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Environmental factors determining the distribution of highland plants at low-altitude algific talus sites

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Abstract

Algific talus is a micro-scale habitat type where highland plants (subalpine and alpine species) are found, disjunct from their typical range, in lowland forests. On algific talus, cold airflows from the interstices between talus fragments create a local microclimate colder than surrounding forests. Despite of the widely-known occurrence of unique vegetation on algific talus, critical environmental factors determining the distribution of highland species in this habitat type are unclear. In order to reveal the environmental factors enabling highland species to inhabit algific talus, we investigated the vegetation and environments of 26 algific talus sites and four reference (non-algific talus) sites in Hokkaido, northern Japan. Several algific talus sites were dominated by highland species, while some algific talus sites and all non-algific talus sites were dominated by lowland species. Community analysis based on detrended correspondence analysis (DCA) and canonical corresponding analysis (CCA) revealed that the algific talus sites dominated by highland species had lower ground temperature, more acidic soil, larger canopy openness, and less diverse vegetation than the sites dominated by lowland species. Highland plants might be maintained under conditions stressful for lowland plants, resulting in less competitive situation. Generalized linear models (GLM), used to evaluate the response of individual highland species to environmental factors, revealed that preferable environmental conditions for highland plants are highly species specific. These results indicate that the maintenance of diverse environments is crucial for the conservation of the unique vegetation and local populations of highland species in algific talus areas.

Key words

Acidic soil, Alpine and subalpine plants, Microhabitat, Refugia, Soil temperature

Introduction

In the current interglacial period, many cold-adapted species are distributed in areas above typical latitudinal and altitudinal limits for forest vegetation (Bliss 1971; Körner and Larcher 1988; Körner 2003). Mountainous areas at mid-latitudes are known to be important refugia for cold-adapted species occurring in landscapes with generally moderate climatic conditions (Gentili et al. 2015a). However, highland plants inhabiting such subalpine and alpine zones are more vulnerable to the risk of local extinctions, because their habitats are commonly small, fragmented, and isolated from each other (Lienert 2004; Gentili et al. 2015b). Marked environmental modifications have progressed in mid-latitude mountain regions. For example, recent climate change has caused the range shifts of many plants and animals toward higher altitudes, which may decrease the abundance of highland plants (Lenoir et al. 2008; Dullinger et al. 2012). Increasing browsing pressure by migrated herbivores is harmful for the maintenance of highland plant populations and species diversity in mountain ecosystems (Baur et al. 2007; Austrheim and Eriksson 2008). Furthermore, human disturbance, such as trail construction, trampling by hikers, and illegal harvesting of rare plant species accelerates the risk of local extinction (Niwa et al. 2000; Pickering and Hill 2007; Nagy and Grabherr 2009; Vásquez et al. 2015). Therefore, conservation of suitable habitats is required to reduce the risk of local extinction of highland plant species.

Small and isolated populations of highland plants exist at “cool spots” below the altitudinal forest-limit at mid-latitudes, where low temperature conditions are maintained at the local scale (sensu Dobrowski 2011). Algific talus is an example of the cool spots (Gentili et al. 2015b) that commonly exist on talus slopes with stony accumulations, where cold airflow comes through the interstices between talus blocks, and low ground temperature is maintained throughout the summer (Nekola 1999; Zacharda et al. 2007). Locally unique vegetation, composed of highland plant species, often develops on this algific talus habitat (Sato 1995; Matsui and Iguchi 2001; Sato 2008; Růžička et al. 2012).

A recent research study reported that low-altitude populations of *Vaccinium vitis-idaea* L. (a common highland species in the mid-latitudes) in algific talus sites have unique genetic structures different from the populations of outlying alpine sites (Shimokawabe et al. 2016). Therefore, algific talus may serve as micro-scale refugia, where plant communities of highland species have been maintained for relatively long periods, independently from otherwise similar communities occurring in the macro-scale refugia in high mountains (Birks 2015). The existence of lowland refugia may facilitate rapid adaptation of species responding to environmental change by which the risk of extinction is reduced (Mosblech et al. 2011; Birks 2015). Furthermore, local adaptation may accelerate the ecological and evolutional divergence of species inhabiting micro-scale refugia (Shea and Furnier 2002; Mee and Moore 2014). Thus, plant communities at algific talus sites should be considered high priority for conservation, although their ecological significance is often overlooked because of their geographic isolation and small habitat size.

