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RESEARCH ARTICLE

Landscape and vegetation structure of domestic reindeer winter pastures in southern Yamal

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Abstract

Winter reindeer pastures in the tundra are spatially heterogeneous systems in which vegetation patterns are closely associated with landscape structure. This study characterises the spatial organisation of vegetation within a tundra winter pasture in southern Yamal using landscape units (urochishches) as the basis for mapping and geobotanical analysis. The study area corresponded to an actual winter grazing territory used by Nenets herders. Landscape mapping on a scale of 1:100,000 covered approximately 200 km², and detailed field studies were conducted within a ~37 km² key site, where 50 geobotanical relevés were completed. We identified 25 types of urochishche and 10 types of plant community. For several urochishches, a relatively consistent association was recorded with a single community type, while others contained two or more community types, reflecting the fine-scale mosaic structure of tundra vegetation. The grass-moss communities occupied the largest proportion of the study area (~51%), followed by the dwarf shrub–moss tundra (13.2%) and the lichen-dominated moss–lichen tundra (12.5%). Although the lichen-dominated communities occupied a relatively small area, lichens occurred within plant communities in approximately 77% of the pasture, while other winter forage plants were also widely represented. The landscape framework therefore provides a spatial basis for relating vegetation composition and potential winter forage components to the landscape structure of an actively used tundra winter pasture.

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Keywords
Arctic, forage resources, landscape structure, plant communities, reindeer herding, spatial heterogeneity, tundra

Introduction

The Yamal Peninsula is a key centre of reindeer herding in the Russian Arctic, where indigenous people, mainly Nenets, practice a year-round nomadic lifestyle migrating with their herds (Stammler 2005; Golovnev et al. 2018). More than 80% of the roughly 200,000 reindeer are owned by private households, whose migration routes differ in configuration and length depending on the administrative affiliation of the households, herd size, and local climatic and forage conditions (Volkovitskiy and Terekhina 2023).

Tundra reindeer herding has a well-defined spatial organisation based on seasonal rotation of pastures. Winter pastures are especially important as they supply the herd with forage during the longest and most challenging period of the year. Their importance depends not only on the composition and abundance of vegetation, but also on the accessibility of forage, which is influenced by snow conditions and terrain heterogeneity (Andreev 1934; Titov, Zarubin 1986; Polezhaev 1993; Dasheev 2013). Classic studies of reindeer forage resources on the Yamal Peninsula have shown that the winter diet includes fruticose lichens, dwarf shrubs, and parts of vascular plants remaining under the snow cover (Andreev 1934; Avramchik 1939; Glinka 1939; Magomedova et al. 2006). The distribution and abundance of lichens have traditionally been used as a key indicator of winter pasture quality. A recent study of vegetation in summer pastures in southern Yamal (Gorbunova et al. 2023) reported a significant decline in lichen forage reserves over the last decade compared to the early twentieth century, whereas green forages have remained unchanged over the past 80 years. Even studies of summer pastures have emphasised the condition of lichens. However, the contribution of lichens to the winter diet varies markedly between regions, depending on their accessibility (Bogdanovskaya-Gienef 1938), and any assessment of the actual forage potential of pastures should also consider vascular-plant resources (Andreev 1933; Titov, Zarubin 1986; Polezhaev 1993). These characteristics are strongly influenced by the spatial structure of the area and the properties of its plant communities.

In studying reindeer pastures, researchers employ geobotanical surveys, remote sensing, and GIS analysis, enabling assessment of vegetation composition and spatial distribution over vast areas (Andreev 1934, 1940; Bogdanovskaya-Gienef 1938; Colpaert et al. 2003; Rees and Danks 2007; Elsakov et al. 2011; Elsakov 2014; Lavrinenko and Lavrinenko 2014). The southern Yamal tundra vegetation studied here is highly patchy, a pattern driven by the interplay of landforms, moisture conditions, surface sediments, and ongoing cryogenic processes (Gribova 1985; Matveeva 1998; Morozova and Magomedova 2004; Magomedova et al. 2006). The spatial distribu-

tion of plant communities is largely determined by the topographic position and local environmental conditions. The fine-scale mosaic of tundra vegetation makes detailed mapping of individual plant communities over large areas difficult, whereas pasture mapping generally requires a broader level of spatial generalisation.

In analysing the structure of seasonal pastures, attention should be paid not only to the distribution of plant communities but also to their association with landforms, moisture regimes, and other environmental factors. A landscape-based approach allows a pasture to be viewed as a combination of landscape units (urochishches), each characterised by a particular set of environmental conditions and associated plant communities (Melnikov et al. 1983). Although previous studies have provided extensive information on Yamal vegetation and plant resources (Morozova and Magomedova 2004; Magomedova et al. 2006; Veselkin et al. 2021, Gorbunova et al. 2023), geobotanical studies have generally not used the landscape structure of pasture territories as the primary spatial framework for characterising the spatial distribution of plant communities. The present study applies this landscape-based geobotanical approach within a specific winter pasture area.

Yamal reindeer herders winter both in the northern taiga south of the Ob River and on the peninsula itself, in the tundra zone (Volkovitskiy and Terekhina 2023). In the latter case, herds spend several winter months on pastures where the composition and accessibility differ from those of forest pastures. This article examines an area of tundra winter pasture whose use by Nenets herders was documented during our fieldwork. An additional feature of the study is that vegetation is analysed within the documented boundaries of an actual winter grazing territory used by particular Nenets reindeer herding households, rather than within an area delineated solely for the purposes of a geobotanical survey.

The aim of this study is to characterise the spatial structure of vegetation in local winter pastures in relation to the landscape organisation of the area. The study consisted of five main stages: (i) identification and description of the landscape structure of the winter pasture area; (ii) description of plant community composition and structure within the defined urochishches; (iii) analysis of the relationships between the identified plant communities and the urochishches; (iv) a description of the spatial structure of the area in relation to the identified urochishches and plant communities; and (v) qualitative assessment of the vegetation cover of the winter pastures in southern Yamal.

This approach broadens the characterisation of winter pastures beyond the assessment of lichen resources alone by considering the spatial combination of different vegetation types and winter forage components within the landscape structure of the pasture.

Materials and methods

Study area

The study area is located in the southern subarctic tundra subzone of the Yamal Peninsula (Walker et al. 2005) in the Russian Arctic. The regional climate is characterised by a short cool growing season, long, cold winters, and snow cover that persists from autumn to late spring (Sokolov et al. 2016; Hofhuis et al. 2021). This subzone includes a combination of tundra, bog, and meadow plant communities. A notable feature of the southern tundra is the widespread occurrence of shrubs, particularly dwarf birch, in upland watersheds. The species richness and strong habitat affinity of many species result in a high diversity of plant communities and heterogeneity of the flora. Southern tundra communities are characterised by dense vegetation cover, increased plant height and vertical complexity, and increased shrub layer height, closure, and floristic diversity. Compared to more northern bioclimatic subzones, species richness, height, and projective cover of the shrub layer as well as species richness, height, and projective cover of the forb-dwarf shrub layer increase significantly (Magomedova et al. 2006).

