

Plant Diversity of the Russian Arctic: Providing a Baseline for Arctic Change and Conservation Research

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Polar desert on Pioneer Island, Severnaya Zemlya archipelago
Photo by Gabriela Schaeppman-Strub, August 2021

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Summary

The Arctic tundra is one of the few biomes that have remained relatively untouched by the direct impact of economic activities. As the Arctic is warming almost four times faster than the global average (Chylek et al., 2022; Rantanen et al., 2022), pressure on the tundra is increasing, complicating efforts to conserve its ecosystems (Ernakovich et al., 2014; Niskanen et al., 2019; Reji Chacko et al., 2023). Plant diversity is a key component of the Arctic tundra as it forms the basis of ecosystem functioning. Plant diversity changes lead to cascading effects throughout the entire ecosystem, and also influence the global climate, primarily via the carbon and energy cycles (Heijmans et al., 2022; Loranty et al., 2014; Oehri et al., 2022). The importance of protecting plant diversity is recognized by Arctic countries through the Arctic Council, and conservation is facilitated by the Conservation of Arctic Flora and Fauna (CAFF) (Barry et al., 2020).

About half of the Arctic tundra is located in Russia, a country where independent research is facing serious challenges. In the Russian Arctic climate change and economic expansion are putting pressure on the ecosystems and thus, weakening their ability to maintain plant diversity (Khapugin et al., 2020; Telyatnikov & Pristiyazhuk, 2014; Yu et al., 2011). With half of the tundra being located in Russia, pan-arctic conservation strategies need to include the Russian territories in order to maintain the intactness of this biome, even though directly influencing the Russian government's conservation decisions may be difficult given the current political context. The successful development of these strategies requires a thorough scientific understanding of the ecosystems and their functioning informed by up-to-date data on the processes affecting the Russian Arctic tundra and its plant diversity, currently largely missing.

Observations on plant diversity in the Russian Arctic have been scattered and mostly not accessible for a comprehensive pan-Arctic analysis. Therefore, in **Chapter 1**, we translated, standardized and digitized 4785 geobotanical plots collected in the Russian Arctic from 1927 to 2022 and presented them as the Russian Arctic Vegetation Archive (AVA-RU), now available to the international community. The plots document

over 1770 plant and lichen species and subspecies, their habitats, and information on the vertical and horizontal structure of vegetation.

Climate is changing fast and human activities are expanding across the Arctic, however, our understanding of how they shape tundra species richness is limited. Therefore, in **Chapter 2**, we utilized AVA-RU data to examine the relative impacts of environmental and anthropogenic factors on community-level plant species richness and its distribution in the Western Siberian Arctic – one of the Arctic regions most affected by anthropogenic pressure. The results reveal an increase in species richness from South-West to North-East, driven mainly by climatic factors, instead of the commonly expected decrease from South to North along the latitudinal gradient. We show that paleoclimatic factors exhibit higher predictive power (up to 21% of explained deviance) even when compared to modern climate, indicating a lasting impact of past climate on tundra vegetation. We suggest that while species richness distribution is mostly driven by environmental factors, a targeted study is needed to assess the human impact. We also show that existing protected areas cover only a fraction of the most species-rich areas.

As the Arctic changes, areas with the most extreme climate are likely the most vulnerable to warming. Documenting their diversity and biomass becomes crucial for establishing a baseline to monitor future changes. Therefore, in **Chapter 3**, we assessed plant and lichen species richness, turnover and biomass, as well as their spatial distribution, in polar deserts — the northernmost biome on Earth. While we only identified 129 species within the 19 surveys, there is a major difference in species richness distribution and turnover. Particularly, 40% of the detected species were found exclusively in a single plot. We also showed that biomass varies widely across the sites, with its maximum on Vize Island, where the mean biomass is comparable to Arctic tundra levels.

Overall, my thesis supports the stewardship of Arctic plant diversity in Russia with new baseline data and applications, with the overarching goal of informing and enhancing conservation strategies at both the national and pan-Arctic levels.

Glossary

Arctic amplification – phenomenon of near-surface air temperature change over the Arctic enhancing 3 to 4 times relative to the global average.

Arctic Vegetation Archive – a circumpolar effort to assemble Arctic vegetation plot data into a standardized, publicly accessible web-based archive and promote its application to northern issues, including a pan-Arctic vegetation classification framework (Walker et al., 2016).

Biodiversity – the variety of life in all its forms, functions, and levels of organization, including genetic, species, community diversity, and ecosystem diversity.

Biome – according to one of the definitions, *'ecological-evolutionary unit, spanning several large-scale spatial levels, including global climatic zones, continents and landscapes at subcontinental and supraregional scales'* (based on Mucina, 2018)

Braun-Blanquet plot – vegetation survey collected according to the methodology developed by Josias Braun-Blanquet (1918). Each plot includes a complete species list of vascular and non-vascular plants sampled in a specific area. The size of the plot varies depending on community characteristics (Westhoff & Van Der Maarel, 1978).

Earth Stewardship – science that facilitates the active shaping of trajectories of social-ecological change to enhance ecosystem resilience and human well-being (Chapin et al., 2011).

Ecosystem functions – physicochemical and biological processes that occur within an ecosystem that influence life, many of which are directly linked to human well-being (Byers, 2022).

Global change – large-scale changes transforming Earth's environment and capacity to support life such as climate change, land use change, species invasion, overexploitation and pollution.

Plant biomass – weight of plant material contained above and below a unit of ground surface area at a given point in time (based on Roberts et al., 1985). In this thesis I focus on aboveground biomass.

Plant community (phytocoenose) – interacting populations of plant species growing in a uniform environment and showing a floristic composition and structure that is relatively uniform and distinct from the surrounding vegetation (based on Westhoff & Van Der Maarel, 1978).

Plant functional types – non-phylogenetic groupings of species that show close similarities in their resource use and response to environmental and biotic controls (Duckworth et al., 2000).

Polar desert – polar biome characterized by single-layer vertical structure, discontinuous vegetation cover, absence of shrubs and leading role of cryptogams in plant communities (based on Matveyeva, 2015). It corresponds to CAVM (2003, 2018) subzone A.

Russian Arctic – the Arctic area within the borders of the Russian Federation, including both lands of the Indigenous people as well as Arkhangelsk oblast'. The thesis focuses only on the terrestrial Arctic, primarily within the Circumpolar Arctic Vegetation map (CAVM team, 2003) borders.

Species richness – number of species within a defined area.

Tundra – a treeless biome in the Northern hemisphere, characterized by continuous vegetation cover, primarily formed by dwarf-shrubs, cryptogams and graminoids, and a major influence of permafrost on ecosystem functioning.

Vegetation – mosaic of plants and their communities within a specific area or across the entire Earth.

1 Introduction

1.1 Russian Arctic: from a pristine land to a new development frontier

The Russian Arctic is one of the last terrestrial frontiers in the Northern hemisphere. This vast and largely uninhabited land stretches for thousands of kilometers, starting from the Norwegian border, crossing the mountainous Kola Peninsula, the plains of the Malozemelskaya and Bolshezemelskaya Tundras, and reaching the Polar Ural mountains marking the boundary between Europe and Asia. It continues through Yamal, Taz, Gydan, and the Taymyr Peninsulas, and the vast Yakutian lands and Chukotka Peninsula, ultimately ending on Ratmanov Island in the Bering Strait — almost diametrically opposite the Kola Peninsula on the Arctic Circle.

Only a few cities are located in the Russian Arctic, particularly to the north of the forest line. However, the sparsity of the human population and the perceived intactness of the Russian Arctic (only approximately 7% of the area is directly affected by industrial activity (Akandil et al., in review)) should not conceal the threats affecting the region. As an integral part of the Earth system, the region experiences the same types of environmental pressures as the rest of the world, often even more pronounced.

The primary pressure is climate change. The Arctic warms almost four times faster than the global average (Chylek et al., 2022; Niittynen et al., 2020; Rantanen et al., 2022) and climate change is already affecting almost every aspect of ecosystem functioning in the Arctic (Callaghan et al., 2012), is shifting vegetation types and zones (Ermokhina et al., 2023; Pearson et al., 2013; Reji Chacko et al., 2023) with particularly strong changes expected in the northernmost polar deserts ecosystems (Barry et al., 2013; Nielsen & Wall, 2013; Weijers et al., 2017). Perhaps the most alarming development is the acceleration of tundra fires (Chen et al., 2021; Hu et al., 2015), more often occurring even far north of the Arctic Circle (Witze, 2020). Fires degrade the permafrost (Jones et al., 2015), enabling plants to root deeper and increasing nutrient availability, favoring vascular plants over non-vascular plants (Blume-Werry et al., 2019). As a result, global warming and associated fires could lead to the transformation

of the tundra into a new stable state (Heim et al., in review), potentially changing the vegetation on a broad scale from lichen and moss to graminoid or shrub-dominated tundra (Heim et al., 2021; Hollingsworth et al., 2021; Myers-Smith et al., 2019), with consequences for a vast array of functions ranging from albedo to reindeer pastures carrying capacity (Chambers et al., 2005; Kuklina et al., 2022). Moreover, the influence of these fires is not solely constrained to the initial area that is directly affected. The resulting release of greenhouse gases to the atmosphere creates a positive feedback loop, accelerating warming, and leading to permafrost degradation which, in turn, brings more fires in the future (Chen et al., 2021; Lasslop et al., 2020). Such feedback loops make the Arctic tundra a very fragile ecosystem, and one of the first victims of the heavy environmental costs of climate change — a canary in the coal mine of the ecological crisis.

The very economic activities that have brought the climate change crisis are expanding in the Arctic today. They include natural resource extraction (Hanaček et al., 2022; Peters et al., 2011), infrastructure building (including the so-called 'strategic infrastructure' developed by the Russian state to facilitate economic expansion and consolidate control over the region) (Povoroznyuk, 2023), commercialization of traditional agriculture including reindeer herding (Pilyasov & Kibenko, 2022), and potentially tourism (Golubchikov et al., 2019; Timoshenko, 2020). While the scale of these activities is relatively local compared to the lower latitudes, it is nevertheless steadily growing (Akandil et al., in review) and expected to accelerate with the likely future Arctic sea ice melting and following Northern Sea route opening (Francois & Rojas-Romagosa, 2013; Makarova et al., 2021). The colonization is promoted by the state which considers the Arctic land as 'free' and encourages its use through programs like the Far Eastern Hectare (2016) and Arctic Hectare (2021)¹ ('Russian homestead act'), as well as a special tax and administrative regime favorable for businesses (Russian Far East and Arctic Development Corporation, 2024).

¹ I received myself an invitation to apply for the 'Arctic hectare' program through the governmental *Gosuslugi* portal email newsletter on 02.11.23 while writing this Introduction.

Recent political developments in Russia, culminating with the full-scale invasion of the Ukraine, have substantially contributed to the destruction of nature. Deregulation has been implemented to compensate industries for sanction losses (Milkin & Volobuev, 2022; Russian Social Ecological Union, 2022; Simonov & Davydova, 2023). Further, repressions against Indigenous Peoples and ecological organizations and activists are growing (Koltsov, 2023; The Moscow Times, 2023). Even respected international NGOs like Greenpeace and WWF have been outright banned, and many smaller ecological NGOs have been labeled as 'foreign agents' (The Moscow Times, 2023). The growing tensions between Russia and NATO have also contributed to the ongoing militarization of the Russian Arctic islands (Gronholt-Pedersen et al., 2022; TASS, 2015), sometimes threatening nature reserves including the UNESCO heritage site Wrangel Island (Konstantinova, 2022). Moreover, the deterioration of scientific connections also reduces the possibility of monitoring the developments (Lopez-Blanco et al., 2024).

It is especially challenging to develop strategies to reduce the risks and safeguard the Russian Arctic biodiversity in such a complex situation. There is no straightforward path to address climate and development threats to its biodiversity, even fewer when compared to the broader Arctic, considering our limited ability to monitor its changes. Yet, this should not distract us from the goal; we should still investigate potential ways. Tackling the threats to biodiversity requires a synergy of knowledge and action, science and policies. While the challenges on the action front are substantial and largely — though not exclusively — political, there is significant room for improvement in the knowledge component as well. Persistent data gaps and uncertainties remain a major hurdle in understanding the changes in the Arctic, especially in the Russian part (Ermokhina, 2018; Lopez-Blanco et al., 2024; Metcalfe et al., 2018; Nature, 2022; Virkkala et al., 2019). Since fieldwork in Russia is currently severely limited, these gaps could be addressed by making better use of existing data available in Russian, through its standardization and translation to English, enabling pan-Arctic scale synthesis. In turn, addressing the gaps will make it possible to develop strategies at both the international and (potentially) national levels, which will form the basis for protecting the biodiversity of the Russian Arctic.

1.2 Ecosystem stewardship: scientific approach and its applications in the Arctic

Different approaches and strategies for ecosystem conservation are widely conceptualized using the term 'stewardship'. For example, according to Chapin et al. (2011), Earth stewardship aims for simultaneous achievement of long-term biosphere stability and ensures equitable access to basic needs for a good life throughout society. Yet, this is not the only possible perspective on stewardship, as this term is used for many different approaches. While sharing the broad definition of collaborative and responsible management of the environment respecting ecosystems and their functions, stewardship approaches vary depending on the degree of their radicalism, agents and facilitators, type of governance, and applied knowledge (Mathevet et al., 2018).

One of the key differences between the approaches is the type of knowledge applied, including scientific and expert knowledge, pragmatic and lay knowledge², as well as their combinations. While primary reliance on expert knowledge (including scientific) is criticized as a facilitator of technocracy, limiting the ability of democratic actors to shape and protect their environment (Taylor, 2013), scientific knowledge remains a crucial component of most approaches. The reason is that the different actors, not only bureaucratic or technocratic, need scientific knowledge to conceptualize and comprehend seemingly isolated events as part of broader processes, such as climate change, which are incompatible with human scale ('hyperobjects', in terms of Morton (2013)). Therefore, scientific knowledge contributes to many stewardship approaches either as a main or supplementary type of knowledge (Fig. 1).

² Lay knowledge – non-scientific forms of knowledge (Turnhout et al., 2019)

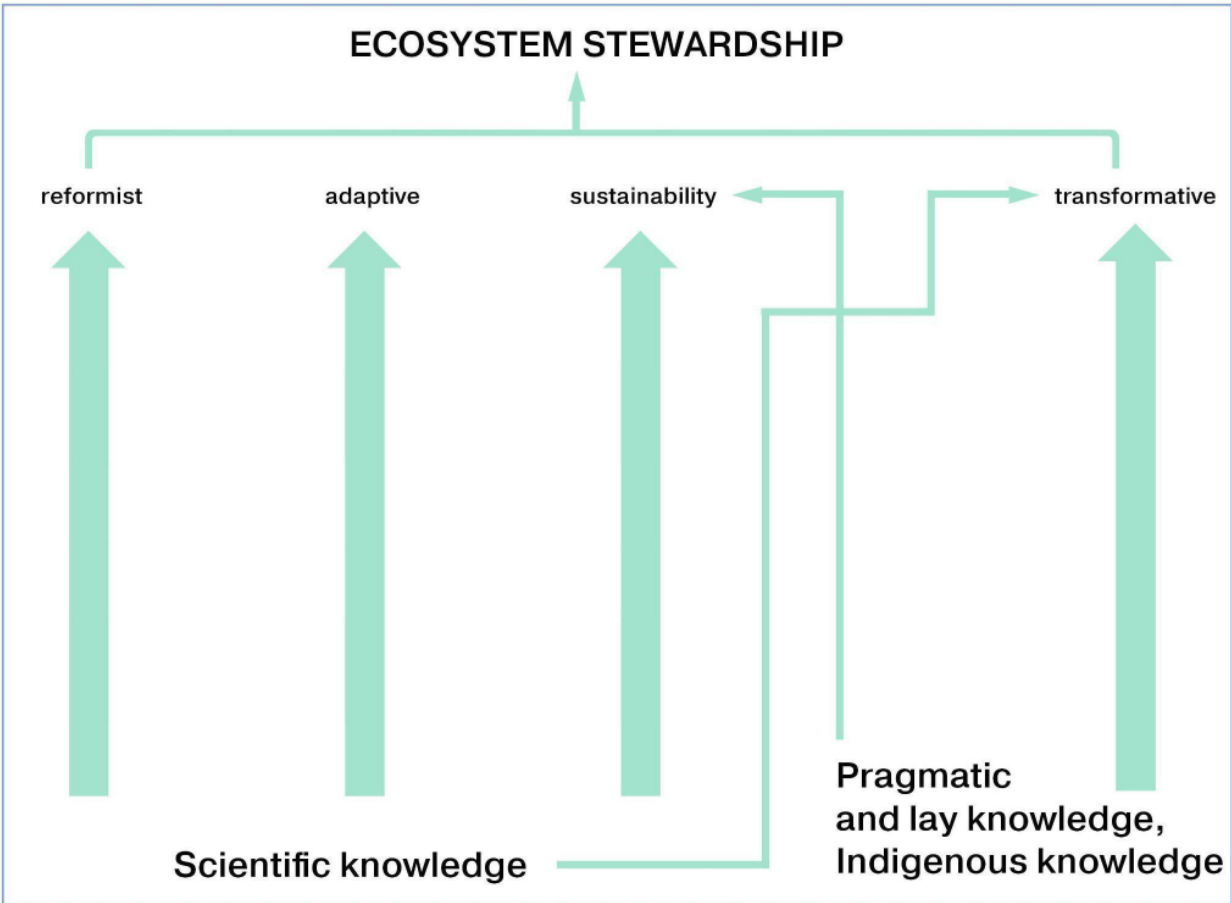


Figure 1. Stewardship approaches and their underlying knowledge (according to Chapin et al., 2011; Mathevet et al., 2018)

There are few global efforts that provide a scientific basis for ecosystem stewardship, particularly with a focus on biodiversity monitoring. Effective and comprehensive global biodiversity monitoring is essential for conservation planning, as it provides the information to identify immediate targets while also showing a broad picture of the state of biodiversity, which is necessary for the development of more systematic approaches. There is a wide range of both international and country-level biodiversity data archives documenting information on species distribution and, sometimes, their abundance. The Global Biodiversity Information Facility (GBIF) is the largest biodiversity data repository, containing information on billions of species occurrences across the globe (<https://www.gbif.org/>). As endangered species are an important focus for monitoring, information on their occurrences is collected and

managed by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (<https://www.iucnredlist.org/>), which relies on country-level lists, including the Russian Red Data Book. In Russia, extensive data on plant occurrences is assembled in the Moscow University Herbarium database, which has recently been integrated into GBIF (<https://plant.depo.msu.ru/>). Citizen science portals such as the international INaturalist (<https://www.inaturalist.org/>) or Russian Plantarium (<https://www.plantarium.ru/>) further contribute to global monitoring of biodiversity.

However, despite the existence of many global and regional biodiversity data portals there remains a lack of data standardization. Few projects are dedicated to address this issue, notably the Map of Life project, assembling and integrating different biodiversity data sources, including GBIF and IUCN, (Jetz et al., 2012), and the newly proposed Global Biodiversity Observing System initiative (GBIOS), with its goal to federate biodiversity observation networks in a similar way as global climate observations (Gonzalez et al., 2023). Another important challenge is the presence of spatial biases due to uneven monitoring capabilities and efforts of data storage and mobilization, which leads to a range of uncertainties and spatial biases, particularly in species distribution modeling (Beck et al., 2014; Geurts et al., 2023). Both challenges are pressing for the Arctic, which has its own research and monitoring infrastructures facing similar problems as the global one.

In the Arctic the scientific approach to conservation and stewardship is represented by the non-governmental International Arctic Science Committee (IASC) and the Conservation of Arctic Flora and Fauna working group (CAFF) of the Arctic Council. CAFF is addressing the conservation of Arctic ecosystems by monitoring, assessments and research group activities (<https://caff.is/about/caff/>), promoting actions to policymakers helping to sustain biodiversity (CAFF, 2013). Specifically, CAFF focuses on conservation of plant diversity through its Circumpolar Flora group (CFG) (<https://www.caff.is/work/projects/cfg-caffs-flora-group/>), encouraging pan-Arctic cooperation among botanists for a unified approach to monitoring, protection and sustainable use of Arctic vegetation.

One of the monitoring projects of conservation importance endorsed by CFG is the Arctic Vegetation Archive. The Arctic Vegetation Archive (AVA) is 'a circumpolar

effort to assemble Arctic vegetation plot data into a publicly accessible web based archive and promote its application to northern issues' (Walker, 2014). Due to the use of different protocols by scientists for vegetation surveys, the collected data often lack compatibility. This incompatibility complicates pan-Arctic scale analysis of vegetation and its responses to climate change (Walker et al., 2019). The AVA initiative addresses the problem by bringing together and harmonizing data from Alaska, Canada, Greenland, Scandinavia and Russia through cross-border cooperation, potentially integrating over 31,000 plots into a single archive (Breen et al., 2017). The prototype for international AVA is the Alaskan Archive (AVA-AK) providing open access to more than 3,000 plots across the state (Walker et al., 2016). The initiative was launched in 2013 at an international workshop in Krakow (Walker et al., 2013) and continued through Prague (2017), Arkhangelsk (2019) and Vienna (2023) workshops, as well as many smaller talks and discussions. Importantly, beyond its primary work on data standardization, the AVA initiative provides an opportunity for discussion among scientists from different countries to exchange their knowledge on Arctic vegetation. This contributes to deeper shared understanding of the common challenges related to mapping and monitoring of Arctic vegetation, necessary for a pan-arctic scale conservation.

1.3 Safeguarding Arctic plant diversity under global change

But what could be a stewardship strategy for the Arctic? And why should protecting Arctic plant diversity be part of the strategy?

When someone mentions 'Arctic nature' they are probably thinking about polar bears and walrus rather than plants. A simple search for this term in Google shows many photos of lifeless glaciated landscapes, icebergs, and cold, frozen seas (Fig. 2). The images of landscapes alternate with pictures of animals: bears, reindeers, ptarmigans, wolves, seals and whales (sometimes incorrectly showing pictures of Antarctic penguins as well). Only a very few pictures on the first several pages of the search display some vegetation, mostly spruce and other trees covered by snow, and almost no picture specifically focusing on plants. This lies in stark contrast with my

firsthand experience from fieldwork in the Arctic, where I observed a diversity of plants and their communities (Fig. 3)

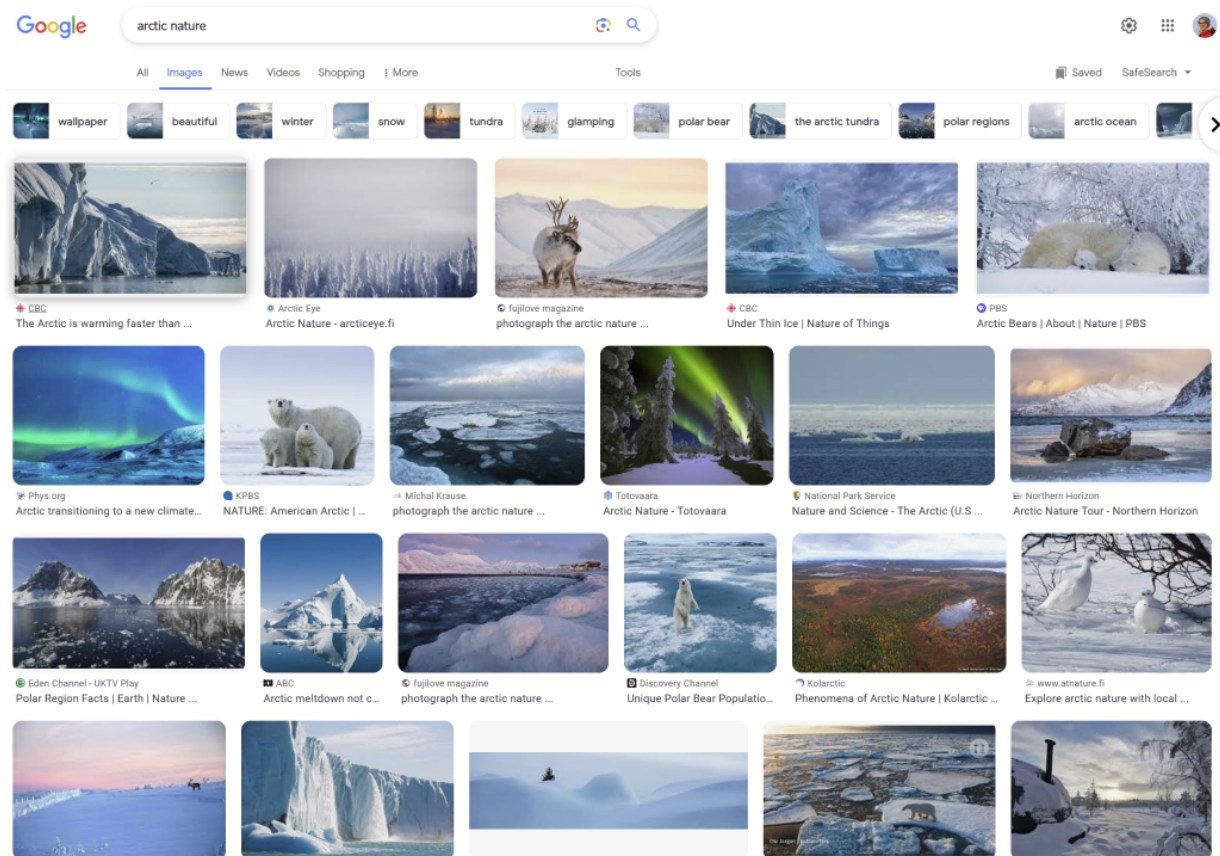


Figure 2. Images displayed from a Google search using the search term 'Arctic nature'. (Google, November 10, 2023; <https://www.google.com/>)



Figure 3. Arctic nature as I see it in the field.

However, deprioritizing Arctic plant diversity goes beyond a public perception issue or search engine bias. The prevailing targeted approach to nature conservation primarily focuses on protecting the most diverse ecosystems, flagship species, or areas that provide important ecosystem services to the human population (Jung et al., 2021, Zhu et al., 2021). The approach is incorporated in global biodiversity agreements such as the Convention of Biological Diversity (CBD) with its 30 by 30 target (designating 30% of the Earth surface as protected areas by 2030, especially the areas with particular importance of biodiversity, ecosystem functions and services) set during COP15 in Montreal (Convention on Biological Diversity, 2022). Adopting the Kunming-Montreal global biodiversity framework is widely recognized as a major step in biodiversity protection, celebrated by many scientists and conservationists across the globe (Gilbert, 2022). Yet, its targeted approach could lead to potential conservation problems. The largely unspoken premise of targeted conservation is that some

ecosystems will be unavoidably further sacrificed to allow economic expansion and GDP growth. Considering that the prevailing approach to conservation is metrics-focused, and species numbers (only 3% of global flora occur in the Arctic (Callaghan et al., 2004)) and human population (estimated at about 10 million in the Arctic and subarctic areas in 2019, accounting for approximately 0.13% of the world's population (Heleniak, 2020)) are comparably low in the Arctic, the targeted approach puts the plant diversity of Arctic terrestrial ecosystems at risk of being deprioritized.

However, Arctic plant communities sustain unique species that are often endangered by climate change (Grundt et al., 2006; Oke et al., 2023; Zhang et al., 2023). Many of these species are cryptogams, which are more diverse but generally less studied than vascular plants (Barry et al., 2013; Matveyeva, 2015). Some of the Arctic regions also demonstrate relatively high endemism, particularly Wrangel Island and other areas of Eastern Beringia, where 48% of endemic vascular plants of the Arctic are found (Ickert-Bond et al., 2013; Talbot, 1999). Apart from its floristic diversity, the Arctic also has diverse plant communities (Matveyeva & Lavrinenko, 2021; Reynolds et al., 2019). Developing under specific conditions of permafrost, low summer temperatures, varying continentality, precipitation, topography, soil chemistry, and prevailing drainage conditions, Arctic communities form 16 distinct vegetation types, varying between bioclimatic subzones (CAVM, 2003; Reynolds et al., 2019; Walker et al., 2005). Each of the vegetation types is characterized by a particular composition of plant functional types, characteristic species and distinct community structure (Walker et al., 2005).

Moreover, Arctic ecosystems and their vegetation are not only unique and highly complex, they also play a vital role in maintaining the global biosphere and climate stability through their ecosystem functions. One of the most crucial functions of tundra vegetation is its role in the global carbon cycle (Meredith et al., 2019). Historically, Arctic ecosystems have served as a carbon sink, storing carbon in plant biomass and, more importantly, in maintaining permafrost (Loisel et al., 2014; Schuur et al., 2015). It is estimated that about 1,700 billion metric tons of frozen carbon are stored in the Arctic permafrost and an unknown quantity of this carbon is under risk of being released due

to permafrost thawing (Miner et al., 2022). Vegetation generally mitigates permafrost thaw in summer by its isolating effect (Blok et al., 2010; Heijmans et al., 2022). Arctic vegetation also influences the climate by altering the albedo, which affects changes in the Earth's surface energy budget (Lorantý et al., 2011; 2014; Oehri et al., 2023). Beyond its impact on climate, Arctic vegetation forms the basis of the terrestrial Arctic food chains. It sustains herbivores, thereby maintaining the diversity of Arctic animals and hence the traditional livelihoods of Indigenous peoples who depend on them (Bogdanova et al., 2021; Magga et al., 2009).

Thus, it is crucial to recognize the importance of the Arctic plant diversity and plant communities for conservation to establish a pan-Arctic nature protection framework. Among other factors, this requires detailed data and a thorough understanding of the processes shaping tundra communities in the Russian Arctic. The challenges of studying the Russian Arctic are currently significant, mainly due to the current limitations on conducting fieldwork, leading to questions about the adequate approaches for its study (Lopez-Blanco et al., 2024). While an apparent solution lies in broadening the use of remote sensing, its effectiveness is limited without ground truth data for validation. However, with the vast amount of data collected in the Russian Arctic by Russian researchers, the big opportunity and challenge lies in its harmonization and systematization (Ivanova & Shashkov, 2016). In addition to field surveys, this could include translating the studies and conducting their meta-analysis, along with the potential use of citizen science portals that continue to function in Russia. By combining these different data sources, it is possible to supplement the remote sensing, providing a baseline for future monitoring of changes and the development of various applications, such as macroecological modeling, in the Russian Arctic, which remains one of the most understudied areas of the entire Arctic (Lopez-Blanco et al., 2024; Metcalfe et al., 2018).

1.4 Research questions

As global change rapidly transforms Arctic ecosystems, it is essential to maintain and protect them in the interests of global biosphere stability, but also for their intrinsic

value. To estimate the scale of ecosystem degradation in the Arctic and develop new conservation strategies we need comprehensive geobotanical datasets with pan-Arctic spatial coverage. Since the ecosystems of the Russian Arctic, especially the polar islands, remain the most understudied parts of the Arctic, I aim to fill the gaps in the geobotanical **data** by collecting extensive datasets on tundra plant communities, their biomass, and habitat characteristics. This allows me and my colleagues to **model** essential biodiversity variables related to species populations and community composition (Pereira et al., 2013). Specifically, we investigate the processes shaping the key characteristic of Arctic plant communities – their species richness. Moreover, we study the distribution of plant biomass – another key parameter of the Arctic ecosystems at the northern margin of life – in polar desert islands. The obtained knowledge on the distribution of plant diversity and biomass, in turn, informs **conservation** strategies across the Russian Arctic and beyond (Fig. 4).

Specifically, in the thesis I address the following research questions:

1. What is the current state of geobotanical data across the Russian Arctic?
2. What are the key factors shaping plant species richness in the Western Siberian Arctic and their relative importance?
3. How is plant diversity and aboveground biomass distributed across the Russian polar desert islands at the landscape scale, and what is their current status?

To address the first question, we consolidated the existing current and historical Russian Arctic Braun Blanquet plots into a single harmonized Russian Arctic Vegetation Archive (<https://avarus.space/>), in Chapter 1.

To answer the second question, using macroecological modeling we explored in Chapter 2 the relative influence of climate (including paleoclimate), topography, and anthropogenic factors on the community-level species richness in the Western Siberian Arctic — one of the Arctic regions most affected by anthropogenic pressure.

To address the third question, we assessed in Chapter 3 the aboveground biomass of different plant functional types in Russian polar deserts — the northernmost

biome expecting major changes because of climate change. Additionally, we modeled the landscape-level plant biomass of the Russian polar islands to provide a baseline for monitoring future changes.

Overall, my thesis aims to support the stewardship of Russian Arctic plant diversity with new baseline data and applications, with the overarching goal of informing and enhancing conservation strategies at national and pan-Arctic level.

