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Citation	Polar Biology, 33(4), 565-570 https://doi.org/10.1007/s00300-009-0727-x
Issue Date	2010-04
Doc URL	https://hdl.handle.net/2115/45093
Rights	The original publication is available at www.springerlink.com
Type	journal article
File Information	PB33-4_565-570.pdf

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Short Notes

Baidzharakhs (relic mounds) increase plant community diversity by interrupting zonal vegetation distribution along the Arctic Sea, northern Siberia

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Abstract

To understand how baidzharakhs (relic mounds enclosing polygonal ice blocks in permafrost) affect the zonal distribution of vegetation, vegetation was measured in 145 50 cm × 50 cm plots on a coastal terrace facing the Arctic Ocean in northern Siberia. Cluster analysis classified five community types that were zonally distributed along the coastline. α-diversities (species richness and diversity) were not different among vegetation types except for vegetation close to the coastline. On and around baidzharakhs, burrows created by lemmings were frequently observed, and plant cover was low, suggesting that baidzharakhs support habitats for rodents. Disturbances by rodent habits caused plant cover to decline but did not change α-diversity. Two vegetation types that developed only on baidzharakhs were found at intermediate distances between the seacoast and inland areas. Because these two vegetation types are azonally distributed, β-and γ-diversities were increased by permafrost-derived topography, i.e., baidzharakh, and/or disturbance by rodents of which suitable nesting habitat is provided by baidzharakh.

Key words baidzharakhs, northern Siberia, permafrost, topography, rodent burrow

Introduction

Numerous baidzharakhs or baidzherakhs (Sakha language) develop on coastal terraces in the northern Siberian arctic tundra facing the Arctic Ocean, and develop around ice wedges and edomas (Matveyeva 1994, Chernov & Matveyeva 1997). Edomas or yedomas, which consist of ice-rich fine permafrost deposits of the Late Pleistocene, are developed from the enlargement of ice wedges (Grosse et al. 2007). A network of baidzharakhs is derived from frozen thermo-erosional mounds in the permafrost zone (Sher et al. 2005). A baidzharakh is a mound several meters high and 3-12 m wide. It is the residual shell formed by the melting of ice wedges in polygonal ground. However, the formation processes have various developmental pathways, including abundant ice pillars covered by a frozen earth layer occurring on glacial terraces, and washing out by flows of earthy veins (Mironenko 2007).

A zonal distribution of plant communities often develops within a short distance of the seacoast. This is due to drastic changes in environmental stresses from the sea, such as salt spray and ground surface instability. These factors are important in vegetation zonation where the soil type is not rock (Wilson & Sykes 1999). Therefore, plant community composition is often related to distance from the shoreline so this distance can be used as a surrogate to investigate vegetation establishment patterns (Ingolfsson 2005, Alvarez-Rogel et al. 2006, Acosta et al. 2007).

Large mammals, such as reindeer and musk ox, as well as small mammals, including rodents, often affect the quality, density and patchiness of plant community structure in various ways (Klein & Bay 1994). For example, plant species diversity is higher in areas close to pocket gopher burrows due to the creation of gaps (Reichman & Seabloom 2002), and small mammals alter plant community structure in the forest-tundra ecotone by selective foraging (Olofsson et al. 2004). The depth and distribution of nests are influenced by thaw depth in permafrost regions, because nests can not be established within the permafrost layer. Therefore, vegetation zonation is likely to be modified as the distribution of rodent nests is altered following the changes in permafrost distribution as

permafrost is degraded by global warming (Jorgenson et al. 2001).

Vegetation patterns in coastal vegetation along the Siberian Arctic Ocean have not been well examined (Doing 1985, Tsuyuzaki et al. 2008). Data were collected to document vegetation differences and the present vegetation data are required. Diversity is often classified into three types: α (within-community diversity), β (between-community diversity), and γ (landscape diversity) (Forman & Godron 1986). Baidzharakh topography may affect these three types of diversity differently. Therefore, the major objectives of this study were to confirm: 1) vegetation zonation patterns along the distance gradient from seacoasts, 2) the effects of baidzharakh topography and related factors on the vegetation patterns, and 3) the contribution of baidzharakhs to α-, β- and γ-diversities.