The southern tundra is characterised by extensive wetlands: mires are widespread in both river valleys and watersheds. Flat-hilled bogs are widespread here and bog and tundra vegetation often forms tundra-bog and bog-tundra complexes. Monodominant tallgrass meadow communities are common in river floodplains, and arctophilous thickets are common along the shores of lakes, oxbow lakes, and at river mouths. Meadow vegetation also includes drained lake basins (khasyreis) and coastal meadows (tamps) (Il'ina et al. 1985; Matveeva 1998; Magomedova et al. 2006).

Reindeer herding is organised through an annual cycle of land use, in which different grazing areas are used by herds during particular seasons (Vasil'ev 1936; Marin 2006; Eira et al. 2023). Winter pastures are the areas used during the winter part of this cycle. The study area (approximately 200 km^2) lies within the Yorkutayakha River basin, about 30 km from the coast of Baydaratskaya Bay (Fig. 1). During the winter season (November–May), corresponding to the snow-covered period, the area provides grazing grounds for 1,000 reindeer owned by four private Nenets households. In the summer, they migrate 140 km northwest to Levdiyev Island. Between May and November, the area is also used as a seasonal migratory corridor by several other households, with a total of up to 4,500 reindeer passing through the area twice annually: once on their northward journey and again on their return to their winter pastures elsewhere. Our long-term field observations and discussions with local herders indicate that the area has been used regularly as a winter pasture for many years and that local herders consider its forage resources sufficient for winter grazing.

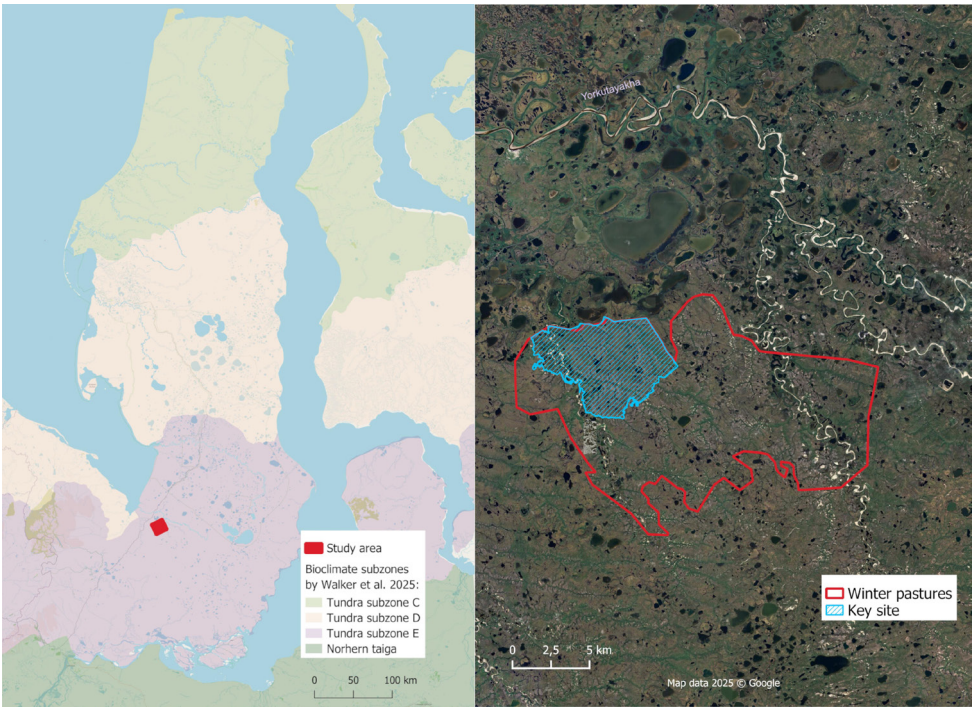


Figure 1. Study area on the Yamal Peninsula.

Landscape and geobotanical research

The spatial structure of the winter pastures was examined by landscape mapping on a scale of 1:100,000. At this scale, the primary mapping unit was the urochishche, a complex landscape unit composed of smaller units, facies, which are relatively homogeneous in nanorelief, plant associations, surface deposits and moisture conditions, heat exchange, and the stage of exogenous geological processes. In the hierarchical classification of landscape units, an urochishche is broadly comparable to the German nanogeochore and the Australian land unit (Khoroshev 2020). The typological similarity of the urochishches is determined by the underlying geological and geomorphological setting, the characteristics of the drainage, the climatic variables, and the intensity of ongoing natural processes. The interaction of these factors produces regular combinations of urochishches that determine the morphological structure of the landscape and patterns in the spatial distribution of vegetation. Each urochishche is characterised by a specific microrelief and a combination of plant communities and soil types. We used the typology of urochishches developed for northern Western Siberia by E. S. Melnikov et al. (1983).

For a detailed landscape and geobotanical characterisation of winter pastures, we used a combination of classical landscape and geobotanical methods to describe the structure of the vegetation cover. The urochishches were delineated during the

desk-based phase through expert visual interpretation of multi-temporal satellite imagery. At the initial stage, we used a WorldView-1/2 imagery mosaic with a spatial resolution of up to 0.5 m, available in QGIS. At the final stage, following fieldwork, the urochishche boundaries were refined using a very high resolution image dated 26 July 2025 (Google, Airbus, Maxar Technologies), available in Google Earth (resolution 0.5 m). The delineation was performed manually, using direct interpretation criteria (tone, texture, shape, and topographic position), and boundaries were drawn on a scale of 1:50,000 – twice the scale of the final 1:100,000 map. No independent quantitative assessment of mapping accuracy was performed. Because the landscape map was produced by expert visual interpretation and manual delineation rather than by automated or supervised image classification, a classification confusion matrix and the kappa coefficient were not calculated. A draft landscape map of the entire winter pasture area (~200 km²) was then produced.

The morphological structure of the landscape was subsequently analysed, and dominant, codominant, and accessory urochishches were identified, and the relative proportion of each urochishche type was calculated for the entire winter pasture area. Based on the spatial patterns identified during the image interpretation, a key site for geobotanical fieldwork (~37 km²) was selected to include all urochishche types identified throughout the entire pasture area (~200 km²). This allowed us to describe the main plant communities typical of each identified urochishche type. As an additional assessment, we compared the relative proportions of the different types of urochishche within the key site and the entire pasture using the Renkonen similarity index. The resulting value (PS = 0.8067) indicated a high degree of similarity in landscape composition between the key site and the entire pasture area (Wolda 1981). This comparison was used as an additional check of the structural similarity of the two areas, rather than as a basis for extrapolating landscape proportions.

The field phase involved a comprehensive study of the key site, comprising detailed geobotanical relevés, vascular plant species inventories, and assessment of the projective cover of valuable forage lichen species. Sampling locations for vegetation descriptions were established within the identified urochishche types. To identify the plant communities most typical of each urochishche, 50 standard geobotanical relevés were made at the key site in July – August 2023. These included three relevés in dominant and codominant urochishche types and one to three in accessory types covering more than 0.5% of the study area. The relevés of tundra communities followed standard methodology on 100 m² sample plots (Lavrenko, Korchagin 1964). For each plot, we identified habitat characteristics and community structure, as well as topographic position, microrelief, moisture conditions, and signs of disturbance. Qualitative field notes on the potential for snow accumulation were made on the basis of topographic position and microrelief; these observations were not treated as direct measurements of winter snow conditions; a similar approach was used by Andreev (1934). Community structure was assessed by recording the composition, cover, and height of the shrub layer, as well as the forb–dwarf shrub and moss–li-

chen layers. For each plot, we determined the species composition and projective cover of vascular plants and lichens and recorded the presence of litter and bare ground. Specimens that could not be reliably identified in the field were collected for laboratory identification. The nomenclature and taxonomic status of vascular plants follow the Plants of the World Online database (POWO 2026), while the lichen nomenclature follows Index Fungorum (2026). Valuable forage species were identified based on Andreev (1934) and Magomedova et al. (2006).