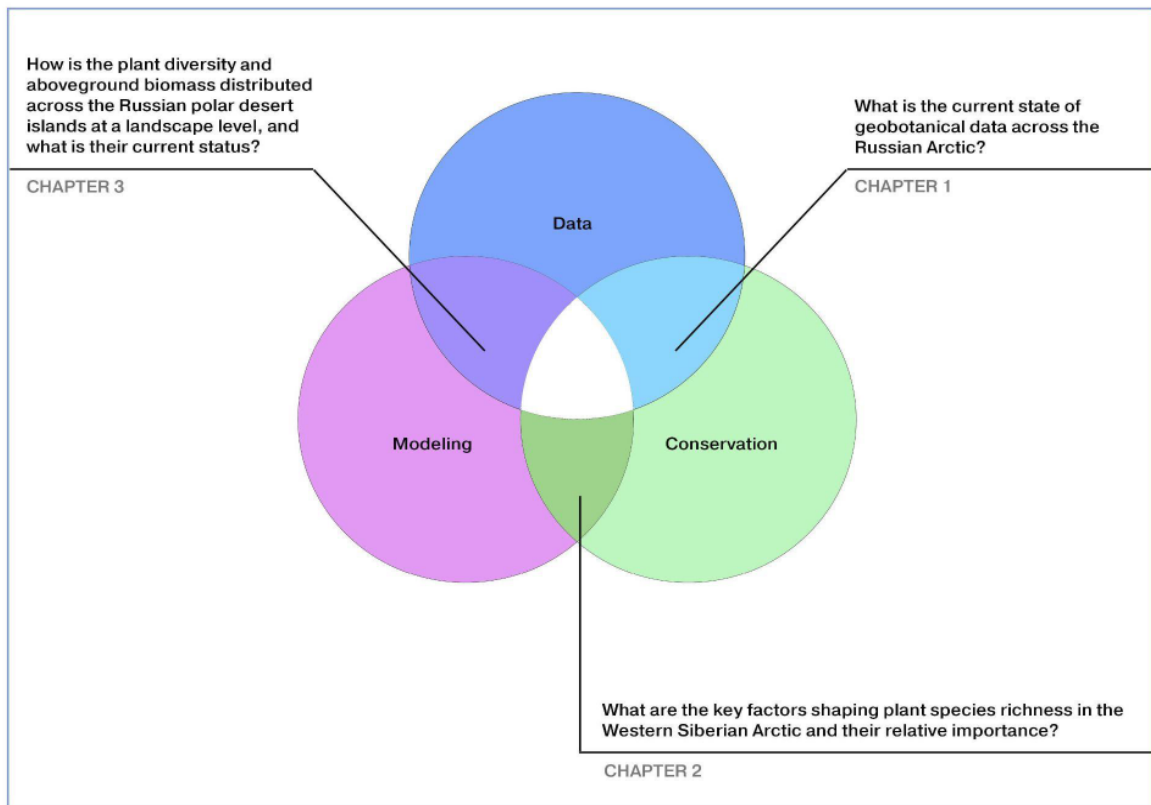


Figure 4. Research questions and conceptual scheme of the thesis.

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2 Russian Arctic Vegetation Archive — A new database of plant community composition and environmental conditions

Zemlianskii, V., Ermokhina, K., Schaepman-Strub, G., Matveyeva, N., Troeva, E., Lavrinenko, I., Telyatnikov, M., Pospelov, I., Koroleva, N., Leonova, N., Khitun, O., Walker D., Breen A., Kadetov, N. Lavrinenko, O., Ivleva T., Kholod, S., Petrzhik, N., Gunin, Y., Kurysheva, M., Lapina. A., Korolev, D., Kudr, E., & Plekhanova, E. (2023). Russian Arctic Vegetation Archive — A new database of plant community composition and environmental conditions. *Global Ecology and Biogeography*.
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Abstract

Motivation: The goal of the Russian Arctic Vegetation Archive (AVA-RU) is to unite and harmonize data of plot-based plant species and their abundance, vegetation structure and environmental variables from the Russian Arctic. This database can be used to assess the status of the Russian Arctic vegetation and as a baseline to document biodiversity changes in the future. The archive can be used for scientific studies as well as to inform nature protection and restoration efforts.

Main types of variables contained: The archive contains 2873 open-access geobotanical plots. The data include the full species. Most plots include information on the horizontal (cover per species and morphological group) and vertical (average height per morphological group) structure of vegetation, site and soil descriptions, and data quality estimations. In addition to the open-access data, the AVA-RU website contains 1912 restricted-access plots.

Spatial location and grain: The plots of 1-100m² size were sampled in Arctic Russia and Scandinavia. Plots in Russia covered areas from the West to the East, including the European Russian Arctic (Kola Peninsula, Nenets Autonomous district), Western Siberia (Northern Urals, Yamal, Taza and Gydan Peninsulas), Central Siberia (Taymyr Peninsula, Bolshevik Island), Eastern Siberia (Indigirka basin) and the Far East (Wrangel Island). About 72% of the samples are georeferenced.

Time period and grain: The data were collected once at each location between 1927 and 2022.

Major taxa and level of measurement: Plots include observations of >1770 vascular plant and cryptogam species and subspecies.

Software format: csv files (1 file with species list and abundance, 1 file with environmental variables and vegetation structure) are stored at the AVA-RU website (<https://avarus.space/>), and are continuously updated with new datasets. The open-access data is available on Dryad and all the datasets have a backup on the server of the University of Zurich. The data processing R script is available on Dryad.

Keywords: Arctic, Arctic Vegetation Archive, biodiversity, Braun-Blanquet plots, tundra, vegetation classification.

2.1 Introduction

Climate warming, industrial activities, and an increase in tourism are increasingly impacting the Arctic environment, its biodiversity, and the livelihoods of Indigenous people (Bartsch et al, 2021; Forbes et al, 2009; IPCC, 2019; Pearson, 2013). Protecting Arctic nature requires broad-scale monitoring activities, such as monitoring plant-community diversity and distributions, wildlife habitat, and modelling changes in the structure and functioning of the Arctic ecosystems. This leads to the necessity of developing large data archives providing information on species and trait diversity for all Arctic regions. Existing projects include the European Vegetation Archive (Chytrý et al., 2017), the Alaskan Arctic Vegetation Archive (Walker et al., 2016), and the Tundra trait database (Bjorkman, 2018). However, especially for the Russian Arctic, the assessment and prediction of plant biodiversity and ecosystem functioning are hampered by a lack of standardized in situ data accessible to the research community (Walker et al., 2016). The development of the Russian part of the Arctic Vegetation Archive (AVA) can fill this gap and deliver full and open access to Russian Arctic vegetation data.

Despite well-established Soviet research (Sekretareva, 1999; Tikhomirov, 1956; Tolmachev, 1978; Yurtsev, 1994) as well as significant Russian and international efforts conducted in the 1990-2010s (Koroleva & Kulyugina, 2015; Koroleva & Kopeina, 2018; Matveyeva 1994, 2006, 2011; Matveyeva et al., 2013, 2017; Matveyeva & Lavrinenko, 2021, 2023; Pospelova & Pospelov, 2010; Rebristaya, 2013; Walker et al., 2018, 2019), the Russian Arctic remains the area most poorly covered by geobotanical research north of the Polar circle (Ermokhina, 2017, 2018). International access to datasets collected by Russian scientists is often hampered by political, bureaucratic, and language barriers. Another important factor that hinders broader data access is the lack of data standardization. It is estimated that about 5000 relevés (phytosociological plots following the Braun-Blanquet method) are published (mainly in Russian), many more are digitised, but not published, or still in field books (Ermokhina, 2017). Harmonization

and integration of the data into internationally available archives would facilitate pan-Arctic vegetation research impeded by existing data gaps.

Here we present a newly assembled Russian Arctic Vegetation Archive (AVA-RU), which consists of 4785 Braun-Blanquet plots (Fig. 1). The goal of AVA-RU is to unite and organize existing Russian Arctic geobotanical data into a single data repository according to international AVA protocols (Walker, 2013). The AVA-RU is part of the international Arctic Vegetation Archive project supported by the Conservation of Arctic Flora and Fauna (CAFF, 1997; <https://www.caff.is/flora-cfg/ava>) and the International Arctic Science Committee's Terrestrial Working Group (IASC TWG). The AVA-RU is the only resource containing historical Soviet geobotanical plots, as well as modern Russian and international data collected in Russia. The data were sampled at 40 major sites ranging from the Norwegian Svalbard archipelago and the Kola Peninsula (Murmansk oblast') in the West to the Indigirka basin (Sakha Republic) in the East, covering all bioclimatic subzones from high polar deserts to forest tundra and northern taiga (CAVM, 2003). Most plots (72%) are georeferenced and can be used for modeling applications. The time range of the data varies from the late 1920s (Kola Peninsula historical data) to 2022 (Yamal Peninsula).

The Arctic Vegetation Archive can be used to address a wide range of scientific and practical issues. We aim to promote the use of AVA-RU datasets for scientific research, biodiversity conservation, and ecosystem restoration.



Figure 1. Overview of locations and number of geobotanical plots included in the Russian Arctic Vegetation Archive (Eurasian Arctic transect data included, status 3 March 2023).

2.2 Data acquisition and harmonization

Data acquisition and compilation

AVA-RU data have been sampled following the Braun-Blanquet sampling method, which is the standard methodology for Russian Arctic vegetation records (Walker et al., 2017). The size and shape of relevés can vary from 1 to 100 m² depending on vegetation type and characteristics of the site. The species cover/abundance is indicated by the percentage of plot area or using a categorical scalar. Whenever possible, photos of the plots were taken (Fig.2).



Figure 2. Russian AVA data collection process. **A:** 2017-2018 field campaign camp (Yamal Peninsula); **B:** Pre-sampling photo documentation; **C:** Photo of the plot (Baidara Bay); **D:** Geobotanical plot sampling; **E:** Plants height measurements; **F:** Soil composition identification; **G:** Plant biomass field sampling; **H:** Plant biomass samples sorting. *Photos by Olga Kulikova, Anton Romanov, Yakov Gunin, Ivan Sergeev and Vitalii Zemlianskii (2017-2018).*

A significant part of the Western Siberian dataset (1003 plots) was compiled by team members during the 2017 expedition to the Yamalo-Nenets Autonomous district (Telyatnikov et al, 2019, 2021), while other datasets were independently contributed by researchers or based on previously published data (Dedov, 1940; Kholod, 2007; Koroleva et al., 2018, 2019; Lavrinenko & Lavrinenko, 2016, 2018; Matveyeva, 2006; Matveyeva & Lavrinenko, 2006; Pospelova & Pospelov, 2010; Telyatnikov et al., 2015, 2022; Walker et al., 2019).

Data-processing algorithms and quality control procedures

We used the standard AVA protocol to enter geobotanical data (<https://arcticatlas.geobotany.org/catalog/dataset/current-turboveg-data-dictionary-and-p-anarctic-species-list-pasl>). To process the species data, the Turboveg data management system was used (Hennekens & Schaminée 2001). Alternatively, some datasets were standardized using R software (R version 4.2.2). In this case, we compared the species name provided by the author with the Pan-Arctic species list (Raynolds et al., 2013), which we used to maintain taxonomic consistency. We indicated species that were not found in PASL, as 'Unknown' in the column 'PASL taxon scientific name', but kept the original name in the column 'Dataset taxon'. The quality of vascular plant and cryptogam data were estimated by the AVA team. Six classes of data quality were used: 1. highest, 2. high, 3. high but incomplete, 4. moderate, 5. moderate and incomplete, and 6. low.

Data description

The AVA-RU contains 4785 geobotanical plots belonging to 40 datasets. All the datasets consist of at least two separate files: a species list and a habitat data list. The species list contains a full species list for each plot, and species abundance is given in classes or percentage. The habitat data list contains information about vertical (average layer height) and horizontal (layer cover) structure of vegetation, as well as a variety of information about habitat and environmental conditions. The full structure of the database is described in the AVA protocol

(<https://arcticatlas.geobotany.org/catalog/dataset/current-turboveg-data-dictionary-and-p>

[anarctic-species-list-pasl](#)) and the most relevant parts are highlighted in Appendix Table 1. The majority of the plots (72%) have handheld GPS (WGS 84 datum) georeferencing.

Some datasets are also supplemented by 'Additional data' files, which contain the data not included in the international AVA protocol such as active layer thickness or plant biomass. These non-AVA format files can also include information about vegetation layer coverage (vascular plants, dwarf shrub (without separation by erect and prostrate dwarf shrubs) or hemi-prostrate-dwarf shrub coverage, etc.).

Future data contributions to AVA-RU

Data owners can contribute their data to the Archive by contacting our team through the AVA-RU website form (<https://avarus.space/profile/about/>). The submitted datasets will be accepted if they meet the following minimal criteria: a) completeness of vascular plant list; b) georeferencing (not mandatory for historical USSR data); c) some habitat data. We encourage small datasets collected in the same region to be contributed as a single archive whenever possible. The AVA-RU team can support the authors with standardizing their data according to AVA-RU rules. For collective datasets, permission of all data owners is required. Datasets can be updated upon the author's request (update history is indicated in the dataset description).

2.3 Data access and rights

AVA-RU data is maintained and updated on the project website, which is available in English and Russian (<http://avarus.space/>). The website contains information about the project, team members, and data use guidelines.

The AVA-RU data can be used for research, education, or conservation and protection of nature. The publication should be cited as follows: Zemlianskii, V., Ermokhina, K., Schaepman-Strub, G., Matveyeva, N., Troeva, E., Lavrinenko, I., Telyatnikov, M., Pospelov, I., Koroleva, N., Leonova, N., Khitun, O., Walker D., Breen A., Kadetov, N. Lavrinenko, O., Ivleva T., Kholod, S., Petrzhek, N., Gunin, Y., Kurysheva, M., Lapina. A., Korolev, D., Kudr, E. & Plekhanova, E., (2023). Russian Arctic Vegetation Archive – a new database of plant community composition and environmental

conditions. *Global Ecology and Biogeography*, <https://doi.org/10.1111/geb.13724>. We encourage AVA-RU data users to inform the AVA-RU team about their publications using the Archive data through a website form (<http://avarus.space/profile/about/>). The titles of the projects will be published on the AVA-RU website in the 'supported projects' section.

Data regimes

Open-access is the default regime for published datasets. Open-access data can be freely and directly downloaded from the AVA-RU website as Creative commons 4.0 (<https://opendefinition.org/licenses/cc-by/>), but citation of the data source is required (see Section 3.2). A copy of the open-access part of AVA-RU data is stored regularly on the external data archive Dryad, using a versioning system. The status of the open-access data as of March 3rd, 2023 (AVA-RU-v.1.0), is accessible on Dryad (<https://doi.org/10.5061/dryad.5tb2rbp8d>). For open-access data, it is necessary to provide references both to the original publication and this AVA-RU data publication. We encourage reporting on any inaccuracies found in the AVA-RU datasets.

Contributors of unpublished datasets can opt for **restricted access**. The use of restricted access data requires permission from the data owner. The restricted access regime lasts for 5 years, after which the datasets are automatically transferred to open-access. Applicants can contact data owner(s) through a website form on AVA-RU and ask for permission and conditions of use. The AVA-RU team checks the data request by the applicant(s) as quickly as possible, normally within 2 weeks, and contacts the data owners, requesting permission to use the dataset. In case of questions from the data owner, the AVA-RU team contacts the applicant(s) directly and requests additional information. Once permission is received from the owner, the team sends the dataset to the applicant. The data users should propose co-authorship to restricted-access data owners. Co-authors should be offered the possibility to contribute to the research and interpretation of the results.

2.4 Applications and published studies

The AVA-RU data have already been used for a broad range of research including vegetation classification and mapping (Koroleva & Kulyugina, 2015; Lavrinenko & Lavrinenko, 2018a, 2018b; Lavrinenko et al., 2016; Matveyeva, 2006; Telyatnikov et al., 2021, 2022), species distribution modeling (Ermokhina et al., 2023) and species richness prediction (Zemlianskii et al., in review). We also plan the import of the AVA-RU datasets into sPlot (s-Plot, 2023; <https://www.idiv.de/en/splot.html>). The publication of the datasets now allows further applications, that might include spatial modeling of vegetation height and plant biomass, and conservation studies.

Data availability statement: The AVA-RU data are stored on the Russian Arctic Vegetation Archive website (<https://avarus.space/>) as well as linked through the CAFF website (<https://www.caff.is/flora-cfg/ava/links>). The open-access data are available on the Dryad repository (<https://doi.org/10.5061/dryad.5tb2rbp8d>). The data processing R script is available on the Dryad repository (<https://doi.org/10.5061/dryad.prr4xgxr1>).

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3 Current and past climate co-shape community-level plant species richness in the Western Siberian Arctic

Zemlianskii, V., Brun, P., Zimmermann, N., Ermokhina, K., Khitun, O., Koroleva, N., & Schaepman-Strub, G. (2024). Current and past climate co-shape community-level plant species richness in the Western Siberian Arctic. *Ecology and Evolution*.

Abstract

Aim: The Arctic ecosystems and their species are exposed to amplified climate warming and, in some regions, to rapidly developing economic activities. This study assesses, models and maps the geographic patterns of community-level plant species richness in the Western Siberian Arctic and estimates the relative impact of environmental and anthropogenic factors driving these patterns. With our study, we aim at contributing towards conservation efforts for Arctic plant diversity in the Western Siberian Arctic.

Location: Western Siberian Arctic, Russia.

Methods: We investigated the relative importance of environmental and anthropogenic predictors of community-level plant species richness in the Western Siberian Arctic using macroecological models trained with an extensive geobotanical dataset. We included vascular plants, mosses and lichens in our analysis, as non-vascular plants substantially contribute to species richness and ecosystem functions in the Arctic.

Results: We found that the mean community-level plant species richness in this vast Arctic region does not decrease with increasing latitude. Instead, we identified an increase in species richness from South-West to North-East, which can be well explained by environmental factors. We found that paleoclimatic factors exhibit higher explained deviance compared to contemporary climate predictors, potentially indicating a lasting impact of ancient climate on tundra plant species richness. We also show that the existing protected areas cover only a small fraction of the regions with highest species richness.

Conclusions: Our results reveal complex spatial patterns of community-level species richness in the Western Siberian Arctic. We show that climatic factors such as temperature (including paleotemperature) and precipitation are the main drivers of plant species richness in this area, and the role of relief is clearly secondary. We suggest that while community-level plant species richness is mostly driven by environmental factors, an improved spatial sampling will be needed to robustly and more precisely assess the

impact of human activities on community-level species richness patterns. Our approach and results can be used to design conservation strategies and to investigate drivers of plant species richness in other arctic regions.

Keywords: Arctic vegetation, macroecological modeling, Arctic Vegetation Archive, community-level plant species richness, paleoclimate predictors, anthropogenic impact.

3.1 Introduction

The documentation of Arctic plant diversity and its distribution under global change is one of the key priorities of international science and policy agendas as coordinated by the Conservation of Arctic Flora and Fauna (CAFF, 1997) of the Arctic Council and the International Arctic Science Committee (IASC). This information is urgently needed for the identification of Arctic biodiversity hotspots, which are a major target for nature protection and conservation (UN Convention on Biological diversity) (CBD, 1992). Plant diversity in the Arctic is usually studied at regional (hundreds of square kilometers), local (square kilometers) and community (square meters) levels. Despite Arctic regional and (to a lesser extent) local plant diversity being relatively well documented, the community-level distribution of plant diversity across broad spatial extents and its drivers remains understudied, especially in the Siberian part of the Arctic (Daniëls et al., 2005, 2013; Khitun et al., 2016; Walker et al., 1994). Yet, the immediate scale at which plant diversity drives ecosystem processes and responds to environmental change is the community scale. Understanding the distribution of plant diversity and its relation to environmental and anthropogenic drivers at the community level is therefore key, especially in regions exposed to amplified global change such as the Arctic.

Species richness across plant communities in the Arctic is strongly related to local abiotic factors such as soil moisture, meso- and microrelief, wind speed and exposure, permafrost and soil conditions (Iturrate-Garcia et al., 2016; Schultz, 2005; Walker et al., 2019), which can promote high heterogeneity among communities at small spatial scales. This heterogeneity is often larger than inter-regional differences

between communities belonging to the same vegetation type (Khitun, 1998; Khitun & Rebristaya, 1998). Furthermore, anthropogenic factors play an increasingly important role in shaping Arctic vegetation, changing community composition, threatening some local species (especially, lichens and mosses) and simultaneously increasing total plant species richness through introduction of new species and habitat change (Daniëls et al., 2013; Forbes 1995, 1997; Nellemann et al., 2001; Povoroznyuk et al., 2022; Rebristaya & Khitun, 1998; Red Book of YANAO, 2010).

The Western Siberian tundra is a rapidly transforming region of the Arctic (Kozlova, 2013; Kumpula et al., 2011, 2012; Walker et al., 2012). The combination of multiple interacting factors including climate change, infrastructure expansion, fossil fuel extraction (Skipin, 2014), reindeer pressure (Egelkraut et al., 2020; Kryazhimskii et al., 2011; Veselkin et al., 2021) and species invasions, contributes to large-scale ecosystem degradation within and beyond areas directly affected by economic activity (Golovatin et al., 2012; Forbes et al., 2009). The high landscape homogeneity (Rebristaya, 2013) and the large extent (about 300'000 km²) contrast with the uneven spatial distribution of anthropogenic impacts, and make the Western Siberian tundra a natural laboratory for studying the relative impact of environmental and anthropogenic drivers on tundra flora and vegetation across biological, temporal, and spatial scales.

Most of the botanical research in the Western Siberian tundra was conducted at the site level, following the 'local flora' methodology (Khitun, 2002, 2003; Khitun et al., 2016; Khitun & Rebristaya, 1998; Rebristaya, 1989, 2013; Rebristaya & Khitun, 1994, 1998). This methodology is based on a complete assessment of vascular plant species in an area of 100-300 km². There are 42 local floras described across the Western Siberian tundra, but their distribution is uneven: about two thirds of the local floras were described on the Yamal Peninsula, while other areas are poorly sampled. Local species pools vary widely: from 215 species in Layakha, west of Taz Peninsula (Fig. 1), subzone E (CAVM, 2003; Rebristaya et al., 1989), and 209 species in Chugoryakha, south-west of Gydan (Fig.1), subzone E (Rebristaya & Khitun 1994; CAVM, 2003), to 75 species on Bely Island, subzone B (CAVM, 2003; Rebristaya, 1995). Generally, regional species richness declines with latitude, but areas at the same latitude at Gydan have richer

floras than at Yamal by 20 to 30 species (Khitun, 1998, 2016; Rebristaya 2013). Although overall summer warmth has been identified as the main contributing factor to floristic richness gradients, other factors such as soil acidity, local topography, glaciation and sea level history of the area are also considered important (Khitun, 1998, 2016; Rebristaya, 2013; Walker et al., 2005). The particular importance of Pleistocene sea level changes has been documented, although accurate quantification of its impact on the contemporary flora has remained challenging due to the lack of Pleistocene palynological data for the region (Rebristaya, 2013).

While earlier studies based on local floristic data provide important insight into regional vascular plant species richness, we still lack an understanding of which factors are structuring the species richness at the community level across the Western Siberian Arctic and how climate, topographic and anthropogenic factors combine to impact community species richness across large spatial extents. Large-scale quantitative studies of community-level species richness have not been carried out in Western Siberia, where existing studies rely either on traditional geobotanical methods or are limited to smaller areas (Forbes & Sumina, 1999; Khitun, 1998; Rebristaya 2013). Here, based on a newly assembled, large geobotanical data set (Zemlianskii et al., 2023), we aim to identify the main drivers and map the patterns of community-level plant species richness, including vascular plants, mosses and lichens, in the Western Siberian tundra. We estimate the relative impact of different contemporary and historical environmental and anthropogenic factors on plot-level community species richness using macroecological models. We model and map the spatial distribution of mean plant species richness across the area and discuss these predictions in context of previous geobotanical studies. We hypothesize that 1) climate factors are more important in explaining patterns of community-level species richness across vast Arctic plains than topographic factors, 2) paleoclimatic factors have higher explanatory power compared to the current climate, 3) anthropogenic factors are as important predictors as natural factors, 4) community-level plant species richness in the area follows the latitudinal diversity gradient, and 5) current protected areas do not sufficiently well cover regions with high species richness.

3.2 Methods

The objective of our research is to estimate the distribution of plant species richness at the community level across the Western Siberian tundra. To this end, we calibrated macroecological models, predicting mean plot-level plant species richness as a function of environmental factors (Guisan et al., 2017; Guisan & Rahbek, 2011) from geobotanical plots sampled across the region. We also estimated the role of anthropogenic factors, using distance from infrastructure as a proxy for anthropogenic impact.

Study area

The Western Siberian tundra is located in the northern part of the Western Siberian plain and covers slightly more than 300'000 km². The area has a low plant species richness at the regional level because of its landscape properties and geoclimatic history. The area belongs to the European-West-Siberian province (Yamal-Gydan subprovince) of the Arctic floristic region (CAVM team, 2003; Yurtsev, 1994). In comparison with neighboring subprovinces, Yamal-Gydan is characterized by almost complete absence of endemism, low vascular plant species richness (the lowest in continental Russia), and a lack of many montane species (Daniëls et al., 2013; Khitun, 1998; Rebristaya, 2013; Sekretareva, 1999; Yurtsev, 1994). In total, the province harbors about 450 species of vascular plants (Koroleva et al., 2011), 276 species of mosses (Chernyadyeva, 2001; Voronova & Dyachenko, 2018) and 250 species of lichens (Magomedova et al., 2006). The flora of the area was shaped by Quaternary climate oscillations as well as marine transgressions and (to lesser extent) glaciations, which had an especially strong impact on Yamal (Rebristaya 2013; Stewart et al., 2016). Landscape homogeneity, high soil acidity, and absence of bedrock exposure also contribute to observed low species richness (Khitun 1998; Rebristaya, 2013).

Geobotanical plots

To estimate community-level species richness we used geobotanical data from the Russian Arctic Vegetation Archive (Ermokhina et al., 2022; Zemlianskii et al., 2023). These data consist of 1483 Braun-Blanquet plots established in homogenous vegetation collected during 2005-2017 field campaigns in the Western Siberian tundra (Fig. 1) (Zemlianskii et al., 2023). The data were collected following the standard international Arctic Vegetation Archive protocol (Walker et al., 2013, 2016, 2018) and include full species lists of vascular plants and, contrary to most other existing floristic studies of the area, also bryophytes and lichens (Elven et al., 2011; Raynolds et al., 2013). For the 12 major sites (100-150 km² sub-areas, with more than 60 plots sampled in each), we collected data representative for all vegetation types found in the area (at least 5 plots per community per major site). In addition, we used 10 minor sites with 4-21 plots per site. The plot size varied from 25 to 100 m² depending on community characteristics (Matveeva, 1998). We divided plots into two classes, large plots (100m²) and small plots (less than 100m²), to test for the effect of plot size on species richness.

The plot-level species richness, which we calculated as plot-wise numbers of present species of vascular plants, mosses and lichens (liverworts data were omitted because of uneven identification quality across the database) was used to build regression-type macroecological models. The response variable of our models was species richness per community. To estimate latitudinal trends at the site-level, we also inferred lichen, moss, vascular plants and total species richness for each major site.

Predictor variables

For each geobotanical plot, we first extracted co-located data from an initial set of 48 contemporary environmental predictors describing climate, topography, vegetation productivity, and anthropogenic impact (Appendix Table S1). Climatic predictors included wind speed from the Global Wind Atlas (Davis et al., 2023; <https://globalwindatlas.info/>), 19 bioclimatic variables (seasonal and annual statistics of temperature and precipitation) from CHELSA (Karger et al., 2017), mean ground temperature from ESA Global permafrost project (Obu et al., 2019), and annual statistics of climate moisture index, total cloud cover, potential evapotranspiration, site

water balance, and growing degree days from CHELSA-BIOCLIM+ (Brun et al., 2022). Topographic predictors included altitude, standard deviation of altitude, topographic position index, log-transformed slope, and aspect, which were derived from the Arctic digital elevation model (Morin et al., 2016; Porter et al., 2018), and topographic wetness index (Marthews et al., 2015). Mean normalized difference vegetation index (NDVI) for the period July-August 2019-2020 as observed by MODIS (<https://modis.gsfc.nasa.gov/>) was used as vegetation-related predictor.

In addition to these contemporary environmental factors we tested the effect of five paleoclimatic variables (mean annual temperature, annual precipitation sum, paleo-elevation, distance to land ice, and maximum (latest) year in the time-series when the location was covered by land ice) since the Last Glacial Maximum period (221 time steps with 100-year temporal resolution extending up to 22.000 years ago), originating from the CHELSA-TraCE21k dataset (Karger et al., 2021) (Appendix Fig. 4-6). Information on these variables at the locations of our geobotanical plots was extracted using a publicly available R script (https://github.com/jakobjassmann/cryo_db_v2). For paleoclimatic variables we (1) identified the timesteps with highest explained deviance for each predictor and (2) performed a selection of optimal timesteps comparing them with other predictors within the full set.

In addition to the environmental predictors mentioned above, we used distance to infrastructure as a proxy for anthropogenic impact, combining disturbance through industrial activities, and increased potential for species invasion into a single predictor. To this end, we downloaded all available data for roads, railroads, settlements, industrial sites, and airports from OpenStreetMap (<https://www.openstreetmap.org>) and converted them to points. Then, we calculated the distance between each standard grid raster cell and the closest infrastructure point using the nearest neighbor method.

We added distance to infrastructure as a predictor to the macroecological models to test its explained deviance. To assess if a possible effect on the model outcome is independent of environmental predictors we generated a residual plots of the GAM model fitted with environmental predictors against distance to infrastructure predictor.

Additionally, we tested the relationship between distance to infrastructure and the presence of those 413 species (out of the 840 species) with 10 or more occurrences individually. To do this, we fitted logistic regression models and looped through all 413 species, calculating p-values and regression coefficients.

From the full set of predictors, we performed a selection for the final model calibration based on univariate predictive performance (see Appendix Table S1) and limited collinearity (absolute pairwise Pearson correlation coefficients <0.7). The results of the selection were used in the final macroecological models.

Raster layers of all predictors were reprojected in QGIS (version 3.12, <https://www.qgis.org/>) to a standard grid in ESRI:102025 projection with 1000 m horizontal resolution. The resampling and predictor selection was conducted in R (version 4.1.2, R Core Team, 2021) using the package raster (Bivand et al., 2021).

Fitting and validating macroecological models

We modeled species richness as a function of non-anthropogenic predictors using four different model algorithms: random forest (RF, Breiman, 2001), gradient boosting machine (GBM, Friedman, 2001), generalized linear model (GLM, McCullagh & Nelder, 1983), and generalized additive model (GAM, Hastie & Tibshirani, 1990) (see Table 1). For RF, we fitted 500 regression trees, considering three predictors for each tree. For GBMs, we set the number of trees to 80, the minimum number of data points per leaf to 10, the learning rate to 0.1 and the error distribution to 'poisson'. For GLM and GAM we assumed a Poisson error distribution and used the 'log' link function. For GLMs, we defined linear and quadratic terms for each predictor. For GAMs, we used smooth terms with four degrees of freedom. For GLM and GAM, we step-wise optimized the Akaike information criterion by removing uninformative predictor terms from the model equation.

Macroecological models were fitted in the R environment (version 4.1.2) using the packages randomForest (Liaw & Wiener, 2002), gbm (Greenwell et al., 2020), and gam (Hastie, 2020). We used 5-fold cross-validation to estimate model performance.

Agreement between observed and predicted species richness was assessed using Spearman correlation coefficients, root mean square error (RMSE) and mean absolute error (MAE).

Spatial projections

We ensembled the spatial projections of species richness of all fitted models (Table 1). Ensemble predictions were generated using the mean of modeled species richness of the four different models. In addition, we derived the model disagreement between models as the prediction span (i.e., maximum - minimum predicted species richness among models per pixel) and displayed our plot locations on the model disagreement map in order to assess the effect of sampling bias on prediction uncertainty (Fig.3). Finally, we intersected the obtained richness map with a shapefile of the borders of Arctic protected areas in our study region (CAFF, 2010).

