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ORIGINAL ARTICLE

# Multivariate Relationships between Snowmelt and Plant Distributions in the High Arctic Tundra

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**Abstract** We investigated multivariate relationships among snowmelt, soil physicochemical properties and the distribution patterns of Arctic tundra vegetation. Seven dominant species were placed in three groups (Veg-1, 2, 3) based on niche overlap (Pianka's Index) and ordination method, and a partial least squares path model was applied to estimate complex multivariate relationships of four latent variables on the abundance and richness of plant species. The abundance of Veg-1 (*Luzula confusa* and *Salix polaris*) was positively correlated with early snowmelt time, high soil nutrients and dense moss cover, but the abundance of Veg-2 (*Saxifraga oppositifolia, Bistorta vivipara* and *Silene acaulis*) was negatively correlated with these three variables. Plant richness was positively associated with early snowmelt and hydrological properties. Our results indicate that the duration of the snowpack can directly influence soil chemical properties and plant distribution. Furthermore, plant species richness was significantly affected by snow melt time in addition to soil moisture and moss cover. We predict that *L. confusa* and *S. polaris* may increase in abundance in response to early snowmelt and increased soil moisture-nutrient availability, which may be facilitated by climate change. Other forb species in dry and infertile soil may decrease in abundance in response to climate change, due to increasingly unfavourable environmental conditions and competition with mosses.

**Keywords:** Arctic tundra, Climate change, Path modeling, Snowmelt, Soil properties, Vascular plants

## Introduction

Vascular plants in the high Arctic tundra must endure combinations of harsh environmental conditions, such as low temperatures, infertile soil and snowpack (Chapin et al. 2012). Therefore, the composition of Arctic tundra vegetation is strongly affected by changes in temperature and snow regime (Walker et al. 2001). According to the Intergovernmental Panel on Climate Change, the speed and magnitude of global warming will be greater in the High Arctic than on other regions, due to raised mean temperatures and altered patterns of precipitation (IPCC 2014). Especially in spring, snow-covered areas decreased in size in the Northern Hemisphere during the 20th century (Serreze et al. 2000).

There have been many studies on relationships between the distribution patterns of Arctic plants and environmental gradients in Arctic tundra regions. Moreau et al. (2006) focused on the relationship between the paraglacial process and plant colonization in the proglacial forelands. Baddeley et al. (2016) carried out experiments to investigate the effect of providing nitrogen and phosphorus on plant photosynthesis and biomass. Wahren et al. (2005) conducted experiments to investigate the effects of winter snow cover and summer air temperatures on Alaskan Arctic tundra vegetation. However, these studies did not reveal the direct and indirect effects of environmental variables on vegetation composition. To understand these effects, path modeling that can deal with interdependencies within natural ecosystems can be applied (Grace et al. 2010; Hodapp et al. 2015).

Here, we investigated multivariate relationships among snowmelt, soil physicochemical properties and the distribution patterns of Arctic tundra vegetation. Previous research showed that the occurrence of alpine plant communities is strongly influenced by snow deposition, which affects soil moisture

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and nutrient availability (Walker et al. 1993; Theodose et al. 1997). However, they were only focused on single environmental factor affecting on plant distribution pattern, so there was a limitation to reveal the complex interdependency between snowmelt and species distributions in Arctic tundra. We applied the partial least squares path model (PLS path model) to disentangle the multiple simultaneous pathways in the Arctic ecosystem. The PLS path model is a statistical method for studying complex multivariate relationships among observed and latent variables (Sanchez 2013).

The primary purpose of our study was to quantify the strength of multiple direct and indirect interactions of snowmelt on soil physicochemical properties and on the distribution patterns of Arctic tundra vegetation. And then, we discussed future changes in the small-scale plant species' distribution patterns and richness.

## Results

In total, 15 species identified, of which 7 selected as representative species in our study site based on importance values. Assessment of niche overlap based on Pianka's Index showed that *L. confusa* exhibited maximum niche overlap with *S. polaris* (Veg-1); the null hypothesis of niche overlap was rejected (0.793, *p*=0.004). Three forb species (*S. oppositifolia, B. vivipara and S. acaulis*) also had significant niche overlap (0.572, *p*=0.007) at the study site (Veg-2). The ecological niches occupied by two species of dwarf shrub (*D. octopetala* and *C. tetragona*) were very similar (0.657, *p*=0.001) (Veg-3). However, the two dwarf shrubs had generally lower niche overlap with other forbs (Fig. 3).