To identify the main plant community types within the study area, we used the dominant (ecological-phytocoenotic) classification system (Sukachev, 1934), as this approach has been applied in previous studies of Yamal vegetation (Andreev 1934; Magomedova et al. 2006). It allows the predominance of particular functional and forage plants and lichen groups (shrubs, dwarf shrubs, grasses, mosses, and lichens) to be demonstrated and allows comparative analysis of vegetation composition and structure with previously published results. At the subsequent desk-based stage, we initially refined the identified urochishche types, identified the plant communities most typical for each type, and determined the spatial structure of the vegetation cover by relating these communities to the mapped urochishche types and calculating their proportional representation throughout the entire winter pasture area.

Multivariate statistical analysis, including data preprocessing, Hellinger transformation, calculation of Bray–Curtis dissimilarity matrices, and subsequent PERMANOVA, was performed using the specialized "vegan" package (Oksanen et al. 2026) in the R statistical programming environment (R Core Team 2026), deployed on the Posit Cloud platform (Posit Software, PBC; electronic resource: posit.cloud). Graphical visualisation of nonmetric multidimensional scaling (nMDS) ordination results and contingency analysis of landscape characteristics (Pearson's Chi-square test with Monte Carlo simulation and calculation of Cramér's V were implemented using built-in base graphics tools and the stats package.

Results

The study area is located within the landscape of the IV marine terrace. Following the typology of Melnikov et al. (1983), 25 types of urochishche were identified both within the entire winter pasture area and within the key site, including two types of aquatic landscape complexes. The original Cyrillic letter indices used by Melnikov et al. (1983) are retained below.

Urochishches periodically flooded by surface waters (Group 2):

2 – bare beaches and spits;

2a – low flat floodplains and khasyrei bottoms with meadows, often including fragments of mires;

26 – flat low floodplains with stunted forb–moss willows, often with numerous small lakes;

2в – runoff hollows and gullies with willows and dwarf birch shrubs, with fragments of flat, lowland grass mires and peatlands;

2г – flat and slightly ridged valleys of small rivers with zonal vegetation, including dwarf-shrub and dwarf shrub–lichen–moss tundra, grass–moss mires, and fragments of meadows and peatlands;

2д – large gullies with steep slopes and sparse forb–dwarf shrub vegetation with shrubs.

Modern (Late Holocene) mires (Group 3):

3б – flat, hummocky dwarf shrub–grass–moss mires;

3г – complex flat mires with fragments of tundra and peatlands;

3д – rim-polygonal grass–dwarf shrub–moss mires.

Peatlands (ancient mires) (Group 4):

4а – flat, hummocky dwarf shrub–lichen peatlands with grass–sphagnum hollows;

4б – flat or gently sloping hummocky dwarf shrub–moss–lichen peatlands with grass–sphagnum hollows, in complex with flat-mound tundra;

4в – flat-polygonal peatlands with hummocky dwarf shrub–moss–lichen communities on polygons and shrub–grass–sphagnum communities in the troughs;

4г – low, flat, lake-dotted, small-hummocky dwarf shrub–sphagnum–lichen peatlands with numerous grass–sphagnum hollows;

4д – flat-mound hummocky dwarf shrub–moss–lichen peatlands with numerous lakes and grass–sphagnum hollows.

Tundra urochishches (Group 6)

Plains and terraces:

6 – flat, with sand blowouts and fragments of tundra vegetation;

6а – flat, smooth, often with spots and frost medallions, dwarf shrub–lichen;

6б – gently undulating, smooth, polygonal, dwarf shrub–moss–lichen;

6в – gently undulating, poorly drained, with a complex of spotted and small-mound tundra with occasional hollows, dwarf shrub–moss–lichen;

6г – flat, poorly drained, small-mound polygonal, spotted with frost medallion, dwarf shrub–grass–moss–lichen;

6з – flat and gently sloped waterlogged surfaces with hummocky, grass–dwarf shrub–moss tundra and fragments of grass–moss mires;

6н – sloping, smooth, or hummocky tundra with forb–lichen–moss willow thickets (slope communities).

Floodplains:

6и – forb–moss and forb-willow and alder thickets with bare ground spots on scroll bars, including dry marginal zones of khasyreis;

6к – flat and gently sloping surfaces, interscroll-bar depressions, or khasyrei bottoms with forb–horsetail–moss willow thickets, with dwarf shrubs.

Natural-aquatic complexes (Group 7):

оз. – lakes;

р. – rivers.

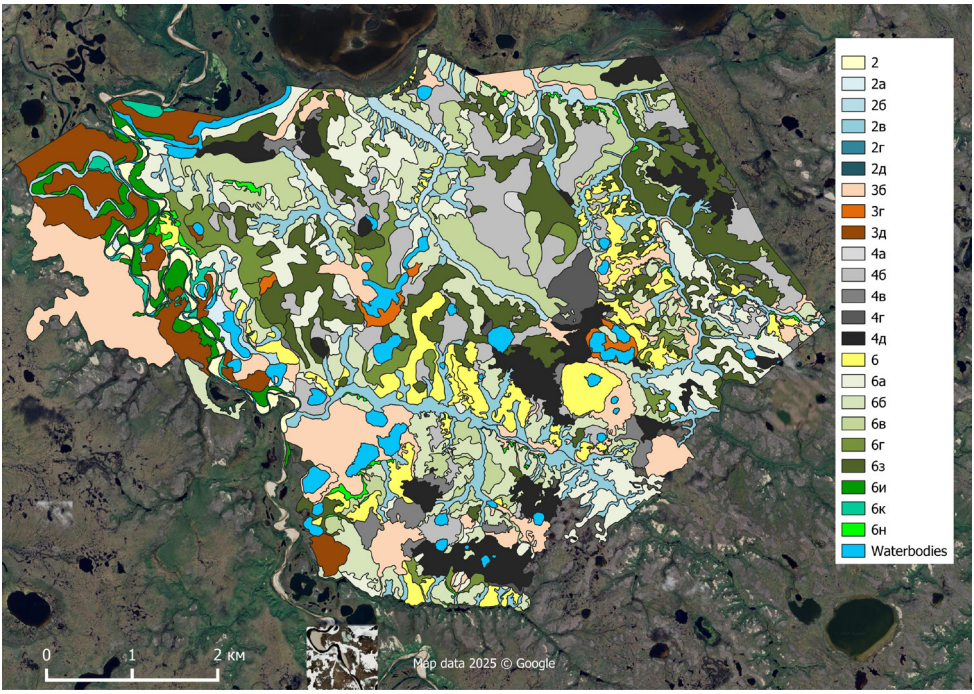


Figure 2. Urochishches of the key site.

