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Research article

Local snow and fluvial conditions drive taxonomic, functional and phylogenetic plant diversity in tundra

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To understand, how the diversity and hence functioning of tundra ecosystems might respond to altering environmental conditions, fine-scale studies are needed as local conditions may buffer broad-scale environmental changes. Furthermore, species functional traits and phylogeny may provide complementary insights to taxonomic diversity patterns as they link plant communities to ecosystem processes often more closely than species count. Here, we examined taxonomic, functional and phylogenetic plant diversity in relation to fundamental environmental factors, namely, growing degree days, snow persistence, soil moisture, pH and fluvial disturbance in northern Norway. The relationships between eight diversity metrics and environmental predictors were investigated using hierarchical generalised additive models. Our results indicated that taxonomic, functional and phylogenetic plant diversity in tundra are all strongly linked to local snow and fluvial conditions, with average variable importance of 0.19 and 0.14, respectively, whereas the importance of other predictors was low (average variable importance < 0.06). The average explained deviance by the models was 0.23. Predicted hotspots of different diversity metrics overlapped notably and were mostly located along the streams. However, when the effect of taxonomic richness was removed from the phylogenetic and functional diversities their connections with environmental predictors were weaker but indicated strongest relationships with snow and soil pH showing distinct diversity hotspots in areas with low species richness. Our study demonstrates that investigating multiple facets of biodiversity enhances understanding on community patterns and their drivers. Furthermore, our results highlight the importance of addressing local hydrological conditions that represent both resources and disturbances for vegetation. As arctic and alpine areas are probably shifting from snow to rain dominated, incorporating snow and fluvial information into the models might be particularly important to better understand tundra ecosystems under global change.

Keywords: arctic-alpine vegetation, biodiversity, fluvial disturbance, snow cover, vascular plants



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Introduction

Ecosystems are facing drastic changes globally due to climatic alterations and land-use changes caused by human actions leading to on-going biodiversity crisis (Steffen et al. 2015). High latitude and altitude tundra environments are particularly under threat as they are expected to warm up to three times faster than the global average, even though direct human impacts are lesser than elsewhere (IPCC 2022). Land area available for cold-adapted arctic–alpine vegetation is constantly shrinking and the decrease of tundra region has been predicted to be vast especially in northern Fennoscandia (Barredo et al. 2020). Alterations in environmental conditions trigger changes in species distributions (Felde et al. 2012), community composition (Bjorkman et al. 2018a, Reichle et al. 2018) and diversity (Niittynen et al. 2020). Furthermore, changes in vegetation patterns have likely effects on the processes and functioning of the whole ecosystems (Myers-Smith et al. 2011). Higher diversity increases ecosystem stability (Craven et al. 2018) and multifunctionality (Le Bagousse-Pinguet et al. 2019), and therefore, investigating diversity patterns and their drivers enhances our understanding of the future of tundra ecosystems.

Looking beyond taxonomic diversity, species functional traits as well as evolutionary history (phylogeny) might provide important insights into community assembly mechanisms and biodiversity (Cadotte et al. 2013, DePauw et al. 2021). Plant functional traits describe species size and structure as well as biogeochemistry concerning plant properties both above (e.g. height and leaf nutrient content) and below ground (e.g. rooting depth and root dry matter content) (Wright et al. 2004, Díaz et al. 2016). Importantly, they relate to key ecosystem processes such as carbon, water and nutrient cycling and productivity (Lavorel and Garnier 2002, Reich 2014). Functional diversity in turn describes the variability of traits in a community providing a more mechanistic approach to biodiversity research, since ecosystem processes are often more directly linked to functional diversity than to species richness (Díaz and Cabido 2001, Roscher et al. 2012). With higher functional diversity, a larger range of traits is present in a community due to niche complementarity leading to more efficient resource use (Díaz and Cabido 2001).

Phylogenetic diversity, in turn, reflects the evolutionary distinctiveness among taxa but likely summarises information on plant trait variability as well (Faith 1992, Tucker et al. 2018). Moreover, phylogenetic diversity is often considered to represent the effect of phylogenetically conserved traits that are important for species survival and reproduction, but challenging to measure, such as traits mediating pathogen effects (Srivastava et al. 2012, Cadotte et al. 2013). Thus, these traits could not be captured in the calculations of functional diversity which usually depend on the easily measurable traits like height or leaf characteristics, for example. Additionally, phylogenetic diversity may also capture interspecific interactions due to the unmeasurable traits (Srivastava et al. 2012) and it does not depend on a priori selection of traits (Tucker et al. 2018). Therefore, considering

species phylogeny may complement the information about the ecological differences of species by accounting for factors that could not be otherwise accounted for (Cadotte et al. 2013). Together functional and phylogenetic diversity hence provide a complementary approach to investigate biodiversity as they can combine information on species richness as well as on community composition but also offer a possibility to examine diversity unrelated to species richness (Villéger et al. 2008, Miller et al. 2016). However, it should be noted, that depending on the used metric, functional and phylogenetic diversity can be heavily influenced by species number (Tucker et al. 2016). Therefore, to disentangle the effect of species traits and phylogeny from richness effect, utilising null models, that control for species richness, might be particularly useful as well as considering different metrics (Miller et al. 2016, Palacio et al. 2022).

In tundra, taxonomic diversity is regionally low, but there can be much variation in the local diversity patterns both in terms of species number as well as community composition as species have adapted to different tundra habitats (Gough et al. 2000, Wilson et al. 2012). Together with heterogeneous local topography, the uneven distribution of snow determines both growing season and overwintering conditions (French 2013, Niittynen et al. 2020) creating microclimatically varying areas, which support different plant communities (Graae et al. 2018). The annual winter snowpack melting, and the subsequent meltwater runoff, redistributes nutrients as well as affects the availability of moisture throughout summer (Westergaard-Nielsen et al. 2020). In addition, meltwater creates microhabitats and causes disturbance for vegetation. Both snow cover duration and fluvial conditions have shown to affect species distributions, richness, and community composition (Löffler and Pape 2008, le Roux and Luoto 2013, Kemppinen et al. 2022). Therefore, drastic effects on tundra biodiversity can be triggered, as cold regions shift from snow dominated towards rain dominated under warming climate (Bintanja and Andry 2017, IPCC 2022). However, locally complex topography and variation in microclimate may buffer the effects of large-scale climatic change, thus increasing the resilience of tundra vegetation (Opedal et al. 2015, Graae et al. 2018). Hence, addressing microclimate in the investigations of tundra biodiversity might be particularly important. Furthermore, microclimate describes the environment at scales more relevant to the plants than the measurements based on free atmosphere (Scherrer and Körner 2011, Lembrechts et al. 2019).

Former studies in tundra ecosystems have investigated taxonomic, functional and phylogenetic plant diversity separately (Stewart et al. 2016, Niittynen et al. 2020, Scharn et al. 2021). However, to our best knowledge, there are no studies combining all three biodiversity facets (DePauw et al. 2021 for boreal forests and Chauvier et al. 2022 for the Alps). Furthermore, most biodiversity studies still investigate species richness possibly due to its simplicity but perhaps fail to reveal more mechanistic linkages between environmental conditions, biodiversity and ecosystem functions (Cadotte et al. 2013, DePauw et al. 2021).

Addressing the different diversity facets together might be particularly important as plant communities can vary notably due to specialised species with distinct characteristics, such as snowbed species in tundra (Choler 2005). This could increase local functional and phylogenetic diversity, even though species number, i.e. taxonomic diversity, would be low (Wookey et al. 2009). Consequently, it could be that different environmental factors are more strongly related to a certain diversity facet. Therefore, utilising functional and phylogenetic diversity metrics could reveal variation in tundra biodiversity that cannot be captured looking at variation in species richness.

To address this issue, we examine taxonomic, functional, and phylogenetic vascular plant diversity in relation to fundamental environmental variables in a local scale study setting in northern Norway. By combining in situ species occurrence and microclimate data, accurate digital elevation model and global trait observations and vascular plant phylogeny we aim to answer to the following questions:

- 1) Do taxonomic, functional, and phylogenetic diversity metrics correlate with each other in tundra plant communities?
- 2) How do different biodiversity metrics respond to the underlying environmental drivers including growing season warmth, snow persistence, soil moisture, soil pH and fluvial conditions? Do functional and phylogenetic biodiversity metrics respond to local environment more strongly than taxonomic biodiversity metrics?
- 3) Can functional and phylogenetic diversity metrics identify biodiversity hotspots in tundra that cannot be identified with taxonomic diversity metrics?

Material and methods

Study area

Our study is located in Finnmark, northern Norway (69°59'24"N, 26°18'36"E, Fig. 1a) at the south-eastern slope of Rásttigáisá mountain in an area 6 km² of size (Fig. 1b). Lowest parts of the study area lie around 400 m a.s.l. and the highest slopes reach above 700 m. Local topography is highly heterogeneous with numerous ridges and depressions that affect the amount of incoming solar radiation and snow cover distribution creating varying microclimate and hydrological conditions. In addition, river Dár (Dárjohka) runs through the north-eastern parts of the area. The average annual temperature varies from -4.5 to -2.5°C and average annual precipitation is 560 mm. During summer the average temperature is around 8.5°C, whereas the average winter temperature is around -12.0°C (gridded climate dataset 1981–2010, Aalto et al. 2017). The bedrock of the area is mainly acidic crystalline rocks, however, a thin layer of nutrient richer shales occurs around the mountain massifs in the region. The bedrock is mostly covered by glacial till, but peatlands and fluvial deposits also occur (Ryvarden 1969).