We fitted ten environmental variables vectors to NMDS ordination axes, and found that seven environmental variables were significantly correlated with the NMDS ordination axes ($p<0.05$). Especially, soil temperature was positively correlated with the abundance of *S. polaris*, and the abundance of two dwarf shrub species was positively correlated with slope gradients. The abundance of three forbs was negatively correlated with soil nutrients (Fig. 3).

Apart from the loading of the slope (A=0.421, B=0.530, C=0.596), Bis (0.366) and Sil (0.595), all values for outer loading were found to exceed the recommended threshold value of 0.7. Average variance-extracted values were higher than the recommended threshold value of 0.5, except for Veg-2 (0.493). Two dwarf shrubs (*D. octopetala* and *C. tetragona*) did not have significant relationships with any latent variables in our initial model.

The final PLS path model revealed significant direct associations (straight lines) of latent variables on Veg-1 (a), Veg-2 (b) and richness (c) (Fig. 4). The abundance of Veg-1 had significant positive correlations with early snowmelt (0.633), chemical properties (chem) (0.348) and moss cover (0.222), indicating that the percentage cover of *L. confusa* and *S. polaris* increased with the level of early snowmelt, soil nutrients and moss cover. In the case of Veg-2, snowmelt (-0.208), chemical properties (-0.246) and moss cover (-0.259) yielded negative path coefficients, indicating that these variables were negatively correlated with the abundance of *S. oppositifolia*, *S. acaulis* and *B. vivipara*. Our results also showed significant total effects (dotted lines) on the abundance of Veg-1 and Veg-2. Snowmelt and soil hydrological properties yielded positive total effects on Veg-1 (Fig. 4A). However, hydrological properties had negative total effects on Veg-2

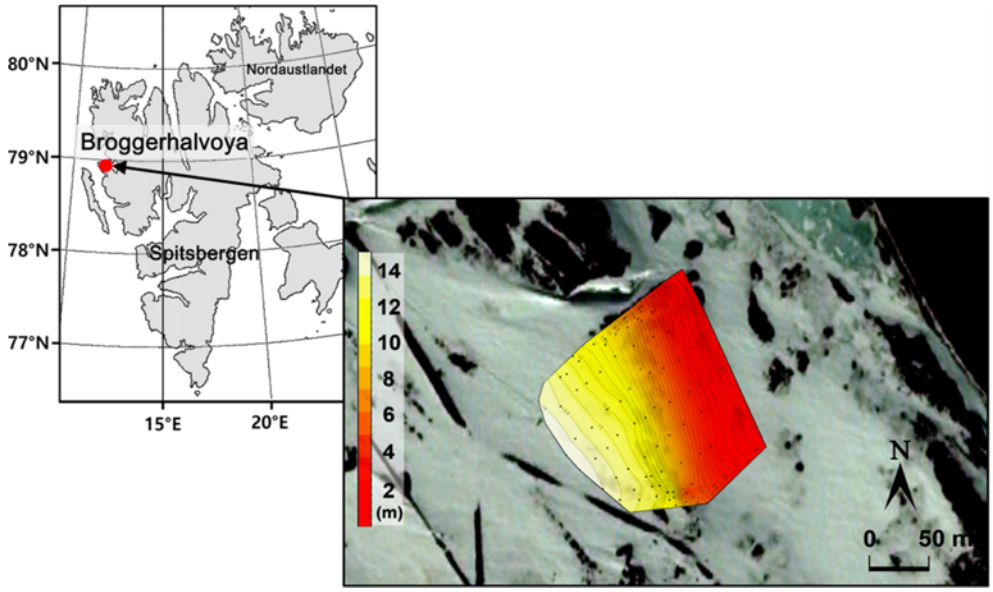

**Fig. 1.** Map of Svalbard and the study site, located on the peninsula Broggerhalvoya. Contour map of relative elevation (m) in the study site.