Six types of urochishches are dominant: 3б – 12.6%, 6 – 10.5%, 6в – 10.1%, 6б – 9.5%, 3д – 8.3%, and 6з – 8.2%. Codominant urochishches (each covering > 1 %): 4б – 6.1%, 4д – 5.6%, 2в – 5.5%, 6а – 5.4%, 6н – 3.0%, 6г – 3.0%, 2б – 2.7%, 4в – 2.0%, 3г – 1.6%, and 6и – 1.6%. Accessory urochishches: 2 – 0.7%, 6к – 0.5%, 4г – 0.2%, 2а – 0.1%, 4а – < 0.1%, 2г – < 0.1 %, and 2д – < 0.1% (Fig. 3).

In terms of areal coverage, dominant urochishches cover 59.1% of the study area, codominant – 36.6%, and accessory – 1.5%, water bodies account for 2.8%. Urochishches that are virtually or completely devoid of vegetation (2 and 6) represent 11.2% of the area. The urochishches 2а, 2г, 2д, 4а, and 4г together cover 0.3% of the study area. Therefore, no geobotanical relevés were conducted in these very rare urochishche types, in the unvegetated or almost unvegetated types 2 and 6, or in water bodies. Overall, the geobotanical survey covered urochishche types that occupy approximately 86% of the entire winter pasture area.

The proportional composition of the types of urochishche within the key site (37 km²) and the entire winter pasture area (200 km²) was also compared using the Renkonen similarity index. The resulting value (PS = 0.8067) indicates a high degree of structural similarity between the two areas (Wolda 1981).

Analysis of geobotanical data identified 10 types of plant community (see Suppl. material 1: Fig. S1) based on the dominant classification system with estimation of

similarities in vegetation layer structure, prevalence of functional and forage plant groups, and their association with different types of urochishche:

urochishches occasionally flooded by surface waters – floodplain communities, comprising several units: shrub–grass (sh-g Fp), shrub–forb–moss (sh-f-m Fp), and grass–moss communities without a shrub layer (g-m Fp);

modern (Late Holocene) mires – grass–moss mires (g-m M);

peatlands – grass–moss peatlands (g-m Pl);

tundra – dwarf shrub–moss tundra (dsh-m T), grass–moss tundra (g-m T), moss–lichen tundra (m-l T), grass–dwarf shrub tundra (g-dsh T), and shrub–forb tundra (sh-f T).

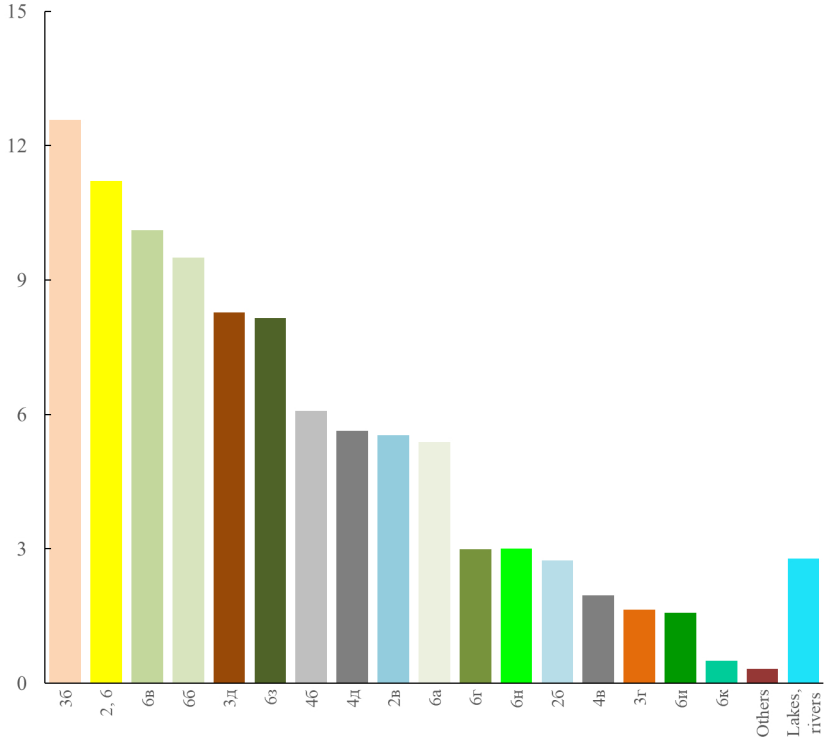


Figure 3. Proportions of types of urochishche within the study area, %. "Others" denotes urochishches 2а, 2г, 2д, 4а, and 4г, together covering 0.3% of the study area.

For each type of plant community, vegetation layers were characterised and dominant and co-dominant species were identified.

Floodplain communities on periodically flooded surfaces. In shrubgrass communities, the shrub layer is sparse (closure ≤ 0.1), composed of low shrubs *Betula nana* L. and *Salix glauca* L. Dwarf shrubs contribute little to the community structure (projective cover, hereafter PC, ≤ 10%). The PC of the grass layer reaches

65% and is dominated by *Carex aquatilis* var. *minor* Boott and *Calamagrostis stricta* (Timm) Koeler; other species are recorded only occasionally. The moss–lichen layer is absent or negligible (PC ≤ 1%).

Shrub–forb–moss communities occur in excessively moist conditions. The shrub layer is sparse, with closure of *B. nana* of 0.1–0.25 and closure of *Salix* spp. of up to 0.05. The structure of the forb–dwarf shrub layer is heterogeneous. Dwarf shrub cover ranges from 2 to 20%, with *Vaccinium uliginosum* L., *Rhododendron tomentosum* subsp. *subarcticum* (Harmaja) G.D. Wallace and *Empetrum nigrum* L. being the most abundant. Forb cover ranges from 10 to 25%, with *Rubus chamaemorus* L. being the most abundant species, accompanied by *Luzula parviflora* (Ehrh.) Desv., *Comarum palustre* L., and *Carex rariflora* (Wahlenb.) Sm.; other species occur only sporadically. The moss–lichen layer is formed by mosses (PC 40–100%), with *Sphagnum* mosses dominating; green forest mosses are rare. Lichens are almost absent.

Grass–moss communities of runoff hollows with moderate moisture have only sporadic shrubs. The grass – dwarf shrub layer is formed by forbs and grasses (PC 15–50%), with *R. chamaemorus*, *C. rariflora*, *C. aquatilis* var. *minor*, and *Eriophorum vaginatum* L. being dominant; other species occur only sporadically. Dwarf shrubs are sparse (PC ≤ 5%), with species encountered only singly. The layer is made up of mosses (PC 70–90%), with the ratio of sphagnum to green forest mosses varying between different sites.

Moderately moist grass–moss communities of modern mires have a poorly developed shrub layer, with B. nana closure ≤ 0.02. Grass is quite abundant in the grass–dwarf shrub layer (PC ≤ 35%), with *Carex rotundata* Wahlenb., *E. vaginatum*, and *Eriophorum angustifolium* Honck. being dominant, while *R. chamaemorus* and *C. rariflora* are co-dominants. Dwarf shrubs are sporadic within the community structure (PC ≤ 7%). The moss–lichen layer is formed by mosses (PC 75 to 100%), with green forest mosses being the most abundant; lichens are sporadic, although plots with lichen PC up to 15% (primarily *Cladonia rangiferina* (L.) Weber ex F.H. Wigg. and *Cladonia arbuscula* (Wallr.) Flot.) occur.