The whole area is located above the forest line and the vegetation is dominated by tundra heath characterised by dwarf shrubs (e.g. *Empetrum nigrum*, *Betula nana*, *Salix herbacea* and *Vaccinium* spp.). Moreover, there are many small streams driven by several long-lasting snow patches (nivations) around the area which create a mosaic of varying habitats ranging from dry wind-blown ridges to dry and moist meadows and even small wetlands (Fig. 1d–i). Vegetation at the ridges consist of stress-tolerant species such as *Juncus trifidus* or *Kalmia procumbens*, whereas meadows provide more favourable growing conditions supporting forbs and graminoids like *Solidago virgaurea*, *Viola biflora* and *Deschampsia flexuosa*. Species around nivations, such as *Ranunculus glacialis* and *Harrimanella hypnoides*, are adapted to long snow persistence. Streams habit disturbance-tolerant species, *Oxyria digyna* and *Micranthes* spp., for example, whereas wetlands are habited by *Rubus chamaemorus* and different willow and *Carex* species. There are also species that occur in several habitats around the area such as *Carex bigelowii* and *Dryas octopetala*, of which occurrence depends on the availability of calcareous substrates (Mossberg and Stenberg 2003).

The area holds 125 study sites (Fig. 1b) which were chosen based on stratified sampling to cover main environmental gradients using elevation, potential incoming solar radiation, SAGA wetness index (SWI, Conrad et al. 2015), snow season length based on satellite images (Niittynen and Luoto 2018) and soil type (peat, fluvial deposits, till, boulders and bare rock) which was digitised based on aerial images and a map of surface deposits (Geological Survey of Norway 2018) combined with field observations and expert knowledge from the area. Environmental variables used in the sampling were derived from raster surfaces at 10 m resolution (Supporting information). To maximally cover the environmental gradients and to also include extreme conditions we weighted the used variables based on the relative frequencies of variable values. First, we created a weighted sampling of 1000 points from which we randomly selected 125 points so that 35 points were considered as extreme points (i.e. having the highest weight) and the rest 90 points were chosen to present average environmental conditions found within the study area. We repeated the sampling several times to find an optimal sample in terms of spatial coverage and representativeness of the environmental gradients covered in the sampled points. Minimum distance of 50 m was considered between the chosen study points to avoid strong spatial clustering. The final pre-selected 125 study points were judged to cover the environmental and spatial space robustly. On average, the study design covered over 80% of the environmental gradients in the entire study area (based on the comparisons of the ranges of the four continuous variables, Supporting information).

From the 125 points, we chose 50 points to install microclimatic data loggers. Logger locations were chosen to represent both environmentally extreme (25 loggers) and average conditions (25 loggers) to cover microclimatic variation within the study area as thoroughly as possible while also considering representative spatial coverage. Multiple samples

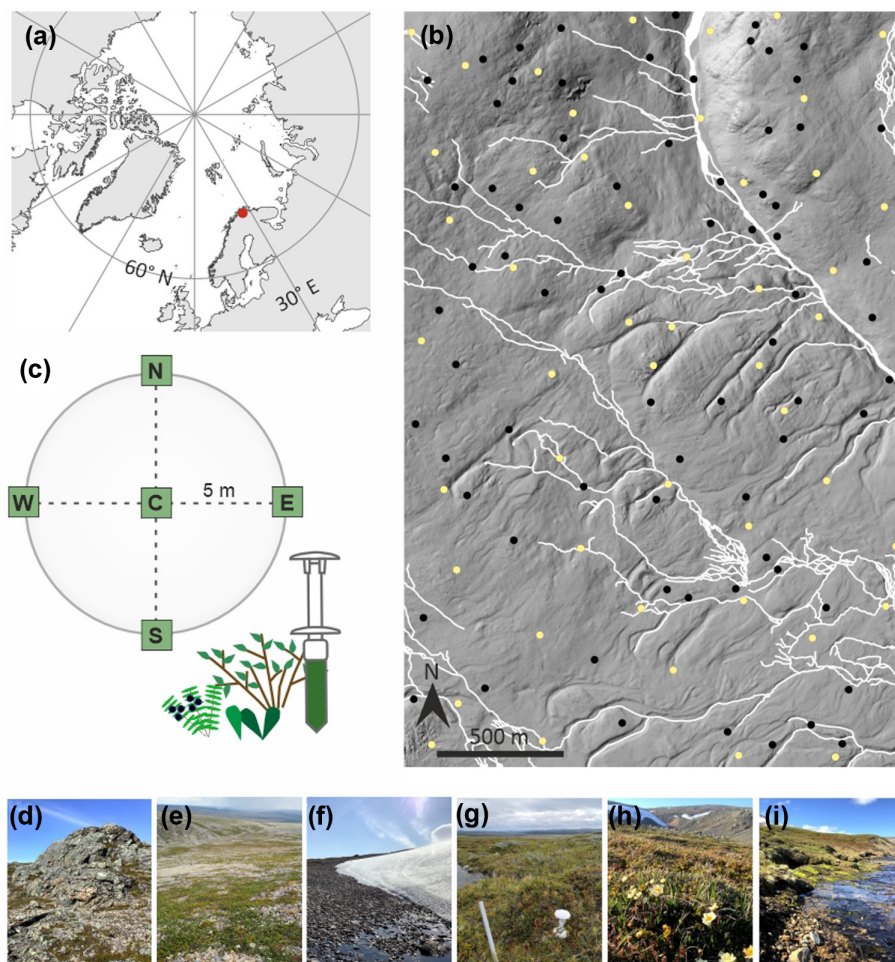


Figure 1. Study area location (a) and the study design (b–c). Yellow points show sites with a microclimatic logger and black points represent study sites without a logger (b). Each site holds five study plots (c) resulting in 561 plots used in the analyses (plots without species observations or with < 3 species were excluded). Main rivers and streams are shown in white (b). Photographs represent key habitats found in the study area: dry ridges (d), tundra heath (e), nivation (f), wetland (g), meadow (h) and meltwater streams and stream banks (i).

of logger placement were evaluated using histograms of the environmental variables at the chosen study points to secure uniqueness and representativeness of the final logger sites. The pre-selected logger points covered almost entirely (98%) the environmental gradients across the 125 study points and over 80% of the gradients within the whole study area (based on the four continuous variables, Supporting information). Final judgement of the pre-selected study points, with and without loggers, was done in the field when founding the study sites in summer 2019 (i.e. changing site location from too hazardous a place, such as very steep slope where a logger would not have stayed in place, to a more secured one). Only a couple of sites out of the 125 had to be moved in the field and a suitable location was mostly found within a few meters. Therefore, we consider that the effect of changing site location on collected vegetation and microclimate data is minor.

Community data

Vascular plant species data was collected during summers 2019–2021 by the authors. At each study site ($n = 125$) five

study plots of 1 m^2 were founded: one to the centre of the site (C plot) and one to each cardinal direction (N, E, S, W plots) with a 5-m radius resulting in 625 study plots (Fig. 1c). From each plot all vascular plant species were identified to species level and their coverage was estimated. *Alchemilla* and *Taraxacum* species with ambiguous taxonomy were identified to genus level, except *Alchemilla alpina* to species level. To utilise the data as fully as possible and to characterise the observed plant communities accurately we included all species observations in the study plot communities. Observations of the two genus level taxa were included as well, as they are prevalent in arctic–alpine communities and trait and phylogeny data were possible to acquire at genus level. For the analyses only plots with at least three species were included resulting in 561 study plots and observations on 105 taxa (Supporting information).

Trait and phylogeny data

Species phylogeny was derived from a global mega tree (GBOTB.extended.TPL) of V.PhyloMaker2 containing 74

529 vascular plant species (Jin and Qian 2022). From our species data 26 species and the two genus level taxa were not found in the mega tree. Hence, they were included in the phylogenetic sub tree created for our community data based on their closely related species or genera using scenario three following Jin and Qian (2019). Species-level phylogenies resolved at the genus-level have been shown to be appropriate to examine phylogenetic structure in species communities (Qian and Jin 2021) and hence should not affect our results.