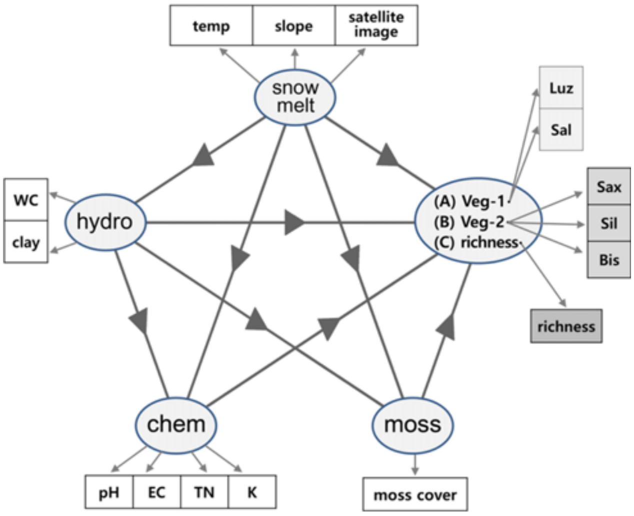

**Fig. 2.** Initial model structure of partial least squares path model, according to our assumptions. Latent variables are displayed in ellipses; manifest variables are represented in rectangles. Arrows depict causal pathways. (hydro, soil hydrological properties; chem, soil chemical properties; veg, vegetation; richness, the number of plant species within plot; temp, soil temperature; WC, soil water content; EC, electrical conductivity; TN, total nitrogen; Luz, *Luzula confusa*; Sal, *Salix polaris*; Sax, *Saxifraga oppositifolia*; Sil, *Silene acaulis;* Bis, *Bistorta vivipara*).

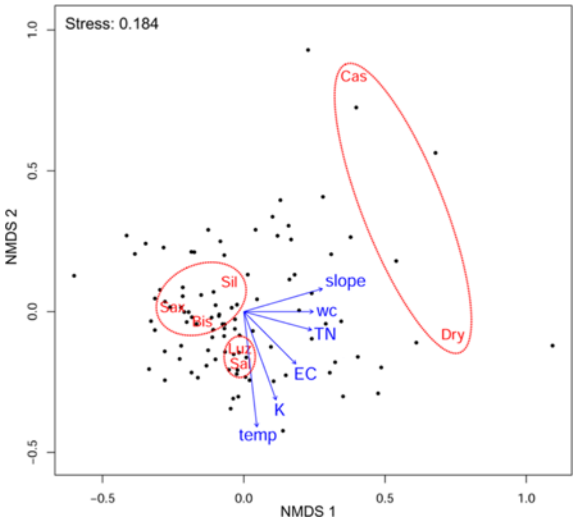

**Fig. 3.** The ordination of nonmetric multidimensional scaling (NMDS), showing the species' scores. Dots represent individual plots at the study site. Blue arrows indicate correlations between environmental variables and the ordination configuration ($p<0.05$). Dotted ellipses represent significant niche overlap in Pianka's Index ($p<0.05$) based on the test statistics of null distribution (1,000 iterations). (temp, soil temperature; WC, soil water content; EC, electrical conductivity; TN, total nitrogen; Luz, *Luzula confusa*; Sal, *Salix polaris*; Sil, *Silene acaulis*; Sax, *Saxifraga oppositifolia*; Dry, *Dryas octopetala*; Bis, *Bistorta vivipara*; Cas, *Cassiope tetragona*).

