	-	-	0	0	0	0	2		0	0	
7         <0.001         0         1         0         1         0         1         26         4           7         <0.001	9	0.026	-	4	0	m	9	12	0	0	-	2	0	0	9	0	7	0	2	
7 <0.001 0 0 0 0 0 31 0	7	<0.001	0	-	0	-	0		26	4	11	2	0	0	-	-	2	5	17	2
	 7	<0.001	0	0	0	0	0	0	31	0	1	0	0	0	0	0	0	0	0	0
7 <0.001 0 0 0 0 0 28 0	7	<0.001	0	0	0	0	0	0	28	0	5	0	0	0	0	0	0	0	0	0

Notations: Max – community type where the species indicator value is maximal, p – significance level.

Species	Мах	d								Cor	Imuni	ty typ	e							
			1	2	Э	4	5	9	7	∞	6	10	11	12	13	14	15	16	2	18
Saussurea pseudo-tilesii	7	0.001	0	0	0	0	0	0	30	0	0	0	4	0	0	0		0	0	0
Atragene ochotensis	7	0.001	0	0	0	0	0	0	27	0	-	0	0	0	0	0	0	0	0	0
Pyrola incarnata	7	0.003	0	0	0	0	0	0	21	0	m	0	0	0	0	0	0	0	0	0
Ribes triste	7	0.018	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0
Carex koraginensis	7	0.024	0	0	2	0	0	0	14		0	0	0	0	0	0	0	0	0	0
Polytrichum juniperinum	7	0.026	0	0	0	0	0	0	14		0	4	0	0	0	0	0	0	0	0
Salix hastata	7	0.030	0	0	0	0	0	0	13	0	-	0	0	0	0	0	0	0	0	0
Racomitrium lanuginosum	7	0.036	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0
Aulacomnium turgidum	7	0.037	0	0	0	0	0	0	13	0	0		0	0	0	0	0	0	4	0
Dicranum fulvum	7	0.045	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0
Salix arctica	7	0.046	0	0	0	0	0	0	11	4	10	0	0	0	0	0	0	0	0	0
Vaccinium vitis-idaea	∞	<0.001	0	0	0	5	-	9	5	29	5	4	0	0	0	5	-	m	5	5
Empetrum nigrum	6	<0.001	0	0	0	0	0	0	9	9	52	0	0	0	5	m	0	~	0	0
Cladonia gracilis	6	0.002	0	0	0	0	0	0	0	0	26	0	0	0	0	0	0	0	0	0
Sphagnum lenense	10	0.046	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
Lerchenfeldia flexuosa	11	0.001	0	0	0	0	1	0	0	0	0	0	28	0	0	2	0	0	0	0
Chamerion angustifolium	11	0.032	0	0	1	0	1	0	2	0	0	0	14	4	°.	1	0	0	2	0
Calamagrostis purpurea	12	<0.001	2	11	13	0	1	0	0	0	0	1	7	39	7	0	2	1	0	0
Chamaepericlymenum suecicum	13	<0.001	1	0	0	0	12	0	0	0	1	0	1	0	44	0	0	0	0	0
Equisetum sylvaticum	13	<0.001	1	0	0	0	-	0		0	2	2	-	2	36	0	4	0	0	0
Rubus chamaemorus	13	<0.001	ю	0	0	0	0	2	0	0	0	-	0	14	37	0	0	0	2	0
Carex globularis	13	0.002	0	0	0	0	0	0	0	0	0	з	0	0	30	0	0	0	4	0
Betula exilis	13	0.008	2	0	0	0	0	0	2	0	1	1	0	0	17	0	0	0	3	0
Dicranum sp.	14	<0.001	0	0	0	0	0	0	0	0	1	1	1	0	0	75	0	0	0	0
Mnium sp.	14	0.001	0	0	0	0	0	0	0	0	1	0	0	0	0	27	0	0	0	0

	Мах	d								Cor	umuu	ity typ	9e							
			1	2	з	4	5	9	7	8	6	10	11	12	13	14	15	16	17	18
cialis	14	0.003	0	0	0	0	0	0	0	2	0		0	0	0	28	0	0		
exicaule	15	0.011	-	0	0	∞	0	0	0	0	0	0	0	0	0	0	15	0	~	0
teri	16	<0.001	0	0	0	0	0	0	9	0	4		0	0	0	0	0	35	0	0
nicrocarpus	16	<0.001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	0	0
fuscum	16	<0.001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	0	0
girgensohnii	16	<0.001	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	88	0	0
capillifolium	16	<0.001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	0	0
sis	16	0.001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	0	0
ium laetum	16	0.002	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	0	0
Istre	16	0.002	0	0	0	2	0	2	6		5	7	0	0	0	4		19	16	17
onecha	16	0.009	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	0	0
ntha	16	0.016	0	0	0	0	0	0	0		0	0	0	0	0	-	0	13	4	0
cosa	16	0.020	0	0	0	0	0	ю	0	З	0	0	1	0	0	0	0	11	0	0
i schreberi	17	<0.001	0	2	0	7	10	2	-	0	e	16	m	0	-	9	4	4	26	-
angiferina	18	<0.001	0	0	0	0	0	-	2	m	m	2	-	0	0	-	0	0	-	41
rbuscula	18	<0.001	0	1	0	0	0	1	0	1	ŝ	7	1	0	0	0	0	0		54
vermicularis	18	<0.001	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	46
m piliferum	18	0.001	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	32
tellaris	18	0.001	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	25
andica	18	0.004	0	0	0	0	0	-	0	0	-	0	0	0	0	0	0	0	0	22
arcticum	18	0.004	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	21
ria nivalis	18	0.007	0	0	0	0	0	2	2	1	0	0	0	0	0	0	0	0	0	16
n tripterocarpum	18	0.017	0	0	0	0	0	0	1	0	∞	1	0	0	0	3	3	0	1	16
i alpina	18	0.025	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	17