Trait observations for eight traits representing species size, structure and biogeochemical properties were derived from six international databases: Tundra Trait Team (Bjorkman et al. 2018b), TRY Plant Trait Database (Kattge et al. 2011), Botanical Information and Ecology Network (Maitner et al. 2018), Ecological indicator and traits values for Swedish vascular plants database (Tyler et al. 2021), Fine-Root Ecology Database (Iversen et al. 2021) and Global root traits database (Guerrero-Ramírez et al. 2020). Species names in the trait databases were harmonised to match the nomenclature of GBIF Backbone Taxonomy by the Global Biodiversity Information Facility with the 'rgbif' R package (www.r-project.org, Chamberlain et al. 2022). Chosen traits were plant height, seed mass, leaf nitrogen content, specific leaf area, root dry matter content, rooting depth, phenology type and pollinator dependence. The chosen traits represent different aspects of species growth, reproduction and dispersal, resource acquisition and competitive ability as well as tolerance for disturbances (Reich 2014, Iversen et al. 2015, Díaz et al. 2016). We calculated a median value (mode for categorical traits), instead of mean, of each trait for each species to decrease the effect of possible outliers. Trait measurements for all traits were not available for every species and the number of species lacking species-specific trait data depended on the trait in question. For example, height and specific leaf area measurements were lacking only from five species, whereas 54 species were lacking rooting depth measurement (Supporting information). However, all species had species-specific trait measurements on some of the used traits (except *Draba nivalis* and *Stellaria borealis*) and on average species-specific measurements were available for six out of eight traits per species (Supporting information). For the missing traits we imputed values based on traits and phylogeny of other species. We included all vascular plant species occurring in Norway, Finland and Sweden in the imputation. We used the 'MissForest' R package (www.r-project.org) which can efficiently handle big datasets including different types of variables with varying rates of missing values (Stekhoven and Bühlmann 2012). The dataset used in imputation included median trait values (or mode in case of categorical traits) for 6460 species considering 248 traits. A high number of species and traits was used to provide enough trait measurements and evolutionary close species for enabling accurate estimation of trait–trait links and phylogenetic signal in the imputation process. This dataset was constructed similarly as the trait data covering the 105 taxa described above. We also used the same methods as described above to construct a phylogenetic tree from the global mega tree to cover the 6460

Fennoscandian species. Next, we used the resulting subtree to calculate 10 first phylogenetic Eigenvectors with *PVRdecomp* function from 'PVR' R package (www.r-project.org, Santos 2018) that describe the phylogenetic relationships across the Fennoscandian species pool. These Eigenvectors were then included as predictors in the imputation algorithm alongside the species level trait values. Average amount of imputed data over the eight traits used here was 25.4% (root traits lacking more measurements than the other traits). To the two genus level taxa (*Alchemilla* sp. and *Taraxacum* sp.) we calculated median (and mode) traits based on species-level traits using species that have arctic-alpine distribution in Fennoscandia (16 *Alchemilla* species and 13 *Taraxacum* species).

Diversity metrics

The three facets of local plant diversity were addressed by calculating eight diversity metrics describing taxonomic, functional and phylogenetic variability. Regarding taxonomy, we calculated species richness (SpRich) i.e. species number per plot, and to take species abundance into account we calculated Shannon diversity index (Shan; Shannon 1948) using 'vegan' R package (ver. 2.5-7, www.r-project.org, Oksanen et al. 2020). For functional and phylogenetic diversity, we calculated three metrics for each. First, we calculated functional richness (FRic; Villéger et al. 2008) and Faith's phylogenetic diversity (PD; Faith 1992) which both take species number into account (Tucker et al. 2018). FRic represents the convex hull volume i.e. the functional space filled by the species and PD represents the total sum of branch lengths on a community's phylogenetic tree. Secondly, to disentangle the effect of traits and phylogeny from species richness we used a null model to calculate standardised effect size (SES) of FRic and PD (FRic_{SES} and PD_{SES}). In the null model, species richness is kept constant while phylogenetic and functional relationships are randomised (Xu et al. 2021, Qian et al. 2022). FRic_{SES} and PD_{SES} were calculated as:

$$\text{Metric}_{\text{SES}} = (\text{Metric.obs} - \text{mean}(\text{Metric.null}))/\text{sd}(\text{Metric.null}),$$

where Metric.obs is the observed value of FRic or PD calculated from the original community data, mean(Metric.null) is the average value for randomised assemblages and sd(Metric.null) is the standard deviation of metric value among the randomised assemblages (Xu et al. 2021). Null metrics were calculated 1000 times from community data which was randomised with 999 iterations using independent swap algorithm which maintains sample species richness and species occurrence frequency (Gotelli 2000). Positive SES values indicate that species within assemblages are less closely related or functionally less similar than expected for a random draw from the species pool (Qian et al. 2022). Lastly, we calculated functional dispersion (FDis) and phylogenetic species variability (PSV) to include another approach to examine functional and phylogenetic diversity patterns unrelated to species richness. FDis represents dispersion of species

in trait space considering species abundances (Laliberté and Legendre 2010) whereas PSV describes mean relatedness of species in a community (Helmus 2007). All functional diversity calculations were done utilising package ‘FD’ (ver. 1.0-2.1; Laliberté et al. 2022) and phylogenetic diversity calculations were performed using package ‘picante’ (ver. 1.8.2, Kembel et al. 2020). Summary statistics and pairwise correlations of the metrics are presented in Fig. 2.

Environmental data

Environmental data used in our study is based on in situ measurements and high-resolution remote sensing products to produce spatially continuous surfaces utilising spatiotemporally accurate data (Lembrechts et al. 2019). All environmental variables were derived to study plots from spatially modelled raster layers (descriptions of each variable below). Raster layers (except fluvial disturbance) were produced utilising three different modelling methods to increase the robustness of the predictions and to decrease the effects of a single method (Araújo and New 2007). Spatial predictions were based on generalised additive models (gam, Hastie and Tibshirani 1986), generalised boosted regression (gbm, Ridgeway 1999) and random forest (rf, Breiman 2001). All raster layers were produced at 2-m resolution. Summary statistics of the environmental predictors are presented in Fig. 2.

Microclimatic data were recorded every 15 min (July 2019–July 2021) using TMS-four-loggers (Wild et al. 2019) located at the centre plot (C in Fig. 1c) of a logger site (n = 50). TMS-four-loggers measure soil temperature in 6 cm depth (T1 sensor), air temperature at ground level (2 cm, T2 sensor) and 15 cm above ground (T3 sensor). Additionally, soil moisture is measured down to 11 cm depth. One of the loggers broke during the first summer and hence microclimatic data is based on the measurements from 49 sites. Furthermore,

there were measurement gaps (i.e. missing measurements or unusable data) in the microclimatic measurements e.g., due to a detached radiation shield or if a logger was detached from the ground, which caused missing values when aggregating the measurement data to calculate the temperature and moisture variables. These gaps in the temperature and moisture variable values were imputed using predictive mean matching and imputations were done separately for each month (van Buuren and Groothuis-Oudshoorn 2011). To investigate relationships between vascular plant diversity and environmental conditions five ecologically relevant variables were chosen to represent known physiological limitations for vegetation (Mod et al. 2016).

Growing degree day (GDD3, Supporting information) was chosen to represent the overall summer thermal conditions in our models and was calculated as an average annual temperature sum over the three measurement years. GDD3 was calculated monthly from the days when the daily mean temperature has been > 3°C (Karlsen et al. 2006). Daily mean temperature was based on the measurements of the T3 sensor. Due to the gaps in the temperature measurements, there were 32 gaps in the monthly GDD3 data that were imputed. GDD3 was modelled to the study area using the logger based GDD3, elevation, annual average temperature, incoming solar radiation, slope, TPI10 (topographic position index at 10 m radius) and SWI. Final GDD3 value extracted to the study plots was the mean of the three model predictions (gam, gbm and rf).

Snow cover and its uneven distribution are fundamental components of cold environments creating a range of habitats with different growing season lengths (French 2013). Snow persistence (Snow, Supporting information), defined using day of year (DOY) of average snow melt, was chosen to describe the length of snow period. Snow persistence was calculated based on surface temperature measurements (T2

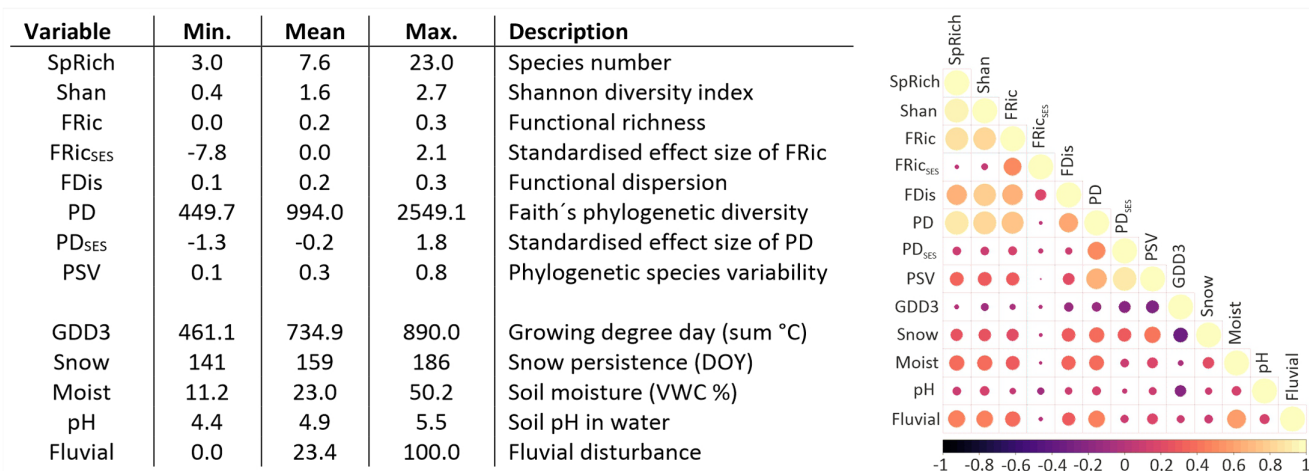


Figure 2. Summary statistics of the investigated diversity metrics and the used environmental predictors as well as their pairwise correlations using Spearman correlation coefficient. The size and colour of the dots show the magnitude and the direction of the pairwise correlation. Bigger dot size indicates a higher correlation, and the colour shows whether the correlation is positive (light) or negative (dark). To save space, the correlation coefficients and their statistical significance are presented in the Supporting information. DOY = day of year, VWC% = volumetric water content.

sensor) from the two winters during the measurement period (2019–2020 and 2020–2021). The snow melting DOY was determined based on the days when the maximum T2 temperature remained $< 1^{\circ}\text{C}$ and the diurnal temperature range (calculated with a 10 day moving average) was below 10°C . Final DOY of snow melt at the logger sites was averaged over the two hydrological years and used to model spatially continuous snow persistence. To model snow persistence within the study area, we used the three modelling methods and geographical location, remotely sensed snow information based on PlanetScope satellite images, elevation, TPI10 and wind index as predictors (Rissanen et al. 2023a). The final snow persistence was the mean of gam, gbm and rf predictions.

