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RESEARCH ARTICLE

# Biodiversity Oases in the Southern Tundra: The Role of shrub-herbaceous communities (Western Siberia)

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## Abstract

The southwestern Gydan Peninsula remains a significant data gap in understanding tundra ecosystem responses to climate change and shrub expansion. Detailed studies linking plant community composition to soil properties in this region are critically lacking. This study provides the integrated analysis of shrub-herbaceous communities and their underlying soils in this region. Based on comprehensive geobotanical and soil surveys at 52 sites, we identified four distinct community types using multivariate analysis. Our results reveal a clear hierarchy of environmental drivers. Primary vegetation patterns and the formation of biodiversity hotspots, including the discovery of several plant species new to the local flora, are predominantly shaped by landscape heterogeneity, such as the mosaic of slopes, valleys, and snow hollows. Soil properties, notably those related to texture, active layer dynamics, and hydromorphy, act as significant secondary filters, structuring communities along a key soil gradient. However, the overall correlation between soil and vegetation matrices was limited, indicating a substantial role for other unmeasured factors. We conclude that plant community assembly in the southern Gydan tundra is governed by an interplay where the geomorphic template sets the stage for diversity, while localized soil conditions fine-tune composition. These findings establish an essential baseline for monitoring and underscore that conserving landscape heterogeneity is crucial for the resilience of these rapidly changing Arctic ecosystems.

## Keywords

Gydan Peninsula, shrub expansion, new floristic records, soil-vegetation relationship, cryosols, edaphic factors, landscape heterogeneity

## Introduction

Ongoing climatic changes in the Subarctic and Arctic (Anisimov and Kokorev 2017; Vasiliev and Drozdov 2020; Kaverin et al. 2021; Fewster et al. 2022) are increasing the length of the growing season, precipitation, and nutrient availability, thereby enhancing vegetation productivity (Wu et al. 2011; Huang et al. 2017; Reichle et al. 2018). This "greening" effect, confirmed by satellite monitoring of the Normalized Difference Vegetation Index (NDVI) (Tishkov and Krenke 2015; Frost et al. 2019; Berner et al. 2020; Myers-Smith et al. 2020), stems not only from increased productivity but also from successional processes. These include the colonization of drained lake basins (Lara et al. 2018; Loiko et al. 2020), landslides, thermokarst depressions (Walker et al. 2009), and most notably, tundra shrubification (Tape et al. 2006; Frost et al. 2013; Tishkov and Krenke 2015). As the most extensive of these successional processes, shrubification is crucial for modeling future landscapes, as it alters tundra ecosystem structure, regional climate, soil-atmosphere exchange, and species interactions (Myers-Smith et al. 2011).

Although shrubification driven by alder, willow, and dwarf birch expansion (Tape et al. 2012) has been extensively studied globally (Vowles and Björk 2019; Chen et al. 2021; Mekonnen et al. 2021), significant gaps remain at the regional scale. The soils and vegetation of the Yamalo-Gydan Ecoregion are poorly documented, even from a primary inventory standpoint (Loiko et al. 2024). While the northern and central Gydan Peninsula are relatively well-studied botanically (Khitun and Rebristaya 1998; Khitun 2002; Telyatnikov et al. 2019; Telyatnikov et al. 2021), data for the south are scarce (Khitun 2003; Loiko et al. 2024). Studies of soils for the peninsula are exceptionally limited (Loiko et al. 2024), contrasting with the better-studied southern boundary of the Yamalo-Gydan Ecoregion (Titov and Potokin 2001; Pismarkina and Byalt 2016; Glazunov and Nikolaenko 2018; Zarov et al. 2022; Loiko et al. 2023).

This regional knowledge gap is critical because these ecosystems are facing dual pressures from climate-driven vegetation change (Frost et al. 2023), alterations in hydrological regimes (Mann et al. 2010), and increasing industrial development that can rapidly alter landscapes (Loiko et al. 2024). Detailed ground-based studies with broad spatial coverage are needed to provide baseline data for vulnerable Arctic ecosystems (Syso et al. 2022) and to interpret trends in tundra productivity from remote sensing like NDVI (Tassone et al. 2024).

In this context, obtaining baseline data on the soils and vegetation of the poorly studied southwestern Gydan Peninsula is a priority. Particular interest lies in ecosystems that act as local biodiversity hotspots and environmental indicators. These include species-rich slopes, ravine and hollow complexes, and streamside communities, where favorable microclimate, drainage, and moisture support highly productive and structurally complex shrub-dominated ecosystems. However, the structure and composition of these shrub-herbaceous communities, as well as their intricate relationships with soil properties, remain poorly studied for this region.

Existing literature provides strong evidence for the profound effects of shrub encroachment on tundra ecosystems (Bonfils et al. 2012; Loranty and Goetz 2012; Frost et al. 2018; Kropp et al. 2020; Liu et al. 2022; Villani et al. 2022). Yet, these studies often treat "shrubs" as a uniform functional group. A critical, understudied aspect is the internal biodiversity of shrub-dominated communities. The distinct composition of older versus newly established thickets, and the specific correlations between this floristic diversity and a suite of soil characteristics, have not been integrally addressed, representing a key knowledge gap in predicting ecosystem trajectories.

Our study continues a series of hierarchical morphogenetic analyses of Western Siberian soils (Loiko et al. 2011; Loiko et al. 2013; Loiko et al. 2015; Konstantinov et al. 2019) and aims to fill the critical gap in understanding the co-evolution of plant communities and soils under shrub expansion in the southern tundra of the Gydan Peninsula. The primary objectives of this work are: 1) to identify and classify the main types of shrub-herbaceous communities in the studied streamsides and slopes, 2) to assess the changes in soil morphological properties and taxonomy resulting from shrub expansion, and 3) to establish the relationships between the identified vegetation clusters and soil characteristics. As shrubs expand and form consortium cores, understanding this plant-soil interplay is essential for predicting the transformation of regional phytodiversity and the trajectory of future landscape changes.

## Materials and methods

### Study Area

The studies were conducted in the southern part of the Gydan Peninsula (Fig. 1). The research area is situated within the Messoyakha subprovince, forming part of the southern tundra subzone in the Gydan province of the Yamal-Gydan tundra region (Atlas... 2004). From a pedological perspective, the territory falls within the subzone of tundra Cryosols and Histic Cryosols characteristic of the subarctic tundra in the West Siberian tundra province, as classified by the soil-ecological zoning of Russia (Map... 2020). The Tazovsky-Gydansky district, where the study was conducted, exhibits diverse soil textures ranging from sandy to clayey, with binomial soil profiles and marine sediments being common features of the local pedogenesis (Loiko et al. 2024).

