



Geostatistical analyses and spatial distribution patterns of tundra vegetation in Council, Alaska

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Abstract

The arctic tundra is an important ecosystem in terms of the organic carbon cycle and climate change, and therefore, detailed analysis of vegetation distribution patterns is required to determine their association. We used grid-sampling method and applied geostatistics to analyze spatial variability and patterns of vegetation within a two-dimensional space, and calculated the Moran's *I* statistics and semivariance to assess the spatial autocorrelation of vegetation. Spatially autocorrelated vegetation consisted of moss, *Eriophorum vaginatum*, *Betula nana*, and *Rubus chamaemorus*. Interpolation maps and cross-correlograms revealed spatial specificity of *Carex aquatilis* and a strong negative spatial correlation between *E. vaginatum* and *C. aquatilis*. These results suggest differences between the species in water requirements for survival in the arctic tundra. Geostatistical methods could offer valuable information for identifying the vegetation spatial distribution.

Key words: alaska, arctic tundra, geostatistics, spatial patterns, vegetation

INTRODUCTION

Northern wetlands are important ecosystems; the arctic tundra covers approximately 5% of global land area and contains approximately 12–14% of the world's total pool of soil organic carbon (Post et al. 1982). Furthermore, the arctic tundra is one of the most sensitive ecosystems in response to climate change because of feedback effects, such as the transition from snow and ice to water and land. Bekryaev et al. (2010) determined that both land and sea-surface temperature have increased rapidly in most parts of the Arctic, with rates up to 1.35°C per decade during 1998–2008, and sea ice has melted approximately 10% per decade between 1979 and 2007 (Comiso et al. 2008). These environmental changes are having effects on the Arctic tundra vegetation, and a detailed analysis of these effects is required.

Arctic vegetation patterns are determined by differ-

ences in climate, topography, and soils (Britton 1967, Peterson and Billings 1980), and several studies of vegetation patterns have been carried out on scales of several meters to a few kilometers. Most past studies described linear vegetation patterns depending on topography by using transect-sampling methods. We used a grid-sampling method and applied geostatistics to analyze spatial variability and patterns of vegetation within two-dimensional space. Geostatistical methods can describe spatial variability in vegetation using semivariograms and correlograms, and can further predict vegetation distribution of unsampled areas using kriging (Goovaerts 1999). Recent studies on vegetation patterns in response to climate change have mainly focused on satellite imagery using the normalized difference vegetation index (NDVI), an important tool for description at the regional scale; but

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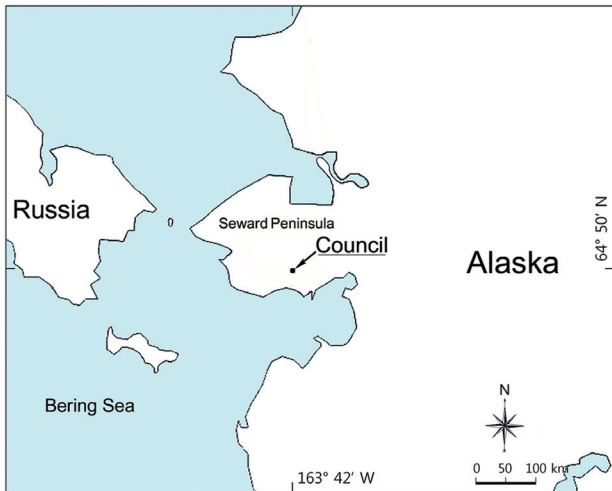


Fig. 1. Map showing the location of the study site, Council, Alaska, USA.

until now, it was not possible to determine each species at the grassland by using the NDVI. In the present study, we analyzed the distributional patterns of each plant species and their associations in the arctic tundra ecosystem.

Plant distribution was estimated by simple inverse distance (Bregt et al. 1992), autocorrelation (Nordbo et al. 1994), or kriging (Heisel et al. 1996). These methods take into account spatial dependence, but only kriging ensures that the estimation is unbiased and has minimum variance (Cressie 1993). Geostatistical methods such as semi-variograms, correlograms, and kriging have been applied to estimate vegetation distribution (Heisel et al. 1999, Rew and Cousens 2001).