Species composition of algific talus vegetation often varies among sites, and some algific talus communities completely lack highland species (Sato 1995). These variations exist even among local algific talus sites within a small area (Shimokawabe et al. 2015), and factors affecting the variation in species composition among algific talus sites are not fully understood. Although low ground temperature must be a predominant factor enabling the growth of highland plants in lowland forests (Saito 1953), the importance of other factors has been suggested (Sato et al. 1993; Matsui and Iguchi 2001). Because of their inherently small size and locality, patches of algific talus vegetation may be sensitive to local environmental factors imparted by surrounding vegetation, such as light, hydrologic and edaphic conditions reported for alpine vegetation (Bliss 1963; Nagy and Grabherr 2009; Takahashi and Murayama 2014). In high mountains, harsh environment, such as cold climate, strong irradiation, desiccation and oligotrophic soil, suppress the dominance of competitive species and contribute to the maintenance of highland species diversity (Choler et al. 2001; Pauchard et al. 2009). Although several factors may affect the growth of highland plants at algific talus sites, there are few studies revealing the relationships between vegetation and environmental factors across algific talus occurrences. Understanding the factors determining the origin and maintenance of highland plant communities at algific talus sites is important for their conservation.

In this study, we aimed to clarify the factors determining plant distribution on algific talus. We compared the responses of highland species, that are typically limited to subalpine or alpine habitats, to environmental conditions across 26 algific talus sites and four reference sites (non-algific talus sites) in Hokkaido, northern Japan. First, we conducted a community analysis to compare the species diversity and environmental conditions among vegetation types distinguished by the presence of highland species. To investigate the environmental factors affecting the occurrence of highland species at the algific talus sites, we focused on ground temperature, humus thickness, soil moisture, soil pH, soil C:N ratio and canopy openness. Second, we examined the probability of occurrence of individual species under specific conditions. Specifically, we attempted to answer the following questions:

(1) To what extent is the presence of algific talus vegetation related to local environmental conditions?

(2) Does the trend of highland plant occurrence responding to the environmental gradients differ among species?

Materials and Methods

Study area

This study was conducted in natural coniferous forests near the town of Engaru (43° 82’ –43° 95’ N, 143° 27’ –143° 42’ E) in the northeastern part of Hokkaido, Japan. Mean monthly temperatures range from –8.3 °C to 19.9 °C with an annual mean of 5.8 °C (data obtained from the Engaru Weather Station, 80 m.a.s.l.). This area has relatively uniform geology, composed of volcanic debris (Geological Survey of Japan AIST 2015). Most algific talus sites are found in montane forests (300–700 m.a.s.l.), where conditions are suitable for some alpine and subalpine species, such as *Vaccinium vitis-idaea* and *Rhododendron palustre* ssp. *diversipilosum* (synonym, *Ledum palustre* ssp. *diversipilosum*) (Shimokawabe et al. 2015). In the southwestern part of this area, there are high mountains (1,500–2,000 m.a.s.l.), and alpine vegetation prevails above more or less 1,500 m.

In 2015, we selected 26 algific talus sites for investigation (Fig. 1). In addition, we set four study sites as references on non-algific talus. All sites exist in the forest zone (300–700 m.a.s.l.). A 5 m × 5 m quadrat was established in each site, centering on the point of lowest surface temperature. The surface temperature was measured at one-hour intervals by infrared thermography (Easy Thermo TP-S, CHINO, Japan).

Vegetation survey

Vegetation surveys were conducted during July to August of 2015. For bryophyte, herbaceous and short tree (< 2 m) species, plant cover (%) of individual species was recorded by visual estimation in each quadrat. Furthermore, the quadrat was divided into 25 grids of 1 m × 1 m square and occurrence of highland species was counted within each grid square. Bioclimatic affinities of highland species, i.e., as subalpine or alpine, was based on Iwatsuki (1981) and Iwatsuki et al. (1993, 1995, 1999).