Grass–moss peatland communities generally lack a shrub layer. Only scattered, low-growing *B. nana* individuals occur (closure ≤ 0.01). The grass–dwarf shrub layer is uneven (PC 20–50%), with grass dominating, while dwarf shrubs are distributed irregularly, ranging from 5 to 20%, with *R. tomentosum* subsp. *subarcticum* and *Vaccinium vitis-idaea* L. being the most abundant, while other species occur only sporadically. Grass PC is 15–35%, with the sublayer formed by *C. rotundata*, *C. rariflora*, *Eriophorum scheuchzeri* Hoppe, *E. vaginatum* and *R. chamaemorus*. The moss–lichen layer is composed of green forest mosses (PC 10–75%) and sphagnum mosses (PC 20–90%); lichen cover ranges from 5 to 15%, the most abundant being valuable forage species, *C. arbuscula* and *C. rangiferina*.

The dwarf shrub-moss tundra with an unevenly developed shrub layer (closure 0.01–0.2) is formed by *B. nana* and willows (*Salix* spp.). The grass–dwarf shrub layer is irregular (PC 15–45%) and dwarf shrubs dominate (PC 10–30%), with the most abundant species, *E. nigrum*, *V. vitis-idaea* and *V. uliginosum*. The grass PC

varies between 5 and 20%. Cyperaceae predominate, including *E. vaginatum*, *Carex bigelowii* Torr. ex Schwein., and *C. aquatilis* var. *minor*; *Anthoxanthum monticola* (Bigelow) Veldkamp also occurs. The moss–lichen layer (PC 50–95%) is formed primarily by green forest mosses (PC 50–90%), while *Sphagnum* mosses occur sporadically (PC 0–5%). Lichens are sparse (PC up to 10%), but on some plots, lichen PC can increase to 40%, including the forage species *C. arbuscula* and *C. rangiferina* (PC up to 10%) and other lichen species (PC up to 20%).

The grass-moss tundra has a sparse shrub layer (closure 0.01–0.15), with scattered *B. nana* and *Salix* spp. The grass–dwarf shrub layer is patchy (PC 20–75%). Grasses dominate (PC 20–75%), while dwarf shrubs contribute 0–10%, with *E. nigrum*, *V. vitis-idaea*, and *R. tomentosum* subsp. *subarcticum* being the most abundant. The grass component is dominated by *R. chamaemorus*, *E. vaginatum*, *E. scheuchzeri*, *C. rotundata*, and *C. aquatilis* var. *minor*. The moss–lichen layer (PC 40–100%) consists of green forest mosses (PC 10–80%) and *Sphagnum* mosses (PC 5–80%). Lichens are generally sparse (PC ≤ 10%), with *C. arbuscula* and *C. rangiferina* being the most frequent (PC ≤ 5%).

Moss–lichen tundra generally lacks a shrub layer; only scattered *B. nana* and *Salix myrtilloides* L. occur (closure ≤ 0.05). The grass–dwarf shrub layer is sparse (PC 10–30%), and both dwarf shrubs and grass are poorly represented (PC 5–20% for each sublayer). The most abundant species are *R. tomentosum* subsp. *subarcticum*, *V. vitis-idaea*, and *E. nigrum*, *E. vaginatum*, *E. scheuchzeri*, *C. bigelowii*, *C. rotundata*, *C. aquatilis* var. *minor*, and *C. rariflora*. The moss–lichen layer (PC 80–100%) is formed by lichens (PC 40–90%), with green forest mosses as co-dominants (PC 10–30%). Layer dominants are valuable forage species – *C. arbuscula* and *C. rangiferina* (5–40% PC for each species) – together with other lichen species (PC 0–50%).

The grass-dwarf shrub tundra lacks a shrub layer, with only occasional individuals of *B. nana*. The grass–dwarf-shrub layer is dense (PC ≤ 65%), dominated by dwarf shrubs (PC ≤ 50%), with *E. nigrum*, *V. uliginosum*, *Arctous alpina* (L.) Nied., *Dryas octopetala* L., *Salix polaris* Wahlenb., and *R. tomentosum* subsp. *subarcticum* being the most abundant. Grasses contribute up to 20% cover, predominantly *C. bigelowii*, *Equisetum arvense* L., *Festuca ovina* L., *Hedysarum hedysaroides* (L.) Schinz & Thell., and *Oxytropis sordida* (Willd.) Pers. The moss–lichen layer is sparse (PC ≤ 10%), with moss (PC ≤ 10%) and only occasional lichens.

The shrub-forb tundra features dense shrub thickets with a closure of 0.7 to 1.0, formed by *S. glauca*, *B. nana*, and *Alnus alnobetula* subsp. *fruticosa* (Rupr.) Raus, with *Salix lanata* L. and *Salix hastata* L. as co-dominants. The forb–dwarf-shrub layer is dense (PC 30–70%) and dominated by forbs (PC 25–70%), including *C. aquatilis* var. *minor*, *Rubus arcticus* L., *Veratrum lobelianum* Bernh., and *E. arvense*. Associated species include *Lycopodium annotinum* L., *Carex chordorrhiza* L.f., *R. chamaemorus*, *C. stricta*, *Aquilegia sibirica* Lam., *A. monticola*, *Bistorta vivipara* (L.) Delarbre, *Angelica archangelica* L. Dwarf shrubs are sparse (PC ≤ 10%), with *V. uliginosum* as the dominant species. The moss–lichen layer is patchy (PC 0–90%), with green forest mosses (PC 0–70%) and *Sphagnum* mosses (PC 0–15%). Lichens

(*C. arbuscula*, *C. rangiferina*, *Cetraria islandica* (L.) Ach., and *Flavocetraria cucullata* (Bellardi) Kärnefelt & A.Thell) are sporadic, contributing up to 10% cover.

In general, we found no significant natural or anthropogenic disturbances to the ground or soil cover at the key site. In many communities, except floodplains and watershed tops, dead plant material accounted for 10–30% of the ground cover, indicating relatively stable vegetation conditions in most of the study area.

Plant communities of Late Holocene mires and peatlands cover 22.5% and 13.7% of the study area, respectively. Each of these urochishche groups supports a single plant community type – grass–moss communities (Fig. 4, Table 1, Suppl. material 2: Table S1).