The purposes of this study are as follow: (1) to present spatial distributional characteristics of 8 tundra plants that are dominant species in council, Alaska; and (2) to assess the spatial association among tundra plant species in a 10,000 m² area.

MATERIALS AND METHODS

Study area

The study was conducted in Council, Alaska (64°50' 38.6" N, 163°42'39.6" W), in an area where representative arctic tundra vegetation was found (Fig. 1). Alaska tundra was classified into 8 broad vegetation types (Johnson and Vogel 1966). More specifically, our study site can be defined by *Eriophorum-Carex* wet meadow, and spruce forest distributed within a few-kilometer-distance region. Tussocks, a growth form of sedges in tundra, are common,

and their size is approximately 20 to 50 cm tall. Permafrost is usually present at depths of 30–50 cm. Soil pH was quite acidic (approximately 4.4), and a negligible amount of nitrate-nitrogen was detected (1 µg/g) while ammonium-nitrogen was 10–100 times higher than nitrate-nitrogen (KOPRI 2013).

Data collection

A grid-sampling method was applied to determine the spatial variability of Alaska tundra vegetation. In July 2010, we placed 66 quadrats at the intersects of a 20 m × 10 m grid within the 100 m × 100 m plot for measuring vegetation coverage. The abundance of vegetation was measured as the coverage within a 50 cm × 50 cm quadrat. Coverage is thought to be an ecologically important single parameter of a species in relation to its community because it is an estimate of how much a plant dominates an ecosystem (Lindsey 1956, Daubenmire 1959). Vegetation coverage was measured in the field, and we took a photograph of each quadrat and checked the coverage in the laboratory using image-analysis software (Image J 1.34 s; Wayne Rasban, National Institutes of Health, USA).

Data analysis

The coverage of 8 species was analyzed using classic statistical descriptors such as mean, coefficient of variance, skewness, kurtosis, and Pearson's correlation coefficient. Diverse transformations were performed to obtain a nearly normal distribution, because geostatistical analyses are sensitive to highly skewed distribution (Jongman et al. 1995). The importance value of each species was calculated based on the relative coverage and relative frequency.

Spatial autocorrelation of species was calculated with a permutation test for Moran's *I* statistic as follows:

$$I = \frac{N \sum_{i=1}^n \sum_{j=1}^n w_{ij} (X_i - \bar{X})}{\left(\sum_{i=1}^n \sum_{j=1}^n w_{ij} \right) \sum_{i=1}^n (X_i - \bar{X})^2},$$

where *n* is the number of observations, *X_i* is the variable value a particular location, and *X_j* is the variable value at another location. *w_{ij}* is a weight index location of *i* relative to *j*. Moran's *I* statistic and its *P*-value were calculated using the "spdep" package ver. 0.5-56 of the R program (Bivand 2013).

The cross-correlogram was applied to figure out the spatial correlation existing between two species. We used the spline cross-correlogram, which is an adaptation of

the nonparametric covariance function (Bjørnstad et al. 1999, Bjørnstad and Falck 2001) that provides a 95% confidence envelope for the function with a bootstrap algorithm. The nonparametric covariance function is calculated as follows:

$$\tilde{\rho}(\delta) = \frac{\sum_{i=1}^n \sum_{j=i+1}^n G\left(\frac{\delta_{ij}}{h}\right) \rho_{ij}}{\sum_{i=1}^n \sum_{j=i+1}^n G\left(\frac{\delta_{ij}}{h}\right)}$$

where G is kernel function with kernel bandwidth h , and δ_{ij} is the geographic separation distance between the values of variables i and j by metric Euclidean distance.