Soil moisture (Moist, Supporting information) presents water available for plants and was transformed from raw logger data into volumetric water content (VWC%) with the transformation function adopted from Kopecky et al. (2021). Moist was calculated as a mean soil moisture during the snowless period when soil temperature (T1 sensor) at the site has been $> 1^{\circ}\text{C}$ as measurements from frozen ground cannot be considered reliable (Wild et al. 2019). Hence, only records from June to September were used. Mean soil moisture was based on the aggregated monthly values (114 gaps that were imputed) and averaged over the snow free periods of the three measurement years. Soil moisture was modelled based on key environmental predictors affecting spatial variation in soil moisture (Kempinen et al. 2018). We used elevation, slope, incoming solar radiation, SWI, soil type and TPI10 and the three presented modelling methods. Final predicted soil moisture value was the mean of the three models' predictions.

Soil pH (Supporting information) was used in our study to represent soil nutrient status (Gough et al. 2000, Hobar et al. 2016). Additionally, as pH was detected from topsoil, which often include both organic and mineral material, the values reflect the organic versus mineral origins of the soil. pH was determined from soil samples collected at the centre plot of each study site ($n = 125$) at 5–10 cm of depth during the vegetation surveys in summers 2019 and 2020. The soil samples were freeze dried and pH was then analysed using water as a solution liquid following the standard International Organization for Standardization 10 390 protocol. Based on in situ measurements pH was modelled using geographic location, elevation, slope, water balance, SWI, edaphic index (Niittynen et al. 2020) and soil type (Rissanen et al. 2023a). Final pH was the median of the three modelling methods.

Fluvial processes create varying habitats, redistribute water and nutrients as well as generate disturbance for vegetation affecting both species richness and community composition (le Roux and Luoto 2013, Kempinen et al. 2022). Fluvial disturbance (Fluvial, Supporting information) was incorporated in our models by calculating distance to running waters using digitised stream network and digital elevation model at 2-m resolution. Stream network was digitised using WorldView satellite images and complemented based on authors' expert knowledge about the study area to include the most important streams within the area. Fluvial effect was calculated as

accumulated cost distance to rivers and streams penalised with slope (i.e. the local slope as the cost surface in the least cost distance calculations). Slope was included in the calculations because the fluvial effect likely reaches further from the stream network over flat terrain and the effect disappears with distance fast when the slope is steep. Furthermore, we set all cost distance values over 100 to 100 and then reversed the index so that pixels just next to the streams get a value 100 and pixels far away a value zero. Calculations were performed in R (ver. 4.0.4, www.r-project.org) utilising SAGA-GIS with package 'Rsagacmd' (ver. 0.1.2, Pawley 2021).

Statistical analyses

All statistical analyses were performed in R (ver. 4.0.4, www.r-project.org) and the analyses codes are available in Zenodo open data repository (<https://doi.org/10.5281/zenodo.7548065>). Prior to model fitting, possible collinearity between the variables was investigated by examining pairwise Spearman correlations. The correlation coefficient did not exceed $|0.7|$ (Dormann et al. 2013, Brun et al. 2019) for any predictor variable combination and hence all five candidate predictors were included in the models (Fig. 2, Supporting information). The relationship between local vascular plant diversity and environmental variables was investigated using generalised additive models utilising package 'mgcv' (ver. 1.8-33, Wood 2011). To consider the possible effect of plot membership within the same study site, we included site as a random factor (random intercept) into our models to produce hierarchical generalised additive models (HGAMS, Pedersen et al. 2019). HGAMS were fitted using restricted maximum likelihood (REML) with smooth parameters using the maximum of three degrees of freedom ($k = 3$) to enable curvilinear relationships but to avoid over-fitting. SpRich was modelled using Poisson distribution and the other metrics using Gaussian distribution. Shan was square root-transformed and PD, PD_{SES} and PSV log-transformed prior to modelling. When predicting (variable importance calculations and spatial predictions), the random factor was excluded.

HGAMS were fitted separately for each diversity metric and model fit, relative variable importance, response curves and spatial predictions were derived. To examine model fit and the importance of each environmental predictor we fitted HGAMS using bootstrapping i.e. the model was fitted hundred times using randomly sampled data. Model fit was expressed as a mean explained deviance (R^2) over the bootstrapping rounds. To focus on the explanatory power of the environmental predictors R^2 was calculated excluding the random effect. Importance of the predictor variables was calculated as follows. At each round we first made a prediction using original data (i.e. the bootstrapped sample). Then we shuffled each predictor at a time and made a new prediction using this data with a shuffled variable. Final variable importance was calculated $1 - \text{corr}(\text{Prediction}_{\text{original}}, \text{Prediction}_{\text{shuffled}})$ (Thuiller et al. 2009). Hence variable importance varies from 0 to 1 and the higher the number the more important the predictor.

To visualise the relationship shape between a diversity metric and an environmental variable we plotted response curves from the HGAMs fitted without bootstrapping (i.e. using the full original data that were not randomly sampled). Furthermore, to investigate the response shapes of the diversity metrics in relation to two environmental gradients at a time we plotted simulated surfaces of the metrics in relationship to all possible pairs of the two predictor variables (here Snow and Fluvial). The surfaces were produced by predicting HGAMs to an artificial dataset that ranged across all possible pairwise combinations of Snow and Fluvial while the other predictors were set to their median values in the original data. HGAMs used to predict the diversity indices to artificial data were fitted similarly as described earlier. Spatial variation in the diversity metrics was visualised producing spatial predictions using the same HGAMs as for response curves and a raster stack of predictor variables at 2 m resolution. From the spatial predictions we then derived the hotspots of each diversity metric by taking the richest or most diverse 5% of cells ($n = 75035$ for each metric) (Niskanen et al. 2017).

Finally, we evaluated the predictive power of HGAMs using leave-one-out cross validation (LOOC) in which the value of each diversity metric at each study plot is predicted once using all other data to calibrate the model. From the LOOC models we derived model fit (R^2) again excluding the random factor to focus on the predictive performance of the environmental variables. Furthermore, the consistency between the observed and predicted metric values was inspected visually with scatterplots and calculating Spearman correlation coefficient (r) and root mean squared error.

Results

Data exploration revealed that Shannon diversity index (Shan), Faith's phylogenetic diversity (PD) and functional richness (FRic) had high correlations with species richness (SpRich) ($r = 0.84\text{--}0.92$) whereas null model-based metrics were scarcely related to SpRich ($r \leq 0.12$) (Fig. 2, Supporting information). Functional dispersion (FDis) showed quite high correlation with the taxonomic diversity indices ($r = 0.66\text{--}0.79$) and PSV was highly correlated with the standardised effect size of PD (PD_{SES}), hence, their results are presented in the appendices to have two metrics of each diversity group in the main results.

Model fit was best for PD and SpRich (mean $R^2 = 0.37$ and $R^2 = 0.35$ respectively) followed by Shan (mean $R^2 = 0.30$) (Supporting information). The same metrics had also the best predictive performance with a correlation coefficient varying from -0.55 to 0.60 between the observed and predicted values and a R^2 ranging $0.30\text{--}0.37$ (Supporting information). Overall HGAMs performed better for the metrics related to species richness than to the null models (FRic_{SES} and PD_{SES}). Model fit and predictive performance of FDis was similar with FRic whereas results of PSV were more alike with PD_{SES} than PD (Supporting information). To address the effect of

site random factor on the model fit we derived R^2 also from the models with a random effect (Supporting information).

The modelling results showed that snow persistence and fluvial disturbance were the most important predictors of taxonomic, functional, and phylogenetic diversity (mean variable importance 0.19 and 0.14 over all eight variables respectively) (Fig. 3, Supporting information). Fluvial disturbance was important especially for taxonomic diversity and FRic causing almost a linearly increasing response whereas snow was a major driver for phylogenetic indices. Diversity metrics showed mostly a unimodal response to increasing snow persistence, however for PD_{SES} and PSV the effect was positive (Fig. 3a–b, Supporting information). FRic_{SES} differed from the other metrics as it was mostly affected by variation in soil pH (mean variable importance 0.35). To explore more closely, how vascular plant diversity varies depending on the two most important predictors, we plotted surfaces of simulated diversity indices in relation to Snow and Fluvial (Fig. 3c, Supporting information). The contour plots showed that diversity metrics related to species richness gain their highest values in areas with high fluvial disturbance and average snow length duration. Leaving out the effect of pH, FRic_{SES} seems to be mostly driven by Snow whereas PD_{SES}, as well as PSV, benefit from both high fluvial disturbance and long snow persistence (Fig. 3c, Supporting information).