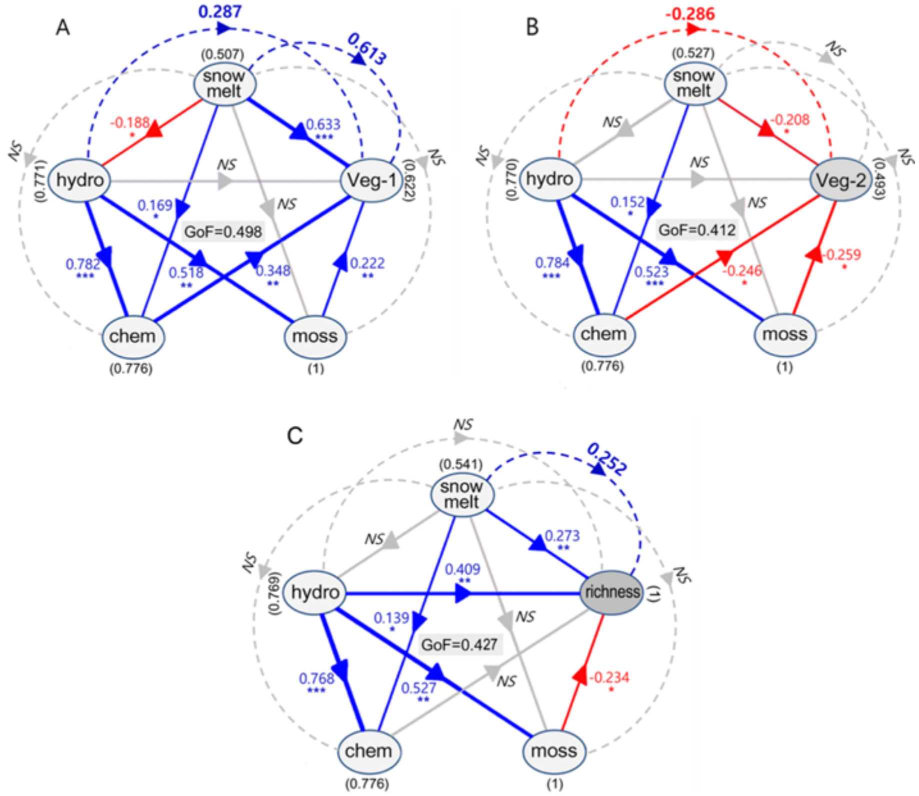

**Fig. 4.** Inner models in the partial least squares path model of effects of environmental parameters on Arctic plant abundance and distribution, showing path coefficients (numbers near the arrows) and average variance-extracted values (in parentheses). Blue arrows indicate positive relationships; red arrows indicate negative relationships. Straight lines indicate direct effects; dotted lines indicate total effects (=direct effects + indirect effects). The significance of each direct effect is estimated based on the regression equation between latent variables (*NS*, non-significant; *$p<0.1$; **$p<0.01$; ***$p<0.001$). The significance of each total effect is estimated based on the simulation-bootstrapped 95% confidence interval.

(Fig. 4B). Plant richness had positive associations with snowmelt and hydrological properties, but richness had a negative correlation with moss cover. Snowmelt also had significant total effects on richness (Fig. 4C).

## Discussion

This study revealed the multivariate nature of the relationships between plant distribution patterns and environmental conditions in the small-scale Arctic tundra. We grouped dominant plant species according to their niche overlap and quantified their associations with environmental variables. Our results showed that *L. confusa* and *S. polaris* mainly occurred in areas with higher soil temperature and more nutrients than those where other herbaceous species occurred. On the other hand, *S. oppositifolia*, *B. vivipara* and *S. acaulis* were frequently found in areas where the soil was dry and lacking in soil nutrients.

The plant species distribution patterns we found are consistent with the results of earlier research. At our study site, *L. confusa* mainly occurred on slopes with early snowmelt and relatively high soil temperature. Coulson et al. (2003) reported that the temperature of the soil beneath *L. confusa* plants was higher than that beneath other species. This graminoid is morphologically and physiologically adapted to the High Arctic tundra environment by having an effective photosynthetic system and a thick boundary layer (Addison and Bliss 1984). At our study site, the distribution of *S. polaris* was also significantly associated with high soil temperature and high levels of soil nutrients. Ohtsuka et al. (2006) observed that habitats with high nutrient levels and moderate water conditions were mono-dominated by the *S. polaris* community. Furthermore, in an experiment involving nutrient applications to Arctic vascular plants, the density of *S. polaris* leaves increased significantly with the addition of N and P (Madan et al. 2007). *S. polaris* is classified as one of the dominant plant species occurring on exposed ridges on Svalbard (Elvebakk 1994).