Study area and methods

The study site is located near Ambarchik on the Arctic Ocean coast (69^{o}40’39”N, 163^{o}47’46”E). The biome is categorized as lowland tundra with low precipitation and temperature (Richter-Menge et al. 2006). The major types of soil deposits close to the seacoast were silt and sand, probably originated from the products of coastal deposition. When we conducted our research in mid-August 1996, it was snowing and the seacoast was covered with enormous drift ice.

We randomly established 145 50 cm × 50 cm plots in ca 200 m × 100 m area from seacoast to inland. Each plot was divided into 25 10 cm × 10 cm cells, and the projected cover of each species was visually estimated. Nomenclature follows Tolmachev (1974) for vascular plants. Mosses and lichens were not identified, except for *Ceratodon purpureus* (Hedw.) Brid. and *Polytrichum* spp. (mostly by *P. inflexum* (Lindb.) Lac.). Plot locations (elevation, distance from the seacoast, and slope direction) were measured using a laser level (Topcon ET-2, Topcon, Tokyo). The number of nest holes was counted in each plot, and the area of mounds was measured. The area of mounds included the mounds contact with plot margins. Therefore, the total area of mounds in a plot occasionally exceeded the plot area. Conspicuous baidzharakhs were not included into the mounds.

The mounds included mounds created by rodents, tussocks, and small baidzharakhs, but the distinction was sometimes difficult. However, tussocks tended to be distributed more on the bottom of baidzharakhs, and mounds created by rodents were more abundant on the top. Small baidzharakhs were recorded as the mounds, although the records were likely to be less because of the size requirement. Elevational difference and gradient within each plot were measured by a clinometer and ruler.

Two-way indicator species analysis (TWINSPAN) was conducted using the percent cover of each taxon (Hill 1979). Three parameters of α-diversity were examined in each plot: species richness, species diversity, and evenness. Shannon-Wiener's species diversity and evenness were used. Differences in species composition, diversity and environmental attributes between TWINSPAN clustering groups were compared by Tukey's honestly significant difference (HSD) test when nonparametric ANOVA (Kruskal-Wallis test) showed significant differences among the clustering groups. Then, non-metric multi-dimensional scaling (NMDS) was applied to investigate relationships between environmental factors and cluster groups, by using all taxa. Since aspect (the azimuth direction of the local slope) was not significantly related to vegetation distribution patterns in a preliminary run before the final DCA, aspect was not used for the final run. TWINSPAN was performed with PC-Ord (ver. 5.19) (Mjm Software, Gleneden Beach, Oregon): other analyses were conducted by the software package R (ver. 2.8.0) (R Foundation for Statistical Computing, Vienna, Austria).

Results

Forty-two plant taxa were recorded from 145 plots. Of these, 38 taxa were from vascular plants. TWINSPAN classified five plant community groups A to E (Fig. 1). The first branching on the dendrogram and highest eigenvalue on the division indicated that the community structure of group E was strongly different from the other four groups. Group E was characterized by *Equisetum arvense* and *Ceratodon purpureus*. Then, groups A and B were separated from groups C and D by six vascular plant species. Groups A and B had

more *Eriophorum scheuschzeri*, *Carex ensifolia* and *Ranunculus borealis* than groups C and D, which had more *Eriophorum vaginatum*, *Phippsia concinna* and *Saxifraga hirculus*. Group A was distinguished from group B by the presence of *Salix polaris*. Group C, which contained more *Ranunculus borealis*, *Saxifraga hirculus* and moss spp., was different from group D, which contained more *Salix pulchra*, *Dryas punctata*, *Dryas viscosa* and *Ceratodon purpureus*. All plots in group D included *Arctagrostis latifolia* and *Salix pulchra*.