Interpolated maps were computed using the block kriging method, which involves estimating values for areas within the unit. Block kriging is more appropriate than punctual kriging methods because average values are more meaningful than single point values (Burgess and Webster 1980). To define the degree of autocorrelation among the measured data points, the semivariance statistic $\gamma(h)$ is calculated for each specific distance interval h in a data set such that

$$\gamma(h) = \frac{1}{2n(h)} \sum_{i=1}^{n(h)} [z(s_i) - z(s_{i+h})]^2,$$

where $n(h)$ is the number of lag pairs at distance intervals of h , and $Z(S_i)$ and $Z(S_{i+h})$ are values of the measured variable at spatial locations i and $i + h$ respectively (Isaaks and Srivastava 1989). Empirical semivariograms were fit to linear or exponential models and the block kriging was applied based on the parameters from the semivariogram model to estimate vegetation coverage in the rest of the area. Geostatistical analyses were conducted using the

“geor” ver. 1.7-2 packages of the R program (Ribeiro and Diggle 2001).

To analyze compositional differences among the plant communities of the 66 surveyed quadrats, Detrended Correspondence Analysis (DCA) ordination techniques were applied using the “vegan” package ver. 2.0-7 of the R program (Oksanen et al. 2007). DCA was developed to overcome the distortions inherent in correspondence analysis ordination, and performs better with simulated data than do correspondence analyses or reciprocal averaging ordinations (Hill and Gauch Jr 1980). The Bray–Curtis coefficient was used for a distance measure because it is known as one of the most robust measures (Faith et al. 1987).

RESULTS

A total of 12 species and 7 families of vascular plants were identified in the study site. The descriptive statistics for the 10 dominant plants are shown in Table 1. The most frequently found vascular plant species were *Vaccinium uliginosum* and *Ledum palustre*, and lichen had the highest coverage among vegetation types in the study area. All coverage data were not normally distributed and had relatively high coefficients of variance, so diverse transformations were applied to the data to improve normality. *Empetrum nigrum* and *Vaccinium vitis-idaea* had both lower importance value and higher variation than other vegetation, so these two species were excluded from the geostatistical analysis.

In our study area, the most important vegetation was

Table 1. Descriptive statistics of percent cover of the 10 dominant plant species and vegetation types in arctic tundra in Council, Alaska. The figures in the brackets are untransformed data values

	Frequency	Importance value	Transformation	Cover	Coefficient of variance	Skewness	Kurtosis
Lichen	44	16.4	Logarithm	0.88 (22.4)	0.86 (1.24)	-0.09	-1.65
Moss	32	10.7	Logarithm	0.60 (13.5)	1.21 (1.59)	0.53	-1.50
<i>V. uliginosum</i>	66	15.7	Arcsine	0.38 (15.8)	0.47 (0.74)	-0.07	0.95
<i>C. aquatilis</i>	43	11.6	Inverse	-0.71 (13.1)	-0.46 (1.54)	0.71	-0.92
<i>E. vaginatum</i>	31	9.1	Inverse	-0.75 (10.9)	-0.44 (1.61)	0.81	-0.95
<i>L. palustre</i>	58	11.1	Arcsine	0.25 (8.3)	0.59 (0.75)	-0.61	-0.78
<i>B. nana</i>	44	9.2	Arcsine	0.21 (7.8)	0.92 (1.23)	0.43	-0.44
<i>R. chamaemorus</i>	42	7.2	Arcsine	0.16 (4.5)	0.96 (1.23)	0.36	-0.95
<i>E. nigrum</i>	26	4.4	Arcsine	0.09 (2.6)	1.53 (1.91)	1.32	0.61
<i>V. vitis-idaea</i>	32	4.6	Arcsine	0.08 (1.5)	1.25 (1.54)	0.81	-0.71