Compared with other species, dominant forbs such as *S. oppositifolia*, *S. acaulis* and *B. vivipara* were frequently found on the dry and low-nutrient soil. *S. oppositifolia* grows under a wide range of environmental conditions; it is found in dry meadows, river bars and exposed ridges with coarse substrate texture. Previous research revealed that aboveground cover of *S. oppositifolia* significantly decreased in plots where N, P and K were added together (Madan et al. 2007). This plant is known as a pioneer-xerophytic species that is found on young moraines in the peninsula Broggerhalvoya (Moreau et al. 2005). Similarly, *S. acaulis* frequently occurs on gelifluction lobes or terracettes that also support xerophytic vascular plants such as *Dryas octopetala*, *Minuartia rubella* and *Cerastium acrticum* (Cannone et al. 2004).

We quantified the direct and indirect associations of snowmelt on soil properties and vegetation distributions using a PLS path model. There are several reports on the importance of snowpack for the distribution of vascular plant species (Walker et al. 1993; Scott and Rouse 1995). Early snowmelt has a profound effect on soil moisture and nutrient cycles during the growing season of vascular plants in Arctic tundra ecosystems.

Elvebakk (1994), working in an older deglaciated area on Svalbard, showed that the ridge-snowbed gradient is a determining factor for the distribution of vegetation. If they become free of snow early in spring, plants have longer growing seasons, but they are exposed to severe stress due to temperature fluctuations, strong winds and dry soil conditions (Walker et al. 2001). Our PLS path model also confirmed that early snowmelt can result in drier soil conditions during the growing season. By contrast, a heavy snowpack reduces the light available for photosynthesis during the growing season, and gas permeability can be decreased by the formation of ice layers in the snowpack (Jones 1999).

The amount of snowpack is affected by topographic characteristics and by wind speed. For example, strong winds can remove snow from exposed ridges and deposit it in areas protected by hillsides. Scott and Rouse (1995) observed that the erection of a snow fence on upland tundra caused a significant change in vegetation types found near the fence, compared with those found in a nearby exposed region. Snow accumulation can increase soil moisture, so that moisture-tolerant species easily establish themselves. Furthermore, soil moisture has an indirect effect on species' abundance and richness through changes in the moss cover. At our study site, the abundance of some forbs (Veg-2) and species richness was decreased in densely moss-covered regions, but the abundance of other dominant species (Veg-1) was positively correlated with moss cover. Mod et al. (2015) examined the effects of biotic interactions on the richness and distribution of vascular plants, bryophytes and lichens, and concluded that the impacts of biotic interactions on individual species varied among the species groups.

Early snowmelt is recognized as a major factor controlling soil nutrient cycles, such as the rate of decomposition and mineralization, in Arctic tundra (Walker et al. 2001). The present study showed that the early snowmelt areas had higher soil nutrient levels than the late snowmelt areas, suggesting that soil nutrients may be directly affected by the higher soil temperature, which is positively correlated with soil microbial activities in Arctic tundra.

Our PLS path model revealed that early snowmelt can exert direct or indirect effects on plant species richness. Previous research on the effects of soil nutrients on Arctic plant diversity showed that plant species richness increases with N and P application (Gordon et al. 2001; Manette et al. 2007). Gough et al. (2000) suggested that soil pH is an important factor affecting regional species richness in Alaskan Arctic tundra. Mod et al. (2016) emphazised the importance of biotic interactions for the richness and distribution of vascular plants, bryophytes and lichens. However, they focused on single environmental factors that exert effects on the distribution of vascular plants in High Arctic tundra. We showed that Arctic tundra plants may be directly influenced by the persistence of snow, due to the effects of light and temperature. Early snowmelt can also have indirect effects on soil moisture and nutrient availability, which are critical factors for vascular plant distribution (Walker et al. 1993).