Distance from the coastline ranged from 30 m to 181 m, and elevation ranged from 1 m to 38 m in height. Terrestrial plants were rarely established in areas less than 30 m from the coastline. The order of vegetation types from seacoast to inland were: E < B < C ≈ D < A (Table 1), showing that groups C and D placed themselves between groups A and B. Group E was established in areas closest to seacoast, and group B in areas second-closest to the seacoast. Group A was established the farthest inland. Groups C and D lay between groups B and A. Since elevation increased with increasing distance from the seacoast, group E was established on the lowest elevation, and group A on the highest. Groups C and D developed mostly on the baidzharakhs, shown by the large area of mounds. Because baidzharakhs are mounds, gradient and elevation differences within a plot became higher in these two groups. When plots were established on and around baidzharakhs, aspect varied. However, most plots on and around baidzharakhs were categorized into cluster groups C and D, indicating that the vegetation did not differ greatly between seaward and inland sides on baidzharakhs. There were burrows created by rodents on and around baidzharakhs (Fig. 2). Even if there were no nest holes in the 50 cm × 50 cm plots, nests were observed on the baidzharakh. We did not observe the rodent species responsible for these disturbances, but based on the form, size and distribution of nest holes, it is likely that the rodents were Siberian brown lemmings (*Lemmus sibiricus*). Since bare ground was observed around burrows, the low plant cover in group C was considered to be caused mostly by mammalian damage. Excavations confirmed that the depth of the permafrost surface was 35 cm in mid-August at the base of baidzharakhs, suggesting that

the depth of rodent nests was restricted to shallow layers where the mounds of baidzharakhs were not developed.

Species richness and diversity did not differ between cluster groups except for group E (Table 1), which had low plant cover derived from disturbances and stresses occurring near the seacoast. Evenness did not differ between any cluster groups. Plot cover was lowest in groups C and E, although the causes of low plant cover were different between them. Group E, established close to the seacoast, received stresses from the sea, and group C received herbivorous damages. *Arctagrostis latifolia* was widespread throughout the surveyed area (Table 2), but slightly decreased in group A, which developed inland. The other species occurred in respective cluster groups (Fig 1). In particular, *Saxifraga hirculus*, *S. hirculus*, *Eriohprum vaginatum*, *Phippsia concinna* and *Dryas puncutata* were established mostly on baidzharakhs (groups C and D). *Salix pulchra* was more frequent (100% occurrence) in group C than in group D, in which frequency of occurrence was 100%. *Eriophorum scheushzeri*, *Ranunculus borealis*, *Salix polaris* and *Equisetum arvense* were less abundant on baidzharakhs.

Of the environmental factors, coefficients of determination (r^2) on NMDS indicated that four factors - distance from seashore, elevation, slope gradient, and number of nest holes - were significantly ($p < 0.01$) related to the plot scores of the axes I and/or II. Of these four factors, elevation and distance were related more to axis I, and slope and number of holes were related to axis II (Fig. 3). Therefore, elevation and distance were the prime determinants of the vegetation development, shown by the positions of cluster groups along axis I, that is, group A showed the highest scores along axis I, and group E the lowest. The factors related to the second axis were different from those related to the first axis. Groups B, C and D overlapped considerably in their scores along axes I and II. Of these, group C, which developed on baidzharakhs, tended to show lower scores on axis II. These results clarified that baidzharakhs developed specific and azonal plant communities, i.e., groups C and D, within the zonal distribution of vegetation between seacoast and inland. There were burrows created by lemmings on baidzharakhs (Fig. 2). Although the

baidzharakhs occasionally collapsed because of the development of burrows, the factors primarily related to axis II was the number of nest holes. In addition, α-diversity did not decline on baidzharakhs inhabited by rodents. This indicated that lemming nests also contributed to the development of groups C and D.