Scrutinising the spatial predictions of the investigated metrics, taxonomic and functional diversity (excluding FRic_{SES}) as well as PD, indeed peak around streams (Fig. 4a, Supporting information). The effect of snow is inevitable in the spatial variation of PD_{SES} and PSV when the predictions are compared with Snow raster (Supporting information) as well as the effect of pH for FRic_{SES} (Supporting information). Hotspots of SpRich, Shan, FRic and PD overlapped heavily, sharing around 80% of the cells with highest diversity (Fig. 4b). In the studied landscape, these areas are often characterised by stream bank meadows like site RL 121 and wetlands like site RL 99 (Fig. 4c). However, functional, and phylogenetic diversity do not always overlap with the hotspots of taxonomic diversity. Hotspots of PD_{SES} and PSV were distinct from those of taxonomic and functional metrics with less than 10% of shared area on average (Fig. 4a, Supporting information). In the case of FRic_{SES} the hotspots were even more distinct from any other metric and the highest shared area was 2% with PSV. In the studied landscape, areas with high phylogenetic and functional diversity (unrelated to SpRich) can be found for example near long lying snow patches (RL11) or ridges (RL2) (Fig. 4b).

Discussion

Here we showed that vascular plant diversity patterns in tundra are strongly linked to local snow and fluvial conditions. Our results showed that taxonomic, functional and phylogenetic diversity metrics may provide both congruent as well as contrasting insights to plant diversity patterns depending on the used metric. Functional and phylogenetic diversity

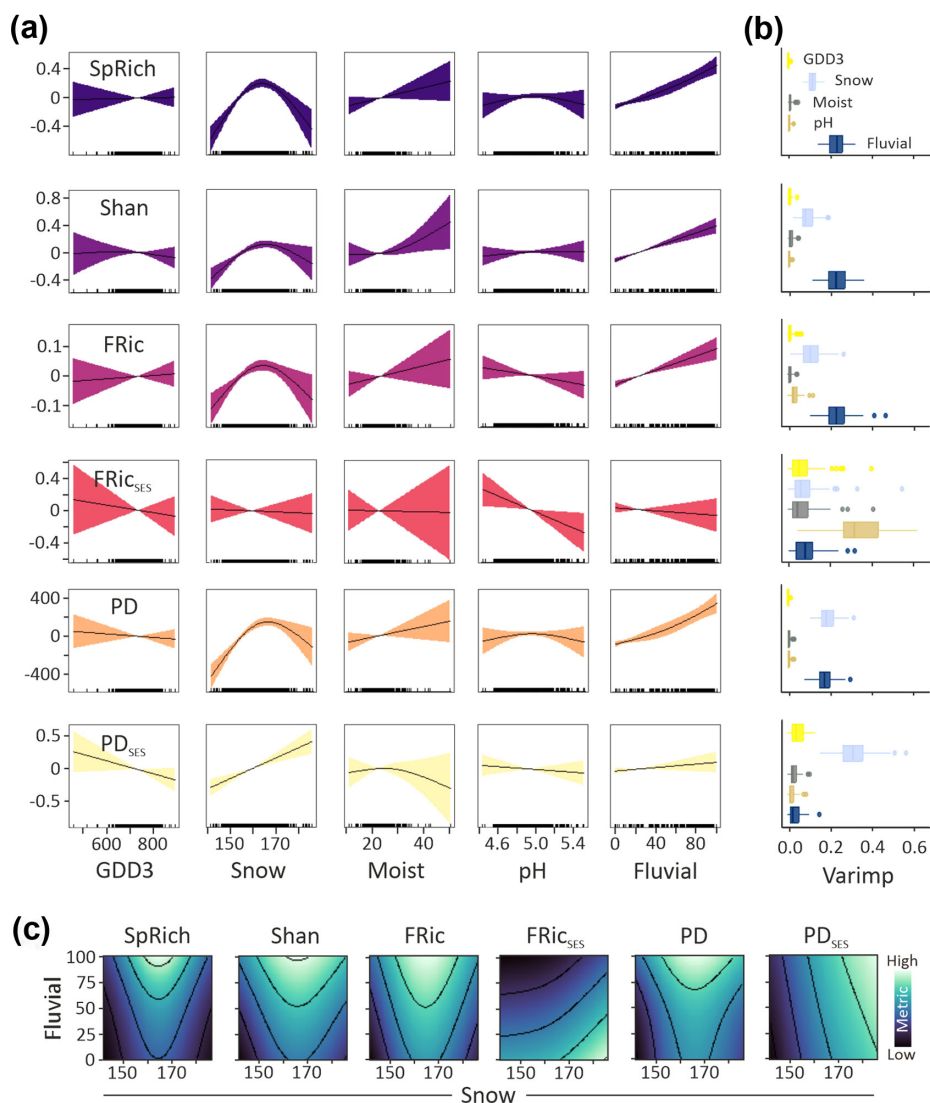


Figure 3. Response curves of the diversity metrics (a) and relative importance of the predictor variables (b) derived from the HGAMs. Response curves are based on HGAMs fitted with non-sampled data. Boxplots show variable importance based on 100 bootstrapping rounds. Box edges show 1st and 3rd quartile, and the thick line shows the median and whiskers extend to 1.5 interquartile range. The lowest panel (c) shows simulated diversity indices in relation to Snow and Fluvial.

metrics that account for species number in a site produced highly similar results with the taxonomic metrics indicating the strong effect of species richness on the tundra biodiversity patterns. However, when the effect of taxonomic richness was controlled for, functional and phylogenetic diversity metrics can reveal biodiversity patterns along environmental gradients that would have remained otherwise hidden. Nevertheless, regardless of the investigated metric, the same key environmental factors shaped plant diversity. Former studies have shown the importance of snow persistence when examining taxonomic (Löffler and Pape 2008, Niittynen et al. 2018) and functional (Niittynen et al. 2020) vascular plant diversity. Likewise, fluvial conditions and other geomorphological features are known to be fundamental predictors of species richness (le Roux and Luoto 2013) and community functional

composition in tundra (Kempainen et al. 2022). Our study corroborates these findings and highlights the importance of snow persistence and fluvial disturbance on phylogenetic diversity as well.

The significance of snow and fluvial conditions for tundra plant diversity can rise from several mechanisms causing them to override the effect of temperature, moisture, and soil pH, which are often found to be significant explanatory variables for tundra diversity (Gough et al. 2000, Nabe-Nielsen et al. 2017, Giaccone et al. 2019). Driven by local topography, uneven distribution of snow cover and stream network, which depends on meltwater, create a mosaic of varying habitats ranging from dry windblown ridges to moist depressions supporting occurrence of different species (Billings and Mooney 1968, French 2013). Various microhabitats can occur even

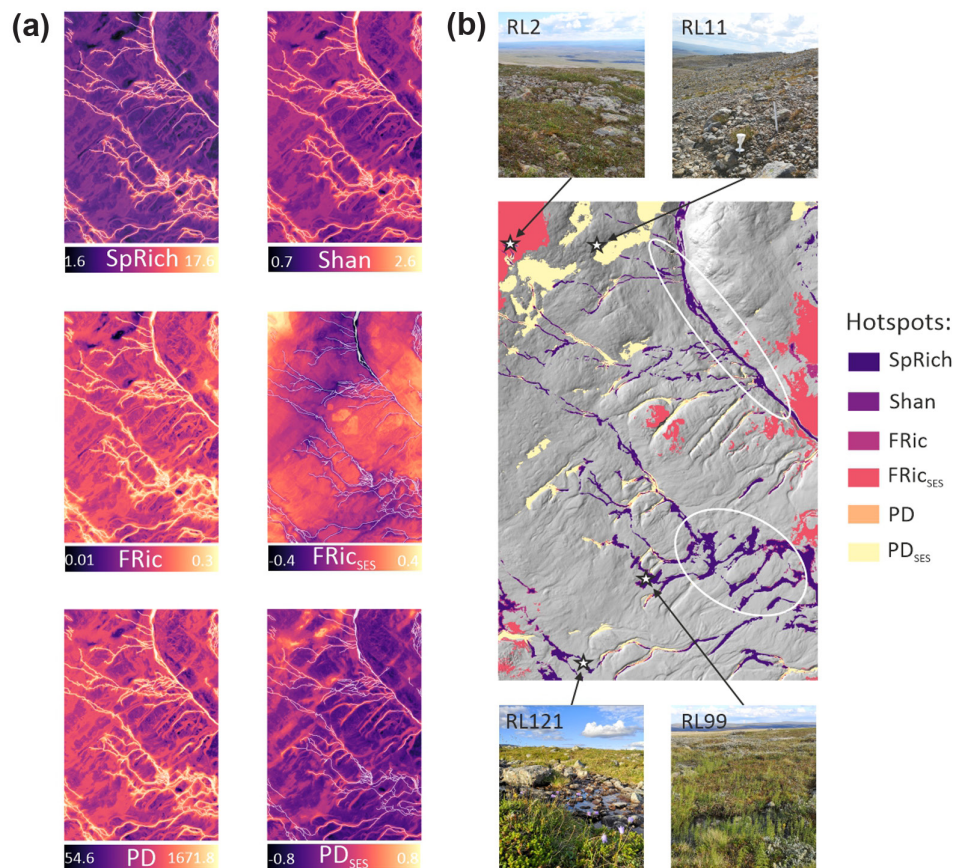


Figure 4. Spatial predictions (a) and hotspots (b) of taxonomic, functional and phylogenetic diversity. Spatial predictions are based on HGAMs fitted with non-sampled data and hotspots are defined as the 5% of cells with the highest metric value. Hotspots of SpRich, Shan, FRic and PD largely overlap especially within the two areas that are circled in white. Photographs show examples of study sites with high vascular plant diversity (RL2–RL121).

very locally along the streambanks, facilitating different plant communities that may host functionally and/or phylogenetically distinct species, which can increase both local species richness as well as the other aspects of diversity. Furthermore, spatiotemporal variation in snow and meltwater runoff provides resources for plants by redistributing nutrients and increasing the amount of plant available water (Westergaard-Nielsen 2020), hence capturing some of the effect of soil moisture and probably also that of pH. Moreover, snow and soil moisture dampen temperature extremes, which are shown to be of high importance in determining plant occurrence (Bokhorst et al. 2009), therefore possibly decreasing the importance of temperature in the models. Furthermore, growing degree day that was used to represent thermal conditions averages the effect of extreme temperatures as well. Additionally, it may be that snow and fluvial conditions can better account for temporal variation in plant available water as well as the extreme dry or wet conditions, which can be decisive for plant species persistence in addition to the average soil moisture (Kemppinen et al. 2019).