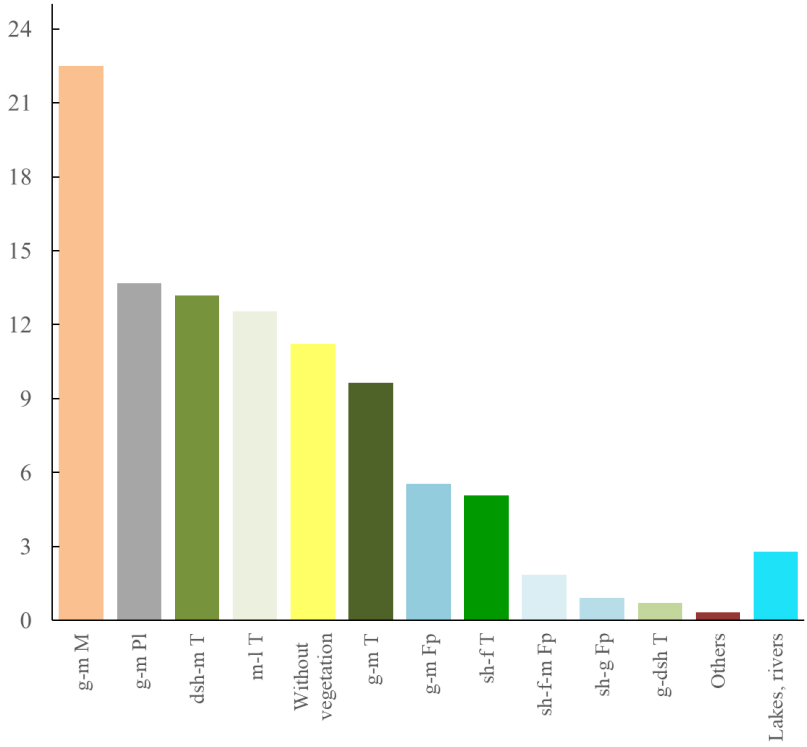


Figure 4. Proportions of plant community types within the study area, %. Plant community abbreviations: g-m Pl – grass–moss peatlands; g-m M – grass–moss mires; m-l T – moss–lichen tundra; g-m T – grass–moss tundra; dsh-m T – dwarf shrub–moss tundra; g-m Fp – grass–moss floodplain communities without a shrub layer; sh-f T – shrub–forb tundra; sh-f-m Fp – shrub–forb–moss floodplain; g-dsh T – grass–dwarf shrub tundra; sh-g Fp – shrub–grass floodplain communities; "Others" denotes the unsurveyed urochishches 2а, 2г, 2д, 4а, and 4г.

Table 1. Dominant plant species, structure, and landscape associations of plant communities in winter pastures of southern Yamal

Group of urochishches	**Periodically flooded by surface waters**		**Modern mires**	**Peatlands**	**Tundra plains and terraces**				**Tundra floodplains**
Urochishche	**2б**	**2б**	**2в**	**3б/3г/3д**	**4б/4в/4д**	**6а/6б/6в**	**6г/6з**	**6а/6б/6г**	**6а**	**6и/6н/6к**
Plant communities	**sh-g Fp**	**sh-f-m Fp**	**g-m Fp**	**g-m M**	**g-m Pl**	**dsh-m T**	**g-m T**	**m-l T**	**g-dsh T**	**sh-f T**
Shrub species	**2**	**10-30**	**0-3**	**1-3**	**1**	**1-20**	**1-15**	**0-5**	**1**	**70-100**
Alnus alnobetula subsp. *fruticosa* (Rupr.) Raus	–	–	–	–	–	–	–	–	–	0-95
Betula nana L.	1	10-25	1-2	0-2	0-1	1-15	1-3	0-5	1	0-70
Salix glauca L.	1	3	<1	–	–	0-3	<1	–	–	0-60
Salix lanata L.	–	–	–	–	–	0-2	0-10	–	–	0-10
Dwarf shrub species	**10**	**2-20**	**5**	**3-7**	**5-15**	**10-30**	**0-10**	**5-20**	**50**	**0**
Arctous alpina (L.) Nied.	1	–	<1	–	–	0-5	<1	<1	10	–
Empetrum nigrum L.	–	3	1	<1	0-3	3-15	0-10	1-5	10	<1
Rhododendron tomentosum subsp. *subarcticum* (Harmaja) G.D. Wallace	2	7	1	0-4	2-7	0-5	0-5	1-7	5	0-2
Salix polaris Wahlenb.	–	1	–	–	–	<1	–	0-2	10	<1
Vaccinium uliginosum L.	7	0-10	1	<1	0-3	1-7	<1	0-5	10	0-10
Vaccinium vitis-idaea L.	–	–	<1	1	0-5	1-10	0-5	0-7	<1	<1
Grass and herb species	**65**	**10-25**	**15-50**	**10-35**	**15-35**	**7-20**	**20-75**	**5-20**	**20**	**25-70**
Anthoxanthum monticola (Bigelow) Veldkamp	–	–	–	–	–	0-10	–	0-2	1	0-3
Calamagrostis stricta (Timm) Koeler	10	<1	–	<1	–	<1	<1	<1	<1	0-7
Carex aquatilis Wahlenb.	40	0-15	0-10	1	–	0-10	0-15	0-3	–	0-30
Carex bigelowii Torr. ex Schwein.	–	–	<1	–	–	0-7	<1	0-5	2	–
Carex rariflora (Wahlenb.) Sm.	–	1	0-10	0-3	0-3	<1	<1	0-10	–	<1
Carex rotundata Wahlenb.	–	<1	<1	3-10	0-10	–	0-7	0-2	–	–
Comarum palustre L.	5	3	1	1	–	–	<1	–	–	<1

Group of urochishches	Periodically flooded by surface waters			Modern mires	Peatlands	Tundra plains and terraces				Tundra floodplains
Urochishche	**2б**	**2б**	**2в**	**3б/3г/3д**	**4б/4в/4д**	**6а/6б/6в**	**6г/6з**	**6а/6б/6г**	**6а**	**6и/6н/6к**
Plant communities	**sh-g Fp**	**sh-f-m Fp**	**g-m Fp**	**g-m M**	**g-m Pl**	**dsh-m T**	**g-m T**	**m-l T**	**g-dsh T**	**sh-f T**
Equisetum arvense L.	–	–	–	–	–	–	–		5	1-30
Eriophorum scheuchzeri Hoppe	–	<1	0-7	0-5	0-10	1	0-10	0-10	–	–
Eriophorum vaginatum L.	–	1-3	0-15	0-12	0-10	0-15	0-15	0-15	–	–
Rubus chamaemorus L.	5	5-10	0-30	1-3	1-30	<1	0-65	<1	–	0-5
Veratrum lobelianum Bernh.	5	–	–	–	–	–	–	–	–	0-25
Moss species	**1**	**40-100**	**70-90**	**75-100**	**80-95**	**50-95**	**40-95**	**10-40**	**10**	**0-85**
Sphagnum sp.	–	35-100	10-80	0-40	20-90	–	5-80	0-10	–	0-15
Green forest mosses	1	0-10	10-80	45-75	5-75	50-90	10-80	10-30	10	0-70
Lichen species	**0**	**<1**	**<1**	**0-15**	**3-15**	**0-40**	**0-10**	**40-90**	**<1**	**0-10**
Cladonia arbuscula (Wallr.) Flot.	–	–	–	0-5	0-5	0-10	0-2	5-30	–	0-2
Cladonia rangiferina (L.) Weber ex F.H. Wigg.	–	–	–	0-10	1-10	0-10	0-3	5-40	<1	0-3
Cetraria islandica (L.) Ach.	–	–	–	<1	<1	0-2	<1	0-2	<1	0-3
Flavocetraria cucullata (Bellardi) Kärnefelt & A. Thell	–	–	–	<1	<1	0-2	0-2	0-2	<1	0-2
Other lichen species	–	–	–	–	–	0-20	–	0-50	–	–

Note: Values represent the range of projective cover (%). The symbol "–" indicates species absence; "<1" indicates species presence as single instances (cover < 1%). Plant community abbreviations: sh-g Fp – shrub–grass floodplain; sh-f-m Fp – shrub–forb–moss floodplain; g-m Fp – grass–moss floodplain without a shrub layer; g-m M – grass–moss mires; g-m Pl – grass–moss peatlands; dsh-m T – dwarf shrub–moss tundra; g-m T – grass–moss tundra; m-l T – moss–lichen tundra; g-dsh T – grass–dwarf shrub tundra; sh-f T – shrub–forb tundra.