We classified the investigation sites into four groups based on the quantity of highland plants in each site as follows: (1) algific talus site with dominance of highland plants (> 80 % cover of highland plants), (2) algific talus site with moderate amounts of highland plants (5–80 % cover), (3) algific talus site with few highland plants (< 5 % cover), and (4) non-algific talus site (reference sites). This criterion was determined with reference to the results of detrended corresponding analysis (see Statistical procedures and Fig. 2a)

Environmental factors

Ground temperature (°Celsius; °C), humus thickness (centimeter; cm), soil moisture (%), soil pH, soil carbon-to-nitrogen ratio (C:N ratio), and canopy openness (%) were measured for each site. Ground temperature at 10 cm of soil depth was recorded at the center of each quadrat at hourly intervals using an automatic data logger (CO-UA-001-08, Onset, USA). Humus thickness and soil moisture were measured randomly at five different points in each quadrat and average score was used as a representative value. Soil moisture (volumetric water content in soil) was measured by a time-domain-reflectometry device (TDR; Hydro Sense, Campbell Scientific, USA) connected to a 12 cm probe; measurements were taken when there was no rainfall for at least one day before the measurement to avoid rainfall effect on soil moisture. For the analysis of soil pH and C:N ratio, five soil samples were collected randomly from each quadrat, at the depth of 5 cm from the ground surface under the litter layer; samples were combined and mixed well. Air-dried soil samples (10 g) were mixed with 250 ml deionized water, stirred, and pH of the supernatant solution of suspension was measured using an EC-pH indicator (WM-22EP, DKK-TOA, Japan). The carbon and nitrogen contents in 10 mg air-dried soil samples were analyzed by a CN analyzer (NCS2500, CE Instruments, UK), and C:N ratio was calculated. Canopy openness was calculated from hemispherical photographs, which were taken at 1.5 m above the ground at the center of each site using a fish-eye lens (180° Fisheye S-Size T-03S, TODA SEIKO, Japan). These photographs were analyzed using CanopOn2 program (Takenaka 2009). Ground temperature was measured from June to October, and all other measurements and soil sampling were conducted during July to August in 2015.

Statistical procedures

To evaluate the significance of environmental factors determining vegetation type, community analysis was conducted using detrended corresponding analysis (DCA: Hill and Gauch 1980) and canonical corresponding analysis (CCA: Braak 1986). We used vegetation cover of all species in each site converted by angular transformation to stabilize the variance (Sokal and Rohlf 1995). First, research sites were ordered on a two-dimensional plane by the DCA. Second, to reveal the specific environmental factors related to the algific talus vegetation, Spearman’s correlation coefficients were calculated between the derived values of the DCA axis and values of each environmental factor, i.e., accumulated ground temperature (daily mean values from June to October), humus thickness, soil moisture content, soil pH, soil C:N ratio and canopy openness. Then, factors having a high correlation with the DCA axes (we defined that absolute value of correlation coefficient ρ is > 0.5 and significance level P is < 0.001) were used in the CCA as explanatory valuables.

In order to further clarify the trend of species diversity across sites, Spearman's correlation coefficients were calculated between the derived values of the DCA axis and Shannon-Wiener's diversity index *H'* of individual sites based on the coverage of individual species.

A generalized linear model (GLM) with binomial error distribution and logit-link function (Hosmer and Lemeshow 1989) was used to analyze the relationship between environmental factors and the occurrence of highland species. In this analysis, abundance of each highland species (rate of occurrence within 25 grids) was set as a response variable and the seven environmental factors mentioned above were used as explanatory variables. All the response and explanatory variables were standardized before the analysis. In this regard, highland species appearing in less than three sites were excluded from the analysis because of insufficient sample size. First, a simple correlation coefficient (ρ) between the occurrence rate of each species and each environmental factor was calculated using Spearman's rank method. Then, full models for individual species were built using selected environmental factors, where absolute ρ values larger than 0.2 were used as explanatory factors. Finally, model selection was conducted based on Akaike's information criteria (AIC), in which the model with the smallest AIC value was defined as the best-fit model for each species. Community analyses were conducted using vegan package (Oksanen et al. 2015) and GLM analyses were conducted using MASS and MuMIn package (Venables and Ripley 2002; Barton´ 2015) in R version 3.1.2 (R development core team 2014).

Results

Species assemblage and environmental factors

In the vegetation survey, 170 species were recorded across the 30 sites. Among them, 13 species were recognized as highland species; they included four spermatophytes (*Vaccinium vitis-idaea*, *Rhododendron palustre* ssp. *diversipilosum*, *Cornus canadensis*, *Rhododendron dauricum*), one pteridophyte (*Lycopodium annotinum*), and eight bryophytes (*Dicranum majus*, *Hylocomium splendens*, *Rhytidiadelphus triquetrus*, *Sphagnum girgensohnii*, *Pleuroziopsis ruthenica*, *Ptilium* *crista-castrensis*, *Bazzania trilobata*, and *Oligotrichum aligerum*) with reference to Iwatsuki (1981) and Iwatsuki et al. (1993, 1995, 1999). Most of the highland species were found at the algific talus sites, except for one reference site, where a small *C. canadense* population was found. The DCA derived four axes and first two axes explained 69 % of total vegetation variance (Table 1). Of 23 algific talus sites, seven sites were classified as the group with highland plants dominance, 11 sites as the group with a moderate amount of highland plants, and eight sites as the group with few highland plants; the remainder were the non-algific talus group (four reference sites). The four identified groups based on the vegetation cover ratio were distinctively ordered in series along DCA1 (Fig. 2a).