3.3 Results

The role of contemporary environmental factors

Testing the predictive power based on univariate predictive performance of the initial set of 48 environmental variables shows that climate-related factors are better predictors of mean community-level plant species richness than factors related to topography or distance to infrastructure (Table 2, Appendix Table S1). Our results confirm that community-level species richness in the Arctic is strongly linked to warmth, but the relationship varies depending on which seasonal temperature statistics is considered. Lower mean January temperature is associated with higher species richness (found primarily on the more continental Gydan Peninsula) though the relationships are non-linear as the warmest temperature (found at the more oceanic coast of eastern Yamal) is also associated with higher species richness compared to colder temperatures of central Yamal and northernmost Bely Island (Appendix Fig. 1c). The trend is different for mean daily maximum air temperature of the warmest month where highest species richness is associated with high temperatures (Appendix Fig. 1f). Moisture factors are also important: both the annual maximum and annual range of the

climate moisture index, and maximum and minimum monthly potential evapotranspiration have relatively high adjusted explained deviance (Appendix Fig. 1b, Appendix Table S1). Cloud area fraction and mean wind speed show moderate explained deviance (5 and 7% respectively) (Appendix Table S1). High species richness is associated with relatively low wind speed and cloud fraction. Topographic relief factors are generally less important for community-level species richness than climate variables. Plant species richness is positively correlated with slope (Appendix Fig. 1e) and standard deviation of altitude (Appendix Table S1). The latter two are the only two topographic relief predictors with an explained deviance higher than 5%. Altitude, aspect, topographic wetness index and roughness (topographic position index), on the other hand, have very low explained deviance (Appendix Table S1).

The importance of paleoclimatic predictors

Paleoclimatic predictors show high explained deviance, partly even higher than any contemporary temperature predictor used, yet they are strongly correlated with contemporary climate predictors. The strongest paleoclimate predictor is temperature from 12.1 thousand years ago, which alone explains 21% of the deviance (1% higher than that of the actual mean annual air temperature – the strongest contemporary temperature-related predictor) (Appendix Figure 2a). The four strongest paleo-predictors are all temperatures from the Pleistocene-Holocene boundary period (11.2-12.7 thousand years ago) and have high explained deviance ($\approx 20.9\%$), while temperatures of 17-22 thousand years ago have lowest explained deviance (12-15%) (Appendix Fig. 6). At the same time, the strongest paleoclimatic predictors (temperature, precipitation, distance to land ice) exhibit high correlation with current mean ground temperature (0.95, 0.83 and 0.72 respectively for a 12.1-thousand-year-old time point) and generally also among each other. The data show no evidence of the presence of either land ice or sea water at the plot locations throughout the entire time period since the Last Glacial Maximum.

Anthropogenic impact

To estimate the anthropogenic impact on species richness, we analyzed the distance to infrastructure as a predictor, which shows moderate explained deviance (11%). At the same time, additional GAM residual tests show limited independent impact of distance to infrastructure on total plant species richness (Appendix Fig. 2). Testing the relationships between single species and distance to infrastructure shows that 159 species exhibit significant positive relationships (91 highly significant), while 92 show negative relationships (38 highly significant) with distance to infrastructure (Appendix Fig. 3, Appendix Table S2). Based on the additional test results, distance to infrastructure was excluded from the final model projection map.

Selected predictors and model performance

The final set of eight environmental predictors used for model calibration included four contemporary climate predictors (annual maximum of climate moisture index, mean January temperature, mean daily maximum air temperature of the warmest month and isothermality), three paleoclimatic predictors (mean annual temperature 12.100 years ago, mean annual precipitation 17.200 years ago, and the distance to land ice 9.300 years ago), and one topographic predictor (log-transformed slope) (Table 2). Plot size was omitted as a predictor during GAM and GLM stepwise variable reduction, so we consider the plot size effect as minor as long as the area of the plots lies within the range assessed here. Multivariate GBM and RF also show the same model performance with and without the use of plot size. A detailed list of all tested and selected predictors can be seen in Appendix Table S1.

Using the 8 selected predictors, GAM, GLM, RF and GBM show close performance statistics (Table 1). Our model predictions to the left-out cross-validation subsets showed a Spearman correlation of 0.58, an RMSE of 10.2 and MAE of 8.0. The best model was GLM with a Spearman correlation of 0.60 and a MAE of 8.0.

The ensemble of models shows low model disagreement (less than 5 species) in most parts of Gydan, Taz Peninsula and some areas of Northern and coastal Western and Eastern Yamal (Fig. 3). We identified high model uncertainty (10 to 15 species) in

Southern and Central Yamal, around Bovanenkovo in the West, and the South Tambej gas field at the eastern coast of Yamal.

Spatial patterns of community-level plant species richness

Our model results show a highly heterogeneous distribution of community-level plant species richness across the Western Siberian tundra (Fig. 2). Mean species richness of the model ensemble map varies from 15 species on Eastern Yamal, Bovanenkovo railroad area (Fig. 3), to more than 40 in the Gydan National Park area. The Yamal Peninsula shows generally lower species richness than Gydan. Furthermore, longitudinal differences between Yamal and Gydan are generally higher than latitudinal differences within both peninsulas. Protected areas (except Gydan National Park) generally cover areas with low species richness. Importantly, the main part of the species-rich area in Northern Gydan remains unprotected as well as smaller species-rich areas in Northern and Eastern Yamal.

It is widely recognized that landscape-level or regional plant species richness in the Arctic tundra is strongly dependent on summer warmth and hence declines with latitude. At the community level, we found an opposing trend: median species richness of lichens, mosses, and vascular plants increases with latitude (reduced warmth) (Fig. 2). Based on the univariate predictive performance, latitude is a relatively strong predictor of community-level plant species richness across the area with 15% of deviance explained (Appendix Table S1). Given its high correlation with other, more direct predictors, latitude was not used in the final model. However, we clearly see a temperature-richness effect that is opposed to the expected decline of richness with latitude and associated decrease in temperature.

3.4 Discussion

Our models reveal a highly heterogeneous spatial distribution of community-level plant species richness across the Western Siberian Arctic. In the study, we tested five hypotheses. As we expected in H.1 climate factors such as temperature and precipitation play key roles in shaping community species richness while topography

plays a secondary role (Table 2). Paleoclimatic factors are shown to be stronger predictors compared to similar contemporary climatic factors, while being strongly correlated with the latter (H.2). While revealing relatively high explained deviance, additional statistical tests showed that the effect of distance to infrastructure on plant species richness is difficult to interpret, contrary to H.3. Contrary to the pattern common in the Arctic at regional scale, we do not find a latitudinal decrease in community-level species richness from South to North, but rather a consistent increase from South-West to North-East (H.4, Fig. 2). Finally, in accordance with H.5, our analysis suggests that the most species-rich areas remain largely unprotected (Fig. 2).

Our results unveil the complex interplay of factors driving community species richness in the Western Siberian tundra. Among contemporary predictors, climate is showing the strongest influence on plant species richness patterns in Western Siberian Arctic. Between climate predictors, temperature-related factors such as mean annual and mean ground temperature, growing degree-days and mean January temperature best explained plant species richness which is in line with previous Arctic studies (CAVM, 2003). Moisture factors are also important – a high annual climate moisture index range is associated with high species richness, presumably because continental parts of the region have higher habitat diversity than oceanic ones. Conversely, areas with high cloud area fraction are associated with low species richness as sunlight is an important limiting factor for plant life in the tundra (Chapin, 1987). Topography-related factors and wind speed are generally weaker predictors of plant species richness than climatic factors. The impact of altitude itself on species richness is low due to the generally flat terrain in our study area and hence low variability in altitude. However, we have demonstrated that terrain roughness, as indicated by factors such as slope and the standard deviation of altitude, is associated with high species richness. This finding aligns with previous research, as some of the species-rich communities in the area, such as tundra meadows, are often found on steep slopes (Rebristaya, 2013; Telyatnikov, 2005). The role of wind speed is less conclusive because areas with the lowest wind speed have few geobotanical plots. However, the areas with highest wind speed exhibit lower species richness, which is in good agreement with the known

negative impact of wind erosion (deflation) on Yamal tundra ecosystems (Ektova, 2008; Ermokhina & Myalo, 2012a,b).

The testing of historical climate predictors indicates that paleoclimate had the strongest impact on plant species richness distribution. Notably, some paleoclimate predictors such as temperature and precipitation exhibited higher explained deviance than their contemporary counterparts, which indicates a legacy effect of past climate on the contemporary community-level richness patterns (Stewart, 2016). According to the CHELSA-TraCE21k dataset, our study area was not affected by glaciation or sea level change over the past 21,000 years, which differs from previous research on the region that indicated some sea transgressions during the Boreal age of the Holocene (9,200-8,200 years ago), although not as pronounced as those in the Pleistocene (Rebristaya, 2013). It is challenging to separate the influence of contemporary from historical climate, as demonstrated at the example of Gydan, where the high species richness is mostly attributed to its historical development (Khitun, 1998).

We found no conclusive evidence that distance to infrastructure affects species richness in Western Siberia. Despite strong evidence of impact of anthropogenic activities on the vegetation of the region (Golovatin et al., 2010; Golovnev et al., 2016; Ektova & Morozova, 2015; Ermokhina et al., 2023; Forbes, 2013; Veselkin et al., 2021), a sensitivity analysis suggests that most of the impact of the distance to infrastructure predictor is attributable to other predictors (Appendix Fig. 2). At the same time, indirect indicators such as relatively high explained deviance of the distance (11%) show that there might be a potential relationship that cannot be confidently detected with the data available. The spatial distribution of some species (such as *Deschampsia brevifolia* R. Br. or *Poa alpina* v. *vivipara* L.) which were found primarily at closer distance to infrastructure (i.e. with significant negative correlations) in our analysis are indeed classified as apophytes (Sekretareva, 1999). In other cases, especially for many species showing strong negative relationships with distance to infrastructure (f.e. *Dactylina ramulosa* Hook. Tuck.), sampling bias (due to a sampling gap on intermediate to long distances) may have played a role. Our model results indicate that a better designed spatial sampling is needed to investigate the direct and indirect impact of

human activities, such as industrial expansion and related herding density change, on spatial patterns plant species richness.

Our results suggest increasing mean community-level species richness from South-West to North-East which is the opposite of the common view of a distinct negative latitudinal richness gradient in the Arctic (Daniëls et al., 2000, 2013; Schultz, 2005; Walker et al., 2005), but in agreement with some earlier site-level studies in Western Siberia (Khitun, 1998; Rebristaya, 2013). We consider the following four main reasons for this consistent but somewhat unexpected increase in plot-level species richness from South-West to North-East in this vast Arctic plain:

1. Climatic gradients (temperature, precipitation, seasonality) do not follow the typical South-North direction of the northern hemisphere in our study region, which might be linked to increasing continentality from West to East, supporting a wider range of plant species. We show that contemporary climate has a strong impact on community-level species richness. Specifically, lower mean temperature in January and higher mean daily maximum air temperature during the warmest month are associated with higher species richness (see Appendix Fig. 1c,f). The combined impact of these two temperature factors is an indicator of continentality and has a positive influence on species richness.
2. Topographic variability: variations in elevation, slope, and aspect can create diverse microclimates and soil conditions, supporting a broader spectrum of plant species adapted to specific ecological niches within the landscape. The Gydan Peninsula in the East of our study area shows larger variation in topography compared to the rather flat Yamal and Taz Peninsulas. Topography has been shown to play an important while clearly secondary role as hilly areas with steeper slopes in coastal and northern Gydan show a higher species richness, as confirmed by our models (Fig. 2, Appendix Fig. 1e).
3. Anthropogenic factors: The patchy but rather low predicted species richness in the southern and western parts of the study area (especially in southern and central Yamal) might also partly result from a combination of intense reindeer herding and land use change related to gas extraction. Although we found some indication of anthropogenic

influence, we lack conclusive evidence to demonstrate that distance to infrastructure influences regional species richness on a broad spatial scale.

4. Historical factors: past geological and ecological events, such as sea level change, glaciation patterns, timing of post-glacial colonization, and post-glaciation climate change, can leave lasting legacies on vegetation patterns. The strong relationship between the contemporary status of vegetation and the history and (paleo)geography of the region was hypothesized to play a key role in earlier studies (Khitun, 1998; Rebristaya, 2013). Northern Gydan, which contained refugia during the last ice age (Khitun, 1998), has a higher richness than the Yamal Peninsula. The latter was completely covered by water during the middle Pleistocene and mostly during the late Pleistocene transgressions, while Gydan kept the terrestrial connections with the relatively rich Taymyr and Central Siberian floras (Khitun, 1998; Rebristaya, 2013). The transgressions from the middle to late Pleistocene fall outside the temporal extent of the paleoclimate dataset used in our study. However, we show that the current spatial distribution of species richness is well explained by late Pleistocene and Holocene paleoclimate, indicating a lasting impact of historical factors on species richness in the Western Siberian Arctic.

Several non-quantified factors might also influence the species richness pattern. The described inverse trend in mean community-level species richness over the West Siberian Arctic could be strengthened by high reindeer grazing densities in Southern Yamal, documented by previous studies (Veselkin et al., 2021). The North-east of Gydan is also characterized by soils generally less acidic than Yamal, Taz and South-West of Gydan permitting several arctic-alpine species to migrate from the east and contribute to the high species richness of the area (CAVM, 2003; Khitun, 1998). Unfortunately, there is a lack of comprehensive, high-resolution and spatially well-sampled data on soil pH and reindeer density, making it challenging to incorporate them in our models.

We conclude that plant species richness across the Western Siberian tundra is shaped by a combination of environmental and anthropogenic factors, whereby the

influence of (paleo-) climate factors is strongest. Our study shows that the capacity of nature reserves to protect plant species in our study area is limited because of the insufficient spatial coverage of areas with highest species richness. In addition to this finding, additional factors, such as the low spatial connectivity between protected areas, their focus on animal protection, and their often weak protection status are caveats for conservation efforts in this area (Barry et al., 2017; Kalyakin et al., 2000). Plant diversity protection requires a complex social-ecological approach that is up to be developed. More targeted evaluation of the impact of industrial development on plant species richness and active participation of Nenets people should be part of the approach towards an effective action plan to protect plant species and their ecosystem functions in the Western Siberian Arctic.

Data availability statement: Data available from the Dryad Digital Repository (<https://datadryad.org/stash/share/bFWEuics4lXhXfj2xvo4or1sUYa-WriskoarUuoVdeU>) (Zemlianskii et al., 2023).

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3.6 Figures and tables

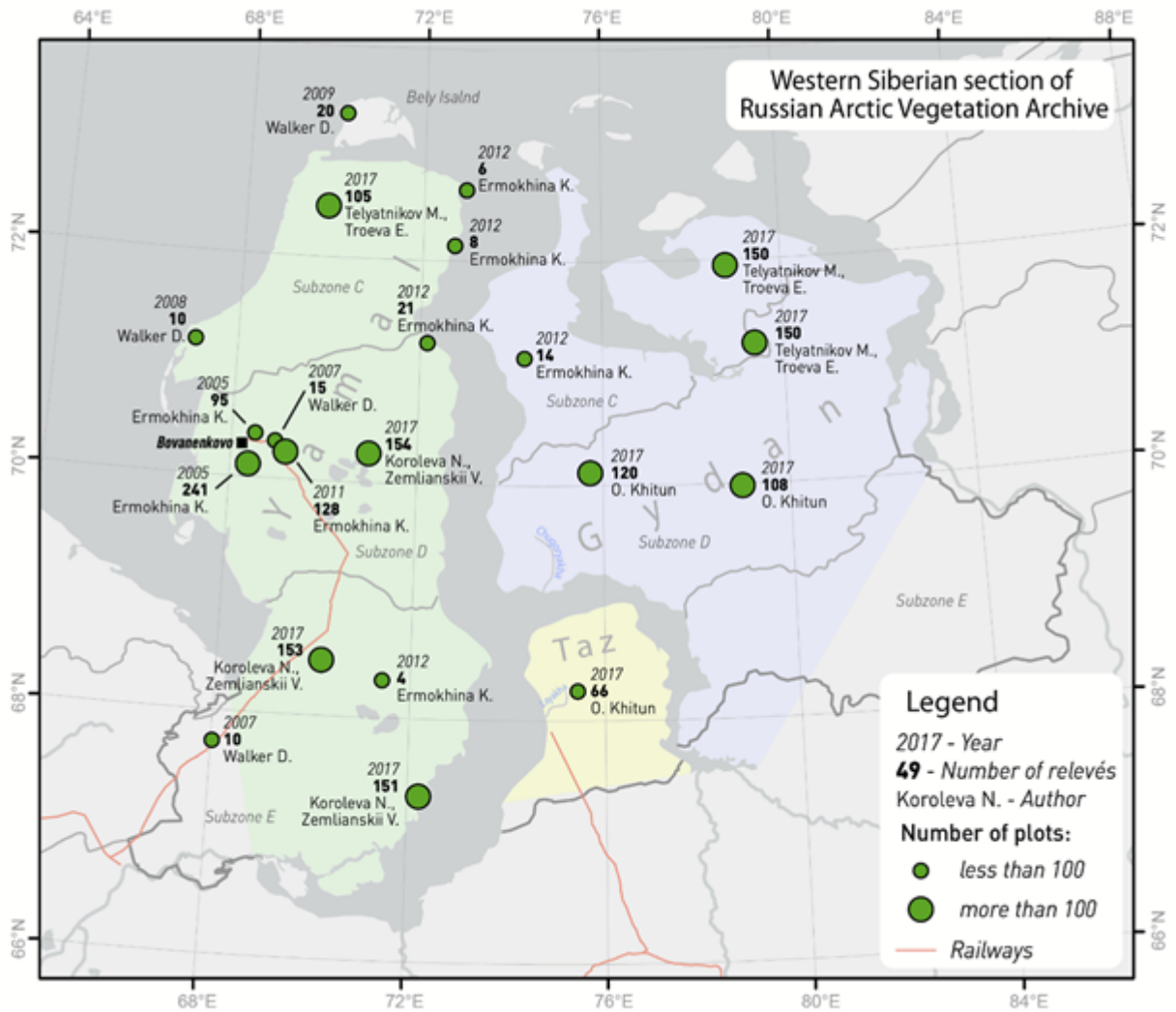


Figure 1. Western Siberian study area, including the location of the major study sites and respective number of geobotanical plots per site (= number of relevés). The Yamal Peninsula is shaded in green, Taz in yellow and Gydan in blue.

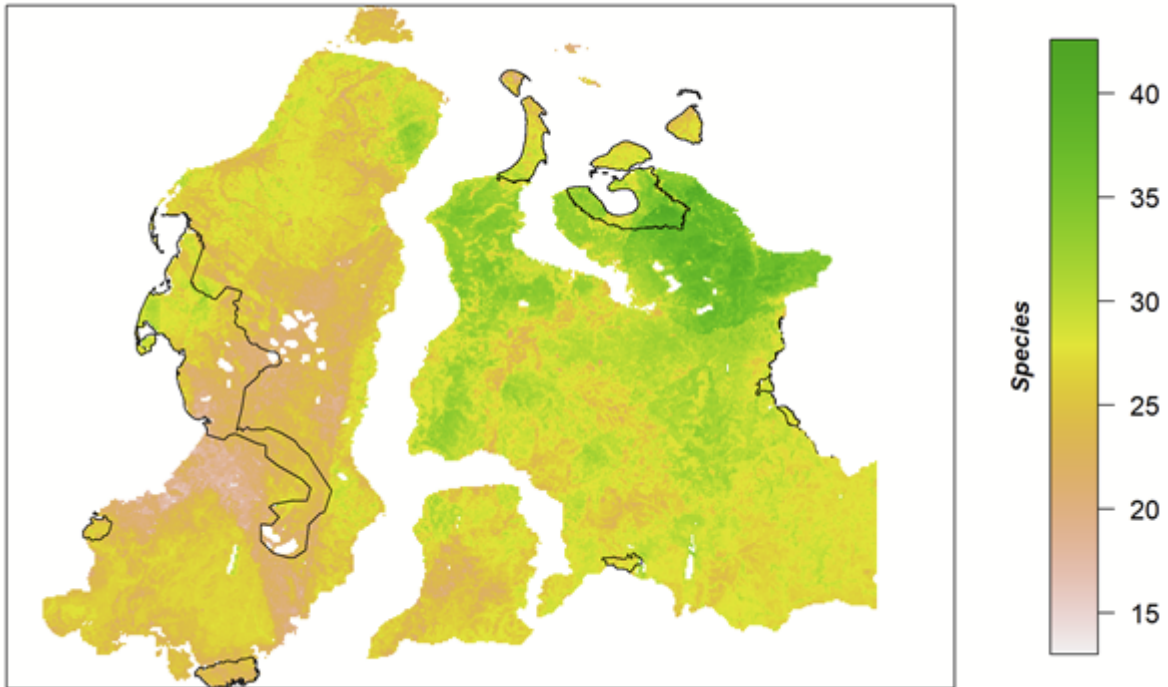


Figure 2. Mean plant species richness distribution in the Western Siberian tundra as predicted by a macroecological model ensemble based on a general additive (GAM), general linear (GLM), gradient boosting machine (GBM) and random forest (RF) model. Black borders show existing protected areas.

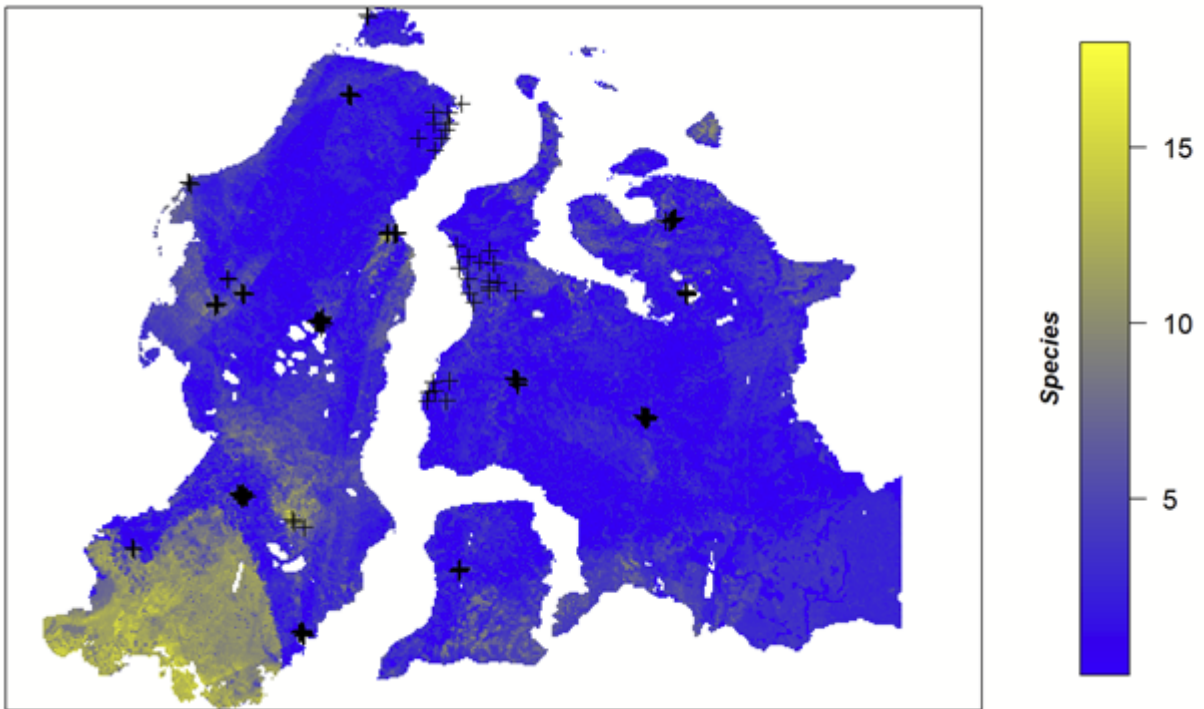


Figure 3. Model disagreement map indicating maximum difference in predicted species number between GAM, GLM, GBM and Random forest. Black crosses indicate geobotanical plot locations.

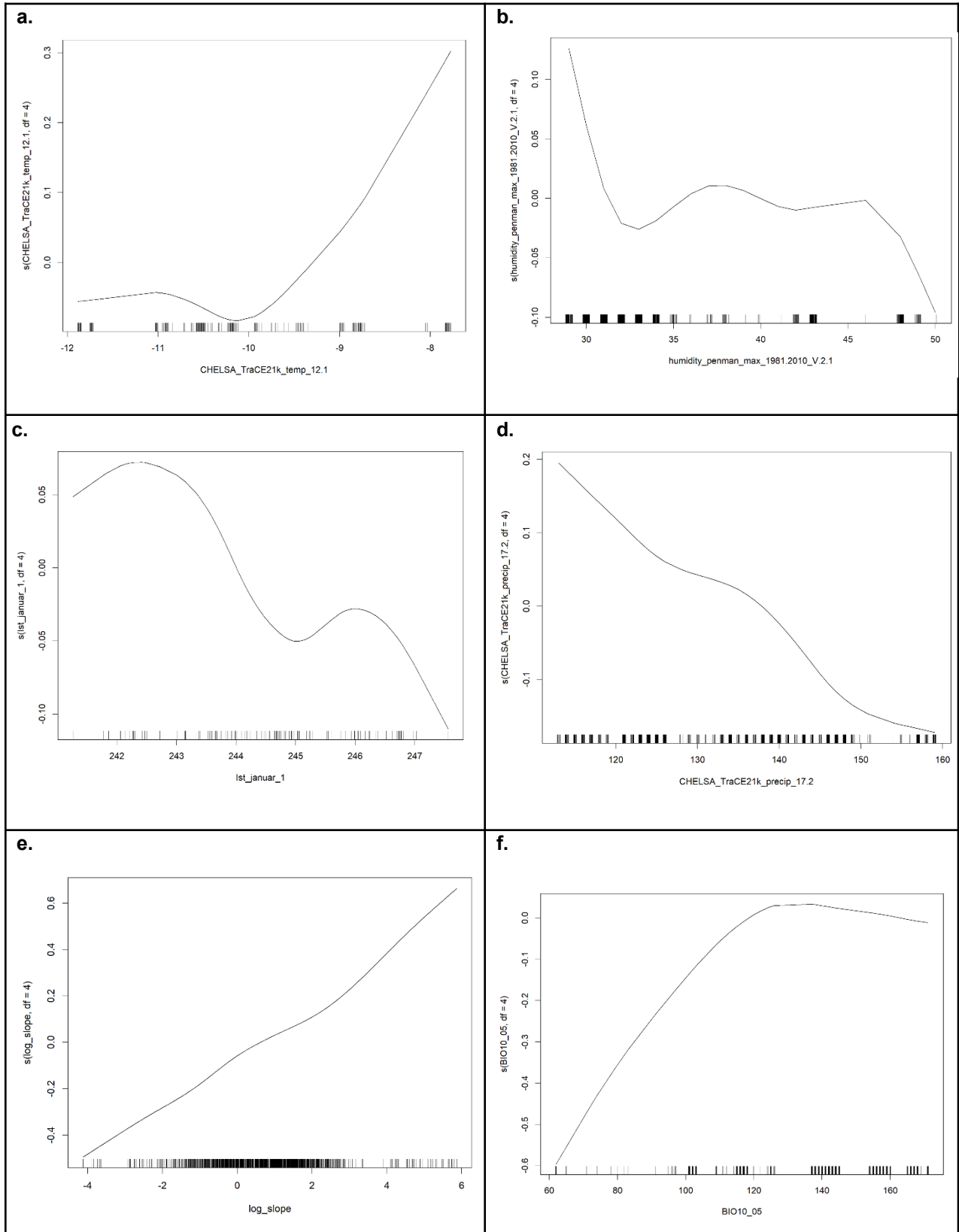
Table 1. Model performance statistics from 5-fold cross-validation (GLM = generalized linear model, GAM = generalized additive model, GBM = gradient boosting machine).

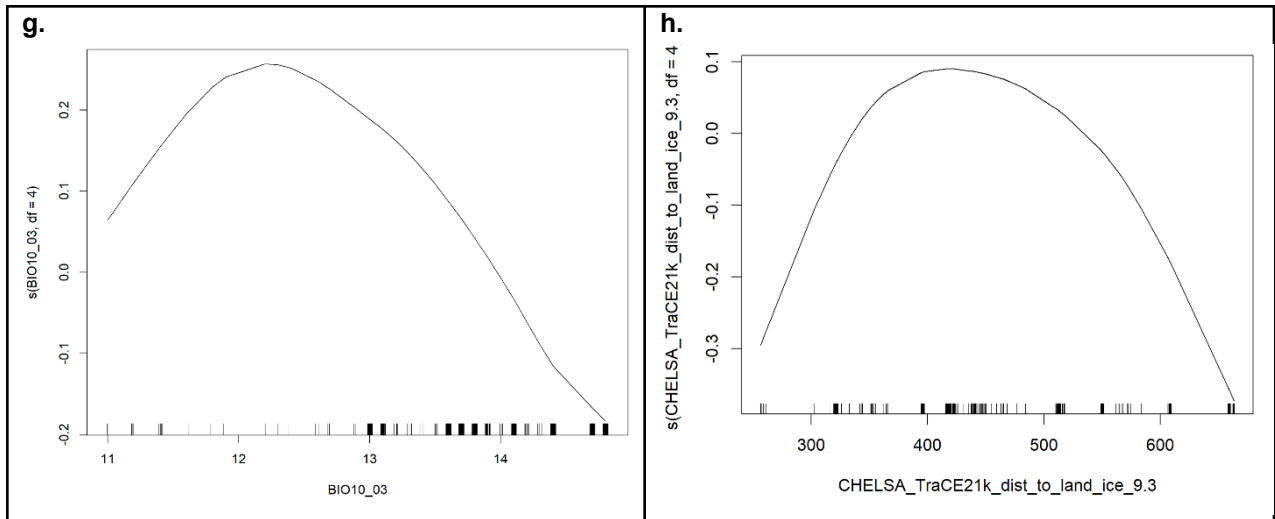
Model	Spearman correlation (0.58 on average)	Mean Absolute Error (8.1 on average)	Root Mean Square Error (10.2 on average)
GLM	0.60	8.0	10.1
Random Forest	0.57	8.2	10.1
GAM	0.56	8.2	10.2
GBM	0.59	8.0	10.5

Table 2. Environmental variables used in the model. The full list of evaluated variables is presented in Appendix, Table S1.