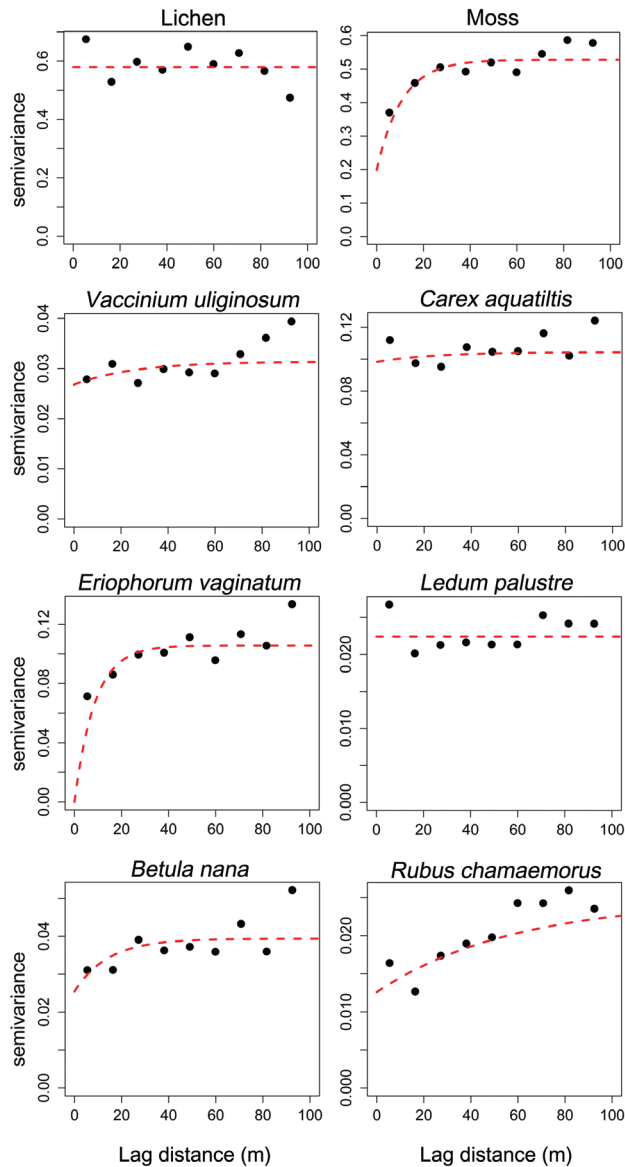


Fig. 2. Omnidirectional semivariograms for 8 dominant vegetations. Black pot represent experimental semivariance value at each lag distance and red broken line are linear or exponential models fitted using maximum likelihood method.

lichen. Moss had an importance value approximately 35% lower than that of lichen. *V. uliginosum* had the highest importance value among 8 vascular plant species, followed by *Carex aquatilis*. To determine the spatial autocorrelation of vegetation, The Moran's *I* and semivariogram results are provided in Table 2 and Fig. 2. Each vegetation displayed differences in their spatial dependence. Lichen, *L. palustre*, *E. nigrum*, and *V. vitis-idaea* showed no spatial autocorrelation. However, some vegetations, such as moss, *Eriophorum vaginatum*, *Betula nana*, and *Rubus chamaemorus*, had a significant spatial autocorrela-