The coordinate value of DCA1 was positively correlated with accumulated ground temperature and soil pH, and negatively correlated with humus thickness and canopy openness ($P < 0.05$). Before the CCA, we selected factors strongly correlated with the abundance of highland plants, those being, factors having $| \rho | > 0.5$ with the DCA1 axis. As a result, accumulated ground temperature ($\rho = 0.61$, $P < 0.001$), soil pH ($\rho = 0.67$, $P < 0.001$), and canopy openness ($\rho = –0.57$, $P < 0.001$) were derived as explanatory variables. The CCA revealed that sites with larger coverage of highland plants tended to have lower temperature, higher acidic soil, and larger openness (Fig. 2b).

The correlation coefficient ρ of coordinate value of DCA1 and biodiversity index H' was 0.74 ($P < 0.001$), indicating a negative correlation between the abundance of highland species and species diversity.

Occurrence of highland species

Table 2 summarizes the standardized partial regression coefficients of the environmental factors that explain the abundance of highland species using best-fit models. Among the 13 highland species, *Sphagnum girgensohnii*, *Pleuroziopsis ruthenica*, *Ptilium crista-castrensis*, *Bazzania trilobata*, and *Oligotrichum aligerum* were excluded from the analyses because they appeared at less than three sites. The environmental conditions affecting the occurrence at the algific talus sites were different among highland species (Fig. 3 and Table 2). Most highland species preferred acidic soil, except for *H. splendens* and *R. triquetrus*. Interestingly, a significantly positive effect of low ground temperature was detected for only four species: *V. vitis-idaea*, *C. canadense*, *R. dauricum* and *H. splendens*. Ericaceous species, *V. vitis-idaea*, *R. palustre* ssp. *diversipilosum* and *R. dauricum*, preferred sites with lower canopy closure. A significant effect of humus thickness was detected for four species: *H. splendens*, *D. majus*, *R. triquetrus*, and *L. annotinum*. *Hylocomium splendens* preferred thicker humus, indicated by larger standardized partial regression coefficients than those for the latter three species. Soil C:N ratio had positive effects on *R. palustre* ssp. *diversipilosum*, *R. dauricum*, and *H. splendens*, but a negative effect on *D. majus*, although the regression coefficients were relatively small in the models.

Discussion

Determinant factors of vegetation pattern

Our analyses revealed that cool soil conditions, acidic soil, and canopy openness are important factors determining vegetation type at low-altitude algific talus sites. Under low soil temperature, development and branching of root systems are often inhibited (Kaspar and Bland 1992). Acidic soil is generally oligotrophic and restricts the growth of many plant species (Pauchard et al. 2009). In contrast, ericaceous plants, including many highland species, are known to grow well under acidic soil conditions because of the mycorrhizal fungi that decompose organic nitrogen compounds and supply nutrients to symbiotic plants as amino acids (Marrs and Bannister 1978; Jansa and Vosátka 2000). Therefore, algific talus with cool and acidic soil conditions may restrict the prevalence of lowland plants, resulting in less competition within these communities. The positive correlation between the coordinate value of the DCA1 axis and the species diversity index supports this prediction, indicating that only stress tolerant species can grow under cool and oligotrophic soil conditions (Grime 1977). Thus, restrictions on lowland plants' invasion contributes to the occurrence of highland plants at low-altitude algific talus sites. Because highland species occurring above the treeline commonly grow under unshaded conditions, algific talus sites under canopy gaps are more suitable for the growth of highland plants in lowland forests.