Higher soil water content has been shown to increase species richness (Nabe-Nielsen et al. 2017) and our results support this both in terms of diversity responses to soil moisture

and specially to increasing fluvial disturbance. It should be noted, however, that the observed almost linearly increasing response to fluvial disturbance does not indicate that e.g. the highest species number would occur in running water or in waterlogged areas as the streams are seasonal and cause temporal variation in ground water content. In the beginning of the growing season strong runoff may occur at a site but later in summer the meltwater decreases, and streams can even dry out. Yet, soil moisture in these sites often remains higher during the whole growing season supporting more diverse vegetation. Additionally, observed responses need to be interpreted in the context of the study setting. Linear trends might relate to the length of the environmental gradients in the studied data as none of the sites is in the middle of a stream and there are only a few wetland sites none of which are on actual wet swamps. Overall, fluvial disturbance seems to drive especially diversity patterns related to species richness (SpRich, Shan, FRic and PD), supporting former studies (le Roux and Luoto 2013, Kemppinen et al. 2019), whereas snow persistence links more strongly to species phylogenetic diversity. Phylogenetic diversity metrics peaked towards increasing snow persistence at areas with low species richness suggesting the presence of a few tolerant, and functionally specialised, species that can

cope with short growing season, thin soil and disturbances caused by long-lasting snow patches (Walker et al. 1993, Komac et al. 2015). However, it is somewhat unclear why snow was particularly related to phylogenetic diversity and not to functional diversity. It could be that in the snowy areas, there are some evolutionary distinct species, which still might have similar trait values in terms of the traits we used. This would then increase the phylogenetic diversity but not functional diversity at these sites. Additionally, it is plausible that phylogenetic information can represent variation in some unmeasurable traits, which cannot be accounted for by the chosen functional traits (Srivastava et al. 2012). Altogether, snow and fluvial conditions might capture small-scale heterogeneity more dynamically than other predictors representing both resources as well as disturbances for vegetation.

Although our study indicated that local snow and fluvial conditions are major drivers of tundra vegetation diversity, partly contrasting patterns and responses of the different metrics highlight the significance of considering multiple aspects of diversity to thoroughly understand tundra ecosystems. Looking beyond species richness is imperative, because even though species number would increase, the functionality of plant communities may be under a threat if co-occurring species are functionally redundant or close relatives, thus lowering functional and phylogenetic diversity (Cadotte et al. 2013, Li et al. 2020). In the light of our results and findings of former research, decrease in biodiversity in tundra would be linked to alterations in the hydrological conditions as high-latitude areas are predicted to change from snow dominated towards rain dominated (Bintanja and Andry 2017). Shorter snow cover duration and decrease in meltwater leading to drier soils, in addition to warming temperatures, poses a great extinction threat to snow dependent and stress-tolerant arctic–alpine species, whereas more generalist boreal species may expand their distribution leading to heathification and shrubification of tundra (Niittynen et al. 2020, Scharn et al. 2021). However, together with complex local topography snow patches and meltwater streams can also sustain arctic diversity by creating varying microhabitats with distinct microclimate conditions that can buffer the effects of large-scale climate change and offer possible refugia for tundra species (Opedal et al. 2015, Graae et al. 2018).

We acknowledge that even though our models seemed to capture variation in investigated diversity metrics quite robustly some uncertainties remain. Firstly, although model fit was reasonable for all three diversity facets it was notable that the study site random effect had a role in explaining the observed patterns. This was clear especially in the results concerning the null model of functional richness which had a particularly poor model fit without the random factor. This might indicate that some relevant environmental predictors explaining variation in functional traits were lacking from the models. A negative response with pH was observed, which could represent the effect of thin, mixed, and resource-poor topsoils hosting only functionally specialised and stress tolerant species, however due to a weak model fit no robust conclusions can be made. Additionally, examinations of functional diversity always

depend on a-priori selection of traits used to calculate the different metrics. This may lead to a weaker performance compared to the models of phylogenetic diversity, which can capture trait variation without subjective choices as well as include information on unmeasurable traits (Tucker et al. 2018). Furthermore, relationships with environmental predictors can alter depending on the used traits affecting the predicted spatial variation in diversity and its hotspots (Díaz and Cabido 2001). Secondly, metrics related to functional traits depend on the type of the used trait values. Here, we used global trait observations, which were considered representative for the studied species as most data were derived from databases of tundra species and the data were inspected for any suspicious values. However, the number of imputed trait values, especially in the root traits, might have affected the results. Additionally, to further increase data accuracy, field-based measurements would be beneficial to account for intraspecific trait variation (Palacio et al. 2022). Lastly, biotic interactions can also be important drivers of biodiversity patterns (Choler et al. 2001, Lortie et al. 2004), especially at fine spatial scales, but are also hard to measure and thus challenging to incorporate realistically into statistical modelling frameworks (Dormann et al. 2018). Therefore, it remains unclear how our results would have altered or refined if biotic elements could have accounted for alongside the abiotic predictors.

To conclude, species richness is unarguably a key component of vascular plant diversity patterns in tundra, however, to sustain the ecosystem functionality, trait and phylogenetic diversity are essential as well, due to possible functional redundancy and species' close kinship. Utilising several approaches in defining and examining diversity can be of high importance for example when targeting conservation efforts. In the context of ongoing environmental change, addressing local snow and fluvial conditions using in situ or other high accuracy data are needed in the predictions of tundra diversity patterns.

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Author contributions

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Investigation (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Olli Kauppi**: Data curation (lead); Investigation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Pekka Niittynen**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Janne Soinen**: Conceptualization (equal); Investigation (equal); Methodology (equal); Supervision (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Miska Luoto**: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Supervision (lead); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Zenodo Digital Repository: <https://doi.org/10.5281/zenodo.7548065> (Rissanen et al. 2023b).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Aalto, J., Riihimäki, H., Meineri, E., Hylander, K. and Luoto, M. 2017. Revealing topoclimatic heterogeneity using meteorological station data. – *Int. J. Climatol.* 37: 544–556.
- Araújo, M. B. and New, M. 2007. Ensemble forecasting of species distributions. – *Trends Ecol. Evol.* 22: 42–47.
- Barredo, J. I., Mauri, A. and Caudullo, G. 2020. Alpine tundra contraction under future warming scenarios in Europe. – *Atmosphere* 11: 698.
- Billings, W. D. and Mooney, H. A. 1968. The ecology of arctic and alpine plants. – *Biol. Rev.* 43: 481–529.
- Bintanja, R. and Andry, O. 2017. Towards a rain-dominated Arctic. – *Nat. Clim. Change* 7: 263–267.
- Bjorkman, A. D. et al. 2018a. Plant functional trait change across a warming tundra biome. – *Nature* 562: 57–62.
- Bjorkman, A. D. et al. 2018b. Tundra Trait Team: A database of plant traits spanning the tundra biome. – *Global Ecol. Biogeogr.* 27: 1402–1411.
- Bokhorst, S. F., Bjerke, J. W., Tømmervik, H., Callaghan, T. V. and Phoenix, G. K. 2009. Winter warming events damage sub-Arctic vegetation: consistent evidence from an experimental manipulation and a natural event. – *J. Ecol.* 97: 1408–1415.
- Breiman, L. 2001. Random forests. – *Mach. Learn.* 45: 5–32.
- Brun, P., Thuiller, W., Chauvier, Y., Pellissier, L., Wüest, R. O., Wang, Z. and Zimmermann, N. E. 2019. Model complexity affects species distribution projections under climate change. – *J. Biogeogr.* 47: 130–142.
- Cadotte, M., Albert, C. H. and Walker, S. C. 2013. The ecology of differences: assessing community assembly with trait and evolutionary distances. – *Ecol. Lett.* 16: 1234–1244.
- Chamberlain, S., Barve, V., Mcglinn, D., Oldoni, D., Desmet, P., Geffert, L. and Ram, K. 2022. rgbif: interface to the global biodiversity information facility API. – R package ver. 3.7.2, <https://CRAN.R-project.org/package=rgbif>.
- Chauvier, Y., Descombes, P., Guéguen, M., Boulangeat, L., Thuiller, W. and Zimmermann, N. E. 2022. Resolution in species distribution models shapes spatial patterns of plant multifaceted diversity. – *Ecography* 2022: e05973.
- Choler, P. 2005. Consistent shifts in alpine plant traits along a mesotopographical gradient. – *Arctic Antarct. Alp. Res.* 37: 444–453.
- Choler, P., Michalet, R. and Callaway, R. M. 2001. Facilitation and competition on gradients in alpine plant communities. – *Ecology* 82: 3295–3308.
- Conrad, O., Bechtel, B., Bock, M., Dietrich, H., Fisher, E., Gerliz, L., Wehberg, J., Wichmann, V. and Böhner, J. 2015. System for automated geoscientific analyses (SAGA) ver. 2.1.4. – *Geosci. Model Develop.* 8: 1991–2007.
- Craven, D. et al. 2018. Multiple facets of biodiversity drive the diversity–stability relationship. – *Nat. Ecol. Evol.* 2: 1579–1587.
- DePauw, K. et al. 2021. Taxonomic, phylogenetic and functional diversity of understory plants respond differently to environmental conditions in European forest edges. – *J. Ecol.* 109: 2629–2648.
- Díaz, S. and Cabido, M. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. – *Trends Ecol. Evol.* 16: 646–655.
- Díaz, S. et al. 2016. The global spectrum of plant form and function. – *Nature* 529: 167–171.
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Cárre, G., Diekötter, T., Márquez, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C. J., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D. and Lautenbach, S. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. – *Ecography* 36: 27–46.
- Dormann, C. F., Bobrowski, M., Dehling, D. M., Harris, D. J., Hartig, F., Lischke, H., Moretti, M. D., Pagel, J., Pinkert, S., Schleuning, M., Schmidt, S. I., Sheppard, C. S., Steinbauer, M. J., Zeuss, D. and Kraan, C. 2018. Biotic interactions in species distribution modelling: 10 questions to guide interpretation and avoid false conclusions. – *Global Ecol. Biogeogr.* 27: 1004–1016.
- Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. – *Biol. Conserv.* 61: 1–10.
- Felde, V. A., Kapfer, J. and Grytnes, J. A. 2012. Upward shift in elevational plant species ranges in Sikkiltdalen, central Norway. – *Ecography* 35: 922–932.
- French, H. M. 2013. The periglacial environment, 3rd edn. – Wiley.
- Geological Survey of Norway 2018. Superficial deposit types, nationwide, full cartography. – https://geo.ngu.no/kart/permafrost_mobil/.
- Giaccone, E., Luoto, M., Vittoz, P., Guisan, A., Mariéhoz, G. and Lambiel, C. 2019. Influence of microclimate and geomorphological factors on alpine vegetation in the western Swiss Alps. – *Earth Surf. Proc. Landf.* 44: 3093–3107.
- Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. – *Ecology* 81: 2606–2621.
- Gough, L., Shaver, G. R., Carroll, J., Royer, D. L. and Laundre, J. A. 2000. Vascular plant species richness in Alaskan arctic tundra: the importance of soil pH. – *J. Ecol.* 88: 54–66.
- Graae, B. J., Vandvik, V., Armbruster, W. S., Eiserhardt, W. L., Svenning, J., Hylander, K., Ehrlén, J., Speed, J. D. M., Klanderud, K., Bråthen, K. A., Milbau, A., Opedal, Ø. H., Alsos, I. G., Ejrnaes, R., Bruun, H. H., Birks, H. J. B., Westergaard, K. B., Birks, H. H. and Lenoir, J. 2018. Stay or go – how