Grass–moss plant communities also occur in other urochishche groups: runoff hollows and gullies with fragments of flat low-lying grass mires (2в), and waterlogged areas of gentle, long slopes (6г and 6з). In general, the largest proportion of the study area (~51%) is covered by grass–moss plant communities. The second most widespread plant community type is dwarf shrub – moss tundra, which represents 13.2% of the area and occurs in urochishches 6а and 6б on the tops of the watershed, and in 6в in the upper sections of gentle, long slopes. The lichen-dominated moss-lichen tundra (PC lichens > 40%) represents 12.5% of the area, occurring on the tops of the watershed (6а, 6б) and in dry and well-drained parts of gentle and long slopes (6г). The bare sandy patches on floodplain bars and watershed areas (2, 6) cover 11.2% of the area and have no forage value. The remaining types of plant community occupy relatively small proportions of the study area. Shrub–forb communities cover 5.1% of the area, occurring in sloping tundra (6н), tundra floodplains (6и, 6к), and sites occasionally flooded by surface waters (2б). Shrub–forb–moss and shrub-grass floodplain communities in 2б cover about 1.8 and 0.9% of the study area, respectively. The grass-dwarf shrub tundra occupies the smallest proportion (0.7%) and occurs in urochishche 6а. The water bodies and their accessibility within the area are an important criterion for pasture quality only in summer (Titov, Zarubin 1986; Dasheev 2013). In winter, water bodies and sand exposures do not have forage value and cover 14.0% of the area.

PERMANOVA (Bray–Curtis dissimilarity with Hellinger transformation) revealed that the species composition of the identified groups differs significantly (Pseudo-F = 4.55, Df = 9, $p \leq 0.001$). The differentiation of communities by urochishches explains 58.5% of the total variability in plant community structure ($R^2 = 0.59$). This confirms that the boundaries between the identified plant community types are objective and closely linked to the landscape structure of the territory (Fig. 5).

Contingency analysis between landscape unit types and the identified groups of plant communities confirmed a statistically significant relationship between urochishche types and plant community groups ($\chi 2 = 254.04$, $p \leq 0.001$, Cramér's V = 0.85).

Discussion

We examined the landscape structure and vegetation cover of the winter pasture area in the southwestern part of the Yamal Peninsula, and identified the relationships between plant communities and the main urochishche types. For most of the surveyed urochishches, a predominant type of plant community could be identified, although the correspondence between landscape and vegetation units was not always one-to-one. Urochishches with moderate to high moisture show relatively homogeneous vegetation. For example, we recorded grass–moss plant communities in all Late Holocene mires (3б, 3г, 3д) and peatlands (4б, 4в, 4г, 4д). Tall shrubs are

characteristic not only of urochishches of Group 2 but also of tundra urochishches 6и, 6н, and 6к, where shrub–forb communities occur. In tundra urochishche 6н, the moss cover in the ground layer is high, while the shrubs are relatively low (50–80 cm). The dense growth of tall shrubs (>1.5 m) in tundra floodplain communities (6и, 6к) results in substantial leaf litter, and such communities often have a well-developed litter layer, with only a small moss cover (PC ≤ 10%). Two tundra urochishche types support only a single plant community type each: dwarf shrub–moss tundra in 6в and grass–moss tundra in 6з, both with moderately moist conditions. Although urochishche 2в is classified as periodically flooded, it does not represent a floodplain, but rather comprises runoff hollows and gullies – well-defined, often waterlogged depressions with potentially prolonged standing water, yet without an active annual flood regime. Therefore, these conditions support grass–moss communities with continuous moss cover in moderate to high moisture conditions.

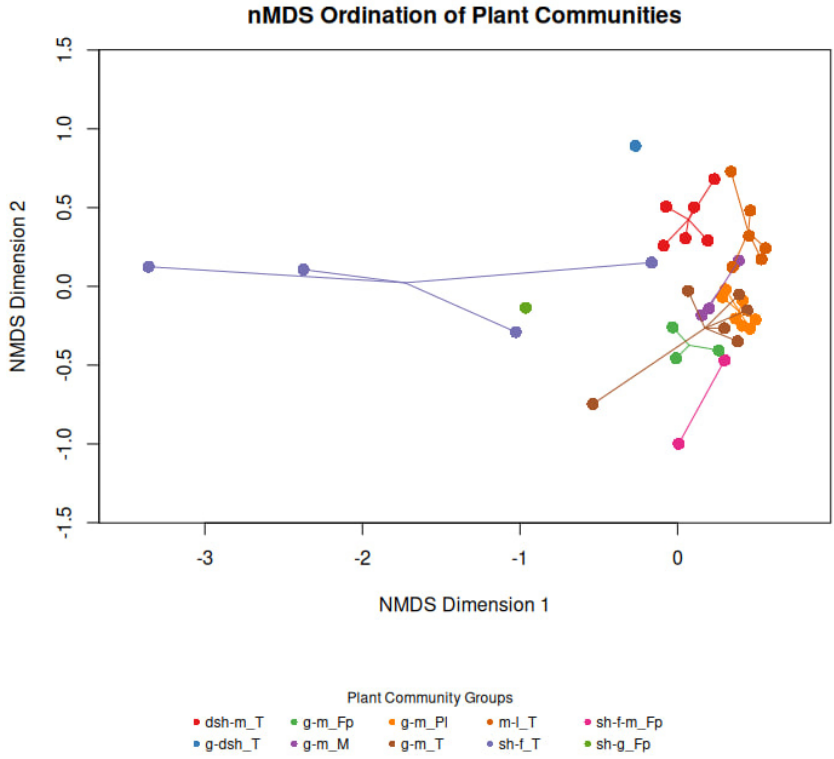


Figure 5. Ordination diagram. Plant community abbreviations: g-m Pl – grass–moss peatlands; g-m M – grass–moss mires; m-l T – moss–lichen tundra; g-m T – grass–moss tundra; dsh-m T – dwarf shrub–moss tundra; g-m Fp – grass–moss floodplain communities without a shrub layer; sh-f T – shrub–forb tundra; sh-f-m Fp – shrub–forb–moss floodplain; g-dsh T – grass–dwarf shrub tundra; sh-g Fp – shrub–grass floodplain communities.

However, in some areas, we found no clear relationship between urochishche type and a single plant community type. This is consistent with the complex structure of an urochishche, which comprises several smaller facies. On the tops of the watershed and the gentle slopes, local variations in substrate moisture are associated with vegetation mosaics within individual urochishches. The diversity of the plant community was particularly high in well-drained urochishches. For example, in urochishche 6a we identified three plant community types – dwarf shrub–moss, moss–lichen, and grass–dwarf shrub tundra. In 66 we recorded dwarf shrub–moss and moss–lichen tundra, and in 6г, moss–lichen and grass–moss tundra. In urochishche 26, the variety of streams and water bodies also gives rise to two variants of the shrubgrass community - one with a well-developed moss layer and one without – depending largely on flooding intensity and duration, and on inorganic sediment deposition from river channels. In general, the observed vegetation heterogeneity is consistent with the fine-scale mosaic structure typical of the southern Yamal tundra (Il'ina et al. 1985; Magomedova et al. 2006).