Discussion

A marked zonation of plant species composition characterizes the seacoast surveyed in the Siberian Arctic, although baidzharakhs interfered with zonation by developing groups C and D. Elsewhere in the world, a complete zonal plant community sequence was found to be lacking in the Mediterranean sand dune ecosystems of Italy, due to human impacts that modify topography (Acosta et al. 2007), suggesting that diverse topography preserves high biodiversity. While baidzharakhs did not contribute to increase α-diversity, β-diversity increased through the modification of vegetation zonation by creating specific vegetation types C and D. This also meant that γ-diversity increased by baidzharakhs. In New Zealand dunes, salt-derived factors (salinity and salt spray) are most important for developing vegetation zonation (Wilson & Sykes 1999). Sharp changes in vegetation types occurred adjacent to baidzharakhs because the raised topography of baidzharakhs protected plants from the harshest effects of the sea, although the aspect was not related to vegetation patterns. These results suggest that the raised topography by baidzharakhs is more important than landward-facing slope for the vegetation development. Vegetation established on the summit areas of costal dunes in Spain shows lower salinity and lower soil moisture than that in depressions on the interdune slopes (Alvarez-Rogel et al. 2006). Therefore, baidzharakhs that created diverse microtopography could contribute to vegetation differentiation and increase the resultant β-and γ-diversities. Sand burial disturbance determines species composition in vegetation at the local scale, while water and nutrient stress more strongly influence regional differences in the vegetation found on French costal sand dunes (Forey et al. 2008). However, the permafrost underlying the Siberian tundra restricts subsurface moisture and nutrient movement except close to the

seacoast where group E is established.

Although lemmings reduced vegetation cover on baidzharakhs by grazing and burrowing, species richness and species diversity did not decrease, even tough it is clear that, as shown by the development of vegetation types C and D, species replacement or substitution occurred on baidzharakhs. Species richness and diversity are not different between areas disturbed and undisturbed by small and large herbivores in a forest-tundra ecotone (Olofsson et al. 2004). Since grazers, including lemmings, select to feed on palatable plants, species palatability to such herbivores is an important determinant of plant community structure in tundra wetlands over both the short- and long- term (Kitti et al. 2009). The collared lemming (*Dicrostomyx exsul*) favors drier habitats dominated by willows (*Salix* spp.) in summer, where it feeds on willows and graminoids (Klen & Bay 1994). In group D where burrows were frequently observed, *Salix pulchra* was most abundant. A graminoid, *Arctagrostis latifolia*, was widespread, and was likely to provide food for lemmings. In a temperate grassland ecosystem, plant community diversity was observed to become highest in areas within several tens of cm of the gateways of pocket gopher (*Thomomys bottae*) nests, by creating gaps for seedling establishment (Reichman & Seabloom 2002). Lemming-vegetation interactions have sustained Arctic ecosystems for millennia (Oksanen et al. 2008). However, if global warming proceeds, Arctic rodents will be replaced by competition from rodents that mainly live in southern regions. Combined with the loss of ground ice and its associated features, differences in foraging and burrowing habits may suggest that vegetation types C and D will disappear in the world.

Conclusion

In conclusion, the development of diverse topography created by permafrost, including baidzharakhs, determines plant community structures (represented here by vegetation groups C and D) in continuous permafrost zones. Furthermore, azonal vegetation is developed by baidzharakh topography, suggesting that changes in baidzharakh distribution

and morphology would induce a decline in β- and γ-diversities in coastal vegetation along the Arctic Ocean.

Acknowledgements We thank Dr. S.A. Zimov and Mr. S. Alexey for field assistance. This work is partly supported by grants from JSPS. We also thank Drs. D. Piepenburg, B. Phillip, and an anonymous reviewer for critical readings of the manuscript.

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Table 1 Mean (± standard deviation) values for plant community characteristics and environmental attributes on a seacoast along the Arctic Sea, northeastern Siberia, examined in 145 50 cm × 50 cm sample plots. The total area of mounds in a plot occasionally exceeded plot size.