- topographic complexity influences alpine plant population and community responses to climate change. – *Perspect. Plant Ecol. Evol. Syst.* 30: 41–50.
- Guerrero-Ramírez, N. R. et al. 2020. Global root traits (GRooT) database. – *Global Ecol. Biogeogr.* 30: 25–37.
- Hastie, T., and Tibshirani, R. 1986. Generalized additive models. – *Stat. Sci.* 1: 297–318.
- Helmus, M. R., Bland, T. J., Williams, C. K. and Ives, A. R. 2007. Phylogenetic measures of biodiversity. – *Am. Nat.* 169: E68–E83.
- Hobara, S., Kushida, K., Kim, Y., Koba, K., Lee, B.-Y. and Ae, N. 2016. Relationships among pH, minerals, and carbon in soils from tundra to boreal forest across Alaska. – *Ecosystems* 19: 1092–1103.
- IPCC 2022. In: Pörtner, H.-O., Roberts, D. C., Tignor, M., Poloczanska, E. S., Mintenbeck, K., Alegria, A., Craig, M., Langsdorf, S., Löschke, S., Möller, V., Okem, A. and Rama, B. (eds.), *Climate change 2022: impacts, adaptation and vulnerability. contribution of working group II to the sixth assessment report of the intergovernmental panel on climate change.* – Cambridge Univ. Press.
- Iversen, C. M., Sloan, V. L., Sullivan, P. F., Euskirchen, E. S., McGuire, A. D., Nurdy, R. J., Walker, A. P., Warren, J. M. and Wullschlegel, S. D. 2015. The unseen iceberg: plant roots in arctic tundra. – *New Phytol.* 205: 34–58.
- Iversen, C. M. et al. 2021. Fine-root ecology database (FRED): a global collection of root trait data with coincident site, vegetation, edaphic, and climatic data, ver. 3. – Oak Ridge National Laboratory, TES SFA, U.S. Department of Energy.
- Jin, Y. and Qian, H. 2019. V.PhyloMaker: an R package that can generate very large phylogenies for vascular plants. – *Ecography* 42: 1353–1359.
- Jin, Y. and Qian, H. 2022. V.PhyloMaker2: An updated and enlarged R package that can generate very large phylogenies for vascular plants. – *Plant Divers.* 44: 335–339.
- Karlsen, S. R., Elvebakk, A., Høgda, K. A., and Johansen, B. 2006. Satellite-based mapping of the growing season and bioclimatic zones in Fennoscandia. – *Global Ecol. Biogeogr.* 15: 416–430.
- Kattge, J. et al. 2011. TRY – A global database of plant traits. – *Global Change Biol.* 17: 2905–2935.
- Kembel, S. W., Ackerly, D. D., Blomberg, S. P., Cornwell, W. K., Cowan, P. D., Helmus, M. R., Morlon, H. and Webb, C. O. 2020. picante: integrating phylogenies and ecology, ver. 1.8.2. – R package, <https://CRAN.R-project.org/package=picante>.
- Kemppinen, J., Niittynen, P., Riihimäki, H. and Luoto, M. 2018. Modelling soil moisture in a high-latitude landscape using LiDAR and soil data. – *Earth Surf. Proc. Landf.* 43: 1019–1031.
- Kemppinen, J., Niittynen, P., Aalto, J., le Roux, P. C. and Luoto, M. 2019. Water as a resource, stress and disturbance shaping tundra vegetation. – *Oikos* 128: 811–822.
- Kemppinen, J., Niittynen, P., Happonen, K., le Roux, P. C., Aalto, J., Hjort, J., Maliniemi, T., Karjalainen, O., Rautakoski, H. and Luoto, M. 2022. Geomorphological processes shape plant community traits in the Arctic. – *Global Ecol. Biogeogr.* 31: 1381–1398.
- Komac, B., Pladevall, C., Peñuelas, J., Conesa, J. V. and Domènech, M. 2015. Variations in functional diversity in snowbed plant communities determining snowbed continuity. – *Plant Ecol.* 216: 1257–1274.
- Kopecky, M., Macek, M. and Wild, J. 2021. Topographic Wetness Index calculation guidelines based on measured soil moisture and plant species composition. – *Sci. Total Environ.* 757: 143785.
- Laliberté, E. and Legendre, J. 2010. A distance-based framework for measuring functional diversity from multiple traits. – *Ecology* 91: 299–305.
- Laliberté, E., Legendre, P. and Shipley, B. 2022. FD: measuring functional diversity (FD) from multiple traits, and other tools for functional ecology, ver. 1.0-12.1. – R package, <https://CRAN.R-project.org/package=FD>.
- Lavorel, S. and Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. – *Funct. Ecol.* 16: 545–556.
- Le Bagousse-Pinguet, Y., Soliveres, S., Gross, N., Torices, R., Berdugo, M. and Maestre, F. 2019. Phylogenetic, functional and taxonomic richness have both positive and negative effects on ecosystem multifunctionality. – *Proc. Natl Acad. Sci. USA* 116: 8416–8424.
- le Roux, P. C. and Luoto, M. 2013. Earth surface processes drive the richness, composition and occurrence of plant species in an arctic-alpine environment. – *J. Veg. Sci.* 25: 45–54.
- Lembrechts, J., Nijs, I. and Lenoir, J. 2019. Incorporating microclimate into species distribution models. – *Ecography* 42: 1267–1279.
- Li, D., Olden, J. D., Lockwood, J. L., Record, S., McKinney, M. L. and Baiser, B. 2020. Changes in taxonomic and phylogenetic diversity in the Anthropocene. – *Proc. R. Soc. B* 287: 20200777.
- Lortie, C. J., Brooker, R. W., Choler, P., Kikvidze, Z., Michalet, R., Pugnaire, F. I. and Callaway, R. M. 2004. Rethinking plant community theory. – *Oikos* 107: 433–438.
- Löffler, J. and Pape, R. 2008. Diversity patterns in relation to the environment in alpine tundra ecosystems of northern Norway. – *Arct. Antarct. Alp. Res.* 40: 373–381.
- Maitner, B. S. et al. 2018. The bien r package: a tool to access the botanical information and ecology network (BIEN) database. – *Methods Ecol. Evol.* 9: 373–379.
- Miller, E. T., Farine, D. R. and Trisos, C. H. 2016. Phylogenetic community structure metrics and null models: a review with new methods and software. – *Ecography* 40: 461–477.
- Mod, H. K., Scherrer, D., Luoto, M., and Guisan, A. 2016. What we use is not what we know: environmental predictors in plant distribution models. – *J. Veg. Sci.* 27: 1308–1322.
- Mossberg, B., and Stenberg, L. 2003. *Den nya nordiska floran.* – Wahlström & Widstrand.
- Myers-Smith, I. H. et al. 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. – *Environ. Res. Lett.* 6: 045509.
- Nabe-Nielsen, J., Normand, S., Hui, F. K. C., Stewart, L., Bay, C., Nabe-Nielsen, L. I. and Schmidt, N. M. 2017. Plant community composition and species richness in the high arctic tundra: from the present to the future. – *Ecol. Evol.* 7: 10233–10242.
- Niittynen, P., and Luoto, M. 2018. The importance of snow in species distribution models of arctic vegetation. – *Ecography* 41: 1024–1037.
- Niittynen, P., Heikkinen, R. K. and Luoto, M. 2018. Snow cover is a neglected driver of Arctic biodiversity loss. – *Nat. Clim. Change* 8: 997–1001.
- Niittynen, P., Heikkinen, R. K. and Luoto, M. 2020. Decreasing snow cover alters functional composition and diversity of Arctic tundra. – *Proc. Natl Acad. Sci. USA* 117: 21480–21487.
- Niskanen, A. K. J., Heikkinen, R. K., Väre, H. and Luoto, M. 2017. Drivers of high-latitude plant diversity hotspots and their congruence. – *Biol. Conserv.* 212: 288–299.
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szöcs, E. and Wagner, H. 2020. *Vegan.* – R package ver. 2.5-7, <https://cran.r-project.org, https://github.com/vegandevs/vegan>.
- Opedal, Ø. H., Armbruster, W. S. and Graae, B. J. 2015. Linking small-scale topography with microclimate, plant species diver-