Although geological conditions are not particularly variable within the study area (Geological Survey of Japan AIST 2015), soil pH varied from 4.0 to 6.5. Soil pH of the algific talus sites with many highland plants were commonly around 4.5, similar to the pH values of alpine regions, where cold climate restricts the decomposition of plant residues by microbes (Bliss 1963; Umemura 1968; Egli et al. 2001). Cold micro-climate on algific talus may restrict microbial activity at low-altitudes, resulting in similar edaphic conditions as those of alpine environments. Indeed, we detected a weak positive correlation ($\rho = 0.49$, $P < 0.01$) between accumulated ground temperature and soil pH, suggesting slow decomposition rates under cold micro-climate. In another case, variation in species composition might affect soil chemistry. As leaves of deciduous species are usually decomposed faster than those of evergreen species (Hobbie and Gough 2004), the forest types around algific talus sites may influence their soil conditions; i.e., soil of coniferous forests is commonly more acidic than that of broad-leafed forests (Street and Kingdom 1997). Furthermore, because many highland species are evergreen species, lower decomposition rates and more acidic situation are expected. This is interpreted as meaning that positive feedback is possible if soil acidification accelerates the exclusion of lowland plants at the algific talus sites.

Previous studies stressed the importance of cold micro-climate on algific talus as the primary factor determining development of this unique vegetation type (Sato et al. 1993; Gude et al. 2003; Růžička et al. 2012). The present study demonstrates that not only low temperature but also acidic soil and open canopy structures contribute to the function of algific talus as a local habitat of highland species.

Responses of highland species to the specific factors

Interestingly, selected factors in the best-fit models varied among species. Although acidic soil is important for the growth of most highland species, positive responses to low ground temperature were detected only for *V. vitis-idaea*, *C. canadense*, *R. dauricum* and *H. splendens*. As mentioned above, low temperature might increase the abundance of highland species indirectly through soil acidification by inhibiting the decomposition of organic matter. Thus, highland species for which the effects of ground temperature were excluded from the best-fit models might be influenced by the indirect effect of low temperature as a condition for rooting.

Although canopy openness was detected as an important factor in the community analysis, the significance of canopy openness was shown only for *V. vitis-idaea*, *R. palustre* ssp. *diversipilosum* and *R. dauricum* in the best-fit model. These species commonly grow in open stony habitats of alpine and subalpine regions (Iwatsuki et al. 1993; Tamai et al. 2009). Because the majority of alpine plants are adapted to high irradiance (Körner 2003), shading stress should decrease the growth and survival of alpine plants although shading effects may not be serious for subalpine plants inhabiting the understory. Therefore, the moderate extent of canopy closure by trees around the algific talus is important for the conservation of species diversity of highland plants.

Humus thickness had positive effects on the occurrence of *D. majus, H. splendens* and *R. triquetrus*. These bryophyte species are common on humus or rotten woody materials found in mountainous areas (Iwatsuki 1981), and some have adaptations for growing on these substrates. *Hylocomium Splendens*, for example, has a sympodial branching in which new modules grow up from modules of the previous year (Økland et al. 1999). This feature may allow *H. splendens* to grow above the thick litter layer. Humus thickness had a marginal negative effect on the occurrence of *L. annotinum*. However, the very low value of the regression coefficient in this species indicates that the effect of humus thickness is considered to be less important.

The C:N ratio of soil showed significant effects on the distribution of several highland species at the algific talus sites. Positive effects were detected in *R. palustre ssp. diversipilosum*, *R. dauricum*, and *H. splendens*. Under high C:N ratio conditions (> 20), the decomposition rate of organic matter is generally low and soil becomes oligotrophic (Craft et al. 2016). Thus, high C:N ratio may inhibit the growth of lowland species, resulting in a positive effect on highland species. Among highland species, only *D. majus* showed a negative response to C:N ratio. Because most C:N ratio values in this study were larger than 20, however, the negative effect of C:N ratio on this species does not seem to matter much.

Conclusion

The present study revealed that the existence of highland species on low-altitude algific talus was strongly related to not only low temperature conditions but also acidic soil, canopy openness and humus thickness. In alpine areas, environmental heterogeneity is important for maintaining species diversity in constituent plant communities (Bliss 1962; Nagy and Grabherr 2009; Takahashi and Murayama 2014). In algific talus areas, the heterogeneity of micro-scale environments is similarly important for the persistence of various highland species at low-altitudes. To conserve the diversity of algific talus vegetation, therefore, maintenance of whole ecosystems including forests surrounding individual algific talus sites should be taken into account.

To clarify the functional role and conservation value of algific talus refugia for cold-adapted plants, studies on the population dynamics of highland species are crucial. Furthermore, records of highland species growing on algific talus are important for the consideration of future vegetation dynamics under global warming. As mentioned before, Shimokawabe et al. (2016) speculate that *V. vitis-idaea* populations at the algific talus sites might be maintained for a long period independent of migration from alpine populations. To test this hypothesis, comparative studies on ecological traits, population dynamics and genetic traits between isolated low-altitude populations and native high-altitude populations are needed.