The relief of the Gydan Peninsula, similar to the entire northern part of the West Siberian Plain, is characterized by a terraced surface. The Yamal-Gydan region features five geomorphological levels (marine terraces) of different ages (Atlas … 1971). The surveyed areas are predominantly composed of the lowest and youngest surfaces of the first and second marine terraces, with absolute elevations ranging from 10 to 25 m above sea level, as well as even lower floodplain areas (Telyatnikov et al. 2021). The highest elevations of the interfluves areas reach up to 40 m above sea level. The upper part of the river catchments is a flat, peaty plains with elevations exceeding 40 m, into which the river valleys and its tributaries are deeply incised (Loiko et al. 2024). The study area constitutes a gently rolling plain, dissected by a network of ravines and numerous lacustrine basins. The lithology of the investigated areas is homogeneous, with sandy deposits prevailing everywhere, while loamy deposits are exceedingly rare (Telyatnikov et al. 2021).

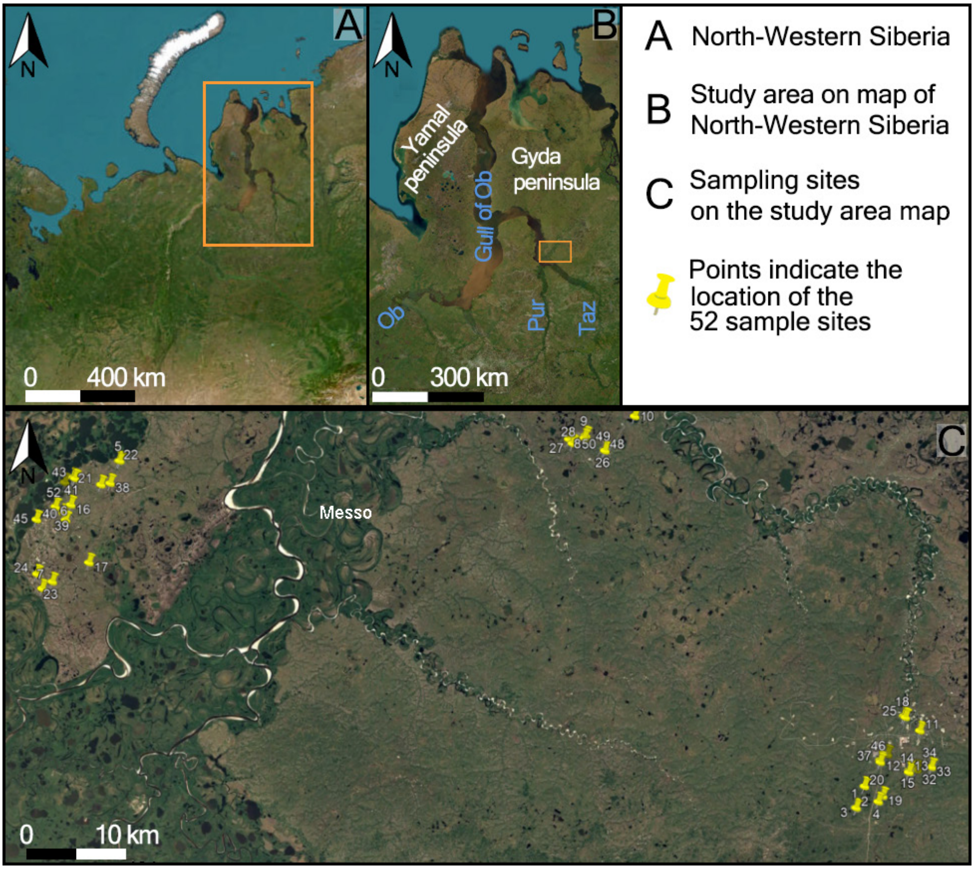

**Figure 1.** Maps and locations of the study sites.

In the southern part of the Gydan Peninsula, the climate is continental, with long and severe winters and relatively brief and cool summers. During coldest month (January), the average air temperature ranges from -27.5 °C to -28.5 °C, while at warmest (July) – it is around 12–14.5 °C. However, on some summer days, temperatures can reach up to 27–30.5 °C. The average annual temperature is between -9.5 and -10.5 °C (Trofimova and Balybina, 2014). Precipitation in this area is approximately 350 mm per year. A stable snow cover usually forms by the end of october and melts by the beginning of June. The snow reaches its maximum depth at the end of April, and there are frequent snowstorms that can cause uneven snow depths, ranging from almost none to 1–2 m, and even more in areas with alder bushes and at the bottom of tundra ravines (Geocryology... 1989).

According to the zonal classification of vegetation cover by I.S. Ilyina (1985), the south of Gydan Peninsula is associated to the subarctic tundra subzone (subzone of southern tundra). This subzone is characterized by the presence of hypoarctic shrubs, including dwarf birch (*Betula nana* L.) and several species of willow (*Salix glauca* L., *S. lanata* L., and *S. pulchra* Cham.). In the southern part of the subarctic tundra, diverse shrub-moss-lichen and shrub-moss tundra with dwarf birches and willows develop on watershed plains. These tundra communities can be found on watershed plains. When waterlogged, these tundra communities on watershed plains transition into shrub-moss, shrub-lichen-moss, or shrub-cottongrass-moss tundra. These tundras have a hummocky or mound-hollow microtopography, and sphagnum moss dominates the vegetation (Ilyina et al. 1985; Pisarenko et al. 2017). In the southern tundra, there are transitional sedge communities with *Carex aquatilis* Wahlenb. and sedge-sphagnum communities that develop in waterlogged lake basins (khasyreys), flow-through depressions, extensive mires of hummock-swamp complexes, and various depressions within waterlogged tundras (Loiko et al. 2020). The moss layer is typically dominated by *Sphagnum obtusum* Warnst. and *S. riparium* Ångstr. (Pisarenko et al. 2017). On elevated terrain, communities with multiple layers of shrubs are widespread. These include alder (*Alnus fruticosa* Rupr.), various types of willows (*Salix glauca* and *S. pulchra*), and dwarf birches (*Betula nana*). Under these shrubs, cloudberries, various herbs and sedges are found, and occasionally larch trees (*Larix sibirica* Ledeb.). Along the banks of larger rivers, alder and willow thickets (*Alnus fruticosa*, *Salix gmelini* Pall.) can be found. Eroded slopes are occupied by communities at different stages of succession as they revegetate after sand blowouts or landslides (Telyatnikov et al. 2021; Loiko et al. 2024).