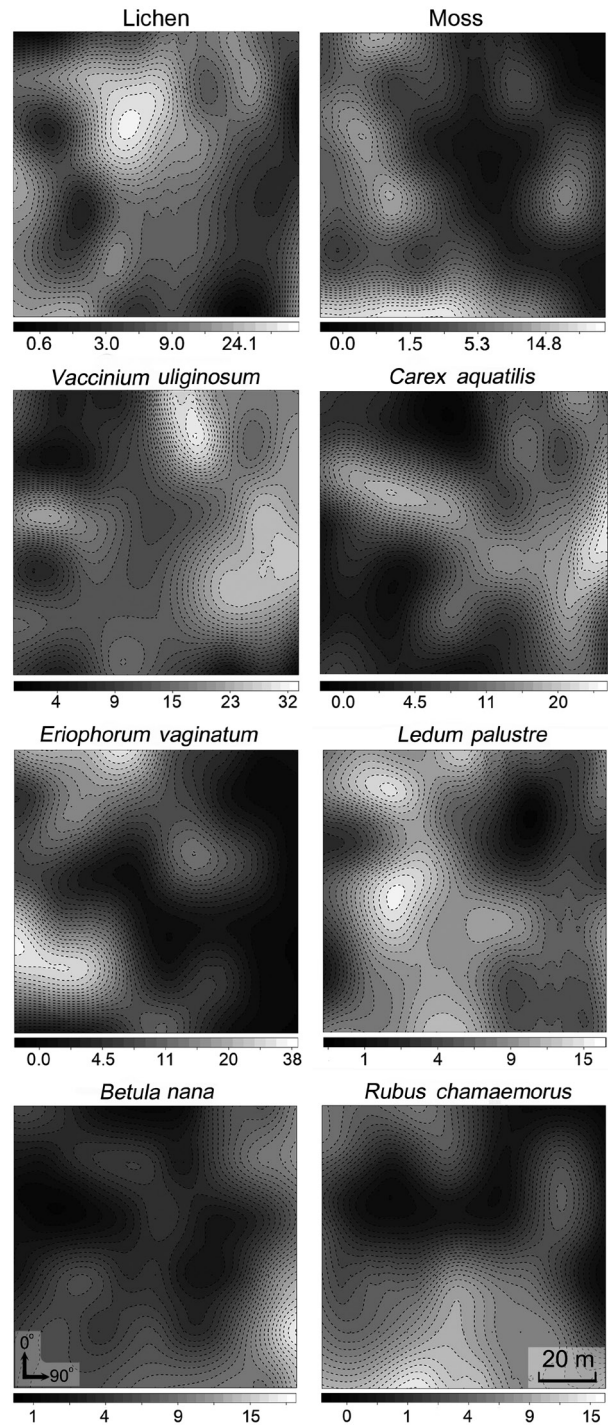


Fig. 3. Interpolation map by using block kriging for 8 dominant vegetations. The legends of each map are percent cover of the vegetations. Scale bar represents the size of sampling plot (100 m × 100 m).

tion, and had diverse range value. For instance, *E. vaginatum* has a range value of 28.83 m and the range of *R. chamaemorus* is 174 m. The proportion spatial structure ($C_1/(C_0+C_1)$; Nugget (C_0), Partial sill (C_1)) represent the

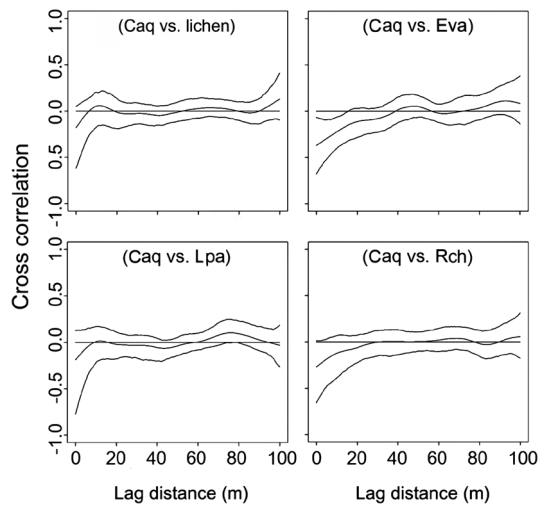


Fig. 4. Spline cross-correlogram between *Carex aquatilis* and other plant species and vegetation types. The x-axes represent the geographic distances between samples and the y-axes represent the cross correlation. The middle lines represent the estimated values and the upper and lower thin lines represent the 95% bootstrap confidence intervals estimated using spline correlogram. Caq, *C. aquatilis*; Eva, *Eriophorum vaginatum*; Lpa, *Ledum palustre*; Rch, *Rubus chamaemorus*.

amount of spatial autocorrelation: as the value approaches 1, the spatial autocorrelation becomes stronger (Cambardella et al. 1994) (Table 2). Our results revealed that *E. vaginatum* had strongest spatial autocorrelation among all the vegetations. The Moran's *I* statistics also showed the same results with the semivariogram model.

The spatial patterns of vegetation at the study plot are presented in Fig. 3. A visual assessment reveals the distri-