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Fig. 1

(a) Study area: forest vegetation near the town of Engaru, Hokkaido, Japan. A 5 m × 5 m quadrat was established in each of 26 algific talus sites and four reference sites, within the enclosed area. (b) Enlarged map of the enclosed area in (a). The 30 sites were divided into four vegetation types based on the ratio (%) of highland plant species. Each site is shown as the classified vegetation type: “algific talus site dominated by highland plants” (circles), “algific talus site with moderate amounts of highland plants” (triangles), “algific talus site with few highland plants” (squares), “non- algific talus site” (crosses)

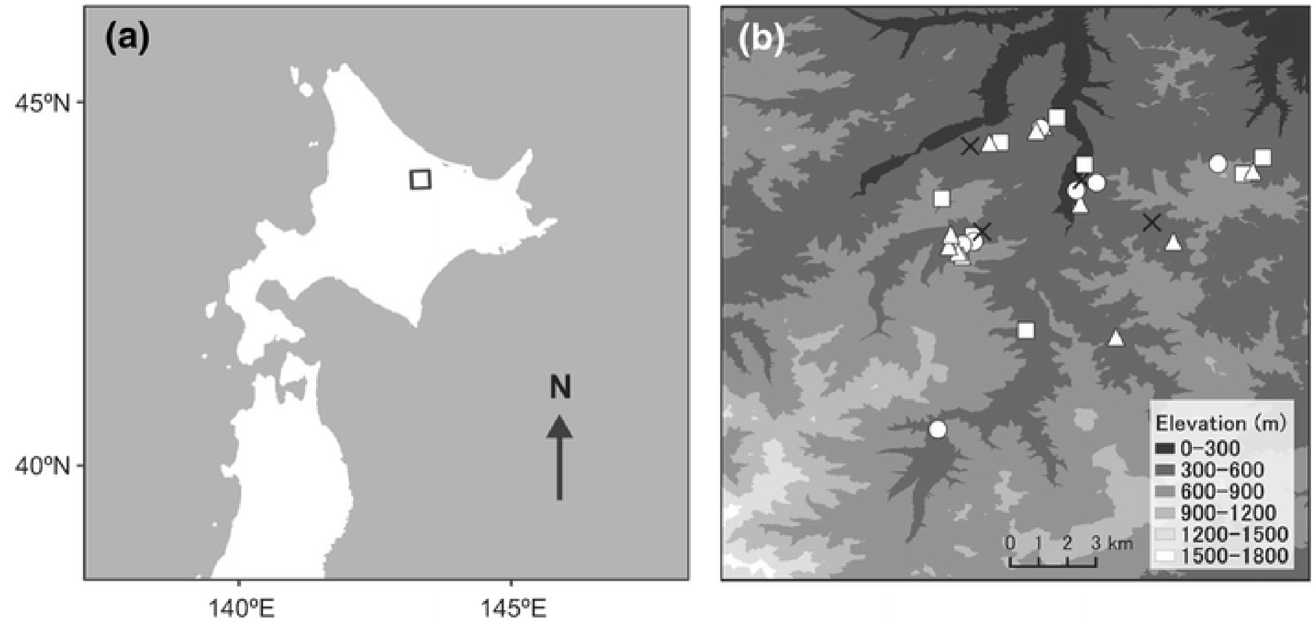

Fig. 2

Ordination of 30 sites by (a) detrended corresponding analysis and (b) canonical corresponding analysis. Symbols correspond with classified vegetation types: “algific talus site dominated by highland plants” (circles), “algific talus site with moderate amounts of highland plants” (triangles), “algific talus site with few highland plants” (squares), “non- algific talus site” (crosses)