## Fieldwork and laboratory analysis

Fieldwork was conducted during the summer of 2024. We surveyed 52 herbaceous-shrub sites characterized by high floristic diversity relative to the surrounding areas. Site selection was based on shrub cover exceeding 40%, with each site measuring 10 × 10 meters. Plant community descriptions were recorded using the presence-absence method. The surveyed communities were classified into 3 distinct habitat types: alder thickets (Suppl. material 1: Table S1), streamside shrub-herbaceous communities (Suppl. material 2: Table S2) and slope/hollow shrub-herbaceous communities (Suppl. material 3: Table S3). In addition to botanical surveys, we described soil profiles at each site (Suppl. material 4: Table S4). We studied soil profiles by digging soil pits, cutting and photographing their front walls, identifying soil horizons and describing them morphologically, followed by sampling.

To identify the plants, they were herbarised. Collected herbarium specimens were transferred to the P.N. Krylov Herbarium (TK) of Tomsk State University for storage. Herbarisation was carried out according to the rules of herbarium (Gureeva 2013). The collected herbarium was identified according to the "Flora of Siberia" (1987–2003) and collection of TK.

Under laboratory conditions, using the collected photographic materials and soil samples, we conducted measurements of the following quantitative parameters (Suppl. material 4: Table S4). Active Layer Thickness (the depth to the permafrost table from the soil surface). Permafrost was not recorded if it was beyond the reach of a 150-cm probe. Thickness of the peat horizon covering the mineral soil surface. Thickness of the AO (moder humus) horizon, where present. Depth from the soil surface to the onset of morphological features diagnostic of gleyization. Thickness of the gleyed layer, measured from the mineral soil surface to a depth of 40 cm. The areal percentage of gley patches within the upper 40 cm of the mineral soil horizons. The percentage of gley patces relative to the total area of the gley horizon, where present. Physical clay content.

## Multivariate analysis

All statistical analyses were performed in R version 4.5.2, using the following packages: «vegan» version 2.7-2 (Oksanen et al. 2025) for multivariate analysis and permutation tests, «cluster» version 2.1.8.1 (Maechler et al. 2025) for clustering algorithms, «ggplot2» version 4.0.1 (Wickham 2016) for data visualization and patchwork version 1.3.2.9000 (Pedersen 2025) for plot arrangement at clusters. Data handling was facilitated by «dplyr» version 1.1.4 (Wickham et al. 2025) and «tidyr» version 1.3.1 (Wickham et al. 2025b).

The original dataset comprised 52 geobotanical descriptions with 117 species recorded in presence-absence format. To reduce the influence of rare species on the analysis, we filtered the dataset to include only species that occurred in more than one sample, resulting in a final dataset of 52 geobotanical descriptions and 82 species for subsequent analysis.

**Analysis of vegetation structure.** During preliminary data analysis, we evaluated multiple approaches to optimize clustering performance by testing two distance matrix measures (Bray-Curtis dissimilarity and Jaccard index, as this measure effectively handles presence-absence data while accounting for joint absences) and several hierarchical clustering methods including average linkage, complete linkage, and flexible beta method with varying beta parameters (β = - 0.25, - 0.30, - 0.35, - 0.40, - 0.45, - 0.50). The final analytical workflow proceeded through five sequential steps:

1. Distance matrix calculation: We computed Bray-Curtis dissimilarity matrices using the vegdist() function from the vegan package.
2. Hierarchical clustering: Cluster analysis was performed using the flexible beta method (β = - 0.25) with the AGNES (Agglomerative Nesting) algo-

rithm implemented in the cluster package. This method was selected for its ability to handle ecological data with varying cluster structures.

3. Cluster determination: The number of clusters was determined through expert assessment of the dendrogram structure, identifying natural groupings based on visual inspection of branch lengths and clustering patterns.
4. Ordination analysis: Principal Coordinates Analysis (PCoA) was conducted using the cmdscale() function to visualize the multivariate data in two-dimensional space.
5. Cluster validation: The quality of cluster assignments was evaluated using silhouette analysis, which measures how well each site fits within its assigned cluster compared to other clusters, and the AGNES coefficient, which assesses the overall strength of the clustering structure.

**Analysis of soil-vegetation relationships.** Prior to the analysis, we assessed multicollinearity among the soil predictors using Spearman's correlation coefficient. Variables E (proportion of gleyed area 40 cm) and F (proportion of gleyed area within the gleyed at 0 to 40 cm) showed a high correlation ($r = 0.88$), indicating potential redundancy. To ensure model stability and interpretability, we retained only variable E in the final RDA model, as it is ecologically more representative of the gradient. The core analysis consisted of several complementary multivariate techniques to quantify and characterize the influence of the eight measured soil variables on plant community composition:

1. Redundancy Analysis (RDA): We used RDA, a constrained ordination method, to model the species presence-absence data as a function of the soil variables. The global significance of the model and the significance of each canonical axis were tested using permutation tests (999 permutations). The relative importance of individual soil variables was assessed by their sum of squared loadings on the first two RDA axes.
2. Mantel Test: To evaluate the overall correlation between compositional dissimilarity and environmental dissimilarity, we performed a Mantel test. A Jaccard dissimilarity matrix was calculated from the species data and compared to a Euclidean distance matrix based on standardized soil variables, using Pearson's correlation and 999 permutations.
3. Non-metric Multidimensional Scaling (NMDS) with Environmental Fitting: We performed an unconstrained NMDS ordination based on Jaccard dissimilarity to visualize the main gradients in species composition. The relationship between the ordination space and individual soil variables was then assessed by fitting environmental vectors using the envfit() function (999 permutations).
4. Indicator Species Analysis: To identify plant taxa significantly associated with high or low values of specific soil parameters, we conducted an indicator species analysis. For each soil variable, samples were split into two groups based on the median value. Associations between species occurrence and these groups were tested using Fisher's exact test.

## Results

### Floristic Diversity and Taxonomic Composition of the Studied Plant Communities

A total of 117 species from 32 families were recorded in the study (Table 1). The vascular flora comprised two families of Lycopodiophyta (Lycopodiaceae, Huperziaceae), one family of Equisetophyta (Equisetaceae), two families of Pinophyta (Cupressaceae and Pinaceae), and 28 families of Magnoliophyta. Among the angiosperms, 25 families belonged to the Magnoliopsida class, and four to the Liliopsida class (Table 1).