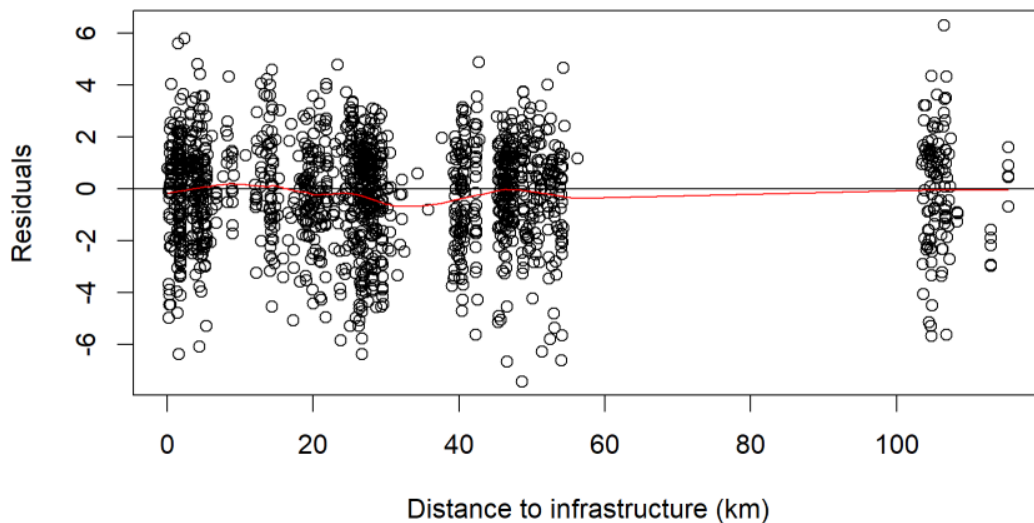
N	Predictors	Explained deviance (%)	Original spatial res. (m)	Source
1	Mean annual paleotemperature (12.100 years ago)	21	30 arcsec (<1000)	CHELSA-TraCE21k dataset (Karger et al., 2021)
2	Climate moisture index (max)	14	30 arcsec (<1000)	CHELSA new (Brun et al., 2022)
3	Mean January temperature	13	1000	MODIS derived 2000-2019 (MOD11A2 MODIS/Terra Land Surface Temperature/Emissivity 8-Day L3 Global 1km SIN Grid V006 [Dataset])
4	Mean annual paleoprecipitation (17.200 years ago)	12	30 arcsec (<1000)	CHELSA-TraCE21k dataset (Karger et al., 2021)
5	Mean daily maximum air temperature of the warmest month (BIO10_05)	11	30 arcsec (<1000)	CHELSA Bioclim (Karger et al., 2016)
6	Isothermality (BIO10_03)	10	30 arcsec (<1000)	CHELSA Bioclim (Karger et al., 2016)
7	(log transformed) slope	10	10	ArcticDEM based (Morin et al., 2016; Porter et al., 2018)
8	Distance to land ice (9300 years ago)	7	30 arcsec (<1000)	CHELSA-TraCE21k dataset (Karger et al., 2021)

3.7 Supporting information

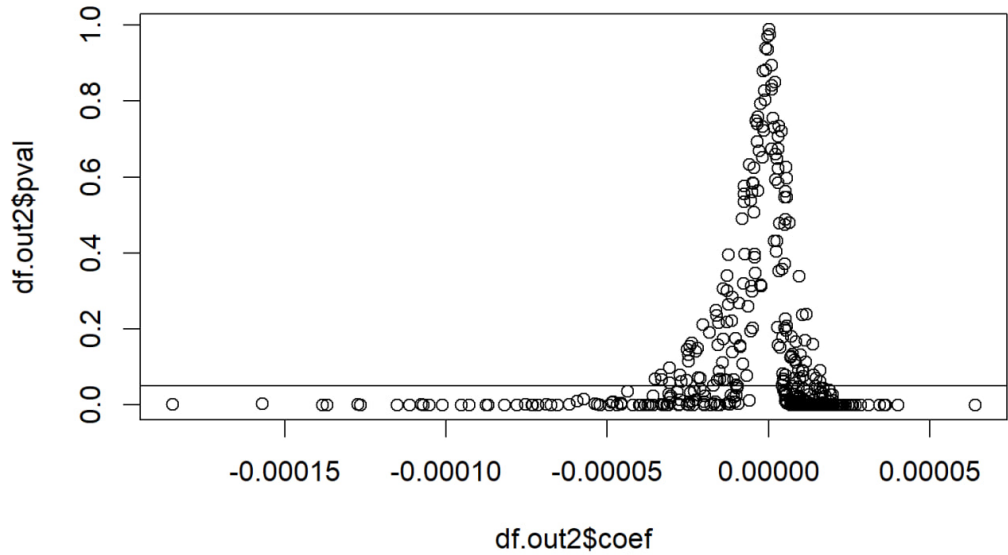




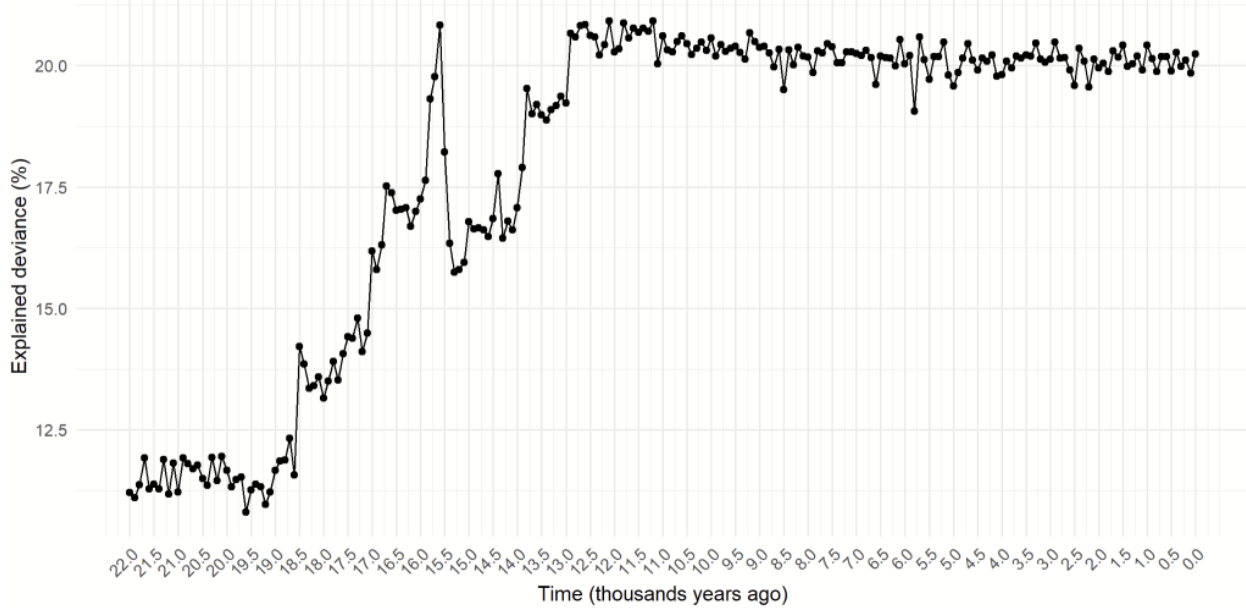
Appendix Figure 1. Response curves for all predictors used in the GAM model of community-level plant species richness of the Western Siberia Arctic region. Response curves are for **a.** 'Mean annual paleotemperature' (12.100 years ago) ($^{\circ}\text{C}$); **b.** 'Climate moisture index (max)' (humidity_penman_max); **c.** 'Mean january temperature' ($^{\circ}\text{K}$); **d.** 'Mean annual paleoprecipitation' (17.200 years ago) (mm); **e.** '(log transformed) slope'; **f.** 'Mean daily maximum air temperature of the warmest month (BIO10_05)' (0.1°C); **g.** 'Isothermality'; **h.** 'Distance to land ice' (9300 years ago) (km).



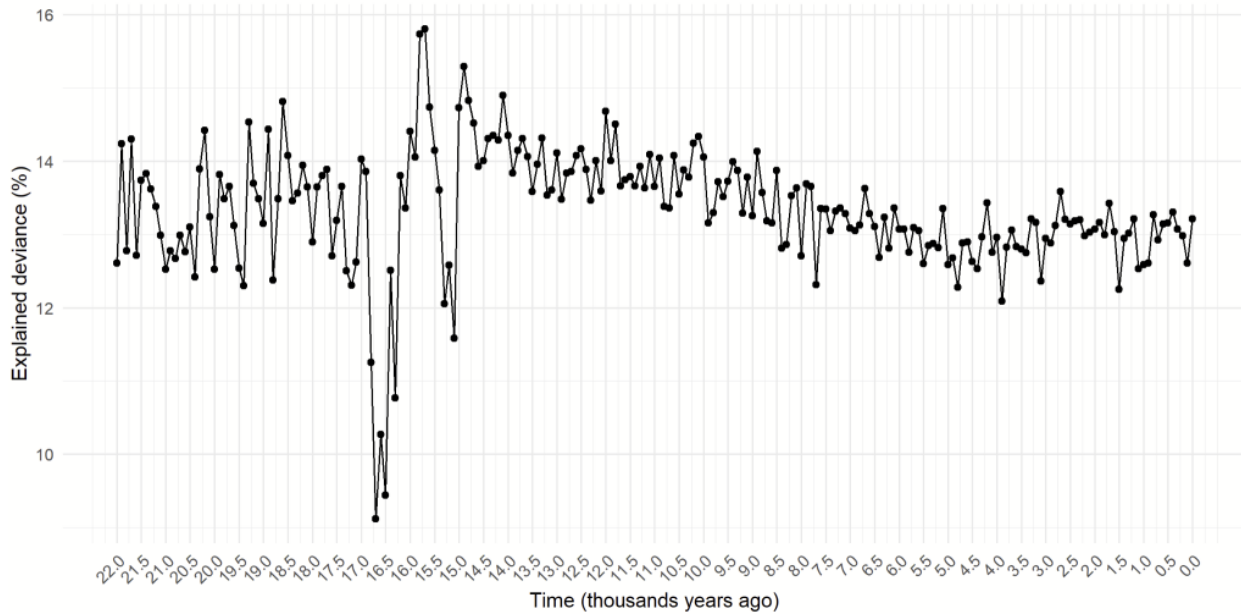
Appendix Figure 2. GAM residuals to distance to infrastructure. Loess function (span 0.3) is used to produce a trend line.



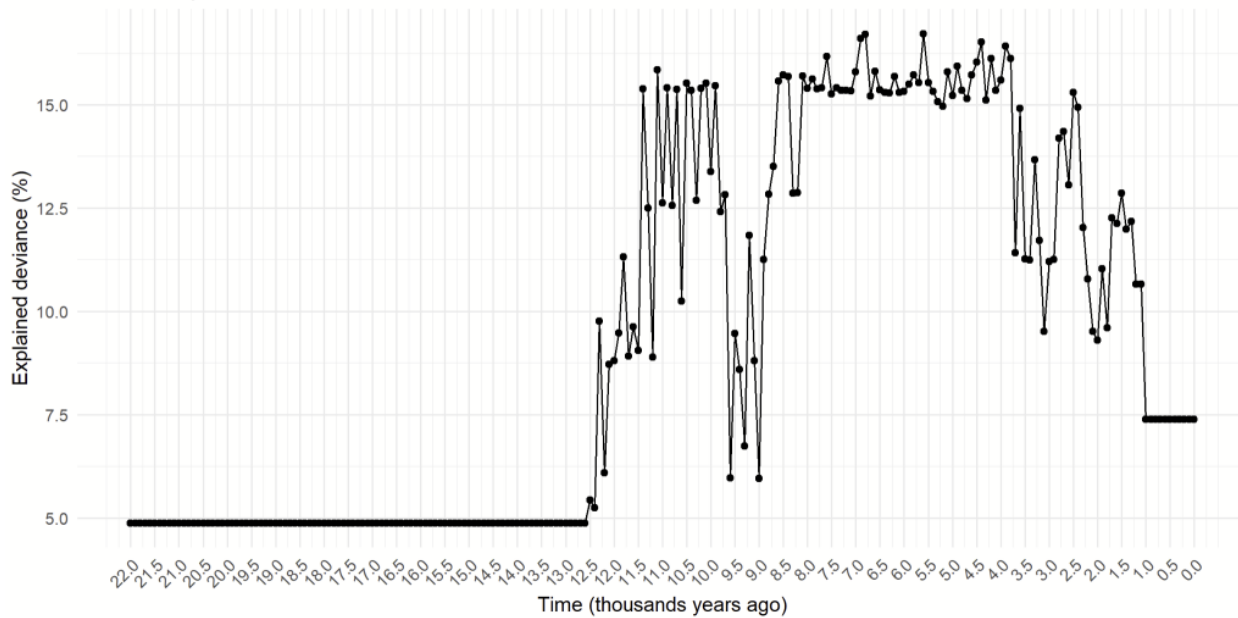
Appendix Figure 3. The relationships between the occurrences of each of the 840 species and distance to infrastructure. The x-axis displays the coefficients of logistic regression models and y-axis displays corresponding p-values. The black line is a threshold, separating statistically significant cases from insignificant ones.



Appendix Figure 4. Explained deviance of 'paleotemperature' throughout the time since the Last Glacial Maximum (22.000 years ago).



Appendix Figure 5. Explained deviance of 'paleoprecipitation' throughout the time since the Last Glacial Maximum (22.000 years ago).



Appendix Figure 6. Explained deviance of 'distance to land ice' predictor throughout the time since Last Glacial Maximum (22.000 years ago).

Appendix Table S1. Full list of tested predictors (green color shows selected predictors in final model, red color - predictors omitted because of their low predictive power, black color – left out due to high correlation with selected predictors). High correlation (>0.7) with other predictors indicated only for predictors with explained deviance higher than 5%. For paleoclimatic predictors explained deviance is given for the time period 12.100 years ago (highest PP tested) as well as for the time period used in the model.

N	Predictors	Explained deviance (%)	High correlation (>0.7) with other predictors	Orig. spatial res. (m)	Source
1	Mean annual temperature (12.100 years ago)	21.0	Mean annual precipitation (12.100 years ago), Mean annual air temperature, MGTM	1000	CHELSA TraCE21k dataset (Karger et al., 2021)
2	Longitude	21.0	Mean January temperature (negative), distance to infrastructure (0.72), temperature seasonality (0.72), climate moisture index range, potential evapotranspiration min (negative)	-	-
3	Mean monthly precipitation amount of the warmest quarter (bio10_18)	20.8	Growing degree days heat sum above 5°C, mean July temperature, MGTM, mean potential evapotranspiration, mean daily maximum air temperature of the warmest month, mean daily mean air temperatures of the warmest quarter (0.74), mean daily mean air temperatures of the wettest quarter, precipitation amount of the wettest month, annual precipitation amount, precipitation seasonality, mean monthly precipitation amount of the warmest quarter; latitude (negative)	1000	CHELSA Bioclim (Karger et al., 2016)
4	Mean annual air temperature (bio10_01)	20.1	Mean July temperature, MGTM, mean potential evapotranspiration, mean daily minimum air temperature of the coldest month, mean daily mean air temperatures of the wettest quarter, mean daily mean air temperatures of the coldest quarter, annual precipitation amount, precipitation amount of the wettest month, mean monthly precipitation amount of the wettest quarter, mean monthly precipitation amount of the warmest quarter; latitude (negative)	1000	CHELSA Bioclim (Karger et al., 2016)

5	Mean annual ground temperatures (MGTM)	18.9	Mean annual air temperature, mean July temperature, mean potential evapotranspiration, mean daily minimum air temperature of the coldest month, mean daily mean air temperatures of the wettest quarter, mean daily mean air temperatures of the coldest quarter, annual precipitation amount, precipitation amount of the wettest month, mean monthly precipitation amount of the wettest quarter, mean monthly precipitation amount of the warmest quarter; latitude (negative), paleotemperature	1000	Global Permafrost project (Obu et al., 2019)
6	Mean monthly precipitation amount of the wettest quarter (bio10_16)	17.9	Growing degree days heat sum above 5°C, mean July temperature, MGTM, mean potential evapotranspiration, mean daily maximum air temperature of the warmest month, mean daily mean air temperatures of the warmest quarter, mean daily mean air temperatures of the wettest quarter, precipitation amount of the wettest month, annual precipitation amount, precipitation seasonality, mean monthly precipitation amount of the warmest quarter; latitude (negative)	1000	CHELSA Bioclim (Karger et al., 2016)
7	Precipitation amount of the wettest month (bio10_13)	17.6	Mean annual air temperature, growing degree days heat sum above 5°C, mean July temperature, MGTM, mean potential evapotranspiration, mean daily maximum air temperature of the warmest month, mean daily minimum air temperature of the coldest month, mean daily mean air temperatures of the warmest quarter, mean daily mean air temperatures of the wettest quarter, annual precipitation amount, precipitation seasonality, mean monthly precipitation amount of the wettest quarter, mean monthly precipitation amount of the warmest quarter	1000	CHELSA Bioclim (Karger et al., 2016)
8	Mean annual precipitation (12.100 years ago)	17.6	MGTM, paleo temperature	1000	CHELSA TraCE21k dataset (Karger et al., 2021)
9	Potential evapotranspiration min	16.6	Longitude (negative)	1000	CHELSA new (Brun et al., 2022)

	(pet_penman_min_1981_2010)				
10	Precipitation seasonality (bio10_15)	16.1	Precipitation amount of the wettest month, mean monthly precipitation amount of the wettest quarter, mean monthly precipitation amount of the warmest quarter and MGTM (0.7); Mean daily mean air temperatures of the driest quarter (negative)	1000	CHELSA Bioclim (Karger et al., 2016)
11	Latitude	15.0	Negative: mean annual air temperature, growing degree days heat sum above 5°C, mean July temperature, MGTM, mean potential evapotranspiration, mean daily maximum air temperature of the warmest month, mean daily mean air temperatures of the wettest quarter, mean daily mean air temperatures of the warmest quarter, annual precipitation amount, precipitation amount of the wettest month, mean monthly precipitation amount of the wettest quarter, mean monthly precipitation amount of the warmest quarter	-	-
12	Mean July Temperature (K) (lst_july)	14.7	Mean annual air temperature, MGTM, mean potential evapotranspiration, mean daily mean air temperatures of the wettest quarter, annual precipitation amount, precipitation amount of the wettest month, mean monthly precipitation amount of the wettest quarter, mean monthly precipitation amount of the warmest quarter; longitude (negative)	1000	MODIS derived 2000-2019 (MOD11A2 MODIS/Terr a Land Surface Temperature /Emissivity 8-Day L3 Global 1km SIN Grid V006 [Data set])
13	Mean daily mean air temperatures of the coldest quarter (bio10_11)	14.1	Mean annual air temperature, MGTM	1000	CHELSA Bioclim (Karger et al., 2016)
14	Climate moisture index max (humidity_penman_max_1981_2010)	14.0	Climate moisture index mean	1000	CHELSA new (Brun et al., 2022)

15	Mean daily mean air temperatures of the driest quarter (bio10_09)	13.9	Precipitation seasonality (negative)	1000	CHELSA Bioclim (Karger et al., 2016)
16	Mean daily minimum air temperature of the coldest month (bio10_06)	12.9	Mean annual air temperature, MGTM, mean daily mean air temperatures of the coldest quarter, precipitation amount of the wettest month	1000	CHELSA Bioclim (Karger et al., 2016)
17	Mean daily mean air temperatures of the wettest quarter (bio10_08)	12.8	Mean annual air temperature, growing degree days heat sum above 5°C, mean July temperature, MGTM, mean potential evapotranspiration, mean daily mean air temperatures of the warmest quarter, annual precipitation amount, precipitation amount of the wettest month, mean monthly precipitation amount of the wettest quarter, mean monthly precipitation amount of the warmest quarter; longitude (negative)	1000	CHELSA Bioclim (Karger et al., 2016)
18	Mean January temperature (K) (lst_january)	12.6	Longitude (negative), climate moisture index range (0.7)	1000	MODIS derived 2000-2019 (MOD11A2 MODIS/Terra Land Surface Temperature /Emissivity 8-Day L3 Global 1km SIN Grid V006 [Data set])
19	Annual precipitation amount (bio10_12)	12.4	Mean annual air temperature, growing degree days heat sum above 5°C, mean July temperature, MGTM, mean potential evapotranspiration, mean daily maximum air temperature of the warmest month, mean daily mean air temperatures of the wettest quarter, mean daily mean air temperatures of the warmest quarter, precipitation amount of the wettest month, mean monthly precipitation amount of the driest quarter, mean monthly precipitation amount of the wettest quarter, mean monthly precipitation amount of the warmest quarter; latitude (negative)	1000	CHELSA Bioclim (Karger et al., 2016)

20	Mean annual precipitation (17.200 years ago)	12.3		1000	CHELSA TraCE21k dataset (Karger et al., 2021)
21	Distance to land ice (12.100 years ago)	12.1	MGTM, paleo temperature	1000	CHELSA TraCE21k dataset (Karger et al., 2021)
22	Climate moisture index range (humidity_penman_range_1981_2010)	11.1	Longitude, temperature seasonality	1000	CHELSA Bioclim (Karger et al., 2016)
23	Mean daily maximum air temperature of the warmest month (bio10_05)	10.8	Growing degree days heat sum above 5°C, mean potential evapotranspiration, mean daily mean air temperatures of the warmest quarter, annual precipitation amount, precipitation amount of the wettest month, mean monthly precipitation amount of the wettest quarter, mean monthly precipitation amount of the warmest quarter, mean monthly precipitation amount of the wettest quarter, mean monthly precipitation amount of the warmest quarter; latitude (negative)	1000	CHELSA Bioclim (Karger et al., 2016)
24	Distance to infrastructure	10.8	Longitude	-	OSM based (https://www.openstreetmap.org/)
25	Growing degree days heat sum above 5°C (gdd_5_1979_2013)	10.7	Mean July temperature, mean monthly precipitation amount of the warmest quarter, mean potential evapotranspiration, mean daily maximum air temperature of the warmest month, mean daily mean air temperatures of the warmest quarter, mean daily mean air temperatures of the wettest quarter, mean daily mean air temperatures of the warmest quarter, annual precipitation amount, precipitation amount of the wettest month, mean monthly precipitation amount of the wettest quarter; longitude (negative)	1000	CHELSA new (Brun et al., 2022)

26	Isothermality (bio10_03)	10.3	Cloud area fraction (negative, -0.72)	1000	CHELSA Bioclim (Karger et al., 2016)
27	Log transformed slope	9.6	-	10	ArcticDEM based (Morin et al., 2016)
28	Mean potential evapotranspiration (pet_penman_mean_1981_2010)	9.3	MGTM, mean annual air temperature, growing degree days heat sum above 5°C, mean July temperature, mean daily maximum air temperature of the warmest month, mean daily mean air temperatures of the wettest quarter, mean daily mean air temperatures of the warmest quarter, annual precipitation amount, precipitation amount of the wettest month, mean monthly precipitation amount of the wettest quarter, mean monthly precipitation amount of the warmest quarter	1000	CHELSA new (Brun et al., 2022)
29	Mean daily mean air temperatures of the warmest quarter (bio10_10)	9.3	Mean monthly precipitation amount of the warmest quarter, latitude, growing degree days heat sum above 5°C, mean, max and range potential evapotranspiration; latitude (negative)	1000	CHELSA Bioclim (Karger et al., 2016)
30	Climate moisture index mean (humidity_penman_mean_1981_2010)	9.2	Climate moisture index max, site water balance	1000	CHELSA new (Brun et al., 2022)
31	Site water balance (swb_1981_2010)	8.4	Climate moisture index mean	1000	CHELSA new (Brun et al., 2022)
32	Cloud area fraction (tcc_max_1981_2010)	7.1	Isothermality	1000	CHELSA new (Brun et al., 2022)
33	Distance to land ice (9.300 years ago)	6.7		1000	CHELSA TraCE21k dataset (Karger et al., 2021)

34	Mean monthly precipitation amount of the driest quarter (bio10_17)	6.7	Annual precipitation amount	1000	CHELSA Bioclim (Karger et al., 2016)
35	Standard deviation of altitude	6.1	Standard deviation of altitude	10	ArcticDEM based (Morin et al., 2016)
36	Slope	5.6	Mean wind speed	10	ArcticDEM based (Morin et al., 2016)
37	Mean wind speed	5.4	Slope	100	Global Wind Atlas (https://globalwindatlas.info/)
38	Temperature seasonality (bio10_04)	5.1	Climate moisture index range, longitude, mean daily minimum air temperature of the coldest month, mean daily mean air temperatures of the coldest quarter	1000	CHELSA Bioclim (Karger et al., 2016)
39	Incidence angle raster map	5.1		10	ArcticDEM based (Morin et al., 2016)
40	Beam irradiance	4.7		10	ArcticDEM based (Morin et al., 2016)
41	Mean monthly precipitation amount of the coldest quarter (bio10_19)	3.5		1000	CHELSA Bioclim (Karger et al., 2016)
42	Mean diurnal air temperature range (bio10_02)	3.3		1000	CHELSA Bioclim (Karger et al., 2016)
43	Diffuse irradiance	3.3		10	ArcticDEM based (Morin et al., 2016)
44	Paleoaltitude	3.2		1000	CHELSA TraCE21k

					dataset (Karger et al., 2021)
45	Global (total) irradiance	3		10	ArcticDEM based (Morin et al., 2016)
46	Precipitation amount of the driest month (bio10_14)	2.7		1000	CHELSA Bioclim (Karger et al., 2016)
46	Terrain wetness index	2.6		1000	High resolution global topographic index values (Marthews et. al., 2015)
47	NDVI	2.6		1000	Sentinel derived (JuneAugust 2019-2020)
48	pet_penman_max_1981_2010	1.8		1000	CHELSA new (Brun et al., 2022)
49	Topographic position index	1.7		10	ArcticDEM based (Morin et al., 2016)
50	pet_penman_range_1981_2010	1.6		1000	CHELSA new (Brun et al., 2022)
51	Annual range of air temperature (bio10_07)	1.3		1000	CHELSA Bioclim (Karger et al., 2016)
52	Climate moisture index min (humidity_penman_min_1981_2010)	1.0		1000	CHELSA new (Brun et al., 2022)
53	modcf_intraannualsd_1	0.9		1000	CHELSA Bioclim (Karger et al., 2016)
54	Aspect	0.9		10	ArcticDEM based (Morin et al., 2016)

55	Altitude	0.2		10	ArcticDEM based (Morin et al., 2016)
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Appendix Table S2. Full list of species tested for their relationship to distance to infrastructure (green species name color indicates statistically significant positive relationships, blue indicates negative, and yellow cell color signifies species with highly statistically significant relationships to distance from infrastructure), sorted from minimum to maximum p-value. Only species with at least 10 occurrences were included in the test.

Species name	coefficient	p-value
<i>Sphagnum riparium</i> Ångstr.	0.000064	<0.000001
<i>Andromeda polifolia</i> s. <i>pumila</i> V.M. Vinogr.	0.000040	<0.000001
<i>Salix pulchra</i> Cham.	0.000026	<0.000001
<i>Sphenolobus minutus</i> Schreb. Berggr.	0.000025	<0.000001
<i>Ptilidium ciliare</i> L. Hampe	0.000023	<0.000001
<i>Aulacomnium turgidum</i> Wahlenb. Schwaegr.	0.000022	<0.000001
<i>Stellaria longipes</i> taxon <i>peduncularis</i>	0.000023	<0.000001
<i>Arctagrostis latifolia</i> Br. Griseb.	0.000021	<0.000001
<i>Cetraria laevigata</i> Rass.	0.000022	<0.000001
<i>Dicranum elongatum</i> Schleich. ex Schwaegr.	0.000017	<0.000001
<i>Dryas punctata</i> Juz.	0.000021	<0.000001
<i>Cladonia chlorophaea</i> Somm. Spreng.	0.000022	<0.000001
Unknown liverwort	0.000022	<0.000001
<i>Pedicularis labradorica</i> Wirsing	0.000034	<0.000001
<i>Valeriana capitata</i> Pall. ex Link	0.000019	<0.000001
<i>Sphagnum balticum</i> Russ. C. Jens.	0.000021	<0.000001
<i>Calamagrostis holmii</i> Lange	0.000017	<0.000001
<i>Minuartia macrocarpa</i> Pursh. Ostenf.	0.000026	<0.000001
<i>Vaccinium vitis-idaea</i> s. <i>minus</i> Lodd. Hultén	0.000015	<0.000001
<i>Rhododendron tomentosum</i> s. <i>decumbens</i> Aiton. Elven. D.F. Murray	0.000015	<0.000001
<i>Micranthes nelsoniana</i> D. Don. Small	0.000018	<0.000001
<i>Tomentypnum nitens</i> Hedw. Loeske	0.000018	<0.000001
<i>Carex concolor</i> R. Br.	0.000015	<0.000001
<i>Dactylina arctica</i> Richardson. Nyl.	0.000014	<0.000001
<i>Eriophorum angustifolium</i> Honck.	0.000014	<0.000001
<i>Eriophorum vaginatum</i> L.	0.000015	<0.000001
<i>Pedicularis oederi</i> Vahl	0.000017	<0.000001

<i>Tofieldia coccinea</i> Richardson	0.000029	<0.000001
<i>Myosotis alpestris</i> s. <i>asiatica</i> Vestergr.	0.000019	<0.000001
<i>Festuca brachyphylla</i> Schult.	0.000036	<0.000001
<i>Pedicularis interior</i> Hultén. Molau. D.F. Murray	0.000021	<0.000001
<i>Lagotis glauca</i> s. <i>minor</i> Willd Hultén	0.000015	<0.000001
<i>Luzula kjellmaniana</i> Miyabe. Kudô	0.000020	<0.000001
<i>Sphagnum squarrosum</i> Crome	0.000019	<0.000001
<i>Dactylina ramulosa</i> Hook. Tuck.	0.000036	<0.000001
<i>Poa arctica</i> R. Br.	0.000013	<0.000001
<i>Eriophorum tolmatchevii</i> M.S. Novos.	0.000021	<0.000001
<i>Asahinea chrysantha</i> Tuck. Culb. C.Culb.	0.000023	<0.000001
<i>Poa arctica</i> s. <i>arctica</i> R. Br.	0.000025	<0.000001
<i>Ranunculus subborealis</i> s. <i>subborealis</i> Tzvelev	0.000015	<0.000001
<i>Salix lanata</i> v. <i>lanata</i> L.	0.000012	<0.000001
<i>Polytrichum juniperinum</i> Hedw.	0.000012	<0.000001
<i>Pedicularis lapponica</i> L.	0.000016	<0.000001
<i>Cladonia pleurota</i> Flörke. Schaer.	0.000014	<0.000001
<i>Saxifraga hirculus</i> L.	0.000021	0.000001
<i>Cladonia gracilis</i> s. lat. L. Willd.	0.000010	0.000001
<i>Sphagnum capillifolium</i> Ehrh. Hedw.	0.000036	0.000001
<i>Parrya nudicaulis</i> L. Regel	0.000016	0.000001
<i>Dicranum spadiceum</i> J. E. Zetterst.	0.000010	0.000003
<i>Lloydia serotina</i> L. Rchb.	0.000018	0.000003
<i>Distichium capillaceum</i> Hedw. Bruch. Schimp.	0.000024	0.000003
<i>Ditrichum flexicaule</i> Schwaegr. Hampe	0.000020	0.000004
<i>Sanionia uncinata</i> Hedw. Loeske	0.000010	0.000004
<i>Eutrema edwardsii</i> R. Br.	0.000019	0.000006
<i>Cladonia cornuta</i> L. Hoffm.	0.000017	0.000007
<i>Bryum species</i>	0.000031	0.000007
<i>Polytrichum hyperboreum</i> R. Br.	0.000010	0.000010
<i>Pertusaria dactylina</i> Ach. Nyl.	0.000018	0.000011
<i>Cardamine polemonioides</i> Rouy	0.000017	0.000012
<i>Salix myrtilloides</i> L.	0.000016	0.000012
<i>Vaccinium uliginosum</i> s. <i>microphyllum</i> Lange. Tolm.	0.000009	0.000013
<i>Pedicularis verticillata</i> L.	0.000019	0.000014
<i>Pleurozium schreberi</i> Willdenow ex Brid. Mitt.	0.000011	0.000014
<i>Salix reptans</i> Rupr.	0.000012	0.000017
<i>Pohlia cruda</i> Hedw. Lindb.	0.000020	0.000018
<i>Warnstorfia exannulata</i> Schimp. Loeske	0.000017	0.000022
<i>Peltigera didactyla</i> s. lat. With. Laundon	0.000027	0.000025
<i>Huperzia arctica</i> Grossh. ex Tolm. Sipliv.	0.000017	0.000026

<i>Eriophorum brachyantherum</i> Trautv. C.A. Mey.	0.000023	0.000033
<i>Polytrichum jensenii</i> I. Hagen	0.000014	0.000034
<i>Poa pratensis</i> s. <i>alpigena</i> Lindm. Hiitonen	0.000011	0.000042
<i>Hedysarum hedysaroides</i> s. <i>arcticum</i> B. Fedtsch. P.W. Ball	0.000019	0.000042
<i>Cladonia stygia</i> Fr. Ruoss	0.000009	0.000055
<i>Limprichtia revolvens</i> Swartz. Loeske	0.000017	0.000060
<i>Pyrola grandiflora</i> s. <i>norvegica</i> Knaben. A. Löve D. Löve	0.000019	0.000077
<i>Sphagnum russowii</i> Warnst.	0.000023	0.000185
<i>Cerastium regelii</i> taxon <i>jenisejense</i> Hultén.	0.000026	0.000196
<i>Aulacomnium palustre</i> Hedw. Schwaegr.	0.000008	0.000198
<i>Cerastium regelii</i> Ostenf.	0.000017	0.000200
<i>Alopecurus borealis</i> Trin.	0.000009	0.000216
<i>Calliergon cordifolium</i> Hedw. Kindb.	0.000019	0.000223
<i>Drepanocladus</i> species	0.000018	0.000246
<i>Alectoria ochroleuca</i> Hoffm. Massal.	0.000008	0.000289
<i>Carex bigelowii</i> s. <i>ensifolia</i> Turcz. ex Ledeb. ined.	0.000007	0.000345
<i>Plagiomnium ellipticum</i> Brid. T. Kop.	0.000016	0.000350
<i>Petasites frigidus</i> L. Fr.	0.000009	0.000434
<i>Micranthes hieraciifolia</i> Waldst. Kit. ex Willd. Haw.	0.000015	0.000488
<i>Hylocomium splendens</i> Hedw. Schimp.	0.000007	0.000595
<i>Cetraria islandica</i> L. Ach.	0.000007	0.000611
<i>Sphagnum fimbriatum</i> Wils.	0.000017	0.000623
<i>Arctocetraria andrejevii</i> Oxner. Kärnefelt Thell	0.000012	0.000771
<i>Chrysosplenium alternifolium</i> L.	0.000018	0.001110
<i>Carex rariflora</i> Wahlenb Sm.	0.000009	0.001133
<i>Dryas</i> species	0.000018	0.001266
<i>Bistorta vivipara</i> L. Delarbre	0.000007	0.001282
<i>Cladonia cyanipes</i> Sommerf. Nyl.	0.000019	0.001299
<i>Rhytidium rugosum</i> Ehrh. ex Hedw. Kindb.	0.000012	0.001406
<i>Cerastium maximum</i> L.	0.000018	0.001460
<i>Micranthes nivalis</i> L. Small	0.000016	0.001529
<i>Astragalus alpinus</i> L.	0.000018	0.001622
<i>Peltigera membranacea</i> Ach. Nyl.	0.000012	0.002161
<i>Sphagnum compactum</i> Lam. DC.	0.000014	0.002175
<i>Coptidium lapponicum</i> L. Tzvelev	0.000014	0.002511
<i>Festuca ovina</i> s. <i>ovina</i> . L.	0.000008	0.002666
<i>Plagiomnium</i> species	0.000019	0.002745
<i>Caltha palustris</i> s. <i>radicans</i> T.F. Forst. Syme	0.000013	0.002790
<i>Chrysosplenium alternifolium</i> s. <i>sibiricum</i> Ser. ex DC. Hultén	0.000019	0.002910
<i>Pedicularis albolabiata</i> Hultén. Kozhevnik.	0.000013	0.003102
<i>Dupontia fisheri</i> R. Br.	0.000013	0.003189