Vegetation cluster code	A	B	C	D	E	Total
Number of plots	22	62	30	17	14	145
Species richness *	6.1 ± 1.5 a	7.2 ± 2.2 a	7.2 ± 2.1 a	7.2 ± 1.7 a	3.4 ± 1.6 b	6.7 ± 2.2
Species diversity (*H'*) *	1.28 ± 0.28 a	1.36 ± 0.35 a	1.30 ± 0.44 a	1.42 ± 0.76 a	0.76 ± 0.83 b	1.28 ± 0.39
Evenness (*J'*)	0.72 ± 0.13	0.69 ± 0.12	0.66 ± 0.16	0.73 ± 0.10	0.63 ± 0.16	0.69 ± 0.14
Plot cover (%)	98.6 ± 3.5 a	90.0 ± 14.9 a	79.1 ± 14.3 b	88.3 ± 8.8 a	68.9 ± 21.0 b	86.8 ± 16.0
Gradient (^{o}) *	1.9 ± 1.0 a	4.0 ± 3.8 a	9.8 ± 11.6 b	4.4 ± 4.0	1.3 ± 0.5 a	4.7 ± 14.5
Elevation difference within a plot (cm) *	8.7 ± 8.3 a	7.4 ± 10.2 a	25.3 ± 14.3 b	28.5 ± 24.9 b	1.2 ± 0.6 a	13.2 ± 15.9
Number of nest holes *	0.0 ± 0.0 a	0.2 ± 0.9 a	1.5 ± 1.3 b	0.5 ± 0.8 a	0.0 ± 0.0 a	0.5 ± 1.0
Area of mounds (cm^2) *	214 ± 314 a	159 ± 385 a	639 ± 561 b	942 ± 701 b	0 ± 0 c	343 ± 533
Elevation (m) *	35.8 ± 3.9 a	13.2 ± 13.0 b	26.8 ± 9.7 a	24.8 ± 11.4 a	5.9 ± 11.7 b	20.1 ± 14.5
Distance from coastline (m) *	156 ± 19 a	69 ± 39 b	118 ± 36 c	107 ± 32 c	45 ± 28 d	95 ± 49

* Means for a given attribute are significantly different among cluster groups A-E at $p < 0.01$ (Kruskal-Wallis nonparametric ANOVA).

abcd Means sharing the same lowercase letter for a given attribute are not significantly different at $p = 0.01$ (Tukey's HSD test).

Table 2 Mean cover (%) and (in parentheses) % frequency of plant taxa in each cluster group. Pseudo-species classified by TWINSPAN are indicated by bold face and enclosing rectangle. All pseudo-species and species with occurrence frequency more than 10% are shown.

Vegetation cluster code	A	B	C	D	E	Total
Vascular plant						
Arctagrostis latifolia	17 (59)	34 (93)	34 (93)	27 (100)	7 (86)	28 (90)
Saxifraga exilis	+ (23)	2 (48)	**2 (70)**	+ (35)	-	1 (43)
Stellaria ciliatosepala	+ (32)	1 (40)	1 (70)	+ (53)	-	+ (43)
Eriophorum scheuschzeri	**17 (73)**	**10 (66)**	-	-	1 (7)	7 (40)
Ranunculus borealis	**+ (14)**	**5 (69)**	**2 (37)**	-	-	2 (39)
Salix pulchra	-	11 (39)	3 (23)	**25 (100)**	5 (14)	9 (34)
Carex ensifolia	**1 (27)**	**11 (65)**	+ (7)	+ (6)	2 (7)	5 (34)
Polygonum viviparum	1 (59)	+ (23)	+ (13)	+ (29)	+ (7)	+ (26)
Dupontia fischeri	3 (45)	+ (16)	3 (33)	6 (35)	-	2 (25)
Saxifraga hirculus	1 (23)	+ (11)	**3 (53)**	**2 (41)**	-	1 (24)
Polemonium acutiflorum	-	2 (39)	-	+ (24)	-	+ (19)
Eriophorum vaginatum	-	+ (2)	**7 (53)**	**5 (41)**	-	2 (17)
Phippsia concinna	-	+ (3)	**7 (50)**	**3 (41)**	-	2 (17)
Salix polaris	**34 (95)**	+ (2)	-	-	-	5 (15)
Equisetum arvense	-	+ (13)	-	-	**11 (57)**	1 (11)
Gentiana algida	+ (9)	+ (10)	+ (13)	+ (18)	+ (7)	+ (11)
Dryas punctata	5 (36)	-	-	**8 (35)**	-	2 (10)
Dryas viscose	-	-	-	**7 (29)**	1 (7)	1 (4)
Moss and lichen						
Moss spp.	37 (95)	23 (63)	**6 (63)**	2 (29)	-	17 (71)
Ceratodon purpureus	-	1 (3)	+ (7)	**6 (35)**	**36 (100)**	5 (17)

+ less than 1%. -: not found.