**Table 1.** Summary of floristic richness: numbers of families, genera, and species

| Taxonomic Group | Number of Families | Number of Genus | Number of Species |
|---|---|---|---|
| Vascular Cryptogams (Lycopodiophyta and Equisetophyta) | 3 | 3 | 5 |
| Gymnosperm (Pinophyta) | 2 | 2 | 2 |
| Dicotyledon Dicots (Magnoliopsida) | 25 | 55 | 80 |
| Dicotyledon Monocots (Liliopsida) | 4 | 13 | 30 |
| Total | 34 | 73 | 117 |

The families with the highest species richness were Poaceae (13 species from 8 genus), Cyperaceae (11 species from 2 genus), Salicaceae (11 species from 1 genus), Asteraceae (11 species from 11 genus), and Ericaceae (8 species from 6 genus). Several families were represented by a moderate number of species: Caryophyllaceae (7 species from 4 genus), Rosaceae (5 species from 4 genus) and Ranunculaceae (5 species from 3 genus). Four families included four species each: Lycopodiaceae (2 genus), Polygonaceae (3 genus), Scrophulariaceae (3 genus), and Juncaceae (*Luzula* genus). Two families were represented by three species each: Rubiaceae (*Galium* genus) and Saxifragaceae (2 genus). Six families were represented by two species: Equisetaceae (*Equisetum* genus), Betulaceae (2 genus), Pyrolaceae (*Pyrola* genus), Caprifoliaceae (2 genus), Fabaceae (2 genus) and Melanthiaceae (2 genus). Thirteen families were represented by a single species in the study area: Pinaceae, Cupressaceae, Boraginaceae, Polemoniaceae, Geraniaceae, Violaceae, Apiaceae, Onagraceae, Primulaceae, Empetraceae, Campanulaceae, Grossulariaceae and Brassicaceae.

### Classification of Shrub-Herbaceous Communities

Silhouette analysis revealed relatively weak clustering structure across all tested parameters. The highest silhouette value (0.2) was achieved using Bray-Curtis dissimilarity with the flexible beta method (β = - 0.25) when the dataset was restricted to taxa occurring in 6 or more sites and specifying 6 clusters. However, such extensive data filtration was considered ecologically inappropriate as it eliminated meaningful biological information. We therefore use a more conservative approach, including all taxa occurring in more than one geobotanical description. Given the minimal differences in silhouette values across cluster solutions (k = 2–10) (Fig. 2C), we employed expert-based cluster determination guided by botanical composition and ecological interpretation rather than lean only on statistical optimization.

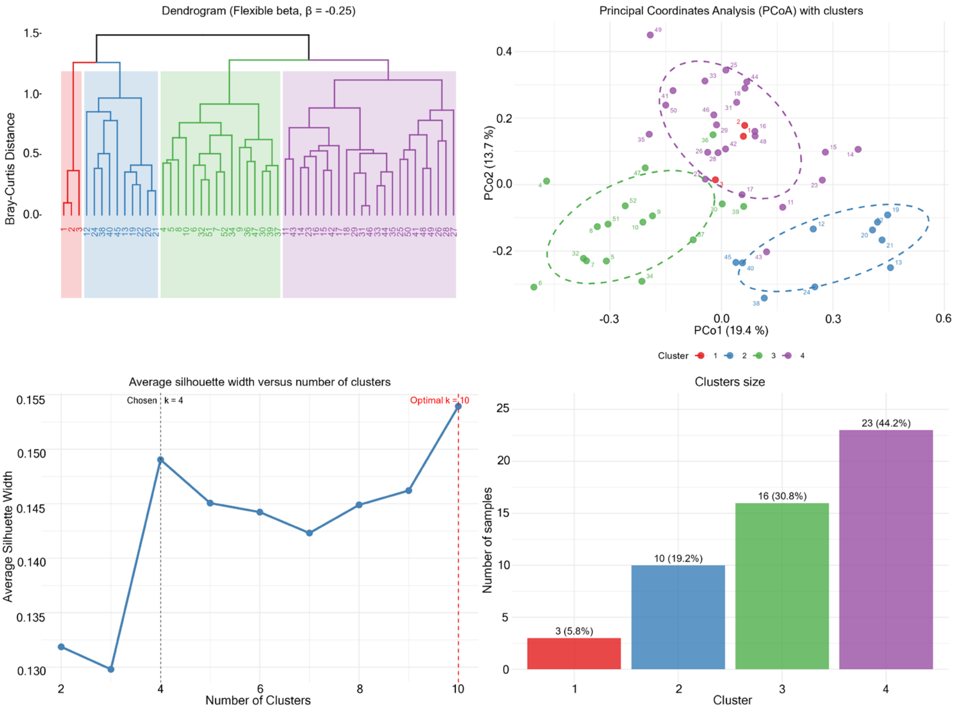

**Figure 2.** Analysis of shrub-herbaceous community based on presence-absence data. **A** – Dendrogram showing hierarchical clustering using flexible beta method (β = – 0.25) with manually identified clusters (k = 4). **B** – Principal Coordinates Analysis (PCoA) ordination. **C** – Plot of average silhouette width versus number of clusters. **D** – Bar plot displaying the size distribution of identified clusters.

Expert assessment of the dendrogram constructed using the flexible beta method (β = - 0.25) revealed four distinct clusters of shrub-herbaceous communities (Fig. 2A). The AGNES coefficient (0.73) confirmed the presence of a reasonably strong clustering structure in the data. However, the average silhouette width (0.15, Fig. 2C) suggested that individual cluster assignments were not well defined, which may reflect the continuous nature of shrub-herbaceous community gradients in the study area. This pattern suggests that while distinct shrub community types can be identified, they form along environmental gradients where intermediate compositions are common.

The Principal Coordinates Analysis (PCoA, Fig. 2B), based on the Bray-Curtis dissimilarity, revealed the underlying structure of the shrub-herbaceous community data. The first two axes explained 19.4% and 13.7%, respectively, of the total variance. A moderate cumulative variance of 33.1% explained by the first two axes is typical for ecological community data, as multiple environmental gradients shape vegetation patterns collectively. Ordination pattern confirm the results of the cluster analysis, showing a partial separation of the four community types in a reduced-dimensional space.

### The four identified clusters varied in size and composition (Fig. 2D):

Cluster 1 (red, 5.8%) represents alder thicket communities. This cluster comprises a single, distinct community characterized by the lowest species richness among all studied alder thickets, with a mean of 8 species. The most frequently occurring species were *Alnus fruticosa*, *Betula nana*, *Solidago lapponica* With., *Polemonium caeruleum* L. and *Carex globularis* L.