<i>Trisetum sibiricum</i> s. <i>litorale</i> Rupr. ex Roshev.	0.000018	0.003714
<i>Cladonia subfurcata</i> NyL. Arn.	0.000009	0.003821
<i>Rumex arcticus</i> Trautv.	0.000011	0.004952
<i>Racomitrium lanuginosum</i> Hedw. Brid.	0.000007	0.005480
<i>Nephroma expallidum</i> NyL. Nyl.	0.000008	0.005518
<i>Juncus biglumis</i> L.	0.000016	0.005531
<i>Cladonia arbuscula</i> s. lat. Wallr. Hale. W.Culb.	0.000006	0.005653
<i>Luzula confusa</i> Lindeb.	0.000006	0.005955
<i>Flavocetraria cucullata</i> Bell. Kärnefelt. Thell	0.000005	0.006498
<i>Ranunculus nivalis</i> L.	0.000015	0.007538
<i>Ranunculus monophyllus</i> Ovcz. s. lat.	0.000017	0.007907
<i>Orthocaulis binsteadii</i> Kaal. H.Buch	0.000012	0.008714
<i>Campylium polygamum</i> Schimp. C. Jens.	0.000019	0.009001
<i>Poa alpina</i> L.	0.000012	0.009554
<i>Pyrola grandiflora</i> Radius	0.000009	0.009929
<i>Bistorta elliptica</i> Willd. ex Spreng. Kom. ex V.V. Petrovsky	0.000008	0.010558
<i>Saxifraga cernua</i> L.	0.000009	0.010613
<i>Carex chordorrhiza</i> Ehrh. ex L. f.	0.000012	0.010776
<i>Betula nana</i> L.	0.000005	0.011160
<i>Gymnomitrium corallioides</i> Nees	0.000011	0.011695
<i>Brachythecium albicans</i> Hedw. B.S.G.	0.000020	0.013121
<i>Astragalus alpinus</i> v. <i>arcticus</i> Sond.n. Lindm.	0.000011	0.013921
<i>Salix polaris</i> Wahlenb.	0.000005	0.014178
<i>Carex rotundata</i> Wahlenb.	0.000007	0.014638
<i>Sphagnum rubellum</i> Wils.	0.000014	0.014707
<i>Lobaria linita</i> Ach. Rabenh.	0.000009	0.016445
<i>Lophozia ventricosa</i> v. <i>longiflora</i> Nees. Macoun	0.000016	0.018996
<i>Hypnum species</i>	0.000010	0.021583
<i>Vaccinium uliginosum</i> L.	0.000008	0.021780
<i>Drepanocladus aduncus</i> Hedw. Warnst.	0.000018	0.024675
<i>Tritomaria quinqueidentata</i> Huds. H.Buch	0.000010	0.025226
<i>Rubus chamaemorus</i> L.	0.000005	0.026845
<i>Nephroma arcticum</i> L. Torss.	0.000012	0.027251
<i>Cladonia subcervicornis</i> Vain. Kernst.	0.000020	0.027609
<i>Pohlia nutans</i> Hedw. Lindb.	0.000006	0.027707
<i>Mnium blyttii</i> Bruch. Schimp.	0.000019	0.027902
<i>Claytonia species</i>	0.000017	0.029141
<i>Polytrichum piliferum</i> Hedw.	0.000007	0.029689
<i>Equisetum arvense</i> L.	0.000005	0.031055
<i>Lophozioopsis polaris</i> R. M. Schust. Konstant. Vilnet	0.000016	0.034495
<i>Gowardia nigricans</i> Ach. P.Halonen	0.000005	0.037191

<i>Cladonia deformis</i> L. Hoffm.	0.000012	0.037892
<i>Cetrariella delisei</i> Bory ex Schaer. Kärnefelt et A. Thell	0.000005	0.040208
<i>Flavocetraria nivalis</i> L. Kärnefelt. Thell	0.000004	0.040543
<i>Veratrum album</i> s. <i>misae</i> Sirj. Tzvelev	0.000019	0.040585
<i>Salix reticulata</i> L.	0.000014	0.042406
<i>Pertusaria panyrga</i> Ach. A. Massal.	0.000011	0.044404
<i>Coptidium pallasii</i> Schltld. Tzvelev	0.000016	0.045090
<i>Timmia austriaca</i> Hedw.	0.000017	0.045125
<i>Calamagrostis neglecta</i> s. <i>neglecta</i> Ehrh. P. Gaertn.	0.000009	0.048253
<i>Festuca rubra</i> s. <i>richardsonii</i> Hook. Hultén	-0.000037	<0.000001
<i>Calamagrostis neglecta</i> Ehrh. P. Gaertn.	-0.000072	<0.000001
<i>Andromeda polifolia</i> L.	-0.000052	<0.000001
<i>Calamagrostis species</i>	-0.000038	<0.000001
<i>Ranunculus subborealis</i> Tzvelev	-0.000105	<0.000001
<i>Polytrichastrum alpinum</i> v. <i>fragile</i> Bryhn. D. G. Long. Hedw. G. L. Sm.	-0.000088	<0.000001
<i>Cladonia species</i>	-0.000028	<0.000001
<i>Polytrichum strictum</i> Menzies ex Brid.	-0.000015	<0.000001
<i>Carex bigelowii</i> Torr.	-0.000137	<0.000001
<i>Stellaria crassifolia</i> Ehrh.	-0.000068	<0.000001
<i>Cladonia mitis</i> Sandst.	-0.000111	<0.000001
<i>Vaccinium vitis-idaea</i> L.	-0.000020	<0.000001
<i>Rhododendron tomentosum</i> s. <i>tomentosum</i> Stokes. Harmaja	-0.000093	0.000001
<i>Leptobryum pyriforme</i> Hedw. Wils.	-0.000107	0.000001
<i>Poa alpina</i> v. <i>vivipara</i> L.	-0.000138	0.000002
<i>Veratrum album</i> L.	-0.000036	0.000003
<i>Puccinellia sibirica</i> Holmb.	-0.000127	0.000004
<i>Poa species</i>	-0.000052	0.000006
<i>Arctous alpina</i> L. Nied.	-0.000016	0.000007
<i>Carex aquatilis</i> Wahlenb.	-0.000038	0.000011
<i>Lophozia ventricosa</i> Dicks. Dumort.	-0.000073	0.000023
<i>Dicranum brevifolium</i> Lindb. Lindb.	-0.000066	0.000037
<i>Pohlia prolifera</i> Kindb. Broth.	-0.000087	0.000074
<i>Oxycoccus microcarpus</i> Turcz. ex Rupr.	-0.000115	0.000192
<i>Salix hastata</i> L.	-0.000042	0.000239
<i>Tetraplodon mnioides</i> Swartz ex Hedw. Bruch. Schimp.	-0.000040	0.000247
<i>Cladonia fimbriata</i> L. Fr.	-0.000078	0.000253
<i>Salix phylicifolia</i> L.	-0.000018	0.000265
<i>Dicranella crispa</i> Hedw. Schimp.	-0.000082	0.000315
Unknown lichen crustose	-0.000073	0.000338
<i>Oxytropis sordida</i> Willd. Pers.	-0.000047	0.000380

<i>Pedicularis species</i>	-0.000032	0.000390
<i>Dicranum acutifolium</i> Lindb.. H. Arn. C. Jens.	-0.000025	0.000396
<i>Cerastium species</i>	-0.000040	0.000405
<i>Armeria maritima s. maritima</i> . Mill. Willd.	-0.000025	0.000571
<i>Oncophorus virens</i> Hedw. Brid.	-0.000031	0.000647
<i>Rubus arcticus</i> L.	-0.000033	0.000786
<i>Cetrariella fastigiata</i> Bory ex Schaerer. Kärnefelt et A. Thell	-0.000023	0.000800
<i>Cladonia decorticata</i> Flörke. Sprengel	-0.000101	0.001131
<i>Deschampsia brevifolia</i> R. Br.	-0.000095	0.001202
<i>Tripleurospermum maritimum s. phaeocephalum</i> Rupr. Hämet. Ahti	-0.000050	0.001233
<i>Aulacomnium species</i>	-0.000028	0.001499
<i>Peltigera scabrosa</i> Th. Fr.	-0.000012	0.001537
<i>Solidago virgaurea s. lapponica</i> With. Tzvelev	-0.000046	0.001566
<i>Festuca species</i>	-0.000033	0.001636
<i>Polytrichum commune</i> Hedw.	-0.000025	0.001646
<i>Cladonia borealis</i> Stenroos	-0.000053	0.001875
<i>Ochrolechia inaequatula</i> Nyl. Zahlbr.	-0.000185	0.001952
<i>Syntrichia ruralis</i> Hedw. Web.. D. Mohr	-0.000069	0.001988
<i>Pedicularis arctoeuropaea</i> Hultén. Molau. D.F. Murray	-0.000076	0.002088
<i>Cladonia macrophylla</i> Schaerer. Stenh.	-0.000062	0.002208
<i>Geranium krylovii</i> Tzvelev	-0.000108	0.002718
<i>Ceratodon purpureus</i> Hedw. Brid.	-0.000020	0.003016
<i>Amblystegium species</i>	-0.000032	0.003072
<i>Hypogymnia physodes</i> L. Nyl.	-0.000127	0.003080
<i>Tephrosieris atropurpurea</i> Ledeb. Holub	-0.000013	0.003179
<i>Chamaedaphne calyculata</i> L. Moench	-0.000157	0.003283
<i>Polemonium boreale</i> Adams	-0.000017	0.004011
<i>Arctocetraria nigricascens</i> Nyl. Elenkin	-0.000054	0.004223
<i>Tanacetum bipinnatum</i> L. Sch.Bip.	-0.000009	0.004532
<i>Equisetum pratense</i> Ehrh.	-0.000046	0.005474
<i>Dicranum scoparium</i> Hedw.	-0.000049	0.006865
<i>Antennaria dioica</i> L. Gaertn.	-0.000031	0.008018
<i>Juncus trifidus</i> L.	-0.000031	0.008097
<i>Eremogone polaris</i> Schischk. Ikonn.	-0.000020	0.008372
<i>Equisetum arvense s. alpestre</i> Wahlenb. Schönswetter. Elven	-0.000011	0.008609
<i>Alnus viridis s. fruticosa</i> Rupr. Nyman	-0.000017	0.008644
<i>Pohlia atropurpurea</i> Wahlenb. H. Lindb.	-0.000048	0.009293
<i>Parnassia palustris s. neogaea</i> Fernald. Hultén	-0.000025	0.009871
<i>Campanula rotundifolia</i> L.	-0.000012	0.009974
<i>Trichophorum cespitosum s. cespitosum</i> . L. Schur	-0.000059	0.010083
<i>Gymnomitrium species</i>	-0.000024	0.011222

<i>Salix nummularia</i> Andersson	-0.000006	0.013053
<i>Stereocaulon glareosum</i> Sav. Magn.	-0.000028	0.013632
<i>Kiaeria glacialis</i> Berggren. I. Hagen	-0.000023	0.014158
<i>Pertusaria geminipara</i> Th. Fr. C.Knight ex Brodo	-0.000057	0.015902
Unknown liverworts leafy	-0.000031	0.020045
<i>Polystichum species</i>	-0.000011	0.021009
<i>Racomitrium species</i>	-0.000020	0.023916
<i>Dicranella subulata</i> Hedw. Schimp.	-0.000030	0.023974
<i>Luzula species</i>	-0.000036	0.024911
<i>Pachypleurum alpinum</i> Ledeb.	-0.000010	0.025617
<i>Sphagnum warnstorffii</i> Russ.	-0.000012	0.026731
<i>Hamatocaulis lapponicus</i> Norrlin. Hedenas	-0.000031	0.029834
<i>Schljakovia kunzeana</i> Huebener. Konstant.. Vilnet	-0.000024	0.033616
<i>Diapensia lapponica</i> L.	-0.000028	0.035730
<i>Calamagrostis neglecta</i> s. <i>groenlandica</i> Schrank. Matuszk.	-0.000020	0.035887
<i>Bromopsis pumpelliana</i> Scribn. Holub	-0.000023	0.036570
<i>Cladonia bacilliformis</i> Nyl. Glück	-0.000044	0.037426
<i>Brachythecium salebrosum</i> Hoffm. ex Web.. D. Mohr. B.S.G.	-0.000021	0.044059
<i>Micranthes foliolosa</i> R. Br. Gornall	-0.000010	0.045560
<i>Bryum pseudotriquetrum</i> Hedw. P.G. Gaertn.	0.000007	0.050917
<i>Pohlia species</i>	0.000014	0.051182
<i>Antennaria villifera</i> Boriss.	-0.000010	0.051236
<i>Psoroma hypnorum</i> Vahl. S.F.Gray	-0.000017	0.051353
<i>Bryocaulon divergens</i> Ach. Kärnefelt	0.000004	0.051853
<i>Hamatocaulis vernicosus</i> Mitt. Hedenas	-0.000010	0.053949
<i>Peltigera rufescens</i> Weis. Humb.	0.000008	0.058900
<i>Hieracium alpinum</i> aggregate	-0.000031	0.059313
<i>Lophozia wenzelii</i> Nees. Steph.	0.000016	0.062405
<i>Cladonia ecmocyna</i> Leight.	-0.000027	0.062767
<i>Hierochloe alpina</i> Sw. Roem.. Schult.	0.000005	0.063017
<i>Ochrolechia frigida</i> Sw. Lynge	0.000005	0.064523
<i>Paludella squarrosa</i> Hedw. Brid.	-0.000016	0.065622
<i>Dianthus repens</i> Willd.	-0.000013	0.065724
<i>Elymus species</i>	-0.000025	0.066234
<i>Sphagnum lindbergii</i> Schimp.	-0.000033	0.066863
<i>Cerastium arvense</i> L.	-0.000014	0.067567
<i>Brachythecium mildeanum</i> Schimp. Schimp.	-0.000011	0.067591
<i>Crepis tectorum</i> s. <i>nigrescens</i> Pohle. P.D. Sell	-0.000035	0.069089
<i>Sphagnum species</i>	-0.000015	0.069463
<i>Peltigera aphthosa</i> L. Willd.	0.000004	0.070123
<i>Draba glabella</i> Pursh	0.000015	0.070606

<i>Oncophorus compactus</i> B.S.G. Kindb.	-0.000021	0.070961
<i>Cladonia furcata</i> Huds. Schrad.	0.000010	0.071879
<i>Peltigera canina</i> L. Willd.	0.000008	0.071916
<i>Lycopodium annotinum</i> s. <i>alpestre</i> Hartm. A. Löve. D. Löve	-0.000022	0.072934
<i>Sphagnum Ångstroemii</i> C. Hart.	0.000011	0.075945
<i>Calliergon stramineum</i> Dicks. ex Brid. Kindb.	-0.000007	0.077468
<i>Stereocaulon alpinum</i> Laur.	0.000005	0.079033
<i>Milium species</i>	-0.000033	0.079783
<i>Limprichtia cossonii</i> Schimp. L.E. Anders.	0.000014	0.079949
<i>Gymnocolea inflata</i> Huds. Dumort.	-0.000028	0.080068
<i>Cladonia coccifera</i> s. lat. L. Willd.	0.000004	0.083402
<i>Loeskygnum badium</i> C.J. Hart. Paul	0.000011	0.090222
<i>Ochrolechia species</i>	-0.000015	0.090407
<i>Brachythecium species</i>	0.000016	0.091071
<i>Polytrichastrum species</i>	0.000010	0.091463
<i>Hierochloe pauciflora</i> R. Br.	0.000009	0.092453
<i>Rinodina turfacea</i> Wahlenb. Körb.	-0.000031	0.097811
<i>Aconogonon ochreatum</i> L. H. Hara	-0.000008	0.108972
<i>Pogonatum urnigerum</i> Hedw. P. Beauv.	-0.000014	0.112405
<i>Deschampsia sukatschewii</i> s. <i>borealis</i> Trautv. Tzvelev	0.000008	0.112773
<i>Cinclidium subrotundum</i> Lindb.	0.000012	0.114097
<i>Japewia tornøensis</i> Nyl. Tønseberg	-0.000025	0.115889
<i>Luzula nivalis</i> Laest. Spreng.	0.000008	0.118885
<i>Sphagnum lenense</i> H. Lindb. ex L.I. Savicz	0.000007	0.126682
<i>Carex lachenalii</i> Schkuhr	0.000007	0.130077
<i>Warnstorfia sarmentosa</i> Wahlenb. Hedenas	0.000010	0.133161
<i>Cladonia grayi</i> G. Merr. ex Sandst.	-0.000025	0.133550
<i>Blepharostoma trichophyllum</i> Linn. Dumortier	0.000007	0.134934
<i>Trisetum species</i>	-0.000011	0.139786
<i>Hypogymnia subobscura</i> Vainio. Poelt	-0.000023	0.141518
<i>Salix rosmarinifolia</i> L.	-0.000025	0.146787
<i>Larix species</i>	-0.000022	0.149898
<i>Cladonia uncialis</i> L. Wigg.	0.000003	0.151533
<i>Artemisia borealis</i> Pall.	-0.000009	0.153406
<i>Icmadophila ericetorum</i> L. Zahlbr.	-0.000025	0.156271
<i>Cladonia pyxidata</i> L. Hoffm.	-0.000009	0.156359
<i>Thamnolia vermicularis</i> s. <i>vermicularis</i> Sw. Schaer.	0.000003	0.158018
<i>Trollius x apertus</i> Perfil. ex Igoschina	-0.000016	0.158207
<i>Cephalozia bicuspidata</i> L. Dumort.	0.000014	0.160226
<i>Bryum weigelii</i> Sprengel	-0.000024	0.163866
<i>Trisetum spicatum</i> L. K. Richt.	0.000008	0.167549

<i>Lichenomphalia hudsoniana</i> H.S. Jenn. Redhead et al.	0.000011	0.171463
<i>Pyrola minor</i> L.	-0.000014	0.173824
<i>Pohlia drummondii</i> C. Müll. Andrews	-0.000010	0.175445
<i>Eriophorum russeolum</i> Fr. ex Hartm.	0.000004	0.180176
<i>Armeria scabra</i> Pall. ex Roem.. Schult.	0.000007	0.181572
<i>Angelica decurrens</i> Ledeb. B. Fedtsch.	-0.000018	0.192128
<i>Comarum palustre</i> L.	-0.000006	0.195407
<i>Polytrichastrum alpinum</i> Hedw. G. L. Sm.	0.000005	0.196601
<i>Luzula wahlenbergii</i> Rupr.	-0.000005	0.202920
<i>Dryas octopetala</i> L.	0.000005	0.203716
<i>Cladonia amaurocraea</i> Flörke. Schaer.	0.000003	0.204726
<i>Oncophorus wahlenbergii</i> Brid.	0.000005	0.208172
<i>Plagiothecium denticulatum</i> Hedw. Schimp.	-0.000021	0.212782
<i>Luzula multiflora</i> s. <i>frigida</i> Buchenau. V.I. Krecz.	-0.000016	0.217864
<i>Sphagnum teres</i> Schimp. Ångstr.	-0.000013	0.219422
<i>Cetraria odontella</i> Ach. Ach.	-0.000011	0.222798
<i>Carex vaginata</i> s. <i>vaginata</i> Tausch	0.000005	0.227052
<i>Minuartia rubella</i> Wahlenb. Hiern	-0.000016	0.236717
<i>Dicranum bonjeanii</i> De Not.	0.000011	0.238554
<i>Hypnum cupressiforme</i> Hedw.	0.000012	0.239878
<i>Pertusaria species</i>	-0.000016	0.249797
<i>Rumex acetosella</i> s. <i>arenicola</i> Y. Mäkinen ex Elven	-0.000006	0.260655
<i>Nephroma species</i>	-0.000013	0.264874
<i>Plagiomnium medium</i> Bruch. Schimp. T. Kop.	-0.000009	0.268904
<i>Deschampsia anadyrensis</i> V.N. Vassil.	-0.000011	0.283628
<i>Cladonia bellidiflora</i> Ach. Schaer.	-0.000005	0.300482
<i>Warnstorfia pseudostraminea</i> C. Müll. Tuom.. T. Kop.	-0.000013	0.302107
<i>Carex canescens</i> s. <i>canescens</i> . L.	-0.000014	0.306619
<i>Sphaerophorus globosus</i> Huds. Vain.	-0.000002	0.313372
<i>Dicranum majus</i> Turner	-0.000005	0.314117
<i>Cladonia rangiferina</i> L. Nyl.	-0.000003	0.316922
<i>Brachythecium turgidum</i> C.J. Hart. Kindb.	-0.000008	0.320661
<i>Sphagnum obtusum</i> Warnst.	0.000009	0.339299
<i>Pertusaria oculata</i> Dicks. Th. Fr.	-0.000013	0.341499
<i>Cladonia stellaris</i> Opiz. Pouzar. Vezda	-0.000004	0.348554
<i>Bryoria nitidula</i> Th. Fr. Brodo. Hawksw.	0.000003	0.352866
<i>Dicranum fuscescens</i> Turner	0.000004	0.358104
<i>Cladonia sulphurina</i> Michx. Fr.	0.000005	0.372763
<i>Peltigera leucophlebia</i> Nyl. Gyeln.	-0.000004	0.390112
<i>Erigeron species</i>	-0.000013	0.395990
<i>Pseudobryum cinclidioides</i> Huebener. T. Kop.	-0.000007	0.397860

<i>Solorina crocea</i> L. Ach.	-0.000004	0.398048
<i>Polemonium acutiflorum</i> Willd.	0.000002	0.405446
<i>Dicranum species</i>	0.000002	0.431723
<i>Salix glauca</i> L.	0.000002	0.432255
<i>Parmelia omphalodes</i> s. lat. L. Ach.	0.000005	0.475461
<i>Oxyria digyna</i> L. Hill	0.000003	0.478112
<i>Sphagnum subsecundum</i> Nees	0.000006	0.480208
<i>Plagiothecium berggrenianum</i> Frisvoll	0.000005	0.489525
<i>Diphasiastrum alpinum</i> L. Holub	-0.000008	0.491078
<i>Arctophila fulva</i> Trin. Andersson	-0.000005	0.508723
<i>Carex brunnescens</i> Pers. Poir.	-0.000008	0.535076
<i>Cetraria species</i>	-0.000006	0.539227
<i>Cetraria ericetorum</i> Opiz	0.000006	0.547883
<i>Epilobium palustre</i> L.	0.000005	0.548013
<i>Scorpidium species</i>	-0.000008	0.556212
<i>Cladonia stricta</i> s. lat. Nyl. Nyl.	-0.000005	0.562190
<i>Cardamine bellidifolia</i> s. <i>bellidifolia</i> . L.	0.000005	0.563938
<i>Cladonia squamosa</i> s. lat. Hoffm.	-0.000003	0.565584
<i>Prasanthus suecicus</i> Gottsche. Lindb.	-0.000008	0.577818
<i>Cladonia verticillata</i> s. lat. Ach. Flot.	-0.000005	0.584188
<i>Ochrolechia androgyna</i> Hoffm. Arn.	-0.000005	0.584969
<i>Peltigera malacea</i> Ach. Funck	0.000003	0.586126
<i>Stereocaulon paschale</i> L. Hoffm.	0.000002	0.594261
<i>Koeleria asiatica</i> Domin	0.000005	0.598074
<i>Peltigera species</i>	0.000003	0.623970
<i>Castilleja lapponica</i> Gand. ex Rebrist.	-0.000005	0.625387
<i>Abietinella abietina</i> Hedw. Fleisch.	0.000005	0.627659
<i>Lophozia savicziae</i> Schljakov	-0.000006	0.633057
<i>Cetraria aculeata</i> Schreb. Link.	0.000002	0.649896
<i>Sphagnum girgensohnii</i> Russ.	-0.000002	0.651957
<i>Artemisia tilesii</i> Ledeb.	0.000002	0.660484
<i>Festuca rubra</i> L.	-0.000003	0.669103
<i>Cladonia crispata</i> s. lat. Ach. Flot.	0.000003	0.674985
<i>Empetrum nigrum</i> L.	0.000001	0.675389
<i>Schljakovianthus quadrilobus</i> Lindb. Konstant. Vilnet	-0.000004	0.693195
<i>Calliargon giganteum</i> Schimp. Kindb.	0.000003	0.708072
<i>Bryum caespiticium</i> Hedw.	0.000004	0.721959
<i>Stereocaulon species</i>	-0.000002	0.722624
<i>Peltigera polydactylon</i> Neck. Hoffm.	0.000002	0.732074
<i>Conostomum tetragonum</i> Hedw. Lindb.	-0.000002	0.733658
<i>Sarmenthyphnum sarmentosum</i> Wahlenb. Tuom.. T. Kop.	0.000003	0.734581

<i>Sibbaldia procumbens</i> L.	-0.000004	0.740753
<i>Sphagnum angustifolium</i> Warnst. C. Jens.	-0.000004	0.749338
<i>Pedicularis hirsuta</i> L.	0.000001	0.755435
<i>Stellaria palustris</i> Ehrh. ex Hoffm.	-0.000003	0.759902
<i>Salix arctica</i> Pall.	-0.000003	0.793425
<i>Cetraria nigricans</i> Nyl.	-0.000001	0.803617
<i>Cladonia cenotea</i> Ach. Schaerer	-0.000001	0.828046
<i>Pogonatum dentatum</i> Menzies ex Brid. Brid.	0.000001	0.831824
<i>Eriophorum scheuchzeri</i> Hoppe	0.000001	0.842335
<i>Silene involucrata</i> Cham. Schltld. Bocquet	0.000002	0.851038
<i>Ranunculus species</i>	-0.000002	0.879684
<i>Calamagrostis lapponica</i> Wahlenb. Hartm.	-0.000001	0.882769
<i>Minuartia arctica</i> Steven ex Ser. Graebn.	0.000001	0.895825
<i>Cassiope tetragona</i> s. <i>tetragona</i> L. D. Don	0.000000	0.937204
<i>Lophozia species</i>	-0.000001	0.939779
<i>Peltigera neckeri</i> Müll.Arg.	0.000000	0.971777
<i>Bryum capillare</i> Hedw.	0.000000	0.976269
<i>Cladonia macroceras</i> Flörke. Ahti	0.000000	0.989790

4 Polar desert islands: plant and lichen richness, turnover and biomass at the margins of life

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Abstract

1. With the rapid Arctic warming a major change is expected in Arctic vegetation and its biomass. Polar deserts are one of the most vulnerable and sensitive to climate change terrestrial biomes of the Earth yet likely the most understudied.
2. Based on vegetation surveys and in-situ plant biomass data collected during the Arctic Century expedition 2021 to the polar islands of the Barents, Kara and Laptev sea region we investigated the plant and lichen richness, turnover and biomass at 8 key sites on Severnaya Zemlya archipelago, Franz Josef Land, Vize and Uedineniya Islands. In addition, we collected high resolution multispectral imagery using drones to extrapolate in-situ plant biomass measurements to landscape scale.
3. We found that although species richness of the visited polar desert areas is low, with a total of only 129 species identified within the 19 sampled plots, they show high species turnover between plots. Notably, 40% of the detected species were found exclusively in a single plot, and 71% were present in no more than 3 plots. Moreover, only 13 species were observed in more than half of the plots, indicating a high degree of specialization within species-poor polar desert communities.
4. We suggest that quantifying cover-biomass relationships at the plot level enables us to extrapolate in-situ aboveground plant and lichen biomass to the landscape scale using linear regression. Our findings reveal that biomass varies widely across different sites, with its maximum on Vize Island, where the mean estimated biomass surprisingly reached $\approx 920 \text{ g/m}^2$, a number comparable to Arctic tundra levels, while other investigated sites have lower biomass (39-138 g/m^2), a level typical for polar deserts. We emphasize that high-precision geolocation, in combination with the use of drones, is crucial for accurately quantifying polar desert biomass and its trends.
5. With our research we aim to deepen the understanding of Arctic plant and lichen richness, turnover and biomass of polar deserts, bridging an important spatial data gap in the Arctic.

4.1 Introduction

Arctic ecosystems are experiencing increasing pressure due to the amplified climate warming (Meredith et al., 2019). As the Arctic warms four times faster than the global average (Rantanen et al., 2022) major changes in its biodiversity and ecosystem functioning are expected in the coming decades (Barry et al., 2013). Vegetation is a key component of the ecosystems and its changes lead to cascading effects throughout the entire ecosystem, and influence the global climate system primarily through carbon and energy cycles (Heijmans et al., 2022; Loranty et al., 2014; Oehri et al., 2022). The change in vegetation and plant diversity include plant functional trait change (Bjorkman et al., 2018), species invasions (Wasowicz et al., 2020), vegetation zone shifts (Ermokhina et al., 2023; Pearson, 2013; Reji Chacko et al., 2022), and complex plant biomass change manifested in either 'greening' or 'browning' trends (Epstein et al., 2013; Callaghan et al., 2022; Myers-Smith et al., 2020). However, since the changes in climate and resulting vegetation response are highly heterogeneous across the Arctic (Myers-Smith et al., 2020; Wu et al., 2020), it is particularly important to investigate regional status of plant and lichen diversity and biomass and their trends, especially in the most climatically extreme and poorly researched areas (Barry et al., 2013; Heijmans et al., 2022; Virkkala et al., 2019).

Russian polar islands remain one of the most understudied parts of the terrestrial Arctic (Virkkala et al., 2019). Franz Josef Land, Novaya and Severnaya Zemlya archipelagos have been largely neglected by geobotanical research due to their remoteness, logistical difficulties, and, often, special military regime (Kholod, 2020; Matveyeva et al., 2015; Walker et al., 2012). Yet, the scientific importance of studying Russian polar islands is high. Together with Ellef and Amund Ringnes Islands of the Arctic Archipelago, northern capes of Ellesmere, Peary Land of Greenland, Nordaustlandet of Svalbard, Cheluskin Peninsula and a few smaller lands, they form the polar desert, or subzone A (CAVM, 2003). The polar desert biome is the most extreme, ecologically unique and likely most sensitive and vulnerable part of the Arctic, according to the Arctic Biodiversity Assessment (Barry et al., 2013).

The polar desert is the northernmost and smallest biome, characterized by sub-zero mean July air temperature (0-3°C), continuous permafrost, relatively low snow depth in winter and often stable fog cover in summer (Bliss et al., 1984; CAVM, 2003; Matveyeva et al., 2015). The extreme climatic conditions lead to a low diversity and cover of vascular plants (cover less than 5% on average) and greater role of bryophytes and lichens (cover up to 40%) in plant communities (CAVM, 2003), which could be described as 'permanent pioneers' due to their simple structure and low intra-community connectivity (Matveyeva et al., 2015). Although polar desert vegetation (cover) is preliminary formed by sparsely distributed small patches of cryptogams and cushion-like forbs, some mesic areas allow development of more continuous vegetation similar to tundra (Daniels et al., 2016).