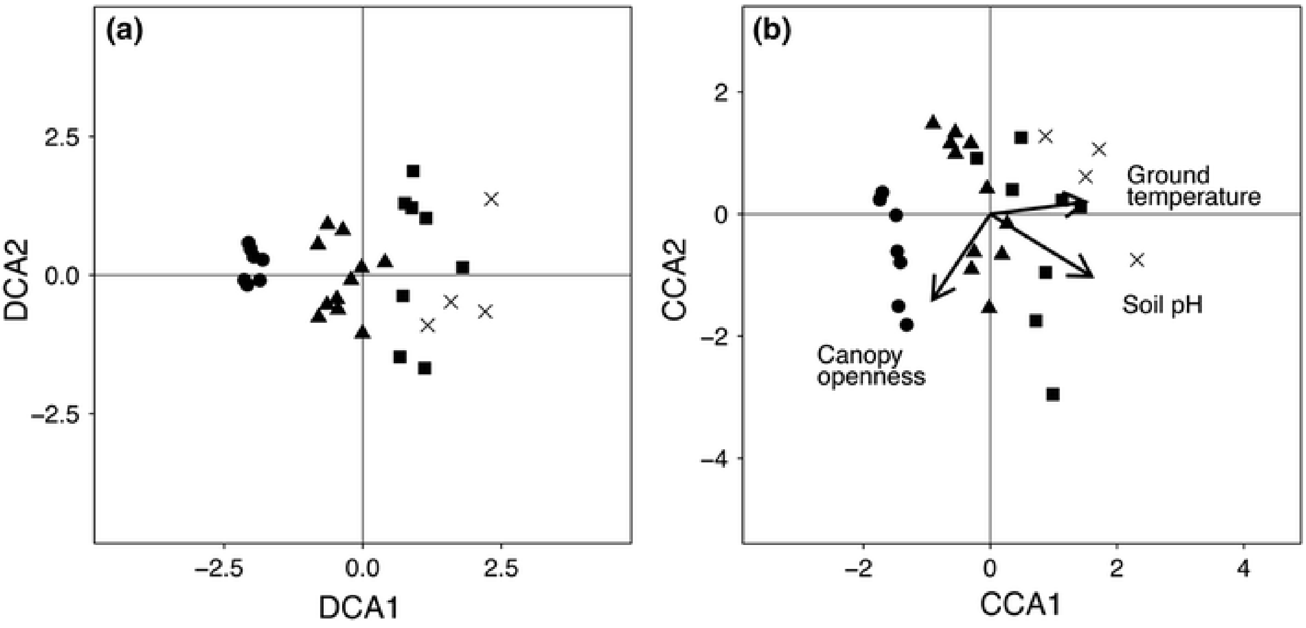

Fig. 3

Probability of occurrence of each highland species, i.e., *Vaccinium vitis-idaea* (VV), *Rhododendron palustre ssp. diversipilosum* (RP), *Rhododendron dauricum* (RD), *Cornus canadense* (CC), *Lycopodium annotinum* (LA), *Dicranum majus* (DM), *Hylocomium splendens* (HS), and *Rhytidiadelphus triquetrus* (RT), that could be regressed by GLM logistic regression in relation to each environmental factor, i.e., (a) soil pH, (b) accumulated ground temperature, (c) canopy openness, and (d) humus thickness