Cluster 2 (blue, 19.2%) consists of the most species-poor streamside communities, with minor representation from hollow and slope habitats (7 streamside and 3 slope communities). The mean species richness for the cluster is 10, driven by the notably low average of about 7 species in the streamside communities that dominate it. The most frequent species were *Betula nana*, *Salix glauca*, *Comarum palustre* L., *Rubus chamaemorus* L., and *Carex aquatilis*. Cluster 2 is likely associated with the most severe waterlogging, as indicated by the constant presence of *Comarum palustre* and *Carex aquatilis*.

Cluster 3 (green, 30.8%) includes both alder thickets and slope communities (7 alder thickets and 8 slope communities). The mean species richness was 16. The most common species included *Equisetum arvense* L., *Betula nana*, *Vaccinium uliginosum* L., *Ledum palustre* L., *Vaccinium vitis-idaea* subsp. *minus* (Lodd.) Hultén, *Empetrum nigrum* L. and *Stellaria peduncularis* Bunge. This cluster represents communities with a significant presence of tundra species, typical of well-drained shrub tundra ecosystems with high taxonomic diversity.

Cluster 4 (violet, 44.2%) contains a mixture of slope shrub-herbaceous communities and streamside communities (14 slope and 10 streamside communities). This cluster had the highest mean species richness (17), which indicates more favorable and heterogeneous conditions. The most common species were *Betula nana*, *Salix glauca*, *Salix pulchra*, *Polemonium caeruleum*, *Equisetum arvense*, *Veratrum lobelianum* Bernh., *Rubus arcticus* L., *Vaccinium uliginosum*, *Viola epipsiloides* Á. Löve & D. Löve and *Pedicularis labradorica* Wirsing.

### Soil-vegetation relationship

The constrained ordination model, Redundancy Analysis (RDA) (Fig. 3A), provided a detailed view of this relationship and was statistically significant (F = 1.43, p = 0.001). It explained 18.6% of the total variance in species composition (Constrained variance = 1.78; Total inertia = 9.60). A permutation test on individual axes confirmed that only the first canonical axis (RDA1) was significant ($p < 0.001$). A Mantel test, assessing the overall correlation between the soil and vegetation distance matrices, confirmed a significant but weak positive relationship (r = 0.157, p = 0.003).

The relative contribution of individual soil variables to the RDA model, assessed by the sum of squared loadings on the first two axes, showed a clear hierarchy. The most influential parameters were physical clay content (H, 0.59), active layer thickness (A, 0.59), proportion of gleyed patches (G, 0.57) and proportion of gleyed patches 40 cm (E, 0.43). The remaining variables showed substantially lower values were peat thickness (B, 0.22), moder humus horizon (AO) thickness (C, 0.20), and gleying depth (D, 0.17).

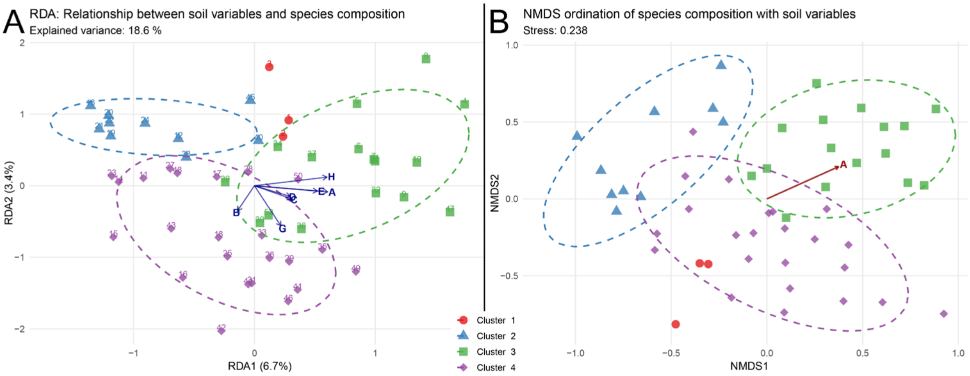

**Figure 3.** The relationship between soil variables and plant community composition. **A** – Redundancy Analysis (RDA) biplot. **B** – Non-metric Multidimensional Scaling (NMDS) ordination based on Jaccard dissimilarity. Soil variable codes: **A** – active layer thickness, **B** – peat thickness, **C** – moder humus horizon (AO) thickness, **D** – gleying depth, **E** – proportion of gleied patches at 40 cm, **G** – proportion of gleyed patches within the gleyed horizon, **H** – physical clay content.

To visualize the main patterns in species composition independently of a predefined environmental model, we performed a Non-metric Multidimensional Scaling (NMDS) (Fig. 3B). This unconstrained ordination (stress = 0.238) represents the overall dissimilarity between samples based solely on species data (Jaccard distance). When soil variables were fitted post-hoc to this ordination space, active layer thickness (A) emerged as the strongest and only statistically significant vector (loadings: NMDS1 = 0.87, NMDS2 = 0.49). This result refines the interpretation of the RDA: while RDA identified a suite of three co-influential factors (A, G, H,) within the constrained model, NMDS suggests that the primary, unconstrained floristic gradient across all samples is most strongly and directly aligned with the cryogenic factor – active layer thickness. The other key variables from the RDA (physical clay proportion and gleyed area) likely contribute to more complex or secondary patterns of community variation.

An indicator species analysis based on Fisher's exact test identified ten statistically significant associations ($p < 0.05$) between plant species occurrences and soil variables (Table 2). The most frequently occurring indicator was *Petasites frigidus* (L.) Fr., which showed significant associations with three soil variables: proportion of gleyed area within the gleyed horizon (G) ($p = 0.0006$), proportion of gleyed area at 40 cm depth (E) ($p = 0.0016$), and physical clay content (H) ($p = 0.0041$).

**Table 2.** Plant species significantly associated with specific soil conditions (Fisher's exact test)

| Soil variable | Species | P value | Plant species frequency | |
|---|---|---|---|---|
| | | | **High soil parameter value** | **Low soil parameter value** |
| Active layer thickness | *Equisetum arvense* | 0.0047 | 0.7692 | 0.3462 |
| | *Stellaria peduncularis* | 0.0034 | 0.5769 | 0.1538 |
| Raw humus horizon thickness | *Empetrum nigrum* | 0.0012 | 0.5625 | 0.1111 |
| | *Tanacetum bipinnatum* (L.) Sch. Bip. | 0.0021 | 0.4375 | 0.0556 |
| Gleying depth | *Trollius asiaticus* L. | 0.0048 | 0.3846 | 0.03846 |
| Proportion of gleyed area 40 cm | *Petasites frigidus* | 0.0016 | 0.5500 | 0.1250 |
| Proportion of gleyed area within the gleyed horizon | *Petasites frigidus* | 0.0006 | 0.5200 | 0.0741 |
| | *Comarum palustre* | 0.0013 | 0.1200 | 0.5556 |
| Physical clay proportion | *Petasites frigidus* | 0.0041 | 0.5238 | 0.1290 |
| | *Chamaenerion angustifolium* (L.) Scop. | 0.0027 | 0.2857 | 0 |

## Diversity and distribution of soil in key biotopes

The most common soils among those studied are Reductaquic Turbic cryosols. These soils were examined at 6 sites. The next most common soils are Reductaquic Turbic Criosols (Arenic) and Histic Reductaquic Turbic Cryosols, studied at 5 and 4 points. Below we provide descriptions of the characteristics of the most common soils under shrubs (Table 3).