High heterogeneity, patchiness and the leading role of non-green cryptogams such as lichens pose methodological challenges for studying the vegetation and its biomass in polar deserts. While satellite-derived estimations of plant cover and biomass are commonly used in Arctic research (Berner et al., 2018; CAVM, 2003; Reynolds et al., 2012), non-linear relationships between observed plant biomass and satellite-derived NDVI complicate the efforts to study plant biomass using satellite data (Myers-Smith et al., 2020). One of the major difficulties lies in matching the scale of ground-truth data with the satellite NDVI having the resolution lower than the size of vegetation patches which leads to a mixing signal with soils (Davidson et al., 2016; Nelson et al., 2022). Drones are considered as a way to bridge in-situ observations and satellite data, providing spatial information on an intermediate scale (Fraser et al., 2016; Kathleen et al., 2022). While there are few studies applying drones to mapping Arctic tundra vegetation and its biomass across several regions (Assman et al., 2018; Fraser et al., 2016; Kathleen et al., 2022; Sievert & Olofsson, 2020), including the Svalbard archipelago (Eischeid et al., 2021; Mora et al., 2015; Thomson et al., 2021), there are no similar studies yet on Arctic polar deserts, particularly in Russia. In combination with sparse and rather incomplete geobotanical data from the region (Alexandrova, 1988; Kholod, 2020; Matveyeva, 2006; Matveyeva et al., 2015; Safronova & Khodachek, 1989; Walker et al., 2012), and almost complete lack of ground-truth biomass data

(Walker et al., 2012), Russian polar islands remain a white spot and an important target for vegetation studies.

During the Arctic Century expedition 2021, we collected a unique dataset combining plot-level plant richness and abundance, vegetation structure, biomass and soil measurements with the first ever-collected high-resolution multispectral drone imagery of Russian polar islands: Graham-Bell, Vize, Uedineniya, Pioneer, Bolshevik, Komsomolets and October Revolution, which represent the major part of Eurasian subzone A (CAVM, 2003). The dataset allows us to gain insight into plant and lichen diversity and vegetation structure of this poorly researched and extremely inaccessible area and to model landscape-level plant biomass on the northernmost extreme of plant life. In this study, we address 3 research questions: 1) What is the plant and lichen species richness across the Russian polar islands? 2) What are the relationships between richness, cover and biomass of these polar island communities? 3) What is the current aboveground plant biomass at landscape level? With the geobotanical surveys, we are aiming to bridge the observational gap by estimating plant and lichen species richness and vegetation structure across the islands, some of which had not been previously visited by geobotanists. With the site-level biomass estimation we contribute to a better understanding of the current plant biomass status of polar deserts and provide a baseline for future plant biomass change monitoring. We hypothesize that plant and lichen species richness is distributed unevenly within the research area, and community structure and plant biomass vary widely across the different sites following variation in plant and lichen species richness, vegetation cover and substrate type.

4.2 Data and methods

Study area and sampling sites

The data were collected during the Arctic Century expedition of 2021, a ship cruise aboard the Akademik Tryoshnikov icebreaker, jointly organized by the Swiss Polar Institute (SPI), the Arctic and Antarctic Research Institute (AARI), in Russia and the Helmholtz Centre for Ocean Research Kiel (GEOMAR) in Germany

(<https://swisspolar.ch/expeditions/arctic-century-expedition/>). The expedition started from Murmansk on 5 August of 2021 and took place in the Barents, Kara and Laptev Seas as well as in the open Arctic Ocean until 6 of September 2021 (Fig.1). During the expedition, our team visited 7 islands (8 sites) either belonging to Franz-Josef Land and Severnaya Zemlya archipelagos or located remotely from the major lands such as Vize and Uedineniya (Solitude) Islands (Table 1). The visited islands are characterized by a high variety of landscapes, and different climate conditions as a result of their location on the north-eastern edge of warm Atlantic water reach (Fig. 2).

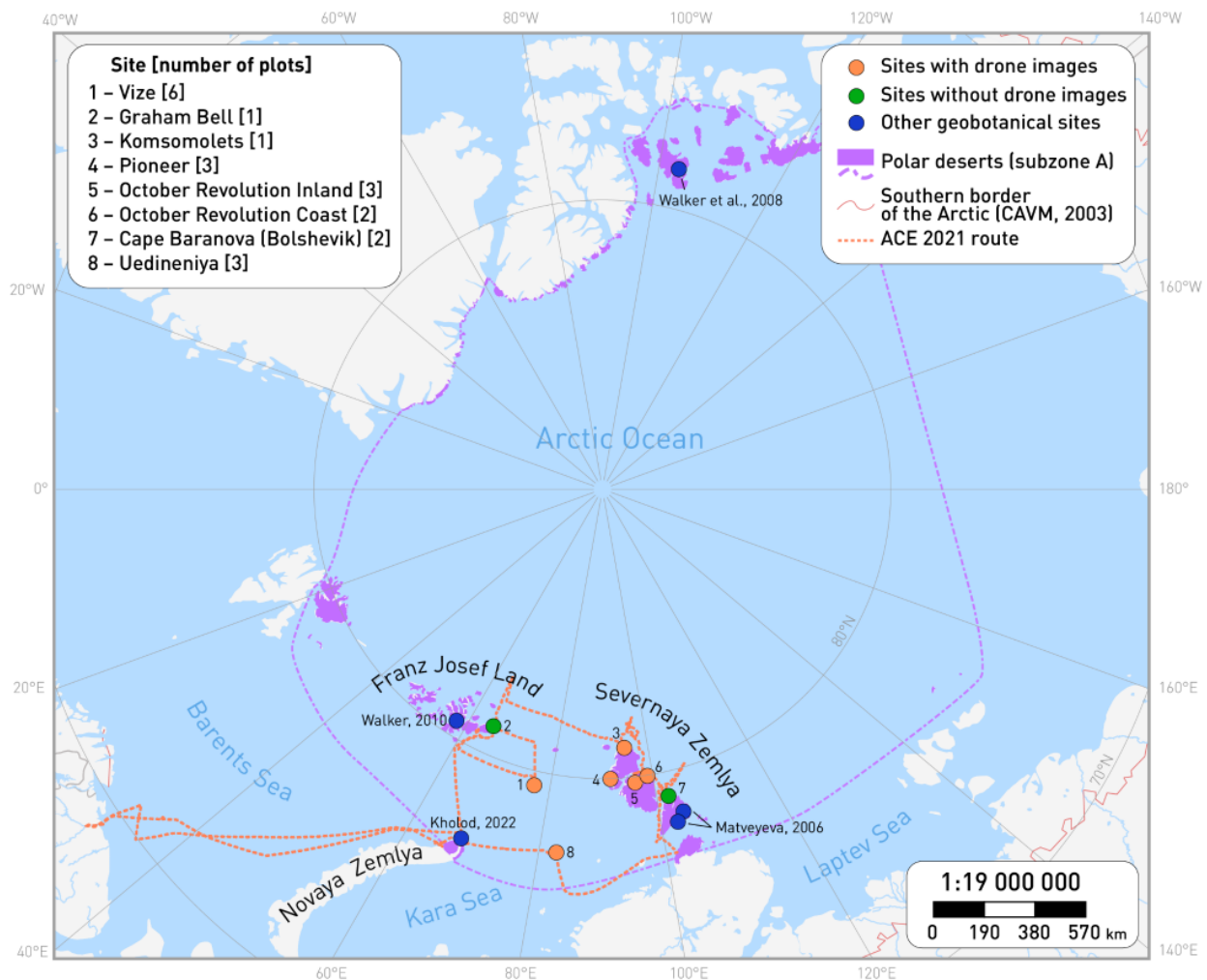


Figure 1. Arctic Century expedition route 2021 and location of the terrestrial sampling sites. Other studies with geobotanical surveys in the Arctic polar desert biome are also indicated.

Graham Bell is the easternmost island of the Franz Josef Land archipelago . The southern and western parts of Graham Bell are covered by the Kupol Vetrenny glacier, while the ice-free area is formed by sandstone. The expedition landing site (Fig. 2a) was located close to Melkoye lake, the largest lake of the island, which is connected to the ocean by a channel. The area is almost completely non-vegetated, apart from rare crust lichens, a few mosses and *Phippsia algida* cushions found in anthropogenically disturbed areas and on whale bones. The island is known for Mesozoic wood fossils, discovered by previous expeditions and apparently abundant at the site (Afonin et al., 2022).

Vize is a non-glaciated island located in the northern part of the Kara sea, halfway between Franz-Josef Land and Severnaya Zemlya archipelagos. Vize is composed of Cretaceous sedimentary rocks, and experiencing strong coastal erosion (2.4-10.9 m per year), intensified by climate change (Baldina et al., 2022). The expedition landing site was located. (Fig. 2b). A distinct feature of the site is its well-developed polygonal microrelief, with 10-12 m frost cracks-formed polygons, and a complex system of erosion valleys that transverse the generally flat and low-altitude island from coast to coast without upper or lower valley section (Pizhankova et al., 2022). The soils of the island are loamy and heavily intermixed with stones. Despite the erosion, Vize is the only island among the visited sites that has predominantly continuous vegetation cover.

Five of the eight visited sites are located on the Severnaya Zemlya archipelago with 4 four major islands: Komsomolets, Pioneer, October Revolution and Bolshevik. Severnaya Zemlya is characterized by a more continental climate compared to Franz Josef Land and Vize, heterogeneous surface geology and relief and large ice caps, covering 47% of the archipelago (Matveyeva, 2015).

The northernmost island of Severnaya Zemlya, Komsomolets, is characterized by the most extreme climatic conditions across the archipelago. Largely covered by the Academy of Science glacier, the island was just once briefly visited by geobotanists (Andreev et al., 1993). The site visited by the Arctic Century expedition (Fig. 2c) is

located in the northwest of the island. The area is a vast fluvio-glacial plain, devoid of any vegetation and covered with scattered stones (a few with lichen crust patches) and occasional pieces of paleowood.

Pioneer is a rocky island with relatively heterogeneous relief. The visited site (Fig. 2d) is located on the northern part of the island on an elevated terrace descending down to the Red Army straight. The area has a few ponds, some of which host colonies of *Nostoc* algae, and a bigger lake, with an outlet river flowing to the sea. Cryogenic processes such as solifluction and cryoturbation created complex surface patterns, often followed by vegetation. Similar to Komsomolets Island, Pioneer is lacking geobotanical data (<http://byrranga.ru/keymap2.htm>).

October Revolution is the largest island of the archipelago. The elevated parts of the island (up to 963 m asl) are covered by 5 major glaciers: Rusanov, Karpinsky, Universiteta, Vavilov and Albanov along with several ones, collectively covering about half of its surface. The non-glaciated areas of the island are characterized by broad river valleys with large flat lowlands (Andreev et al., 2008). During the expedition 2 sites were visited, one in a major river valley with red, iron-rich soils to the south of Rusanov Glacier (Fig. 2e) and the second one on the predominantly rocky eastern coast of the island, north-east from Karpinsky Glacier (Fig. 2f). Currently the vegetation of the island is sparse (<10% of cover on average). However, studies indicate that under the Pleistocene and early Holocene climatic conditions, tundra-steppe and shrub tundra vegetation were common on the island, including areas covered by the modern glaciation (Andreev et al., 2008).

The southernmost island of the archipelago, Bolshevik, is likely the most extensively studied area by botanists in the polar desert (Matveyeva, 2006; Matveyeva & Zanolkha, 2008; Melles et al., 1997; Potemkin, 2000; Potemkin & Matveyeva 2004; Zhurbenko & Matveyeva, 2006). During our expedition, we visited Cape Baranova and its polar station which is located in the north of the island (Fig. 2g). The site is a rocky, anthropogenically disturbed area with small lakes and rather dense vegetation (preliminary, moss) cover.



Figure 2. Landscapes and vegetation of the visited sampling sites.

Uedineniya (Solitude) (Fig. 2h) is an isolated, small (<20 km²), non-glaciated island in the central part of the Kara sea. The western part of the island, visited by our expedition, is a sandstone low-terraced plain (20-27 m asl) with few erosive valleys, while the eastern part is a wet sandy lowland just slightly above the sea level (1-2 m asl) with many small lakes and lagoons (Potemkin & Safronova, 2015).

Geobotanical plots

At the 8 sampling sites visited we collected 19 10x10m Braun-Blanquet plots in total. Each vegetated site is represented by at least 2 plots, Uedineniya and Pioneer by 3, and Vize by 6 plots (Fig. 1, Table 1). The sites on Komsomolets and Graham Bell are not covered by vegetation so the confirmed absences were documented. The plots were surveyed in a 10x10 m area using the standard Arctic Vegetation Archive protocol (Walker et al., 2013, 2016, 2018; Zemlianskii, 2023). The center of each of the plots was geolocated using a handheld GPS (WGS 84 datum). We compiled a full species list for all plots following the Pan-Arctic Species List taxonomy (Raynolds et al., 2013). The species lists include vascular plants (forbs and graminoids), bryophytes, and lichens along with plot-level cover (%) of each species. We also documented horizontal (cover of plant functional types (PFTs) and litter in percentage) and vertical (height of PFTs in centimeters) community structure, as well as some habitat (active layer thickness, soil type and moisture) information. Photos were taken from the four corners of each rectangular plot area. In addition to the plot-level species list, we collected data and samples of species not found within the plots to compile site-level species list.

To estimate the variation of species richness and cover of four plant functional types (lichens, bryophytes, forbs, graminoids) across the sites, we assessed them at plot level and presented the site-level means of the plot-level richness and cover as ggplot2 bar plots (Wickham, 2016). To detect the species with the highest abundance and the most common species we analyzed species composition and cover across the plots.

Table 1. Data collected by geobotanical team during the Arctic Century expedition.

Site	Vize	Graham Bell	Komsomolets	Pioneer	October Revolution Inland	October Revolution Coast	Cape Baranova	Uedineniya
Latitude, Longitude	79°35.9683' N, 76°40.7617' E	81°05.5177' N, 65°13.5166' E	81°00.2441' N, 94°28.3620' E	80°4.12' N, 91°52.184' E	79°43.6339' N, 96°34.0966' E	79°57.7613' N, 99°24.5434' E	79°17.0152' N, 101°38.148' E	77°30.4705' N, 82°17.2605' E
Date	14.08.2021	16.08.2021	20.08.2021	24.08.2021	25.08.2021	26.08.2021	27.08.2021	02.09.2021
Drone Images/ Resolution (cm)	4765/7.36	-	3285/7.54	4185/7.78	3745/8.75	3555/7.7	-	2950/7.65
Vegetation	+	-	-	+	+	+	+	+
Snow cover	-	-	-	-	-	+	-	-
Braun-Blanquet plots	6	1	1	3	3	2	2	3
Subplots (biomass samples)	18	0	0	9	12	6	6	9
Active layer thickness measures	+	+	+	+	+	+	+	+

Plant and lichen biomass assessment

In each of the 19 plots, we collected 3 plant biomass samples (60 in total, including 3 additional samples of October Revolution Inland) within a 25x25 cm area (subplot) within the main Braun-Blanquet plots. We randomly selected subplot locations within each plot area to establish the subplots using 50x50 cm metal frames with a 10 cm grid. The cover of the main 5 biomass types (lichens, bryophytes, forbs, graminoids and dead biomass) was estimated at the subplot-level, and we took nadir photos of the subplots. The topsoil layer within a subplot area was extracted using a knife, along with all plants and crusts. We first removed the soil and then classified the aboveground part of the collected vegetation samples into 5 categories (dead biomass, lichens, bryophytes, forbs, and graminoids). We separated non-decomposed dead moss from

peat and lichen crusts from the soil. We labeled each biomass sample, oven-dried it, and weighed it on a high-accuracy balance (Sartorius Weighing technology GmbH, MSU125P-000-DA), recording the weight with 0.0000X g accuracy. We recalculated the sampled biomass as g/m².

Consequently, we used in-situ plant biomass measurements to estimate the relationships between plot-level species richness and the mean subplot-level biomass (representing the plot-level biomass) of each of the four plant functional types (lichens, bryophytes, forbs, graminoids) through linear regressions. We quantified the relationships between subplot-level cover and biomass for four sites (Vize, Pioneer, Uedineniya, and October Revolution Inland), first separately, and then produced a regression for 3 sites that showed statistically significant relationships and high R² which was later applied for our site-level biomass estimations.

Drone imagery

We acquired drone imagery over the five sites (Vize, Pioneer, October Revolution Inland, October Revolution Coast, Uedineniya) at the end of the vegetation season 2021 (Table 1). We collected 5-band multispectral imagery to separate vegetation and substrate using a MicaSense RedEdge-MX camera (MicaSense Inc., Seattle, WA, USA). This camera was mounted on a fixed-wing drone eBee X (senseFly SA, Cheseaux-Lausanne, Switzerland). The approximate flight height was 80-120 meters. To geolocate the drone imagery with accuracy of 1 cm we used a virtual dGNSS reference station (senseFly GeoBase, senseFly SA, Cheseaux-Lausanne, Switzerland) and post-processed kinematics (PPK). We post-processed the imagery and produced a mosaic using Pix4D Mapper software (version 4.8.1, Pix4D SA, Prilly, Switzerland) for the four sites where we had concurrent drone imagery and in-situ plant biomass measurements (Vize, Pioneer, Uedineniya, October Revolution Inland).

Site-level biomass estimations

To estimate site-level biomass, we quantified site-level fractional vegetation cover using a classification of the drone imagery. We first cropped the drone imagery of 4 sites (Vize, Pioneer, Uedineniya and October Revolution) to a standard 320x630 m extent.

We then created a water and ice mask, using the blue spectral band to filter out ice with values > 0.4 and NDWI values > 0.05 to exclude water. Next, we performed a binary (substrate/vegetation) land cover classification using the K-nearest neighbor algorithm. For this, we selected 13-20 training samples for each class per site, depending on the landscape heterogeneity (more samples were selected for more heterogeneous sites), using the Semi-automated classification plugin in QGIS (Congedo, 2021). We trained the classifier independently for each site. We converted the classification samples of each site to shape files and extracted values of near-infrared (NIR), NDWI, and NDVI to train the classifier using the 'caret' package in R (Kuhn, 2008). To ensure the reliability of the classification output, we performed 12-fold cross-validation and calculated a confusion matrix.

We spatially resampled the resulting map to align with the in-situ Braun Blanquet plot size (10x10m) grid using the 'motif' package in R (Nowosad, 2021), obtaining a fractional vegetation cover map, showing the fraction (%) of the grid area which is covered by vegetation. To account for the uncertainty in the GPS geolocation of in-situ plots, we conducted focal lookup on the fractional vegetation cover map. We first created a 10x10 m square buffer to represent our plots. Given the standard 3 m standard uncertainty in GPS coordinates, we then produced 10-meter buffers at incremental shifts of 1, 2, and 3 m in each direction, resulting in a total of 48 buffers (Appendix Fig. 3). We calculated the mean fractional vegetation cover in each of these buffers, as well as from the original central coordinate of the plot buffer, totaling 49 samples. This method was consistently applied across all plots. Lastly, to validate our estimations we tested the relationships (p-values and R^2) between minimum, maximum and mean sampled fractional vegetation cover of the 49 samples representing each plot and the in situ plot estimations (i.e. mean of the visually estimated vegetation cover of our 3 subplots for each plot). Subsequently, we projected our linear regression model (see 2.3), which quantifies the relationship between in-situ subplot-level live vegetation cover (%) and in-situ subplot-level live biomass ($\text{g}/625\text{cm}^2$), to the drone-based fractional vegetation cover map to produce a site-level biomass estimation map (g/m^2). We indicated the mean of the biomass (g/m^2) for each site, along with the minimum and maximum confidence intervals according to our model. Additionally, we evaluated the

spatial uncertainty of our estimations by generating an uncertainty map that illustrates the difference between the upper and lower model confidence interval projections.

4.3 Results

Plant and lichen species richness and turnover

We identified 21 vascular plant (5 graminoids and 15 forbs), 64 bryophyte (57 mosses and 7 liverworts), 45 lichen species within the boundaries of the 19 geobotanical plots (Fig. 4). Two sites are characterized by particularly low total species richness (aggregated richness across the plots of each site): October Revolution Inland (12 species) and Uedineniya (29 species). Both sites are especially poor in cryptogam species: for Uedineniya 11 bryophyte and 5 lichen species were detected across the all plots, while only 3 bryophyte and no lichen species were found on October Revolution Inland. Four other sites have a total richness of approximately 50-60 species: Pioneer (49), October Revolution Coast (50), Vize (57), and Cape Baranova (Bolshevik) (59). However, the contribution of plant functional types varies across sites. The rocky October Revolution Coast has only 2 vascular plant species but the highest lichen contribution (27 species) to total species richness. The loamy Vize site, in contrast, has the highest bryophyte contribution (33 species) and, after Uedineniya, the highest number of vascular plant species (12 species). In general, rocky sites demonstrate higher species richness than sites with light and dynamic substrate such as sand and, to a lesser extent, loam (Appendix Fig. 1).

Analyzing species occurrence across plots we found that vascular plants in the area are more generalistic compared to more site-specific cryptogams (Appendix Fig. 2). Within the 10 most common species across the area 6 are vascular plants, while they consist only 16% of the total detected flora. The most common species are *Saxifraga oppositifolia* L. and *Minuartia macrocarpa* (Hook.) Mattf. (found in 15 of 19 vegetated plots), closely followed by *Papaver polare* (Tolm.) Perf. (14/19) and *Phippsia algida* (Sol.) R. Br. (14/19). High occurrence is found also for *Saxifraga cernua* L. (12/19), and *Stellaria crassipes* Hult. (12/19). With a few exceptions (*Saxifraga oppositifolia*, *M. macrocarpa*, *P. algida*, and *Stellaria crassipes* are absent on October

Revolution East, the latter also on Pioneer), most of the listed vascular plant species (17 of 21) are found in all sampled vegetated sites. Among bryophytes high occurrence is found for *Bryum* sporophytes (which could belong to different (sub)species) (12/19) as well as for *Distichium inclinatum* (Hedw.) Bruch et al. (10/19), which was not found on October Revolution Inland and Uedineniya sites. Among lichens, the most common are *Thamnolia vermicularis* (Sw.) Schaer. var. *vermicularis* (12/19) and *Flavocetraria cucullata* (Bellardi) Kärnefelt & A. Thell (10/19) present everywhere except October Revolution Inland, where no lichen species were detected. In total, only 13 species were found in more than half of the plots, while 40% of the species (51 species) were identified in just a single plot, and 40 more species in 2 to 3 plots (Appendix Fig. 2). This is particularly pronounced for lichens, for which 23 out of 45 species are found in just a single plot.

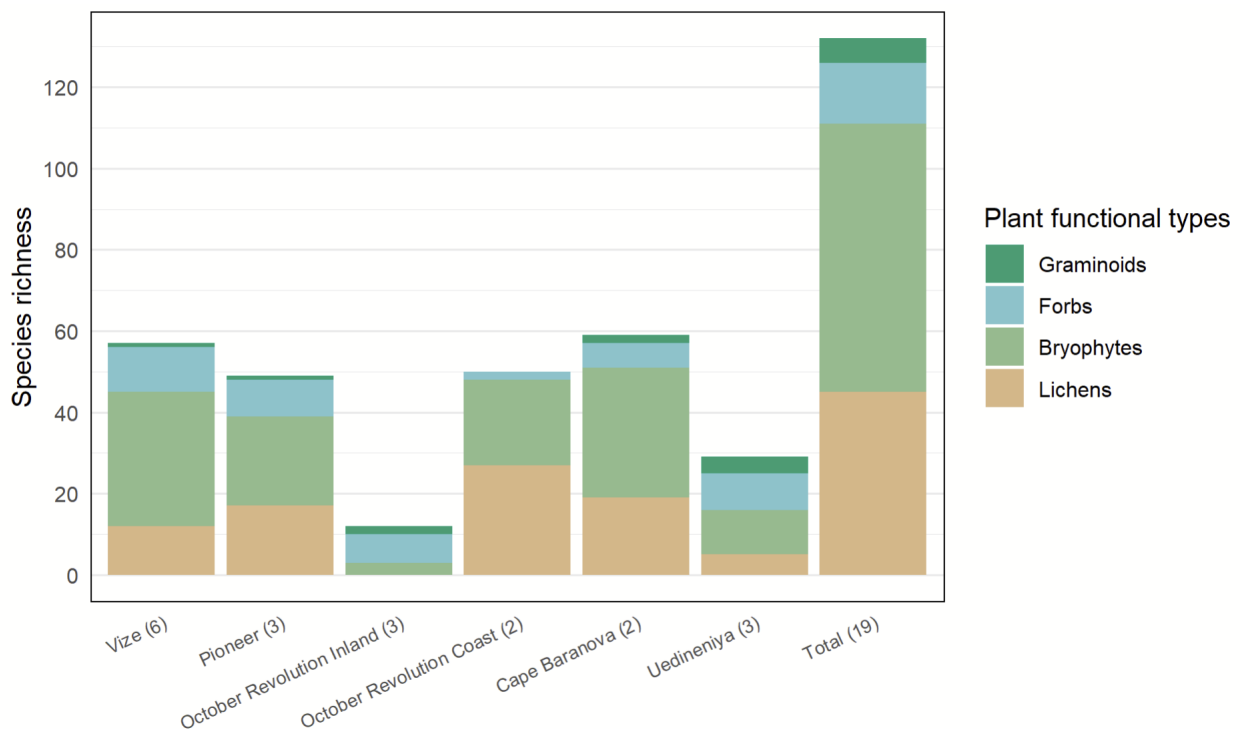


Figure 4. Species richness grouped by plant functional types on polar desert island sites in the Barents, Kara and Laptev Seas (excluding species found outside of plots).

Plot-level plant biomass and its relationships with species richness

Aboveground plant and lichen biomass was found to be highly heterogeneous across the Russian polar islands, with different groups contributing most to the local plant biomass across sampling sites (Fig. 5). The highest median subplot-level biomass was observed at October Revolution Coast (56 g/m^2), while October Revolution Inland, the inland part of the same island, is characterized by the lowest biomass (4 g/m^2). Vize, along with October Revolution Coast and Cape Baranova (Bolshevik) sites, is characterized by the highest biomass of bryophytes (ranging from 31 to 46 g/m^2 * - here and further the median values are given). Lichen biomass is high on rocky sites, such as October Revolution Coast and Pioneer (20 - 30 g/m^2). At the latter, the biomass of lichens exceeds the combined biomass of other plant functional types (20 g/m^2). Although the median biomass of cryptogams is generally higher than the biomass of the vascular plants, there are 2 sites where the biomass of vascular plants is higher. The biomass of graminoids is low or completely absent at most sites, with the exception of Uedineniya where they have relatively higher biomass (5 g/m^2), along with (mostly graminoid) litter (5 g/m^2). In contrast, the contribution of forbs is low but relatively consistent across most of the sites (1 - 3 g/m^2), with the exception of Pioneer (6 g/m^2). Across all the sites, bryophytes are by far the group contributing most to total biomass ($\approx 12 \text{ g/m}^2$), while the biomass of lichens and vascular plants is comparable (Fig. 5).

Testing the relationships between species richness and biomass of different plant functional groups showed no significant linear dependency of biomass on species richness of the visited sites for most of the groups (Fig. 6). Neither bryophytes nor forbs are found to have statistically significant relationships. However, moderately strong ($0.61 R^2$) and highly statistically significant relationships were detected for lichens (p -value = 0.00007). Apart from lichens, moderately strong ($0.6 R^2$) statistically significant relationships were found for graminoids (p -value = 0.0001). However, low species richness of graminoids across most of the sites (with a maximum of 4 species at Uedineniya-1) complicates the estimation of the actual richness-biomass relationships for graminoids.

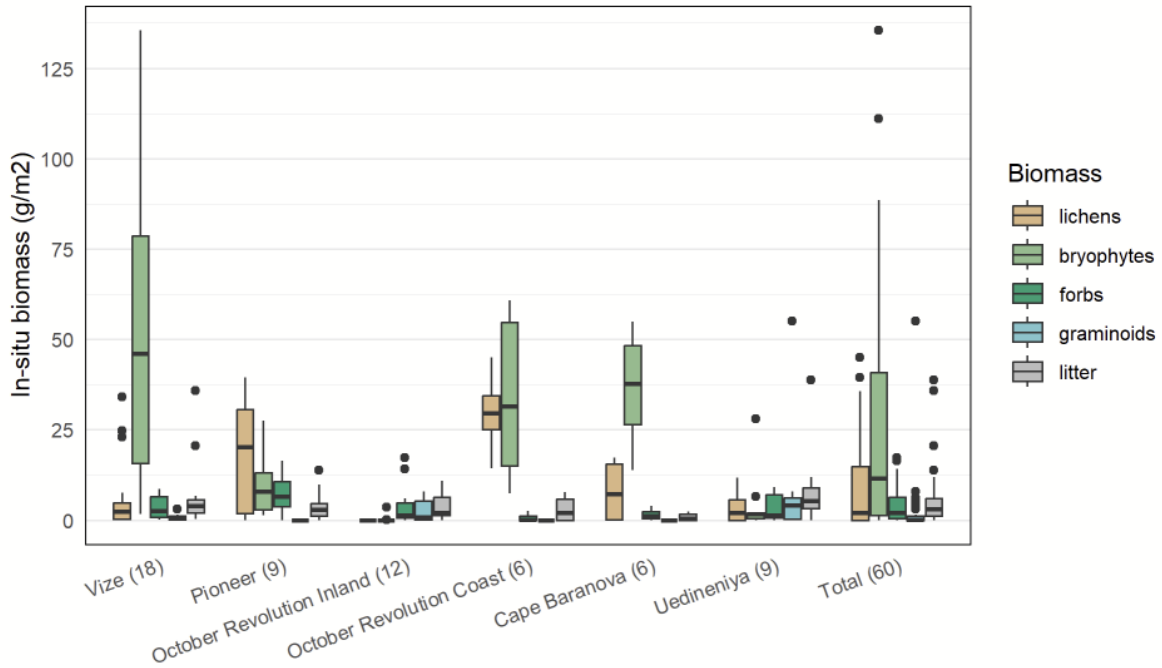


Figure 5. Median in-situ biomass per site (g/m²), for each site the number of sampled subplots is indicated.

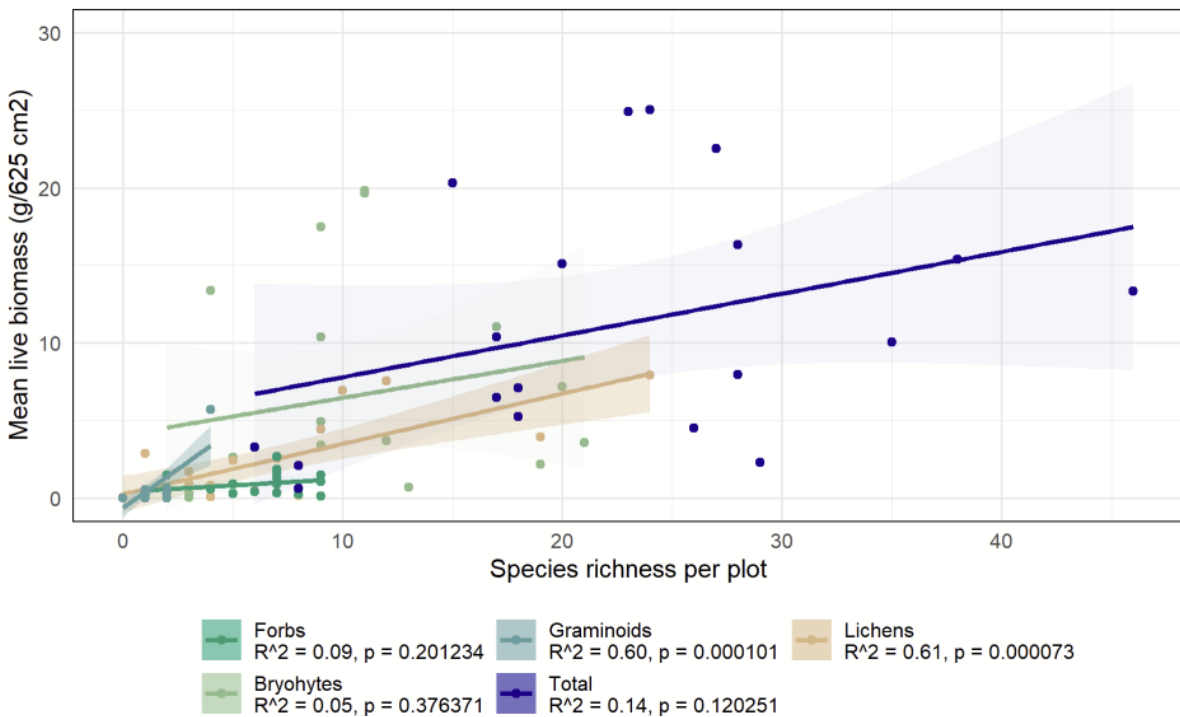


Figure 6. Plot-level in-situ species richness (x) and in-situ plot-level (mean of 3 subplots) biomass (y) relationships.