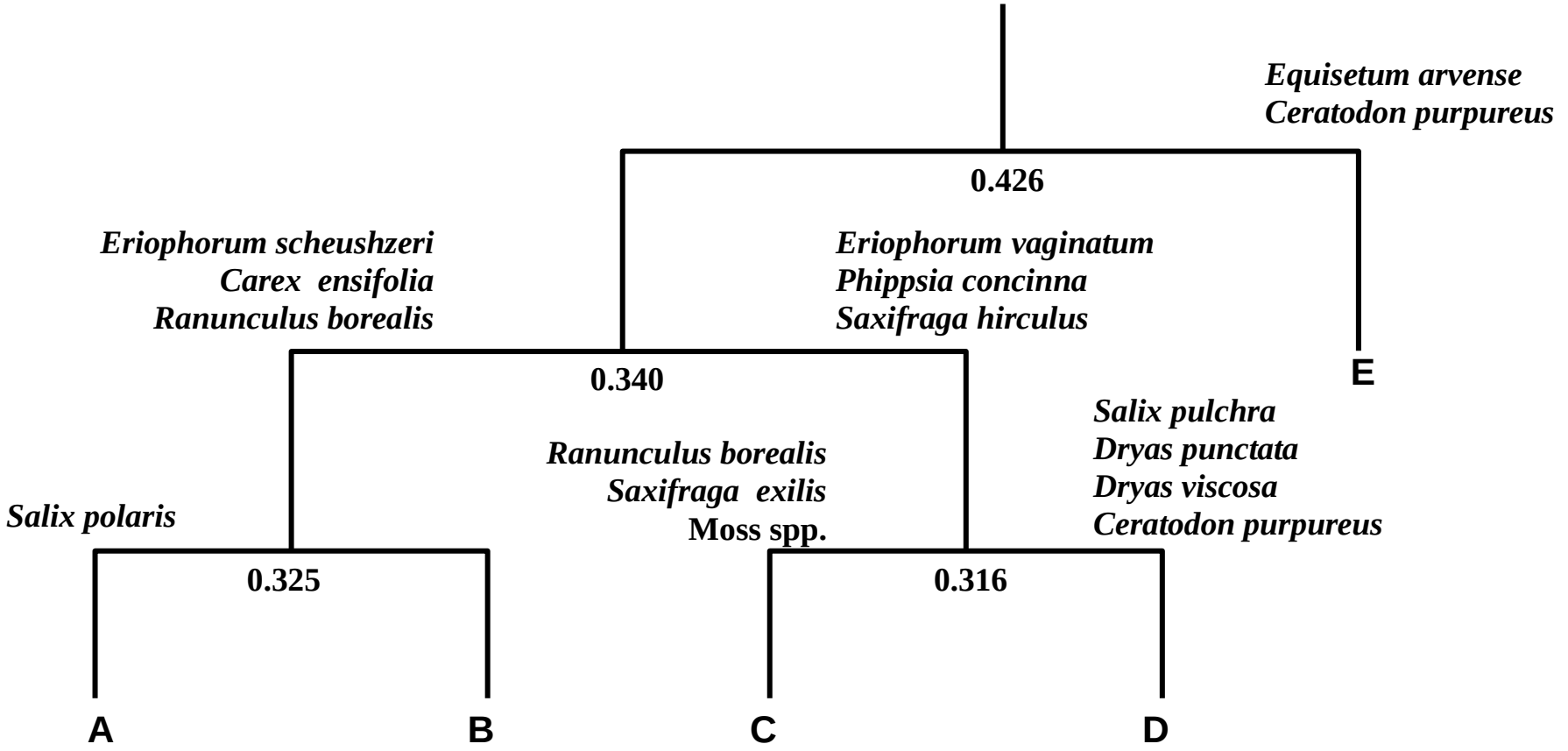

Fig. 1 Vegetation patterns determined by TWINSPAN in 145 quadrats on a seacoast along the Arctic Sea, northeastern Siberia. Each number indicates an eigenvalue at the division point. Indicator species that were used for divisions are shown on the left and right sides of cluster branches.