**Reductaquic Turbic Cryosols** are more often formed on gentle slopes with a steepness of 3 to 5°. The upper part of the profile of these soils is characterized by a cryoturbated suprapermafrost part and abundant gleying. Gleyization appears as grey-blue and rusty-ochre patches and swirls, indicating periodic changes in oxidation-reduction conditions. Cryoturbations in the active layer are found almost everywhere. Cryoturbation results in the burial of significant amounts of carbon through the burial of organogenic particles and charcoal. The granulometric composition varies across the profile from light to heavy loam and clay. Permafrost occurs at a depth of 30–70 cm and often contains ice veins.

**Table 3.** Soil classification (WRB 2022) of the study sites

| Soil name | Site number |
|---|---|
| Reductaquic Turbic Cryosols | 25, 26, 8, 35, 36, 21 |
| Reductaquic Turbic Cryosols (Arenic) | 22, 23, 24, 30, 34 |
| Reductaquic Cryosols | 19, 20 |
| Histic Reductaquic Turbic Cryosols | 18, 29, 7, 32, 28 |
| Fibric Histosols | 5 |
| Pantofluvic Fluvisols (Arenic) | 15 |
| Fluvisols (Arenic) | 1 |
| Gleyic Epifluvic Fluvisols (Arenic) | 31 |
| Stagnic Pantofluvic Fluvisols (Ochric) | 6 |

**Reductaquic Turbic Criosols (Arenic)** are less common and are confined to the lower parts of slopes, stream valleys, and ancient lake terraces. The upper part of the profile has been significantly influenced by cryoturbation processes. The soil-forming substrate consists of ancient alluvial deposits with a sandy texture. Gleyization is mostly confined to the suprapermafrost part of the profile. The alluvial genesis of the parent rock is also identified in the upper part of the profile, but it has been heavily transformed by cryoturbation. The depth of permafrost varies from 25 to 100 cm.

**Reductaquic Cryosols** are found in the valleys of ephemeral (temporary) watercourses. The upper part of the profile (0-10 cm) consists of weakly decomposed peat. This is underlain by a thin layer (less than 5 cm) of raw-humus material. Beneath this raw-humus interlayer, a mineral horizon with signs of humus illuviation is present. A thixotropic horizon with gleyic features lies below. The texture class is light loam. The permafrost table is found at a depth of 25-30 cm.

**Histic Reductaquic Turbic Cryosols** are characterized by a Histic horizon (15-20 cm thick) of highly decomposed peat at the surface. It is underlain by a mineral horizon impregnated with illuvial organic matter. The texture varies from sandy to light loam. The permafrost table is found at 30-80 cm.

**Fibric Histosols** are formed at the confluence of two streams. The soil is represented by a well-decomposed peat horizon with a thickness of 60 cm.

**Pantofluvic Fluvisols (Arenic)** are confined to the floodplains of small and medium-sized rivers, stream valleys, where sandy alluvium predominates. The soils are distinguished by their layered structure with layers of varying thickness. The thickness of the layers is determined by the intensity of sedimentation and the composition of the suspended matter. Burial of surface horizons is often found in the layers. For a significant period of time during the year, soils are affected by waterlogging, which is manifested in the presence of gleying of the profile, which is more characteristic of the lower part of the profile.

**Fluvisols (Arenic)** have formed on the bed of an ephemeral watercourse. The soil profile is composed of layered, sandy alluvial deposits from the surface and exhibits signs of gleyic properties throughout.

**Gleyic Epifluvic Fluvisols (Arenic)** The upper part of the profile (down to 50 cm depth) consists of layered alluvial sandy deposits. These are underlain by gleyed, cryoturbated light loamy deposits. The permafrost table is found at a depth of 55 cm.

**Stagnic Pantofluvic Fluvisols (Orhric)** are characterized by an organic horizon in the upper part of the profile, interlayered with sandy alluvial material. The mineral part of the profile consists of alternating sandy and light loamy layers. The permafrost table occurs at a depth of 110 cm. Gleyic features are confined to the upper 20–30 cm of the soil profile.

## Discussion

### Landscape heterogeneity as a driver of diversity and floristic discoveries

The formation of high plant diversity zones in Arctic environments is often driven by local environmental heterogeneity (Tape et al. 2012; Loiko et al. 2024). Our results demonstrate how specific geomorphic features, such as snow accumulation hollows, well-drained slopes, and stream valleys, create a mosaic of contrasting ecological conditions that support distinct plant assemblages and enhance regional taxonomic diversity in the southern Gydan tundra.

Analysis of species richness across the researched habitats identified several consistent biodiversity hotspots. The high number of co-existing species is attributed to the proximity to contrasting landforms such as southern slopes and stream floodplains, which support the unique microclimatic regime of these habitats.

The most prominent hotspots were ecosystems associated with drained southern slopes (20–25 species, sites 7, 9, 41, 47), stream valleys (20–23 species, sites 16, 17), and hollow ecosystems (20–25 species, sites 28, 49, 50). The latter represent topographical depressions, sheltered by shrubs and experiencing snowmelt two to four weeks later than the surrounding plains, functioning as micro-refugia.

High floristic diversity was also a consistent feature of other contrasting habitat types – particularly in late-successional slope shrub communities recovering from anthropogenic impact (29 species, site 10) and in vegetation complexes adjacent to lake terraces (26 species, site 42). This further demonstrates that floristic richness in southern tundra is primarily associated with areas of high environmental heterogeneity.

However, the relationship between habitat type and community structure is not unidimensional. We observed that within the same broad categories of slopes, hollows, and valleys, certain plots exhibited an alternative ecological strategy: low to moderate species richness (3–9 species, e.g., sites 3, 6, 12–14, 19–22, 30, 34) coupled with apparent high productivity and often strong dominance of one or a few species. This pattern suggests that environmental heterogeneity drives not only peaks in taxonomic diversity but also the emergence of highly productive, low-diversity patches. These areas may represent more stable, mature, or nutrient-enriched states within the landscape mosaic, where competitive exclusion reduces species number, or particularly favorable microsites that allow for vigorous growth of a limited set of well-adapted species (Walker et al. 2009; Liljedahl et al. 2020).