In the near future, what changes in the vascular plant communities are likely to occur at our small-scale Arctic tundra site? Global climate change models predict further increases in temperature and precipitation in the Arctic region (Vavrus et al. 2012; IPCC 2014). Increasing temperatures result in the thawing of the permafrost, which is associated with the thickness of the active layer during the growing season. In addition, increased soil temperatures will lead to higher microbial activity and may promote increasing nutrient availability in the shallow soil layers. A meta-analysis of warming experiments in tundra ecosystems revealed an increase in graminoids and deciduous shrubs, but a decrease in mosses and lichens, in response to raised temperatures (Walker et al. 2006). We can predict, based on our results, that *L. confusa* and *S. polaris*, which are, respectively, the representative graminoid and deciduous shrubs at our study site, may increase in abundance in response to earlier snowmelt and increased soil moisture and nutrient availability. This result is in agreement with the dynamic tundra vegetation model (van der Kolk et al. 2016). Meanwhile, other forbs living in dry and infertile soil may decrease in abundance due to unfavourable environmental conditions and increasing competition with mosses. Earlier snowmelt and increased moisture availability may enhance overall plant richness in Arctic tundra.

In summary, the distribution of vascular plants at our study site was influenced by multiple environmental factors such as snowmelt, soil moisture, nutrient levels and biotic interactions. The duration of the snowpack can control soil physicochemical properties and plant distribution shifts in Arctic tundra. However, at the landscape scale, proglacial chronosequence, disturbances by runoff and climate factors can also determine species' distributions (Hodkinson et al. 2003; Moreau et al. 2005 ). At a local scale, reindeer grazing can play a significant role in plants' distribution and richness (Olofsson 2006; Pajunen et al. 2008). Therefore, studies are needed of interactions between more diverse environmental gradients and species' responses in tundra ecosystem.

## Materials and Methods

### Study Area

The study site is located on the peninsula Broggerhalvoya, close to Ny-Ålesund (78° 54' N, 11° 57' E), Svalbard (Fig. 1). The northern coast area of the peninsula Broggerhalvoya was deglaciated ca. 11,000–13,000 years ago (Cannone et al. 2004), but only a small portion of the study area was covered by mature vegetation. A representative ridge slope in the polar semi-desert vegetation zone of the High Arctic was selected considering common vascular plant occurrence and topographical gradient, in which a study area of approximately 2.4 ha was defined. The most common bryophytes were *Sanionia uncinata*, *Aulacomnium turgidum* and *Dicraonweissia* sp.; vascular plants such as *Luzula confusa*, *Dryas octopetala*, *Saxifraga oppositifolia*, etc. were dominant in an older deglaciated region (Cannone et al. 2004). Climatological data from the Ny-Ålesund meteorological station (1993–2011) showed that the mean January temperature ranges from -17.0°C to -3.8°C, whereas the mean July temperature ranges from 4.6°C to 6.9°C. The melt season starts around June, and the terrain is usually snow-free during the summer period (from June to September). The snow cover usually remains stable after October. The mean annual precipitation is 570 mm (Ny-Ålesund meteorological station, 1996 to 2015).

### Data Collection and Soil Analysis

The plot sampling method (1 $m^2$) was used to determine the abundance of Arctic plants. In July 2014, sampling plots ($n$=100) were placed on the ridge slope, taking topographical variation into account. Within each plot, the percentage cover of each vascular plant and bryophyte species was measured. Species cover was estimated visually using a scale of 0.1–100%: 0.1, 1, 5, 10, 15, 20, 30, 40…100. The coordinates of each sampling plot were measured using differential GPS (Trimble® GeoXT, USA), which has sub-meter accuracy, and relative elevation and slope were calibrated using a laser distance rangefinder (DISTO™ D810, Leica, Germany).

Soil sampling was conducted in each plot ($n$=100) to collect data on soil physicochemical properties. Soil taken from three of each plot's corners was mixed thoroughly, to produce a composite sample for each sampling plot. The soil was sealed in plastic bags and stored in a cooled room at 4°C prior to analysis. Soil temperature was measured at a depth of 5–10 cm, with five replicates in each sampling plot, using a thermometer (AquaTuff 352, Atkins, USA). Early snowmelt plots were selected based on google satellite image, 3rd June 2008 (dummy variables: 1 for plots that were free of snow, 0 for plots that were still covered in snow).

Soil texture was determined using the hydrometer analysis method (Day 1965). Soil electric conductivity (EC) and pH (soil:distilled water, 1:5) were measured using an electrical conductivity meter (Orion model 150A, USA) and pH meter (Orion model 720A+, USA), respectively. Soil water content was determined by measuring the amount of weight lost after drying the samples in an oven at 105°C for 48 h. The total nitrogen was determined using an element analyzer (EA1110; CE Instruments, UK) at the National Center for Inter-University Research Facilities, Seoul National University. The minerals K, Na and Ca were extracted using Mehlich-III extract solution (Cater and Gregorich 2007) and measured using an ICP (Inductively Coupled Plasma) Optical Emission Spectrometer (ICP-730 ES, Varian, Australia).