Fig. 2 Mounds and holes on a baidzharakh. The baidzharakh was collapsed by burrows constructed by rodents.

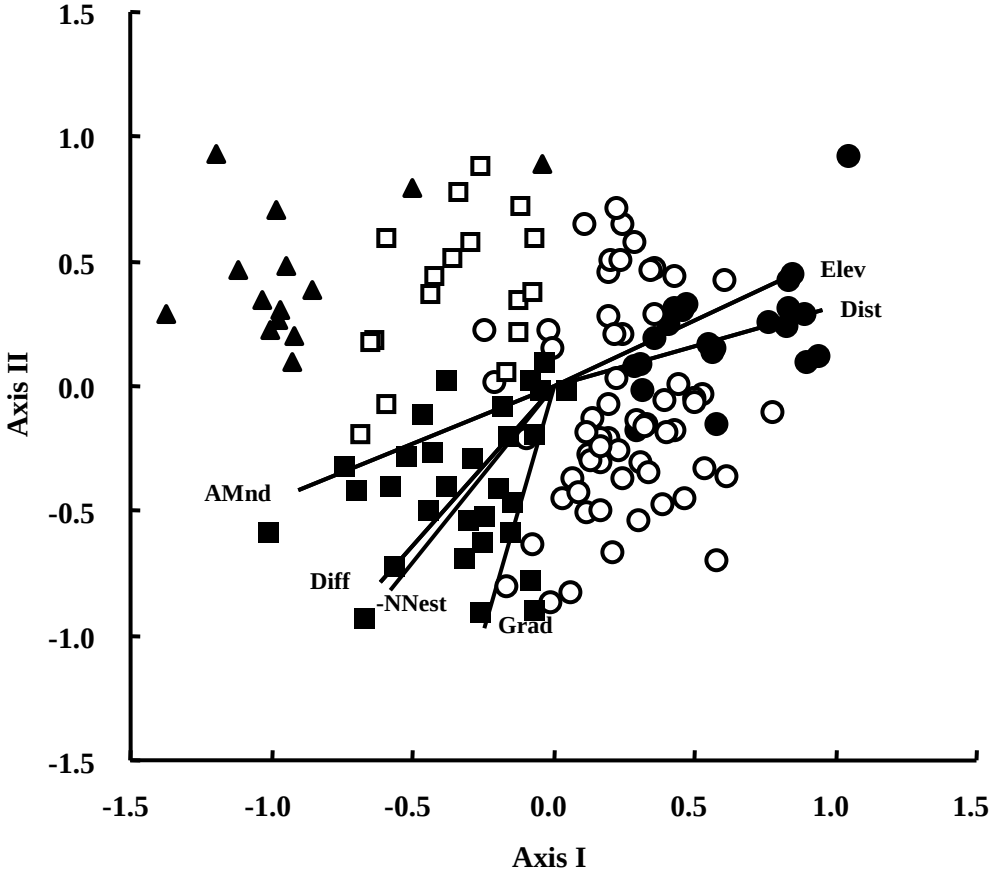

Fig. 3 Plot scores on NMDS (non-metric multidimensional scaling) and examined explanatory variables. Lengths of environmental vectors indicate strength of the relationship of the variable to the NDMS axis. Closed circles, open circles, closed squares, open squares and closed triangles, respectively, indicate cluster groups 1 to 5. Environmental factors: Elev = elevation, Dist = distance from seashore, AMnd = area of mounds, Diff = elevation difference within a plot, NNest = number of nest holes, Grad = local slope gradient.