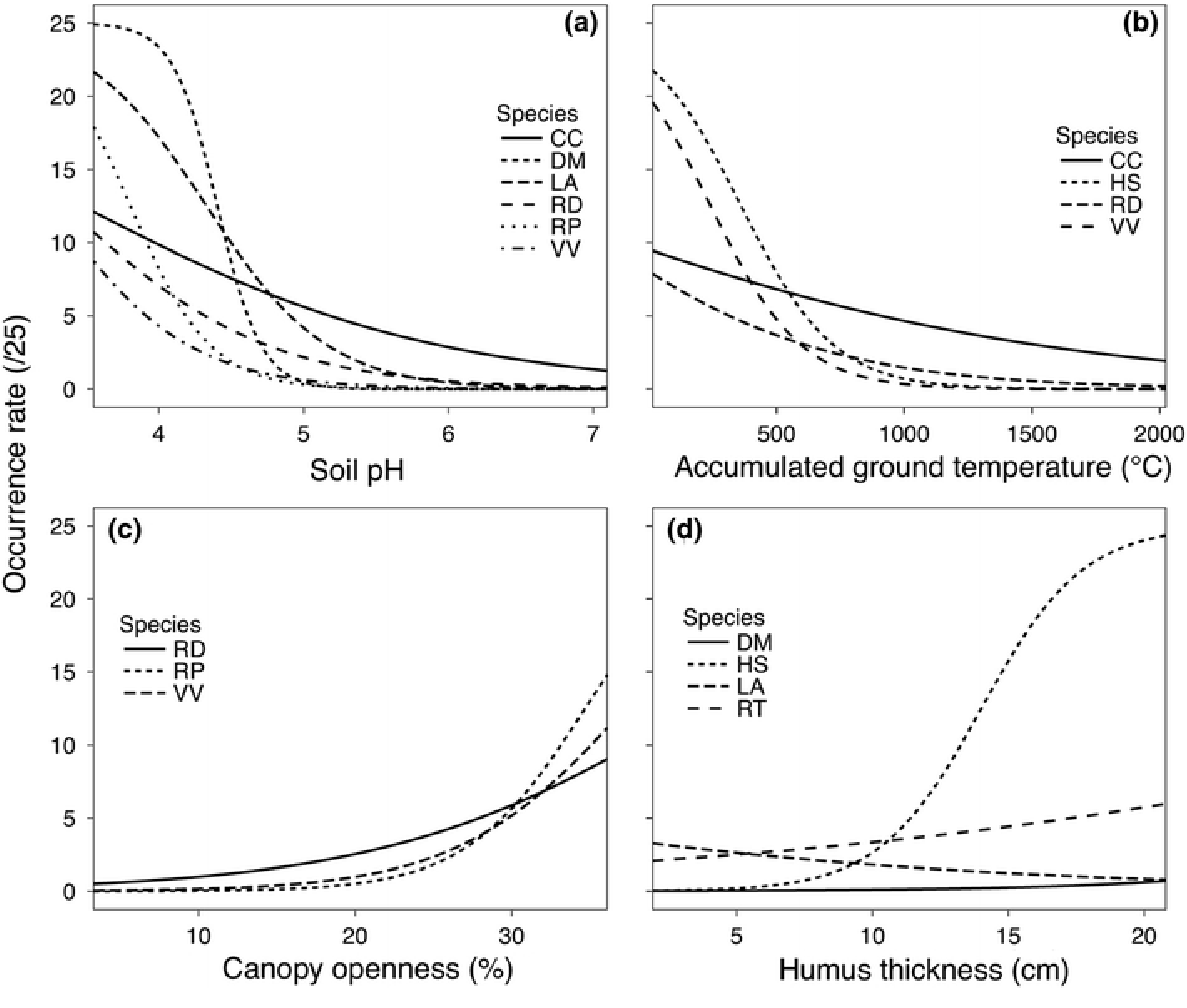

Table 1

The eigenvalues of each DCA axis and Spearman's rank-order correlation coefficients between coordinate values of each DCA axis and the characteristics of study sites (species diversity index and six environmental factors).

DCA axes	1	2	3	4
Eigen values	0.65	0.45	0.27	0.22
Accumulated ground temperature	0.61 ***	0.00	0.18	0.11
Humus thickness	–0.38 *	–0.10	0.13	–0.11
Soil moisture	0.1	–0.47 **	–0.24	0.00
Soil pH	0.67 ***	0.58 ***	0.33	0.10
Soil C:N ratio	–0.49 **	0.01	–0.05	0.24
Canopy openness	–0.57 ***	0.43 *	0.06	0.32
Species diversity *H'*	0.74 ***	–0.09	0.15	–0.07

* $P < 0.005$, ** $P < 0.01$, *** $P < 0.001$

Table 2

Summary of the best-fit models of occurrence of highland plants. Each value represents the standard partial regression coefficient of each environmental factor for eight highland species: *Vaccinium vitis-idaea* (VV), *Rhododendron palustre* ssp. *diversipilosum* (RP), *Rhododendron dauricum* (RD), *Cornus canadense* (CC), *Lycopodium annotinum* (LA), *Dicranum majus* (DM), *Hylocomium splendens* (HS), and *Rhytidiadelphus triquetrus* (RT)

	VV	RP	RD	CC	LA	DM	HS	RT
(Intercept)	–4.31 ***	–5.44 ***	–2.79 ***	–1.48 ***	–2.33 ***	–5.93 ***	–3.56 ***	–2.04 ***
Accumulated ground temperature	–2.79 ***	–0.40	–1.00 ***	–0.49 ***	—	—	–2.73 ***	—
Humus thickness	—	–0.31	—	—	–0.32 **	0.70 ***	2.10 ***	0.26 *
Soil pH	–1.40 ***	–2.41 ***	–0.95 ***	–0.54 ***	–1.59 ***	–4.38 ***	—	—
Soil C:N ratio	—	0.66 **	0.37 *	—	—	–1.71 ***	0.67 ***	—
Canopy openness	1.74 ***	2.46 ***	0.94 ***	0.18	—	—	—	—

* $P < 0.005$, ** $P < 0.01$, *** $P < 0.001$