The study area is a winter reindeer pasture, so a key priority was to estimate the extent of vegetation dominated by or containing a substantial lichen component, as lichens are traditionally considered the main winter forage for reindeer. Lichen-dominated communities account for approximately 13% of the area, while those with a substantial lichen component (PC up to 10–15%) account for approximately 64%. In total, communities containing lichens in the ground layer cover approximately 77% of the study area. Thus, the relatively small area occupied by lichen-dominated communities does not reflect the overall distribution of lichens within the winter pasture: lichens occur in a much larger proportion of the area.

A comparison of our results with previous studies in Yamal shows that the proportion of lichen-dominated plant communities falls within the range previously reported for the region, although direct comparison is complicated by differences in spatial scale. Andreev (1934) revealed that among the Yamal regions that are geographically and structurally closest to our study area, the lichen tundra occupies about 10% and the moss-lichen tundra 2%. These values are broadly comparable with our own result: 12.5% moss–lichen tundra in which lichens predominate. However, in the entire Yamal (Nenets) National Okrug, the proportion of lichen and moss–lichen tundra ranged from 1 to 30%. Plant communities dominated by lichens reached their highest share (23%) in the northern forest tundra and the Arctic tundra. According to Andreev's data, grass–moss plant communities were most widely represented in the southern tundra.

Recent regional assessments of vegetation composition and structure of the Yamal Peninsula and its tundra subzones differ substantially in the completeness and scope of their data (Magomedova et al. 2006; Ermokhina et al. 2017; Gorbunova 2026). Magomedova et al. (2006) found that lichen-dominated communities occupy approximately 3% of the southern subarctic tundra and 4–7% in the Arctic and northern subarctic tundras. Communities in which lichens form a substantial part of the cover occupy approximately 19–20% of the southern tundra - three to

four times less than in the area we surveyed – and 3 to 6% in the more northerly regions. Grass–moss vegetation accounts for about 40% of the southern tundra – compared to approximately 51% in our study area. The proportions of many other plant communities are also comparable to our results. Thus, the main similarity between the two datasets lies in the predominance of grass–moss vegetation, whereas the share of lichen-dominated communities in the winter pastures we examined is considerably higher. However, these differences should be interpreted with caution, since previous assessments pertain to the entire southern tundra subzone, whereas our study covers a much smaller, clearly localised area used as winter pasture.

Ermokhina et al. (2017) list the main plant communities throughout the Yamal Peninsula, while Gorbunova (2026) focuses on the summer pastures in the Yorkutayakha River basin; both describe their association with relief elements. Neither data on the proportions of these types within their respective study areas provides, making comparison with our results impossible. In particular, studies from the last decade have recorded dwarf-shrub-dominated communities on the Yamal Peninsula that V. N. Andreev did not identify in the early twentieth century and that Magomedova et al. (2006) described as heavily grazed variants of lichen tundra on watershed tops.

In the studies reviewed above, the descriptions of the plants community are provided with varying degrees of detail: they report high variability in the cover of the plant and lichen groups, their association with relief elements, and substrate and/or moisture conditions. A comparison of our study area with previous work on the Yamal Peninsula shows that the proportion of lichen plant communities in the winter pasture area is broadly comparable with or even considerably higher than the values reported by other authors.

At the same time, the assessment of winter forage resources should consider not only lichens, but also other plant groups, as well as spatial differences in potential snow accumulation. For example, sedges are an important forage component in early winter and spring, as they can retain green parts for long periods even beneath snow, and are among the first fresh greens in spring (Glinka 1939). Standing dead grasses from the current growing season, as well as some dwarf shrub species are also important components of the reindeer winter diet (Andreev 1934).

Valuable dwarf forage shrubs (*S. polaris*, *V. uliginosum*, *V. vitis-idaea*) were recorded in most communities within the study area (Suppl. material 2: Table S2), but with low abundance (PC ≤ 10% for individual species). Graminoids are scarce, occurring in four community types with low abundance (PC ≤ 10%). Cyperaceae species are the most diverse and abundant, with individual species cover ranging up to 10%, but their total cover in a community could reach 40%.

The highest number of valuable winter forage species (Andreev 1934), including lichens, was recorded in dwarf shrub–moss, grass–moss, and moss–lichen tundra, in urochishches 6а, 6б, 6в, 6г, and 6з, which together cover about 36% of the study area. The conditions of possible snow accumulation differ among these landscape units due to their contrasting topographic positions. In urochishches 6а, 6б, and

6в which occupy watershed tops and upper parts of slopes, snow accumulation is potentially lower. However, even such sites may become less accessible to reindeer when ice crusts form. In 6г and 6з, which occupy lower parts of watershed hills and depressions between them, greater snow accumulation can be expected, although the formation of a deep snowpack takes time. Thus, an assessment of winter forage availability must consider not only snow depth, but also the timing of snowpack formation, its maximum accumulation, and the appearance of ice crusts caused by rain-on-snow events and thaws (Makeev et al. 2014; Serreze et al. 2021).

In general, the results show that winter pastures contain a wide spatial mosaic of plant communities that provide different combinations of lichen and vascular plant forage resources. Approximately 77% of the study area supports communities where lichens are present, while other winter forage plants are also widely distributed. The winter accessibility of these forage resources is likely to vary between landscape units depending on topographic position, snow accumulation, and episodic ice crust formation.

Conclusion

In this study of the spatial organisation of vegetation within the winter pasture area, we examined the landscape structure and the composition and structure of the main types of plant community and demonstrated the association between communities and landscape elements on the urochishche scale. The study area corresponds to an actual winter grazing territory used by Nenets households, allowing the vegetation structure to be analysed within the boundaries of currently used winter pastures.

At the same time, the relationship between urochishche and the type of plant community is not always one-to-one due to the mosaic nature of tundra vegetation. We found the highest community diversity on well-drained watershed tops, as well as on river floodplains, where community composition is associated with frequency of flooding and inorganic sediments. Traditional evaluations of winter pastures have placed particular emphasis on lichen-dominated communities. In the pastures studied, the communities account for only about 13% of the area, while communities with a notable component cover about 64% and lichens are present in communities that cover approximately 77% of the area. The proportion of lichen-dominated communities recorded here is broadly comparable to or higher than the values reported in previous studies of Yamal and other Arctic regions.

The relatively small extent of lichen-dominated vegetation should therefore not be interpreted in itself as evidence of insufficient winter forage. The area has been used as a winter pasture for many years, the herds using it have remained broadly stable, and local herders consider its forage resources sufficient for winter grazing. This is consistent with the larger distribution of lichens across different types and with the presence of other winter forage plants, including sedges, grasses, dwarf shrubs, and standing dead grasses. Therefore, a comprehensive assessment of winter

pasture quality should consider not only the composition of the forage vegetation, but also the landscape position of the plant communities and potential differences in snow accumulation conditions, which may influence the forage.

The combination of botanical and landscape approaches provides a framework for characterising winter pastures as spatial mosaics of plant communities that differ in the composition of forage resources and in the environmental conditions that affect their potential accessibility. Landscape mapping of the entire pasture area, combined with detailed geobotanical surveys of the key site, makes it possible to relate the characteristics of the plant community to the spatial structure of the whole territory. This approach broadens the assessment of tundra winter pastures beyond the extent of lichen-dominated vegetation alone, while retaining lichens as a central component of winter forage.

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Supplementary material 1

Figure S1. Plant communities and their landscape associations in winter pastures of southern Yamal

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Supplementary material 2

Table S1. Structure, plant and lichen species composition across urochisches and plant community types in winter pastures of southern Yamal
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