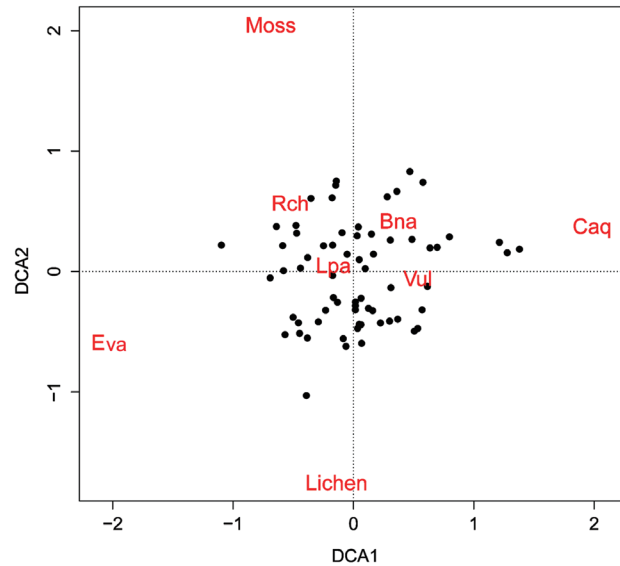


Fig. 5. Detrended correspondence analysis (DCA) ordination of 8 plant species or vegetation types. Black dots represent sampling quadrats and red letters indicate vegetation. Vuj, *Vaccinium uliginosum*; Caq, *Carex aquatilis*; Eva, *Eriophorum vaginatum*; Lpa, *Ledum palustre*; Bna, *Betula nana*; Rch, *Rubus chamaemorus*.

bution patterns and spatial correlation among vegetation. *Eriophorum vaginatum*, *B. nana*, and *R. chamaemorus* showed a distinct aggregation within a narrow area, and *V. uliginosum* and *L. palustre* were not as concentrated as other plants. Kriging maps also showed the negative spatial correlation between *C. aquatilis* and *E. vaginatum*. The cross-correlograms in Fig. 4 show the spatial correlation between *C. aquatilis* and other four vegetation types

Table 2. Parameters of the semivariogram model and Moran's *I* statistics for the 10 dominant vegetations in arctic tundra, Council

	Semivariogram Model	Nugget (C_0) ^a	Partial sill (C_1) ^b	Range ^c	$C_1/(C_0+C_1)$	Moran's <i>I</i>	<i>P</i> -value
Lichen	Linear	0.572	0	–	0	0.017	0.310
Moss	Exponential	0.199	0.328	32.27	0.622	0.217	0.002
<i>V. uliginosum</i>	Exponential	0.027	0.005	76.58	0.156	0.096	0.070
<i>C. aquatilis</i>	Exponential	0.098	0.006	72.02	0.057	0.024	0.328
<i>E. vaginatum</i>	Exponential	0	0.106	25.83	1	0.240	0.002
<i>L. palustre</i>	Linear	0.022	0	–	0	0.091	0.088
<i>B. nana</i>	Exponential	0.026	0.014	42.64	0.35	0.170	0.007
<i>R. chamaemorus</i>	Exponential	0.013	0.012	174.02	0.48	0.312	0.001
<i>E. nigrum</i>	Linear	0.019	0	–	0	0.101	0.052
<i>V. vitis-idaea</i>	Linear	0.009	0	–	0	0.011	0.489

^aNugget (C_0): The height of the jump of the semivariogram at the discontinuity at the origin.

^bPartial sill (C_1): Limit of the variogram tending to infinity lag distances.

^cRange: The distance in which the difference of the variogram from the sill becomes negligible.

Range is not calculated in linear semivariogram model (–).

depending on the lag distance. The most significantly correlated species were *C. aquatilis* and *E. vaginatum*, which were negatively correlated from 0 to 40 m. Other species were also negatively correlated with *C. aquatilis*, but was not statistically significant according to the 95% bootstrap confidence intervals.

The four DCA axes had eigenvalues of 0.20, 0.16, 0.13, and 0.11, and the first two axes were used to generate the scatter plot shown in Fig. 5. *Eriophorum vaginatum* appeared on the left of axis 1 (low axis-1 score) and *C. aquatilis* was on the right of axis 1 (high axis-1 score). Lichen had the lowest axis-2 score and moss had the highest axis-2 score of all the plant types and species. These results indicated that *E. vaginatum*, *C. aquatilis*, lichen, and moss had distinctive spatial distributions pattern each other.

DISCUSSION

Understanding vegetation distribution patterns may be an important step for recognition of arctic tundra ecosystems and their response to climate change. Geostatistics can be a suitable method for understanding spatial variability and interpolation of vegetation distribution maps (Heisel et al. 1999, Jurado-Expósito et al. 2004). In the arctic tundra, several studies have applied geostatistical methods using NDVI datasets for recognition of vegetation patterns at the broad scale (Allen et al. 2004, Spadavecchia et al. 2008), but few studies have applied geostatistical methods to shrubs or herbaceous plants at the micro-habitat scale.