Despite this variation in diversity patterns, the capacity of these heterogeneous habitats to act as biodiversity reservoirs is unequivocally demonstrated by our floristic discoveries. The discovery of several vascular plant species previously undocumented for this part of the Gydan Peninsula provides direct, taxon-specific evidence for the refugial capacity of these heterogeneous landscapes. According to the collections of the P.N. Krylov Herbarium of Tomsk State University and the National Depository Bank of Live Systems (https://plant.depo.msu.ru/?d=P), our research documents the first local records of the following species, many of which were found precisely within the identified hotspot habitats (Fig. 4).

*Carex rostrata* Stokes (Fig. 4A), found in slope communities (Suppl. material 3: Table S3, site 38), previously known from the Pur-Taz interfluve and the Yenisei River floodplain.

Stellaria palustris Retz. (Fig. 4B), recorded in streamside habitats (Suppl. material 2: Table S2, sites 15, 16, 27), with prior findings across the Taz Peninsula, northern Gydan, and the Yenisei floodplain.

*Bistorta elliptica* (Willd. ex Spreng.) Kom. (Fig. 4C), located on a southern slope near a stream (Suppl. material 2: Table S2, site 16), previously observed in the Pur-Taz interfluve and on the Taz Peninsula.

*Arnica iljinii* (Maguire) Iljin (Fig. 4D), documented on an upper southern slope of a river valley (Suppl. material 2: Table S2, site 26), known from the Taz Peninsula and northern Gydan.

*Salix reticulata* L. (Fig. 4E), found in snow accumulation hollows near a stream surrounded by shrubs (Suppl. material 2: Table S2, sites 26, 27), previously recorded on the Taz Peninsula and in the Yenisei floodplain.

*Vaccinium myrtillus* L. (Fig. 4F), found in a slope ecosystem (Suppl. material 3: Table S3, site 42), previously recorded in the Pur-Taz interfluve, on the Taz Peninsula, and in the Yenisei River floodplain.

*Dianthus repens* Willd. (Fig. 4G) found at the eroded sandy margin of an alder thicket (Suppl. material 1: Table S1, site 7), previously known from the Taz Peninsula, the central part of the Gydan Peninsula, the Arctic part of the Yenisei floodplain, and the south near the village of Tolka on the Taz River.

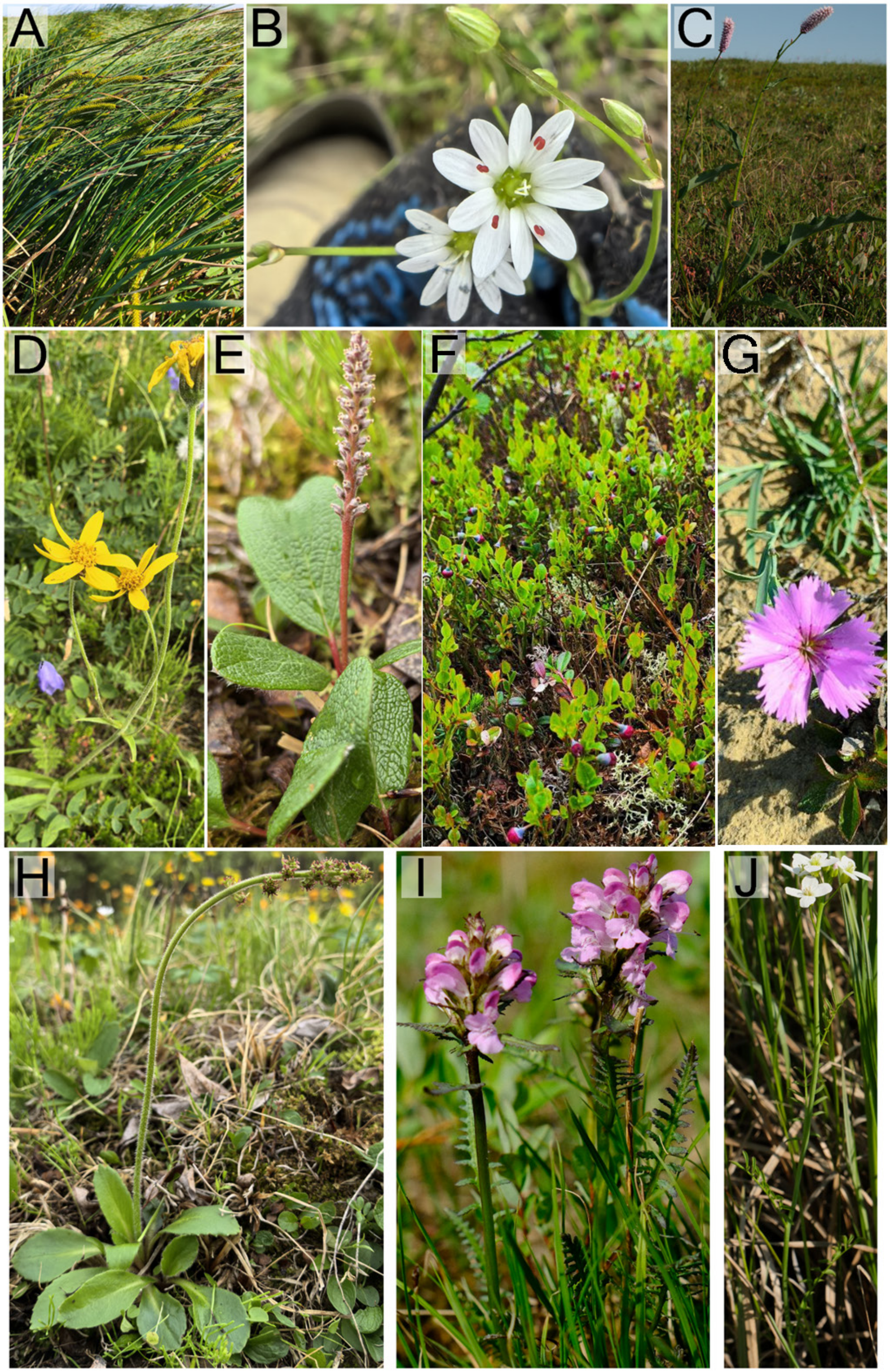

**Figure 4.** Newly reported plant species for the study area. **A** – *Carex rostrata*, **B** – *Stellaria palustris*, **C** – *Bistorta elliptica*, **D** – *Arnica iljinii*, **E** – *Salix reticulata*, **F** – *Vaccinium myrtillus*, **G** – *Dianthus repens*, **H** – *Micranthes hieraciifolia*, **I** – *Pedicularis sudetica*, **J** – *Cardamine nymanii*.