### Statistical Analysis

The percentage cover of each vascular plant species was transformed to an ordinal scale from 0 to 8 for further statistical analysis: 0: 0%; 1:

<1%; 2: 1–5%, 3: 6–10%, 4: 11–20%, 5: 21–40%, 6: 41–60%, 7: 61–80%, 8: 81-100% (van der Maarel 2007). To minimize stress and maximize correlation between variables with ordination configuration, we selected 7 dominant plant species based on the importance values (IV > 5), which were calculated the average of the relative coverage and relative frequency.

Dominant plant species were classified based on their scores for two-dimensional nonmetric multidimensional scaling (NMDS) ordination and niche overlap (Pianka's Index), which was calculated from ordinal transformed percentage cover at each plot. To test the significance of niche overlap between vascular plant species, the observed niche overlap was compared with the values obtained by randomising the original matrix (1,000 iterations) using the RA3 algorithm of the R package 'EcoSimR' (Gotelli et al. 2013). NMDS ordination plots were produced from the Euclidean distance, which is inherently used in eigenvector methods of ordination. The goodness-of-fit of NMDS configuration, representing the rank order of dissimilarity scores, was assessed by the loss or stress function. The stress value was 0.184 for the two-dimensional solution, which is lower than the generally accepted maximum stress value of 2 (Legendre and Legendre 1998). Environmental variables were fitted to NMDS ordination axes scores. The significance of the fitted vectors ($p<0.05$) was assessed using 3,000 permutations of environmental variables. NMDS ordination was conducted with the R package 'vegan' (Oksanen et al. 2013).

The PLS path model is a statistical method for studying multivariate relationships among manifest and latent variables. Latent variables are unobservable variables that are indirectly described by blocks of manifest variables (observed variables or indicators). The PLS path model is composed of the outer model (the measurement model) and the inner model (the structure model). The PLS path model method is more suitable for data that are not normally distributed and for small sample sizes than covariance-based structural equation models (Hulland et al. 2010). Five latent variables were calculated in a reflective way, which means that manifest variables are considered to be caused by the latent variables (Sanchez 2013). The PLS path model depicts the direct and indirect relationships between the latent variables. An initial PLS path model was set up based on the theoretical assumption that environmental factors affect species' abundance in direct and indirect ways (Fig. 2). Specifically, soil moisture is strongly influenced by snowmelt, which leads to a cascade of changes in soil chemical properties, moss cover and the abundance of plant species (Walker et al. 1993; 2001). Based on the correlation and theoretical background, we aggregated the 9 manifest variables into 3 latent variables: early snowmelt (soil temperature, slope, satellite image), soil hydrological properties (soil water content, clay content), soil chemical properties (pH, Electrical conductivity, total nitrogen, potassium). The abundance of *L. confusa* and *S. polaris* were used as indicator variables for the latent variable Veg-1 and the abundance of *S. oppositifolia, B. vivipara* and *S. acaulis* served as indicators for Veg-2. The number of plant species within plots and moss cover was employed as manifest variables of the latent variables of richness and moss, respectively.

To assess the PLS path model, the value of pseudo-goodness-of-fitness (GoF) was used. GoF is calculated as the geometric mean of the average communality and $R^2$ value. The main drawback of the GoF index is that there is no threshold to determine its statistical significance. Outer loading, cross-loading and the significance of the regression equation of the inner model were also checked. Average variance-extracted value (AVE > 0.5) and Cronbach's alpha (> 0.6) were used to check for unidimensionality of the path model (Götz et al. 2010). Lastly, bootstrapping was applied to estimate the precision of the model parameters. The PLS path model was conducted with R package 'plspm' (Sanchez 2013).

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## Author's Contributions

JSP and DJS performed the experiments and data analysis. YKL, JHY and EJL designed the experiment, and all authors read and approved the final manuscript.

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