Cover-biomass relationships

Polar desert islands are characterized by low and patchy vegetation cover (Matveyeva, 2015). Our results show that for none of the sites plot-level (10x10m) mean live vegetation cover reaches 40% (with 30% maximum mean cryptogams cover on Cape Baranova (Bolshevik), and 13% maximum mean vascular plants cover on Vize), while the mean plot-level cover across all the sites is 17% (standard deviation = 10%) (Fig. 7). The observed cover is close to the typical for polar deserts (<40% cryptogam and <5% vascular plant cover), although the vascular plant cover on Vize and Uedineniya sites is higher than average (CAVM, 2003). Cape Baranova (Bolshevik) and Vize sites are found to have the highest mean plot-level cover (30-34%), whereas the lowest mean plot-level cover is found for October Revolution Inland (6%).

Mean plot-level **graminoid** cover varies from 8% on Uedineniya (with *Phippsia algida* (Sol.) R.Br. as the dominant graminoid on the site and the most common across the islands) to almost zero on Pioneer where minimal presence of *P. algida* was detected at the plot borders, while on October Revolution Coast no graminoids were detected. The mean cover of graminoids across the all plots is 4%, and standard deviation is 4%. **Forb** cover is distributed slightly more homogeneously with maximum 6% on Vize and 1% on October Revolution Coast. The species with highest plot-level cover across all sites are found to be *Saxifraga oppositifolia* L. (up to 3%), *Minuartia macrocarpa* (Pursh) Ostenf. (up to 2%), *Papaver polare* (Tolm.) Perf. and *Saxifraga cernua* L. (up to 1%) found on Vize and Pioneer Islands. The mean cover of forbs across the plots is 4% and standard deviation is 4%.

Similar to species richness, cryptogams have the highest contribution to the plot-level vegetation cover for 4 out of the 6 sampled sites. Both **bryophytes** (23%) and **lichens** (8%) cover are the highest on Cape Baranova (Bolshevik Island) site. Among bryophytes, relatively few species have high plot-level cover at least at one site: on Cape Baranova (Bolshevik) site 17 species are found to have more than 1% of cover with *Racomitrium lanuginosum* (Hedw.) Brid., *Polytrichum juniperinum* Hedw., *Drepanocladus aduncus* (Hedw.) Warnst. and *Aulacomnium turgidum* (Wahlenb.)

Schwägr. found with up to 4% cover. At the other sites, *Polytrichastrum alpinum* (Hedw.) G.L.Sm. is found with up to 10% cover on Vize, while most of the species have low and sporadic plot-level cover. The mean cover of bryophytes across the all plots is 9% and standard deviation is 8%. Among lichens, the highest plot-level cover was found for *Stereocaulon* species (Vize, up to 4%) and *Cladonia macroceras* (Delise) Hav. (Cape Baranova (Bolshevik), 12%). The mean cover of lichens across the sites is 4% and standard deviation is 6%.

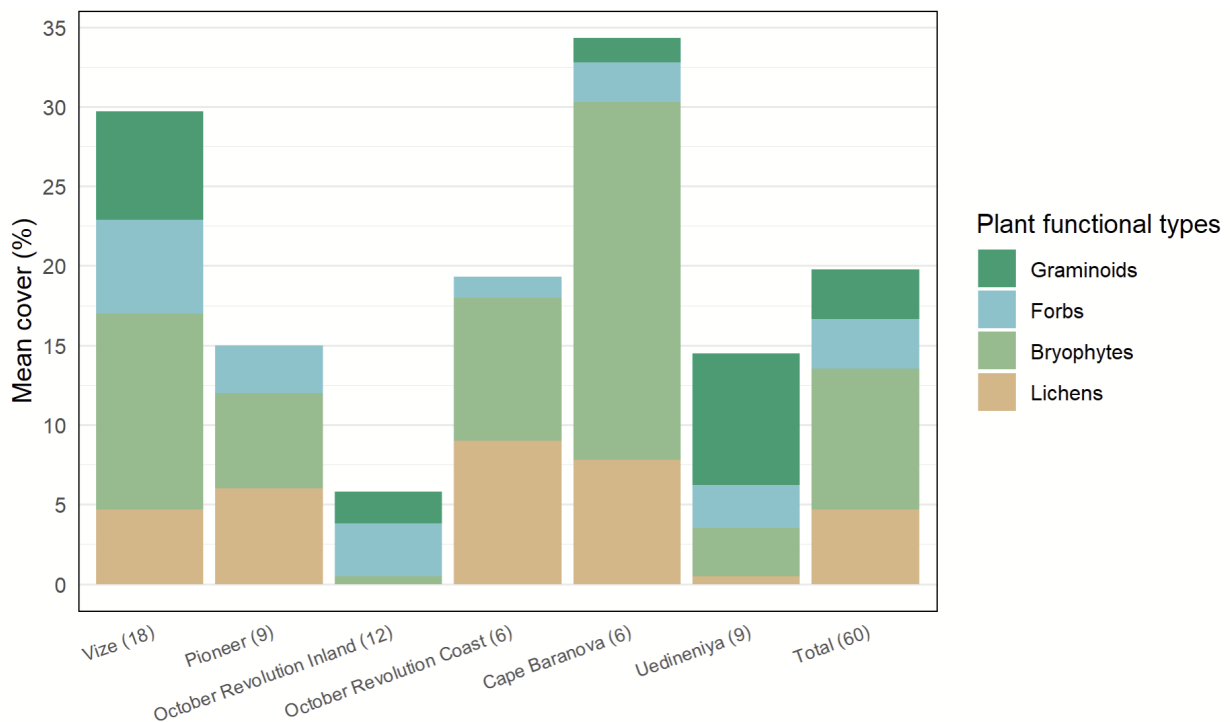


Figure 7. Mean plot-level (10x10m) cover (%) of plant functional types (graminoids, forbs, bryophytes, lichens) per site (non-vegetated sites excluded).

Testing the relationships between in-situ subplot-level live biomass and cover showed similar linear relationships at three of the four explored sites (Fig.8). Vize, Pioneer and Uedineniya sites demonstrate statistically significant relationships with relatively high explanatory power of subplot-level cover (0.59, 0.66, and 0.8 R^2 , respectively). The exception is October Revolution Inland, which shows no significant relationships between subplot-level live biomass and cover (p -value = 0.13). The linear regression based on the combined data from Vize, Pioneer and Uedineniya

demonstrates high statistical significance (p -value < 0.000001) and moderately high explanatory power ($0.61 R^2$).

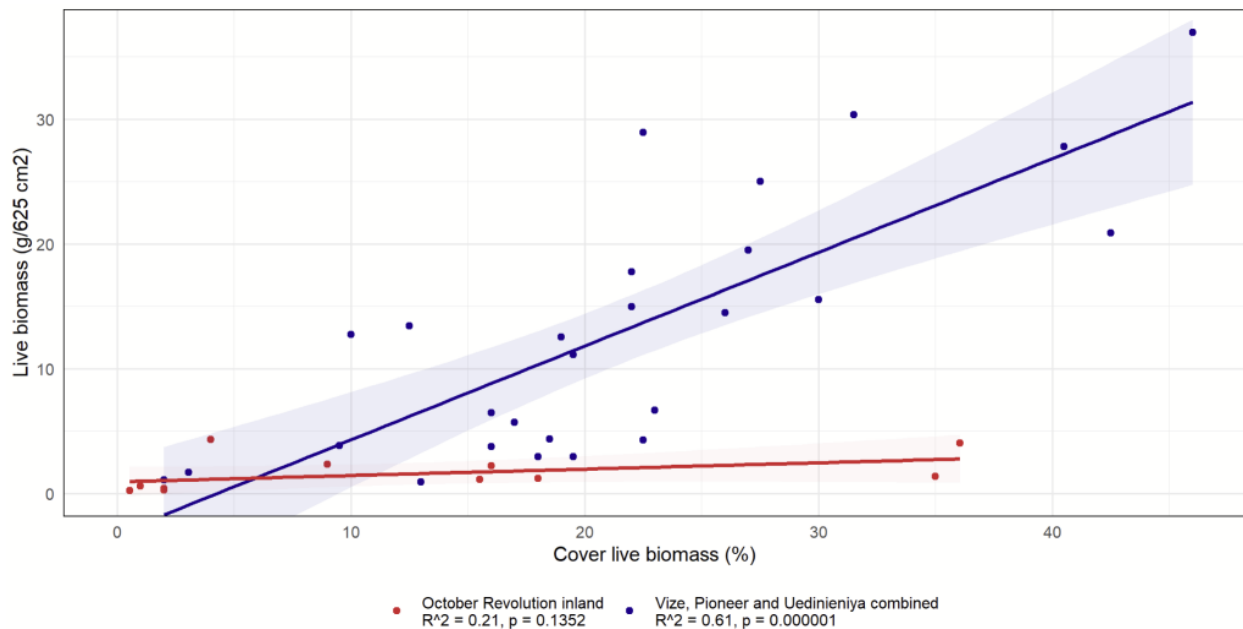
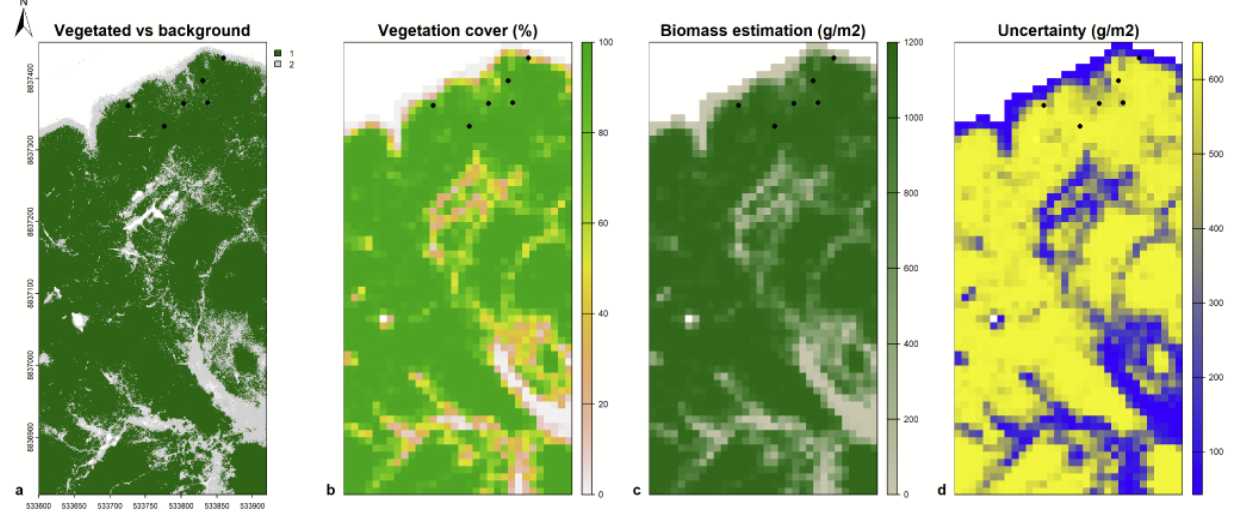


Figure 8. Biomass-cover relationship at subplot level for Vize, Pioneer and Uedineniya sites. October Revolution Inland does not show a significant subplot-level biomass-cover relationship.

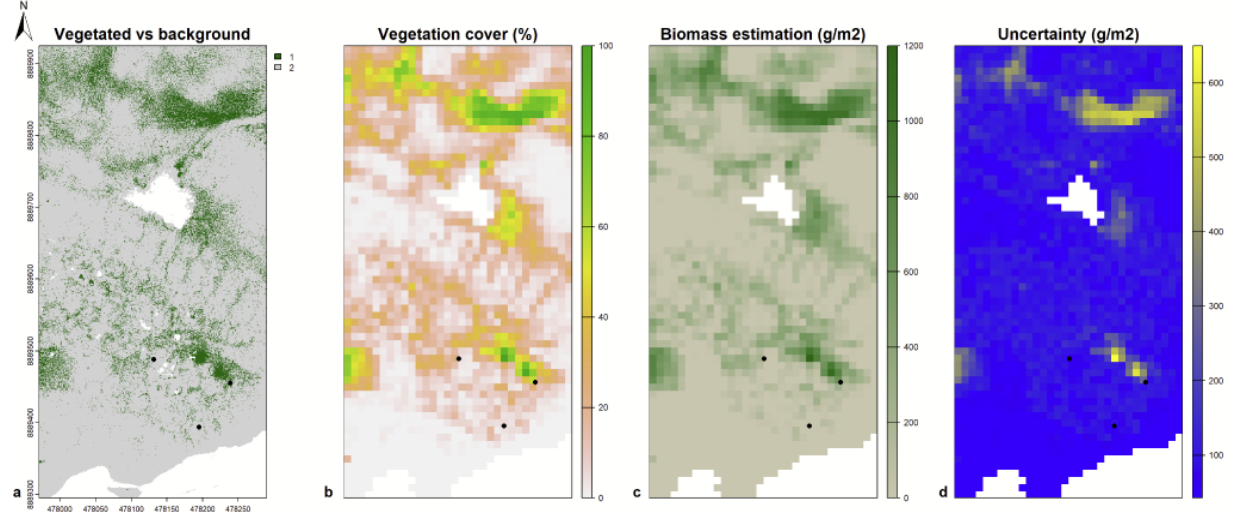
Landscape-level plant biomass estimation

The estimation of site-level vegetation cover based on drone imagery was performed for 4 sites: Vize, Pioneer, Uedineniya, and October Revolution Inland. 12-fold cross-validation with plot-level in situ measurements showed high performance across all sites: an average classification accuracy of 99% for Vize ($Kappa = 1$), 99% for Pioneer ($Kappa = 0.98$), and 98% for Uedineniya and October Revolution Inland ($Kappa = 0.97$). The classification results indicate significant differences in site-level vegetation cover across the sites. Vize is the most continuously vegetated island (site-level cover = 73.8%), while Pioneer (13.6%), Uedineniya (4.5%), and October Revolution Inland (1%) have very low vegetation cover at site-level (Fig. 9a).

Vize Island (mean biomass: 916 g/m², CI: 673-1162 g/m²; median biomass: 1100 g/m²)



Pioneer Island (mean biomass: 138 g/m², CI: 100-203 g/m²; median biomass: 46 g/m²)



Udedineniya Island (mean biomass: 39 g/m², CI: 28-94 g/m²; median biomass: 0 g/m²)

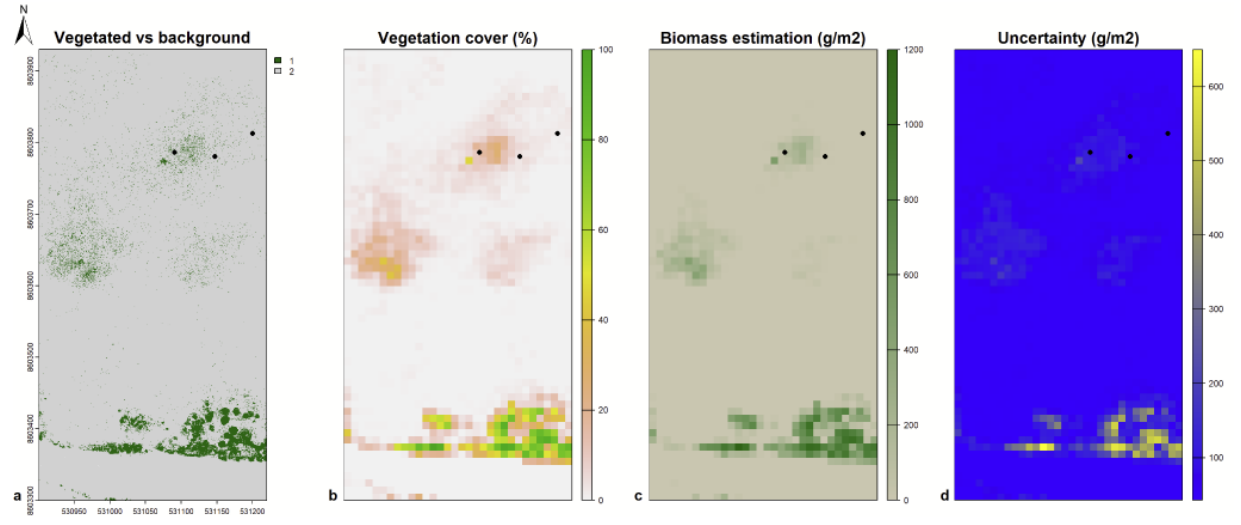


Figure 9. Site-level maps of vegetation cover and biomass distribution. Left to right: a) Cover and biomass maps resulted from drone imagery supervised classification (1: vegetation; 2: substrate; white: water and ice); b) aggregated 10x10 m fractional vegetation cover; c) mean estimated biomass (g/m^2); d) biomass uncertainty estimation (uncertainty = upper CI - lower CI). Dots in the maps indicate geobotanical plots locations.

The aboveground live plant and lichen biomass was estimated for 3 sites (October Revolution Inland was excluded due to the non-significant subplot-level cover-biomass relationship). The estimated mean biomass is highest on Vize, while Pioneer and Uednineniya demonstrate relatively low biomass (Fig. 9c). Uncertainty is highest for the areas with the highest estimated site-level vegetation cover (Fig. 9d).

The results of the focal lookup analysis showed statistically significant results for minimum, median and maximum fractional vegetation cover values within the tested focal windows, though for minimum values the results are on the border of a statistical significance (Appendix Table 2). The highest explanatory power ($0.57 R^2$) and lowest p-value (0.004) are found for the maximum sampled fractional vegetation cover value, while the mean shows intermediate results. The majority of the plots tend to have higher fractional vegetation cover estimates compared to mean in-situ cover, even taking into account the spread of fractional vegetation cover estimates (Appendix Fig. 4). This is especially the case for Vize, where 5 of 6 plots have overestimated fractional vegetation cover, while for Uednineniya, on the contrary, the fractional vegetation cover estimates tend to be lower than the in-situ mean cover for all 3 plots. The largest range (11-90%) is found for a plot on Vize, bordering the non-vegetated slope shoulder, while for most of the plots the span stays below 10%.

4.4 Discussion

Our research reveals that plant and lichen richness and biomass are distributed highly heterogeneously across the Barents, Kara and Laptev polar desert islands. We found that while most of the vascular plant species (both forbs and graminoids) maintain little variation in presence across the visited sites, cryptogams are mostly site- or even plot-specific, with 70% of the species occurring on 3 or fewer plots and 40% observed

just in a single plot. Our findings indicate that lichen biomass has a moderately high positive linear relationship with lichen species richness, whereas bryophytes and vascular plants do not show significant relationships. We document that while bryophytes and lichens have the highest contribution to total biomass across 4 sites (Vize, Pioneer, October Revolution Coast, Cape Baranova (Bolshevik)), vascular plants are the main contributor at 2 sites (Uedineniya and October Revolution Inland). We found that landscape-level plant and lichen aboveground biomass varies significantly, ranging from an almost complete absence of plant biomass on Komsomolets and Graham Bell to mean live aboveground biomass of 39 g/m² on Uedineniya and 138 g/m² on Pioneer, to 916 g/m² on Vize – a level expected in Arctic tundra rather than polar deserts).

Species richness is low though heterogeneously distributed across the Russian polar deserts which was confirmed by our results. Previously researched areas in the southern parts of polar deserts, such as Bolshevik Island (Matveyeva, 2006) and Northern Novaya Zemlya (Kholod, 2020), detected higher species richness for vascular plants and cryptogams compared to our study. For example, Kholod (2020) reported 31 species of vascular plants, 159 bryophytes, and 74 lichens in 150 Braun-Blanquet plots at Cape Zhelaniya (Novaya Zemlya), which are respectively 10, 95, and 29 more species than in our study. The documented species richness on Bolshevik Island is even higher; in 159 plots Matveyeva observed 68 vascular plant species, 155 bryophytes, and 69 lichens (Afonina & Matveyeva, 2002, 2003; Matveyeva, 2006). This can be partly attributed to the smaller sample size of our study, but also to more extreme climatic conditions and higher isolation of the northern islands, where the total species richness is significantly lower down to 7-8 vascular species on Komsomolets and Pioneer Islands (Matveyeva, 2015). However, the species richness of most of our sites is similar to Krenkel Island (Franz Josef Land), (Walker et al., 2012). On Krenkel Island, 11 vascular plant species (10 forbs and 1 graminoid), 25 species of bryophytes, and 28 species of lichens were observed within 10 Braun-Blanquet plots (Walker et al., 2012). All vascular plant species documented by Walker (2012) on Krenkel were also found in our research area, indicating a high homogeneity of vascular plant flora. In contrast, cryptogams showed much greater variation between the sites, with 16

bryophytes (64%) and 16 lichens (57%) from Krenkel were not observed in our research sites. This suggests a high site-specificity and potentially narrow ecological niches of polar desert cryptogams, with their diversity in the area remaining largely understudied due to the lack of field data (Potemkin, 2000, 2004; Zhurbenko & Matveyeva, 2006).

Similar to other low-vegetation communities (Jiang et al., 2017; Kathleen et al., 2022; Röttgermann et al., 2000), polar deserts have been found to exhibit relatively linear relationships between plant and lichen biomass and their cover. This can be explained by their simple vertical structure, described by Matveyeva (2015) as 'almost two-dimensional': our observed mean height of any layer never surpasses 4 cm, with a mean community height of 1.5 cm. The only exception to the linear trend is October Revolution Inland showing no significant relationships between subplot-level biomass and cover. This could be partly attributed to the high contribution of graminoids in the biomass, coupled with the absence of lichens (Fig.5): the biomass of relatively tall graminoids with low cover could be larger compared to the biomass of flat moss mats. For most of the plant functional types, we did not find relationships between species richness and biomass (Fig. 6), as few species of mosses and forbs, such as *Polytrichastrum alpinum* (Hedw.) G.L.Sm., *P. sexangulare* (Bridel) G.L. Smith, *Aulacomnium turgidum* (Wahlenb.) Schwägr., *Drepanocladus species*, or *Saxifraga oppositifolia*, can have relatively high cover in polar deserts. However, we found a moderately strong relationship for lichens, which could be explained by their higher site-specificity (Appendix Fig. 2). This likely indicates greater niche specialization, allowing us to suggest that high lichen species richness uses space more efficiently, in turn leading to higher biomass. As for graminoids, which also showed linear relationships similar to the lichens, the trend may be attributed to the small sample size. With only 5 graminoid species detected across the sites, we suggest that the relationship might not be observed with a larger sample size.

Heterogenous biomass distribution could be explained by differences in substrate, soil conditions and microrelief (Raynolds et al., 2006). Similar to species richness, plant and lichen biomass is found to be the lowest at sites with dynamic and light substrates such as Uedineniya and October Revolution Inland, while loamy and

rocky sites such as Pioneer, Cape Baranova (Bolshevik), Vize and October Revolution Coast have higher than average total biomass, mostly due to higher lichen and bryophyte contribution. Contrary to soil factors, latitudinal climatic gradients are likely less important as the southernmost site (Uedineniya) has the second lowest biomass across the research area and two October Revolution sites located on the same latitude have major differences in biomass. Comparing our results with other research on plant biomass in the High Arctic, we see that our biomass estimates from various sites are mostly similar with other polar desert estimates (CAVM, 2003; Walker et al., 2012), with the exception of Vize. The nearest sampled location is Krenkel Island on Franz Josef Land (Fig. 1), where the detected plant biomass is about 108 g/m² (Walker et al., 2012). The total biomass estimate for Krenkel is similar to our site on Pioneer Island (138 g/m²), which has an estimate between that of Krenkel and Isachsen, another polar desert site in the Canadian archipelago with biomass of 171 g/m² (Walker et al., 2008, 2012). Thus, Pioneer, together with Uedineniya, have biomass typical of polar deserts (CAVM, 2003), while Vize shows a higher than expected biomass more typical for continental Arctic tundra (Bliss, 1984; Gould et al., 2003; Räsänen et al., 2022; Walker et al., 2008, 2012). The high estimated biomass at Vize could partly be attributed to its relatively continuous vegetation cover, similar to certain mesic habitat communities in polar deserts documented by other researchers (Daniels et al., 2016; Matveyeva, 2015). Additionally, contrary to our research, Walker et al. (2012) did not include soil crusts in the total biomass estimate, while mentioning that crust contribution could be 98-221 g/m², depending on the substrate - almost twice more than non-crust biomass detected. Despite this, estimation uncertainties, such as the potential overestimation of site-level vegetation cover during classification, likely also played a role in the landscape-level biomass estimation (Fig. 9).

There are few potential sources of uncertainty in our estimation of plant and lichen aboveground biomass. Although the classification of vegetation and substrate demonstrated very high performance (Kappa: 0.98-1), visually separating vegetation from substrate in some sites (especially Vize) during supervised classification remains challenging despite the high resolution of drone imagery (Table 1). Two main factors contribute to the difficulty: the high intermixing of small stones and vegetation on Vize,

and the signal from soil algae and crusts that provide an NDVI signal similar to vegetation, issues common in polar vegetation mapping (Sotille et al., 2022; Vaczi & Batrak, 2022). Combined, these reasons could lead to the overestimation of fractional vegetation cover, and hence plant and lichen biomass on Vize, while the estimates for Pioneer and Uedineniya are likely more reliable. Additionally, geolocation accuracy is another source of uncertainty for biomass estimations. Although we accounted for the uncertainty in the GPS locations of the center of the 10x10 m plots to ensure the reliability of our fractional vegetation cover estimates (Fig. 9), the limited accuracy of handheld GPS and the absence of subplot coordinates still contribute to high overall uncertainty (Fig. 9,10).

Characterized by low vascular plant species richness, polar deserts are found to have a surprising species richness of bryophytes and lichens. Differences in vegetation characteristics and environmental conditions result in varying biomass, ranging from almost zero to levels similar to Arctic tundra, primarily due to changes in biomass of cryptogams. As 36% of polar desert lichens are found exclusively in the Arctic (Matveyeva, 2015), it is crucial to recognize the diversity of polar deserts and to protect the biome from both warming and potential anthropogenic disturbances. Documenting the species and communities of the biome and studying their ecological niches is hence crucial, as it helps to comprehend the conditions that would lead the 'permanent pioneer' vegetation of polar deserts to shift towards tundra. With our data and research we provide baseline geobotanical data and plant biomass estimations for one of the most understudied regions of the Arctic.

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Data availability statement: All data (species list, environmental variables, biomass) supporting the results of this chapter will be made available upon publication through Dryad and the Russian Arctic Vegetation Archive.

Conflicts of interest: We declare no conflict of interest.

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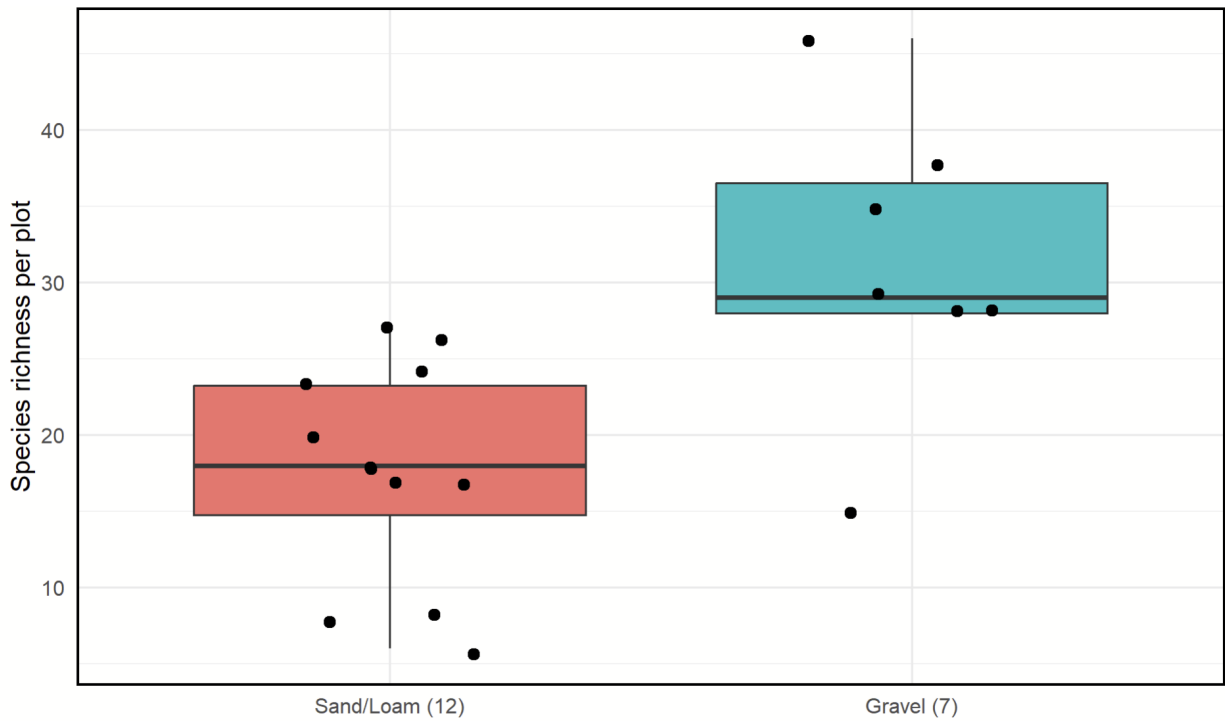
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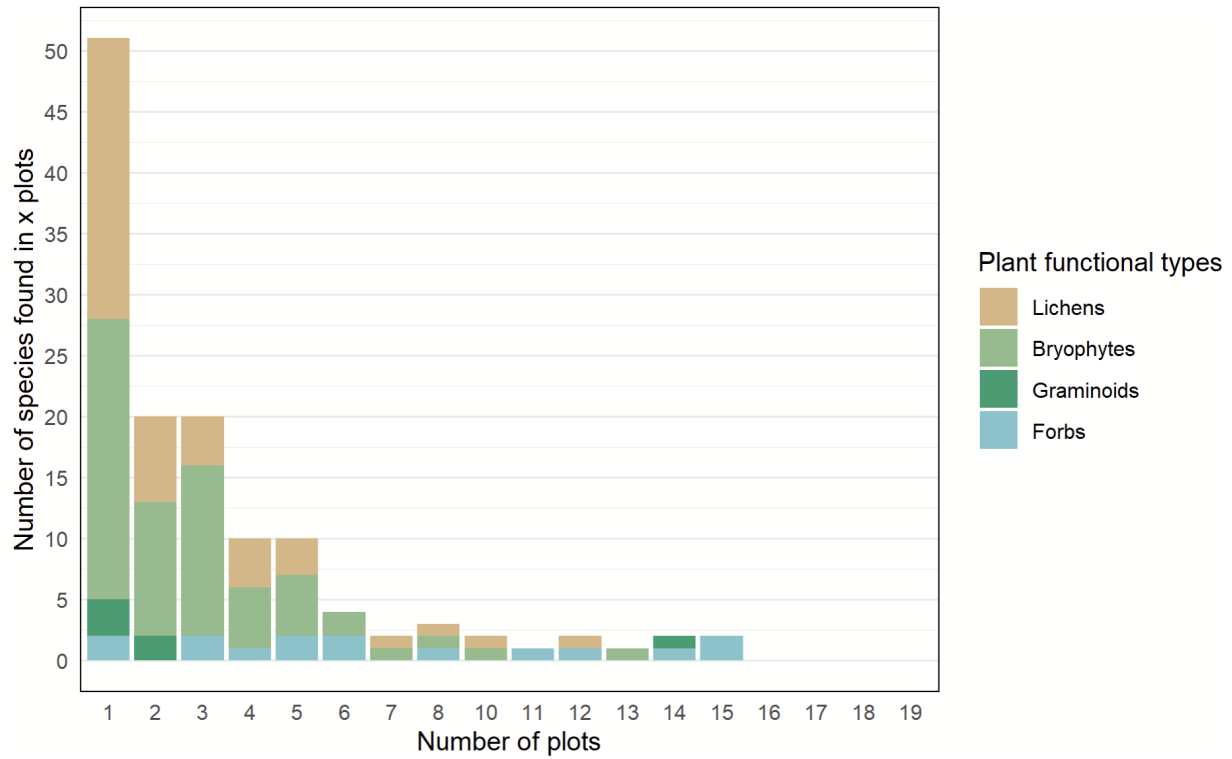
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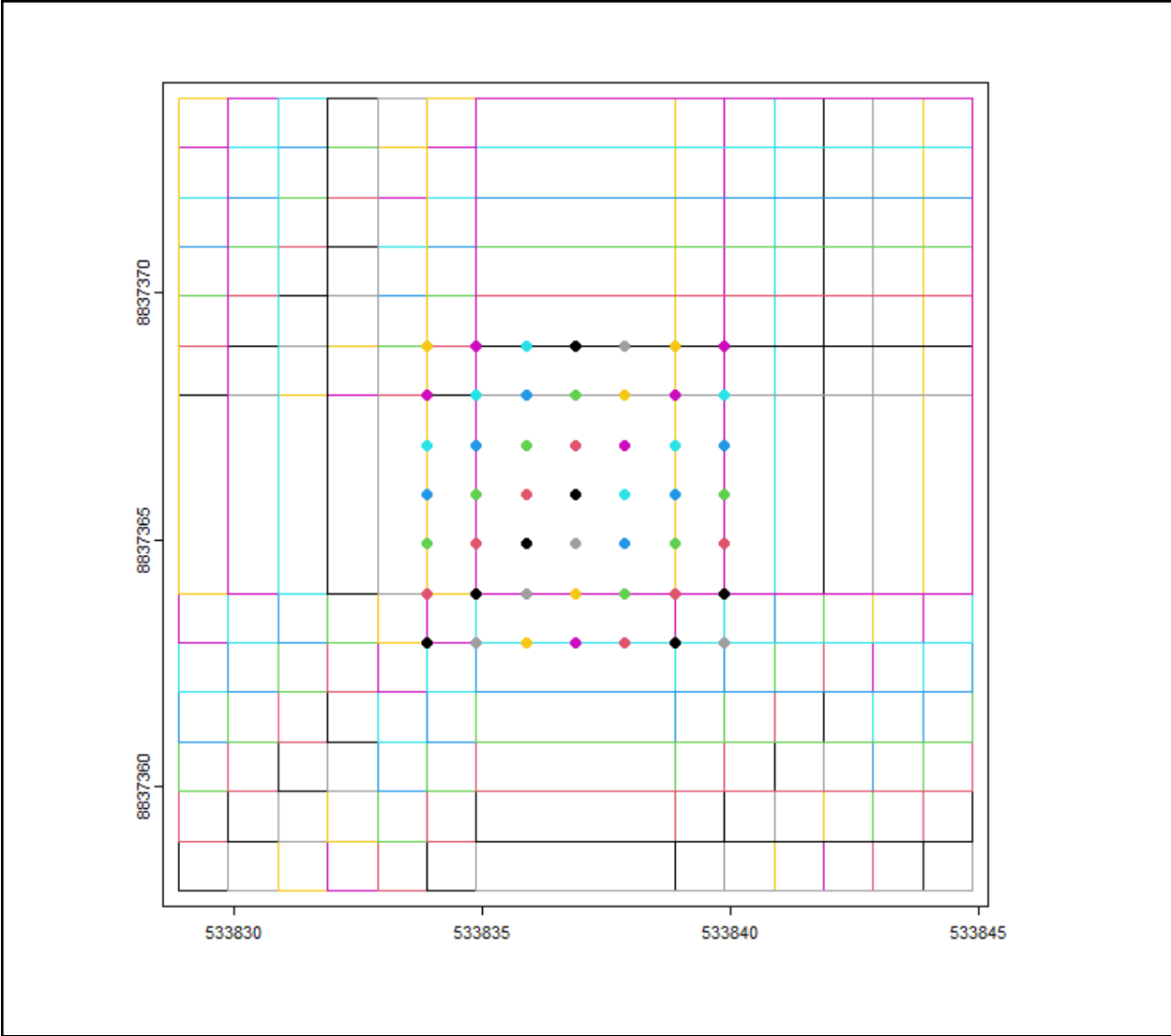
4.6 Supporting information