*Micranthes hieraciifolia* (Waldst. & Kit. ex Willd.) Haw. (Fig. 4H), located in a hollow within snow accumulation ecosystems (site 49; Suppl. material 3: Table S3), previously known from the Taz Peninsula and northern Gydan.

*Pedicularis sudetica* Willd. (Fig. 4I), found in thermokarst stream valleys (Suppl. material 2: Table S2, site 17) and shrub-dominated slopes (Table S3, sites 44, 45, 47, 50), documented earlier on the Taz Peninsula and in central Gydan.

*Cardamine nymanii* Gand. (Fig. 4J), recorded in waterlogged stream valleys (site 5; Suppl. material 1: Table S1) and near-lake shrub systems (Suppl. material 2: Table S2, site 15), previously known from the northern Gydan Peninsula and Norilsk areas.

In summary, the southern Gydan tundra shrub-herbaceous communities supports a complex mosaic driven by geomorphic heterogeneity. This mosaic includes both high-diversity microrefugia evidenced by species-rich sites and the discovery of new floristic records and high-productivity, lower-diversity patches. The co-occurrence of these distinct community types within the same landforms strongly supports the hypothesis that landscape heterogeneity is the primary architect of both taxonomic and functional diversity. The identified hotspots are not merely areas of high species count but function as essential microrefugia and productive nodes, providing the stable, buffered niches necessary for species coexistence, the persistence of rare taxa, and the optimization of biomass production under different local conditions. This underscores the paramount importance of conserving the full spectrum of landscape heterogeneity to maintain the ecological integrity and resilience of Arctic tundra ecosystems.

## The role of soil drivers at vegetation structure

Our integrated analysis confirms that specific soil properties are significant, yet secondary, factors for plant community assembly in the studied tundra landscapes. The significant RDA model ($p=0.001$) and Mantel correlation ($r=0.157$, $p=0.003$) unequivocally demonstrate an soil signal. However, the modest proportion of explained variance (18.6%) and the weak Mantel correlation indicate that the measured soil parameters are not the primary determinant of vegetation structure. Within this constrained variance, a clear hierarchy emerged: soil texture (physical clay proportion, H), cryogenic conditions (active layer thickness, A), and hydromorphic features (proportion of gleyed area within the gleyed horizon, G) were the principal drivers. This hierarchy aligns with the known mechanisms of shrub-soil feedbacks in the Arctic, where shrub expansion is frequently linked to altered soil texture, deepened active layers, and modified hydrology (Frost et al. 2018; Kropp et al. 2020)

These factors govern base conditions like moisture regime and rooting depth. The significance of only the first RDA axis ($p < 0.001$) indicates that the primary variation in plant communities is primarily driven by a single dominant factor as a complex interplay of soil development and hydrology, shaped by these key factors.

The indicator species analysis provides concrete evidence for these relationships, with species like *Petasites frigidus* showing significant associations with multiple variables from this core group (proportion of gleyed area within the gleyed horizon, G; proportion of gleyed area at 40 cm, E; and physical clay proportion, H).

However, the modest overall explanatory power of our soil model is itself an insightful result. It underscores a key principle in contemporary tundra ecology: while soil properties provide an important filter, vegetation patterns at the landscape scale are emergent properties of a more complex interplay (Myers-Smith et al. 2011; Heijmans et al. 2022). Thus, the obtained results suggest that, despite the identification of specific significant soil parameters, they control only a part of the observed vegetation structure. A substantial proportion of the variation (81.4%) is likely due to other factors not accounted for in this model. This explains the overall weak relationship identified by the Mantel test and points to the complex nature of plant community formation in the studied ecosystems of Gyda Peninsula.

## Conclusions

This integrated study provides novel baseline data on the co-evolution of plant communities and soils in the poorly documented southwestern Gydan Peninsula. Our findings offer several key insights into the drivers of tundra ecosystem diversity:

1. Landscape-scale geomorphic heterogeneity – the mosaic of slopes, valleys, and hollows – emerges as the primary architect of both taxonomic and functional diversity. These features create essential microrefugia that support high-diversity hotspots and are directly evidenced by the discovery of several plant species previously unreported for this region. This underscores the critical importance of conserving the full spectrum of landscape heterogeneity to maintain ecological resilience.

2. While a significant soil signal was detected, its measured influence was quantitatively limited compared to the overarching landscape template. A hierarchy of key soil drivers was identified, with properties related to texture, cryogenic conditions, and hydromorphy being the most influential. However, the substantial portion of vegetation variation unexplained by the soil model points to the dominant role of other factors.

3. Vegetation structure itself exhibits a continuous gradient, suggesting that shrub-herbaceous communities assemble along environmental continua rather than as discrete units. The strong alignment of the main floristic gradient with active layer thickness highlights the fundamental role of this cryogenic factor.

In summary, our research establishes a critical baseline for monitoring change. It demonstrates that the transformation of the southern Gydan tundra is governed by a hierarchy where the landscape template sets the stage, while localized soil and cryogenic processes fine-tune community composition. Future studies should prioritize quantifying the microclimatic and historical drivers behind the unexplained variation to improve predictive models of ecosystem trajectory under ongoing climate change.

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## Supplementary material 1

### Table S1. Taxonomical composition of shrub-herbaceous alder thickets communities

Authors: Nikita V. Shefer, Ivan V. Kritskov, Georgyi I. Istigechev, Sergey V. Loiko
Data type: table

Link: https://journal.asu.ru/biol/article/view/18536/15943

## Supplementary material 2

### Table S2. Taxonomical composition of shrub-herbaceous streamside communities

Authors: Nikita V. Shefer, Ivan V. Kritskov, Georgyi I. Istigechev, Sergey V. Loiko
Data type: table

Link: https://journal.asu.ru/biol/article/view/18536/15944

## Supplementary material 3

### Table S3. Taxonomical composition of shrub-herbaceous communities of slopes and hollows

Authors: Nikita V. Shefer, Ivan V. Kritskov, Georgyi I. Istigechev, Sergey V. Loiko
Data type: table

Link: https://journal.asu.ru/biol/article/view/18536/15945

## Supplementary material 4

### Table S4. Morphological parameters of soil profiles

Authors: Nikita V. Shefer, Ivan V. Kritskov, Georgyi I. Istigechev, Sergey V. Loiko
Data type: table

Link: https://journal.asu.ru/biol/article/view/18536/15946