Viereck et al (1992) classified Alaska tundra according to a five-level criterion. Our study site, Council, Alaska, may belong to tussock tundra because tussock (*E. vaginatum*) is one of the dominant species and low shrubs (*V. uliginosum* and *B. nana*) often grow between the tussocks. In addition, moss and lichen are common in our study site. However, *C. aquatilis*, a dominant species in floodplains and wet meadows, was the second most frequently found vascular plant species. This is because our study sites included a small waterway. Tussock tundra is widespread in northwest Alaska in poorly drained and acid soil meadows and is known as very stable and as climax vegetation (Viereck et al. 1992).

In our study site, 5 out of 12 species were included in family Ericaceae, which is common in nutrient-poor sites such as heathland and arctic tundra. The soil at our site was also barren in terms of nitrogen content. The presence of mycorrhizae in Ericaceae plants may help to enhance nitrogen absorption (Strandberg and Johansson

1999), which may be main reason why Ericaceae flourish in our study site, arctic tundra. In addition, the most dominant vascular species in our study site was *V. uliginosum*. Other researchers have reported that this species is generally found on acidic and poorly drained wet soil and that it is the most successful species among other coexisting dwarf shrubs in terms of competition for light (Karlsson 1987b, Jacquemart 1996). Another important factor determining distribution of *V. uliginosum* is nitrogen availability. Karlsson (1987a) found that *V. uliginosum* appeared to be the most competitive of 4 dwarf shrub species in nitrogen-rich sites in subarctic regions.

Geostatistics results showed diverse distributional pattern of tundra vegetation. Semivariance ideally increases with lag distance, and the distance where the model first flattens out is called as the range; sill is semivariance value at the range. Samples separated by distance closer than the range are related spatially. Whereas, those separated by distances greater than the range are not spatially related (Cambardella et al. 1994). Theoretically, the semivariance should be zero at zero separation distance. However, the semivariance usually does not have zero. This is called the nugget effect. The nugget effect is often caused by spatial sources of variation at distances smaller than the sampling interval (Zhao et al. 2009). Our results showed that many species had relatively high nugget values, except for moss and *E. vaginatum* (Table 2 and Fig. 2). The species had too high nugget value to estimate spatial dependence on our grid sample scales (20 m x 10 m), which suggesting that the plants distribute at a shorter distance than field sampling interval or have too low frequency. Our results suggest that smaller scale grid sampling may be more useful to find out spatial autocorrelation of tundra vegetation. Spatial short autocorrelation (short range) of *E. vaginatum* may represent of its short distance dispersal ability or limited environmental preference.

Spatial partitioning of resources and interactions with other species can determine the distribution of species (Chapin III and Shaver 1985). On the contrary, spatial distribution of well-known species can provide clues about limiting environmental factors or competition with other species. Interpolation maps, cross-correlograms, and DCA biplot revealed the spatial specificity of *C. aquatilis*, which confirmed that *C. aquatilis* is the obligate hydrophytes in our study site (Tiner 1991). Our results showed the strong negative spatial correlation between *C. aquatilis* and *E. vaginatum*, suggesting that *E. vaginatum* often grows in relatively dry soil. Lichen also had a negative spatial correlation with *C. aquatilis*. We could estimate that the amount of soil water is one of the most important fac-

tors in determining distribution of vegetation in tundra. However, lichen and *E. vaginatum* did not demonstrate positive spatial correlation. This result suggests unknown environmental associations between these plants, except for soil water contents.

In summary, our study site is representative tussock tundra comprising a small waterway. *E. vaginatum* and *C. aquatilis* are distinctive plants in terms of their spatial distributional pattern. This suggests that two species had different environmental preference in relation to soil water contents. Furthermore, most of vegetation had weak spatial dependence based on our grid sampling scheme except for moss and *E. vaginatum*. Therefore, to figure out detailed spatial distributional pattern and association, careful grid sampling scheme including environmental factors should be applied.

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