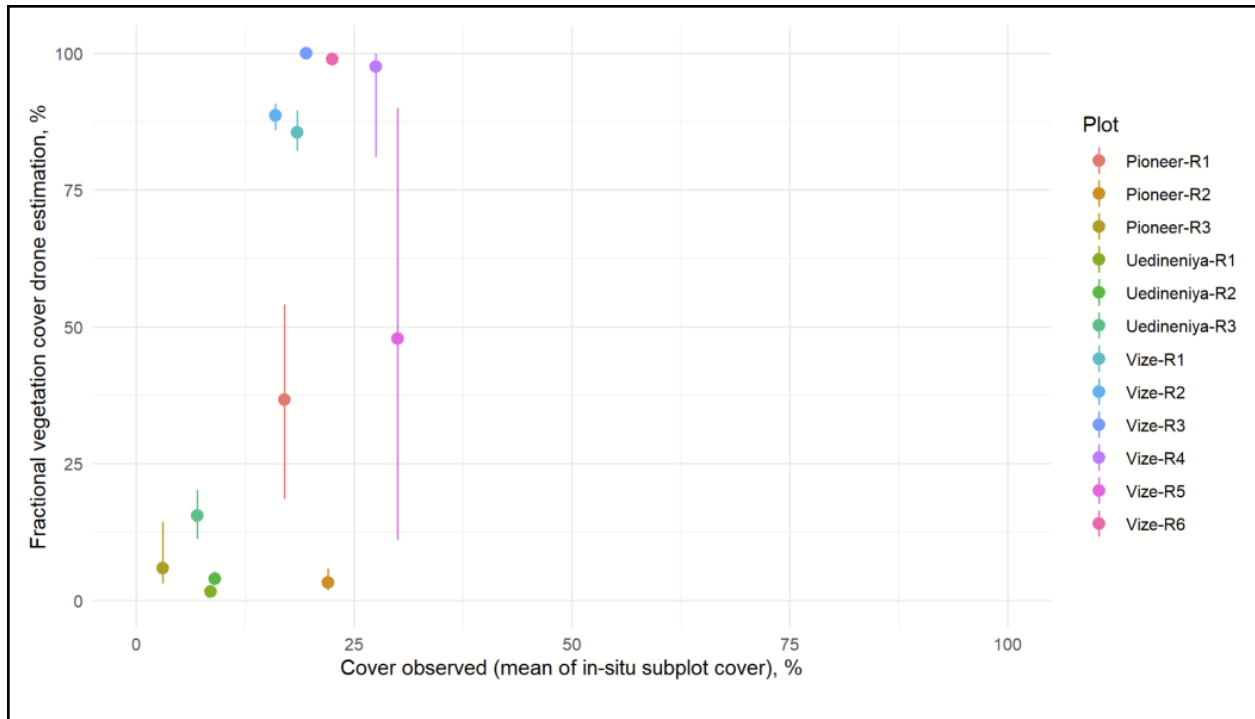
Appendix Figure 1. Relationships between substrate type and species richness. Amount of plots is indicated in brackets.



Appendix Figure 2. Species occurrence across 19 study plots. X-axis: the number of plots where each unique species is found. Y-axis: number of plots. This graph shows in how many plots a species was found. For example, there are no species occurring in 16 plots or more, but two species occurring in 15 plots and 4 species occurring in 6 plots.



Appendix Figure 3. Focal lookup window: the in-situ plot coordinate is located at the center, with 48 additional hypothetical center points placed around it at distances of 1-3 m in 8 directions. Each of the 49 center points is surrounded by a 10x10 meter buffer.



Appendix Figure 4. Focal lookup analysis results. Maximum, minimum and median of fractional vegetation cover from 441 focal lookup windows taking into account 3m GPS uncertainty (Table 2).

Appendix Table 1. Species data

5 Contributions as co-author

In the framework of this PhD thesis, I have additionally contributed to other Arctic studies as a co-author, as listed below.

5.1 Published papers

1. Oehri, J., Schaepman-Strub, G., Kim, J.-S., Grysko, R., Kropp, H., Grünberg, I., **Zemlianskii, V.**, Sonnentag, O., Euskirchen, E. S., Reji Chacko, M., Muscari, G., Blanken, P. D., Dean, J. F., di Sarra, A., Harding, R. J., Sobota, I., Kutzbach, L., Plekhanova, E., Riihelä, A., ... Chambers, S. D. (2022). **Vegetation type is an important predictor of the arctic summer land surface energy budget.** *Nature Communications*, 13(1), 6379. <https://doi.org/10.1038/s41467-022-34049-3>

Abstract

Despite the importance of high-latitude surface energy budgets (SEBs) for land-climate interactions in the rapidly changing Arctic, uncertainties in their prediction persist. Here, we harmonize SEB observations across a network of vegetated and glaciated sites at circumpolar scale (1994–2021). Our variance-partitioning analysis identifies vegetation type as an important predictor for SEB-components during Arctic summer (June-August), compared to other SEB-drivers including climate, latitude and permafrost characteristics. Differences among vegetation types can be of similar magnitude as between vegetation and glacier surfaces and are especially high for summer sensible and latent heat fluxes. The timing of SEB-flux summer-regimes (when daily mean values exceed 0 Wm^{-2}) relative to snow-free and -onset dates varies substantially depending on vegetation type, implying vegetation controls on snow-cover and SEB-flux seasonality. Our results indicate complex shifts in surface energy fluxes with land-cover transitions and a lengthening summer season, and highlight the potential for improving future Earth system models via a refined representation of Arctic vegetation types.

I contributed to the paper by classifying the local vegetation at each study site according to the categories of the Circumpolar Arctic Vegetation map (CAVM, 2003).

2. Ermokhina K., Terskaia, A., Ivleva T., Dudov, S., **Zemlianskii, V.**, Telyatnikov, M., Khitun, O., Troeva, E., Koroleva, N., & Abdulmanova, S. (2023). **The High-Low Arctic boundary: how is it determined and where is it located?** *Ecology and Evolution*, 13(10). <https://doi.org/10.1002/ece3.10545>

Abstract

Geobotanical subdivision of landcover is a baseline for many studies. The High–Low Arctic boundary is considered to be of fundamental natural importance. The wide application of different delimitation schemes in various ecological studies and climatic scenarios raises the following questions: (i) What are the common criteria to define the High and Low Arctic? (ii) Could human impact significantly change the distribution of the delimitation criteria? (iii) Is the widely accepted temperature criterion still relevant given ongoing climate change? and (iv) Could we locate the High–Low Arctic boundary by mapping these criteria derived from modern open remote sensing and climatic data? Researchers rely on common criteria for geobotanical delimitation of the Arctic. Unified circumpolar criteria are based on the structure of vegetation cover and climate, while regional specifics are reflected in the floral composition. However, the published delimitation schemes vary greatly. The disagreement in the location of geobotanical boundaries across the studies manifests in poorly comparable results. While maintaining the common principles of geobotanical subdivision, we derived the boundary between the High and Low Arctic using the most up-to-date field data and modern techniques: species distribution modeling, radar, thermal and optical satellite imagery processing, and climatic data analysis. The position of the High–Low Arctic boundary in Western Siberia was clarified and mapped. The new boundary is located 50–100 km further north compared to all the previously presented ones. Long-term anthropogenic press contributes to a change in the vegetation structure but does not noticeably affect key species ranges. A previously specified climatic criterion for the

High–Low Arctic boundary accepted in scientific literature has not coincided with the boundary in Western Siberia for over 70 years. The High–Low Arctic boundary is distinctly reflected in biodiversity distribution. The presented approach is appropriate for accurate mapping of the High–Low Arctic boundary in the circumpolar extent.

I contributed to the paper by a) collecting geobotanical data during the 2017 and 2018 expeditions; b) analyzing subzonal border area species richness and presenting the results in box plots; c) producing overview and reindeer grazing impact maps; d) supporting the manuscript writing.

5.2 In review

3. Heim, R., Rocha, A., **Zemlianskii, V.**, Barrett, K., Bültmann, H., Breen, A., Frost, G. V., Hollingsworth, T. N., Jandt, R., Kozlova, M., Kurka, A., Jorgenson, M. T., Landhäusser, S. M., Loranty, M. M., Miller, E. A., Narita, K., Pravidolyubova, E., Hölzel, N., & Schaepman-Strub, G. (in review). **Arctic tundra ecosystems under fire – potential trajectories for stable state shifts.**

Abstract

Ongoing climate change is expected to lead to shifts in the composition, structure and functioning of Arctic tundra ecosystems. Tundra fires are increasing in frequency, severity and extent and have the capacity to trigger transitions of tundra vegetation to different stable ecological conditions, also called stable states. A stable state shift of the tundra vegetation may not only impact the local ecosystem, but also the subsistence-based livelihoods of Arctic people. It might furthermore contribute to surpassing the tipping point of permafrost degradation, thereby increasing greenhouse gas emissions.

Post-fire vegetation trajectories observed in field studies can inform possible stable conditions the ecosystem may shift to. The recovery after fire of different plant species and plant functional types after a tundra fire depends on specific abilities such as fire resistance, resprouting, seedbank persistence, and seed dispersal mechanisms.

As a consequence woody plants, graminoids, and mosses can often profit strongly from tundra fires while lichens almost always show a strong decline.

Based on existing empirical data, we found that two trajectories towards alternative stable states are most likely for different Arctic tundra vegetation types. The first trajectory is towards a shrub-dominated state after an unusually severe fire. Post fire, woody plants can gain dominance due to their resprouting ability and taller stature, a response that is further amplified by modern warmer climate conditions. The second trajectory is towards a grass-dominated stable state induced by high fire frequency, with short intervals between fires that promote fires resistance graminoids and do not allow other functional types to recover. These trajectories can vary in course, depending on the pre-fire tundra vegetation, local site conditions, and fire characteristics.

In the future, we need to address several sources of uncertainty regarding possible stable state transitions of tundra ecosystems after fires, using methods that allow the coverage of larger temporal and spatial scales. Similarly, more case studies, especially in so far underrepresented regions and Arctic tundra vegetation types, are essential to broaden the empirical basis for forecasts and possible fire management.

I contributed to the paper by collecting vegetation data on a fire scar in the Western Siberian forest-tundra in 2018 and participating in the discussion and writing of the paper.

6 Synthesis

6.1 Bridging the knowledge gaps on Russian Arctic vegetation

Despite significant geobotanical efforts in the Russian Arctic, many 'white spots' remain, both in terms of plant diversity data and in understanding the processes shaping Russian Arctic ecosystems. With this thesis, I contribute to the geobotanical knowledge of the Russian Arctic by providing baseline data and conducting applied research on the diversity and distribution of plant and lichen species in the Russian Arctic (Chapters 1-3), and the current status and distribution of aboveground plant biomass on Russian polar islands (Chapter 3).

As only a few non-Russian geobotanists have systematically worked in Russia, and since most of the data collected by scientists followed different protocols, there was a lack of internationally accessible, standardized data on Russian tundra plant communities suitable for comprehensive pan-Arctic analysis (Walker et al. 2016). Therefore, the first goal of my thesis was to assess the state of existing data, identify the gaps, and potential datasets for standardization, translation, and integration. With the newly obtained data, we addressed the gaps by creating a comprehensive Russian Arctic Vegetation Archive (AVA-RU), consisting of 4785 vegetation surveys across the Russian Arctic, previously not available to the international scientific community (Chapter 1). AVA-RU contains information on the presence or absence of rare and endangered plant species and their communities, providing data for nature conservation planning.

With the publication of AVA-RU, we developed a core archive for Russian Arctic vegetation data, enabling further modeling applications. In Chapter 2, we conducted the first community-level plant species richness modeling for the Western Siberian Arctic. We utilized the macroecological models to investigate the relative roles of various environmental factors in shaping community-level plant and lichen species richness, thereby improving our understanding of what drives species richness distribution in the Arctic. We discovered an uneven distribution of species richness, with a maximum

species richness in the northeast of the Western Siberian Arctic and the lowest in the southwest, driven mostly by contemporary and ancient climatic factors, while the role of relief is secondary. The resulting maps have enabled an assessment of the effectiveness of existing nature protection areas in conserving regions with the highest species richness. As the first regional-scale case of plant species richness modeling in the Russian Arctic, our research successfully demonstrated the feasibility of the approach, opening the door for similar pan-Arctic analyses as the consistent pan-Arctic data of similar quality will become available.

An additional knowledge gap we addressed in the thesis is the lack of data on plant and lichen diversity and biomass distribution on polar desert islands (Barry et al., 2013; Virkkala et al., 2019). During the Arctic Century expedition of 2021, we collected 19 plots from Franz Josef Land and Severnaya Zemlya Archipelagos, Vize and Uedineniya Islands, thereby bridging the existing diversity data gap of the High Arctic and providing a baseline for monitoring of its future changes. Our analysis of Russian polar desert vegetation surveys revealed a highly uneven distribution of cryptogam species down to the plot level. This is in contrast to vascular plant species, which exhibited a relatively consistent presence across the visited sites. Furthermore, we assessed the in-situ biomass of graminoids, forbs, bryophytes, lichens, and litter across six different sites across five Arctic islands. Modeling landscape-level biomass in polar deserts demonstrated that biomass varies widely across the sites. It reaches a maximum on Vize Island, where the mean estimated biomass surprisingly reached 920 g/m², a number comparable to Arctic tundra levels. Conversely, Pioneer and Uedineniya Islands have lower biomass (39-138 g/m²), a level typical for polar deserts. Combined with the data and results of Chapters 1 and 2, the knowledge of plant and lichen diversity, biomass, and species richness on the polar islands enables the study of vegetation across the entire West Siberian Arctic gradient, from the polar deserts in the north to the Tazovsky Peninsula in the south, complementing existing efforts of the Eurasian Arctic Transect (Epstein et al., 2020; Walker et al., 2019).

6.2 Geobotanical data on the Russian Arctic: remaining gaps and future directions

Many data and knowledge gaps on Russian Arctic vegetation still remain and should be addressed by future geobotanical research. A potential field is the integration of local flora data, based on a complete assessment of vascular plant species within an area of 100 – 300 km². Extensive local flora data for the Russian Arctic, including more than 240 localities (Khitun et al., 2016), are far from being integrated into existing open data archives and remain largely undigitized. Digitizing and unifying the local flora archives would enable landscape-level pan-Arctic species distribution modeling, which could be used for a range of different applications, including more accurate subzone delineation (Ermokhina et al., 2023), as well as for predicting species distributions under future climate change (Niskanen et al., 2019).

Another important direction for improving data availability is the digitization and harmonization of data on rare and endangered species. Federal and regional red books in Russia provide information on the distribution and status of rare species, with updates over time (Red Book of Russia, 2023; Red Book of YANAO, 2010). However, although regional red books are available to the public, species occurrence data from them are not openly available in a format suitable for quantitative analysis. Combining this data into a single digital archive, along with existing knowledge from the Red books about the factors endangering these species (Khapugin et al., 2020), could facilitate their conservation both in Russia and in the wider Arctic. Analysis of these data would also provide insight into the impacts of different global change drivers on rare species, deepening our understanding of the ongoing transformation of the Arctic ecosystems. This includes the broad-scale effects of infrastructure, mining and other economic activities on plant diversity, which have so far been poorly quantified and largely absent from broad scale infrastructure effects assessments (Chapter 2; Povoroznyuk et al., 2022).

Finally, despite the progress made in standardizing geobotanical data through AVA-RU, there is still room for development and updating of the project, requiring further

communication with data owners to provide open access to their archived and new data. In combination with the development of a common vegetation classification framework (Matveyeva & Lavrinenko, 2021; Walker et al., 2016), a comprehensive community data archive would enable modeling of the distribution of plant communities, including rare ones (Green Book of Siberia, 1996), which is not possible with species occurrence data alone. This would contribute to our understanding of plant community niches, thus improving our ability to protect communities from global change.

The main challenge in addressing the data gaps is the lack of connectivity and coordination among researchers, both within Russia and internationally. This problem has worsened in the last two years, as scientific connections between Russia and other Arctic countries have deteriorated (The Moscow Times, 2024). While there are more than 3000 datasets contributed to GBIF from Russia (<https://www.gbif.org/country/RU/summary>), coordinated efforts with known data applications will have a greater impact compared to individual contributions. Potential solutions may be in self-governing bodies responsible for managing national archives. There is an interest in creating a national biodiversity data archive in Russia, which would naturally include at least some of the Russian Arctic data (Ivanova & Shashkov, 2016). However, it is important that these efforts remain coordinated at the international level and share the internationally-accepted protocols. With global initiatives developing to organize biodiversity monitoring in a more coordinated and federalized way (Gonzalez et al., 2023), there is the potential for the development of such initiatives, even in the current political climate. The successful development of the AVA-RU, based on the common Arctic vegetation protocol agreement, suggests there is reason to be optimistic in this area.

6.3 Tundra vegetation and biosphere stability: valuing low diversity ecosystems

Far from being a lifeless desert, the Russian Arctic is home to thousands of plant species and subspecies, including bryophytes and lichens, whose diversity has not been yet fully estimated (Barry et al., 2013; Lewis et al., 2017). Part of the reason for

the underestimation of plant diversity in the Russian Arctic is the lack of access of the international scientific community to Russian vegetation data. This inaccessibility is caused by the lack of data access, standardization, and difficulties in efficiently searching Russian journals. In **Chapter 1**, we addressed this issue by translating and standardizing 4785 plots and presenting them as the Russian Vegetation Archive, taking a step towards the creation of the International Arctic Vegetation Database (<https://www.geobotany.uaf.edu/ava/>). The AVA-RU documented more than 1770 vascular plant and cryptogam species and subspecies, their habitats, and information on the vertical and horizontal structure of plant communities. The archive shows a wide diversity of plants adapted to different climatic conditions of the Arctic, even as extreme as conditions of polar deserts, with low, but highly specialized and unique diversity of bryophytes and lichens, as shown in **Chapter 3**.

In **Chapter 3**, lichens are shown to be an important component of the Arctic ecosystems — in the extreme environment of the Russian polar islands, lichens and bryophytes form a majority of the total biomass. Importantly, polar desert lichens also show a moderately strong positive relationship between their species richness and total biomass, which, in combination with their highest site specificity across all plant functional types (23 of 45 lichens species were found in just a single plot within the study area), makes them a particularly crucial component of the northernmost ecosystems, yet not as recognized as vascular plants. Moreover, lichens are also major contributors to the biomass in tundra biome, providing food to reindeer and thus sustaining the traditional livelihood of Indigenous Peoples (Bogdanova et al., 2021; Joly et al., 2003). As our group's research shows, lichen tundra is likely to undergo a transition to new stable states such as shrub- or grass-dominated communities in the future due to the climate-driven increase in the frequency and severity of tundra fires (**Co-authored paper 3: Heim et al.**, In review.), which are particularly common in Siberia.

As we discuss in **Chapter 2**, climate is the main factor shaping plant species richness in the Western Siberian Arctic, having a lasting effect on its plant diversity, as the high predictive power of paleoclimatic factors shows. However, the relationship

between climate and vegetation is far from being one-dimensional. Our research group has shown that vegetation types and bioclimatic subzones are two of the three most important predictors of variance in Arctic net radiation, affecting the Earth's energy budget (**Co-authored paper 1: Oehri et al., 2022**). Thus, climate-driven shifts in vegetation types and bioclimatic subzones in turn influence the climate, effectively creating a feedback loop. As delineation of vegetation subtypes is interlinked with bioclimatic subzones, this leads to a necessity to develop a comprehensive criteria for bioclimatic subzone delineation. We accomplished this for the case study of Western Siberia, demonstrating a northward shift of 50-100 km compared to previous estimates (**Co-authored paper 2: Ermokhina et al., 2023**).

As shown above, the plant and lichen diversity of the Russian Arctic, although not as diverse as in lower latitudes, is highly valuable, not only for its uniqueness and intrinsic value, but also for its role in maintaining biosphere stability. However, as we show in **Chapter 2**, the current natural reserves of western Siberia do not cover the areas with the highest species richness. This provides additional evidence to support the notion that current protected areas in the Arctic are insufficient in the context of climate change (Reji Chacko et al., 2022), leading us to question what could be a more effective stewardship strategy for conserving Arctic plant diversity, including the plant diversity of the Russian Arctic.

As humanity rapidly approaches the planetary boundaries (Newbold et al., 2016; Rockström 2009, 2023), the area of the natural ecosystems is decreasing every year. This raises questions about the effectiveness and desirability of a targeted approach to nature conservation. Considering the highest importance of protecting the Arctic ecosystems, alternative approaches should be considered, which would inevitably require a deep transformation of the society (Büscher et al., 2017; Moranta et al., 2021). However, as transformative change is often perceived as distant and utopian, intermediate tangible targets should also be identified.

There is a positive case of Antarctica, where at the height of the Cold War (1959) and despite the territorial claims of many countries, an international Antarctic Treaty was

signed to prevent economic and military expansion in the region, while protecting Antarctica for scientific research (<https://www.ats.aq/e/antarctictreaty.html>). While a similar agreement for the Arctic is difficult to imagine in the current political context (it also likely would include more different stake- and rights-holders), the concept still provides a good ideal model for an open and collaborative Arctic, where natural ecosystems are protected. The willingness to discuss such ideas could itself create a constructive space in which new positive solutions could emerge.

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Post scriptum on power and powerlessness of science

The impressive progress in acquiring knowledge of nature has made it possible to model and predict the development of the Earth's system on a large scale. Thanks to this progress, we have solid evidence that the Arctic ecosystems are undergoing rapid transformation, which will result in a wide range of negative consequences for both the biosphere and humanity. Unfortunately, despite this evidence, sufficient actions have not been taken.

There is evidence that intellectual knowledge alone is insufficient. To result in meaningful actions, knowledge must be connected to specific experiences, which is something that scientists, policymakers, and the general public of wealthy nations often lack. We study things that are *remote* from us, both geographically and sensually. We are also not the people who bear the main costs of the crisis.

This separation of intellectual knowledge and social (including, importantly, political) practice partly protects science from being driven by ideologies or contaminated by specific interests. However, this also renders scientific knowledge akin to 'high' knowledge, similar to art or philosophy, which safeguard 'high' truths but remain largely powerless in their actual realization. We should be impartial to obtain the knowledge, but the very impartiality makes us powerless to make the best use of our study results, including their effective communication. I believe it is important to keep this limitation in mind in any research on global change.

There is still an inherent value in knowing, and the knowledge we gain has the potential to be utilized by others, despite its limited power to stop the ecological crisis. As my journalist colleagues reporting on the repressions in Russia rightly point out, even if we cannot prevent bad things from happening, we can still witness and document. This is the least that we, as scientists, can do for Arctic nature.

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Curriculum Vitae

Vitalii Zemlianskii

Date of birth: 24 June 1994

Place of origin: Vladimir city, Vladimir oblast', Russia

Education

- 2012-2016. B.Sc. (*Hons*) in Ecology (Moscow State University, Faculty of Geography, Department of Biogeography). Thesis title: Anthropogenic transformation of plant communities in Northern Yamal.
- 2016-2018. M.Sc. (*Hons*) in Ecology (Moscow State University, Faculty of Geography, Department of Biogeography). Thesis title: Vegetation of typical and southern tundra of Yama-Nenets Autonomous District: ecological and geographical analysis.

Working experience

- Conservation NGO 'Verkhovye' (2017-2019)

Fieldwork experience (selected)

- **July 2022** – Toolik research station, Alaska, USA, post-fire biomass recovery study;
- **August-September 2021** – Arctic Century Expedition, Russian polar islands, vegetation study;
- **July 2020** – Kytalyk, Sakha republic, Russia, expedition of Spatial Ecology and Remote Sensing group, study of vegetation of the site;
- **June 2019** – Utrish natural reserve, Krasnodar region, Russia, geobotanical mapping of the reserve;
- **June-August 2018** – Polar Ural, Yamal-Nenets autonomous district, Russia, expedition of Arctic research center of the Yamal-Nenets autonomous district, assessment of reindeer pasture conditions;

- **July-August 2017** – Yamal, Yamal-Nenets autonomous district, Russia, expedition of Arctic research center of the Yamal-Nenets autonomous district, assessment of reindeer pasture conditions;
- **August 2016** – Yamal, Yamal-Nenets autonomous district, Russia, study of plant ecology on the South Tambey gas field;
- **June 2016** – Kerzhenets Nature Reserve, Nizhny Novgorod Oblast, Russia, wildfire succession research;
- **August 2015** – Yamal, Yamal-Nenets autonomous district, Russia, study of plant ecology on the South Tambey gas field;
- **July–August 2015** – Tigiretsky Nature Reserve, Altai Krai, Russia, project of Russian Geographical society 'An estimation of West Altai plant species diversity as the basis for mountains ecosystem conservation', geobotanical field work;
- **August 2014** – Yamal, Yamal-Nenets autonomous district, Russia, study of plant ecology on the South Tambey gas field.

Teaching experience

- Spatial Ecology and Remote Sensing (UWW 250) course (190 hours): assisting GIS practicals;
- Introduction to Earth System Science (ESS 101) course (30 hours): teaching biodiversity seminars;
- Ecosystems and climate (UWW 182) (37 hours), Principles of Remote Sensing (GEO 233) (4 hours), and Remote Sensing Technologies and Methods (GEO 371) courses (4 hours): exam supervision and corrections.

Courses and training

- **Fall 2022**: Basic German 1; A1 (2 ECTS, 5.75);
- **Spring 2022**: ECO 311 Writing a Scientific Manuscript (2 ECTS, Pass);
- **Spring 2022**: ECO 340 Ecological Theory Part 2 (1 ECTS, Pass);
- **Fall 2020**: Landscape Modelling of Biodiversity: From Global Changes to Conservation (ETH Zurich) (5 ECTS, 5.5).

Peer-reviewed publications

- **Vitalii Zemlianskii**, Philip Brun, Niklaus Zimmermann, Ksenia Ermokhina, Olga Khitun, Natalia Koroleva, Gabriela Schaepman-Strub. 'Current and past climate co-shape community-level plant species richness in the Western Siberian Arctic.' *Ecology and Evolution* (2024).
- **Vitalii Zemlianskii**, Ksenia Ermokhina, Gabriela Schaepman-Strub, Nadezhda Matveyeva, Elena Troeva, Igor Lavrinenko, Mikhail Telyatnikov, Igor Pospelov, Natalia Koroleva, Nadezhda Leonova, Olga Khitun, Donald Walker, Amy Breen, Nikita Kadetov, Olga Lavrinenko, Tatiana Ivleva, Sergey Kholod, Nataliia Petrzhik, Maria Kurysheva, Yakov Gunin, Anna Lapina, Denis Korolev, Ekaterina Kudr, Elena Plekhanova. 'Russian Arctic Vegetation Archive — A new database of plant community composition and environmental conditions.' *Global Ecology and Biogeography* (2023). <https://doi.org/10.1111/geb.13724>
- Oehri, Jacqueline, Gabriela Schaepman-Strub, Jin-Soo Kim, Raleigh Grysko, Heather Kropp, Inge Grünberg, **Vitalii Zemlianskii** et al. 'Vegetation type is an important predictor of the arctic summer land surface energy budget.' *Nature Communications* 13, no. 1 (2022): 6379. <https://doi.org/10.1038/s41467-022-34049-3>
- Ermokhina, Ksenia A., Anna I. Terskaia, Tatiana Yu Ivleva, Sergey V. Dudov, **Vitalii A. Zemlianskii**, Michael Yu Telyatnikov, Olga V. Khitun, Elena I. Troeva, Natalia E. Koroleva, and Svetlana Yu Abdulmanova. 'The High–Low Arctic boundary: How is it determined and where is it located?' *Ecology and Evolution* 13, no. 10 (2023): e10545. <https://doi.org/10.1002/ece3.10545>

Scholarships

- Swiss Government Excellence Scholarship (2019.0075)

Conference contributions (selected)

- 2023. Arctic Summit Science Week, Vienna. Poster: *Environmental and anthropogenic factors co-shape plant species richness across the Western Siberian tundra*;
- 2023. Arctic Summit Science Week, Vienna. Talk: *Russian Arctic Vegetation Archive update*;
- 2022. World Biodiversity Forum, Davos. Talk: *Biodiversity of the Russian High Arctic islands*;
- 2022. World Biodiversity Forum, Davos. Poster: *Environmental and anthropogenic factors explain plant species richness across Western Siberia tundra*;
- 2021. Arctic Summit Science Week, Lisbon. Talk: *Progress of the Russian Arctic Vegetation Archive*;
- 2020. World Biodiversity Forum, Davos. Poster: *Status and development of the Russian Arctic Vegetation Archive*;
- 2019. Arctic Summit Science Week, Arkhangelsk. Poster: *Plant species composition of tundra vegetation in subzone D and E, West Siberia: the approach to comparative analysis*.