- sity and intraspecific trait variation in an alpine landscape. – *Plant Ecol. Divers.* 8: 305–315.
- Palacio, F. X., Callaghan, C. T., Cardoso, P., Hudgins, E. J., Jarzyna, M. A., Ottaviani, G., Riva, F., Graco-Roza, C., Shirey, V. and Mammola, S. 2022. A protocol for reproducible functional diversity analyses. – *Ecography* 2022: e06287.
- Pawley, S. 2021. Rsagacmd: linking R with the open-source ‘SAGA-GIS’ Software. – R package ver. 0.1.2. <https://stevenpawley.github.io/Rsagacmd>.
- Pedersen, E. J., Miller, D. L., Simpson, G. L. and Ross, N. 2019. Hierarchical generalized additive models in ecology: an introduction with mgcv. – *PeerJ*. 7: e6876.
- Qian, H. and Jin, Y. 2021. Are phylogenies resolved at the genus level appropriate for studies on phylogenetic structure of species assemblages? – *Plant Divers.* 43: 255–263.
- Qian, H., Deng, T. and Ricklefs, R. E. 2022. Evolutionary assembly of the Arctic flora. – *Global Ecol. Biogeogr.* 31: 396–404.
- Reich, P. B. 2014. The world-wide “fast-slow” plant economics spectrum: a traits manifesto. – *J. Ecol.* 102: 275–301.
- Reichle, L. M., Epstein, H. E., Bhatt, U. S., Reynolds, M. K. and Walker, D. A. 2018. Spatial heterogeneity of the temporal dynamics of Arctic tundra vegetation. – *Geophys. Res. Lett.* 45: 9206–9215.
- Ridgeway, G. 1999. The state of boosting. – *Comput. Sci. Stat.* 31: 172–181.
- Rissanen, T., Niittynen, P., Soininen, J., Virkkala, A.-M. and Luoto, M. 2023a. Plant trait–environment relationships in tundra are consistent across spatial scales. – *Ecography* 2023: e06397.
- Rissanen, T., Aalto, A., Kainulainen, H., Kauppi, O., Niittynen, P., Soininen, J. and Luoto, M. 2023b. Data from: Local snow and fluvial conditions drive taxonomic, functional and phylogenetic plant diversity in tundra. – Zenodo Digital Repository, <https://doi.org/10.5281/zenodo.7548065>.
- Roscher, C., Schumacher, J., Gubsch, M., Lipowsky, A., Weigelt, A., Buchmann, N., Schmid, B. and Schulze, E.-D. 2012. Using plant functional traits to explain diversity–productivity relationships. – *PLoS One* 7: e36760.
- Ryvarden, L. 1969. The vascular plants of the Rastigaissa area (Finnmark, northern Norway). – *Acta Borealia* 26: 1–56.
- Santos, T. 2018. PVR: phylogenetic eigenvectors regression and phylogenetic signal-representation curve. – R package ver. 0.3, <https://CRAN.R-project.org/package=PVR>.
- Scharn, R., Little, C. J., Bacon, C. D., Alatalo, J. M., Antonelli, A., Björkman, M. P., Molau, U., Nilsson, R. H. and Björk, R. G. 2021. Decreased soil moisture due to warming drives phylogenetic diversity and community transitions in the tundra. – *Environ. Res. Lett.* 16: 064031.
- Scherrer, D. and Körner, C. 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. – *J. Biogeogr.* 38: 406–416.
- Shannon, C. E. 1948. A mathematical theory of communication. – *Bell Syst. Tech. J.* 27: 379–423.
- Srivastava, D. S., Cadotte, M. W., MacDonald, A. A. M., Marushia, R. G. and Mirotchnick, N. 2012. Phylogenetic diversity and the functioning of ecosystems. – *Ecol. Lett.* 15: 637–648.
- Steffen, W., Richardson, K., Rockström, J., Cornell, S. E., Fetzer, I., Bennett, E. M., Biggs, R., Carpenter, S. R., de Vries, W., de Wit, C. A., Folke, C., Gerten, D., Heinke, J., Mace, G. M., Persson, L. M., Ramanathan, V., Reyers, B. and Sörlin, S. 2015. Planetary boundaries: guiding human development on a changing planet. – *Science* 347: 1259855.
- Stekhoven, D. J. and Bühlmann, P. 2012. MissForest—Non-parametric missing value imputation for mixed-type data. – *Bioinformatics* 28: 112–118.
- Stewart, L. et al. 2016. The regional species richness and genetic diversity of Arctic vegetation reflect both past glaciations and current climate. – *Global Ecol. Biogeogr.* 25: 430–442.
- Thuiller, W., Lafourcade, B., Engler, R., and Araújo, M. B. 2009. BIOMOD—A platform for ensemble forecasting of species distributions. – *Ecography* 32: 369–373.
- Tucker, C. M., Cadotte, M. W., Carvalho, S. B., Davies, T. J., Ferrier, S., Fritz, S. A., Grenyer, R., Helmus, M. R., Jin, L. S., Mooers, A. O., Pavoine, S., Purschke, O., Redding, D. W., Rosauer, D. F., Winter, M. and Mazel, F. 2016. A guide to phylogenetic metrics for conservation, community ecology and macroecology. – *Biol. Rev.* 92: 698–715.
- Tucker, C. M., Davies, T. J., Cadotte, M. W. and Pearse, W. D. 2018. On the relationship between phylogenetic diversity and trait diversity. – *Ecology* 99: 1473–1479.
- Tyler, T., Herbertsson, L., Olofsson, J. and Olsson, P. A. 2021. Ecological indicator and trait values for Swedish vascular plants. – *Ecol. Indic.* 120: 106923.
- Walker, D., Halfpenny, J., Walker, M., and Wessman, C. 1993. Long-term studies of snow-vegetation interactions. – *BioScience* 43: 287–301.
- van Buuren, S. and Groothuis-Oudshoorn, K. 2011. mice: Multivariate imputation by chained equations in R. – *J. Stat. Softw.* 45: 1–67.
- Westergaard-Nielsen, A., Balstrom, T., Treier, U. A., Normand, S. and Elberling, B. 2020. Estimating meltwater retention and associated nitrate redistribution during snowmelt in an Arctic tundra landscape. – *Environ. Res. Lett.* 15: 034025.
- Wild, J., Kopecký, M., Macek, M., Šanda, M., Jankovec, J. and Haase, T. 2019. Climate at ecologically relevant scales: a new temperature and soil moisture logger for long-term microclimate measurement. – *Agric. For. Meteorol.* 268: 40–47.
- Villéger, S., Mason, N. W. H. and Moullot, D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. – *Ecology* 89: 2290–2301.
- Wilson, J. B., Peet, R. K., Dengler, J. and Pärtel, M. 2012. Plant species richness: the world records. – *J. Veg. Sci.* 23: 796–802.
- Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. – *J. R. Stat. Soc. B* 73: 3–36.
- Wookey, P. A., Aerts, R., Bardgett, R. D., Baptist, F., Bråthen, K. A., Cornelissen, J. H. C., Gough, L., Hartley, I. P., Hopkins, D. W., Lavorel, S. and Shaver, G. R. 2009. Ecosystem feedbacks and cascade processes: understanding their role in the responses of Arctic and alpine ecosystems to environmental change. – *Global Change Biol.* 15: 1153–1172.
- Wright, I. J. et al. 2004. The worldwide leaf economics spectrum. – *Nature* 428: 821–827.
- Xu, Y., Liu, J.-J., Li, H.-N., Liu, K., Burgess, K. S. and Ge, X.-J. (2021). The effects of evolutionary and environmental variance on estimates of phylogenetic diversity in temperate forest plots. *J. Plant Ecol.* 14 :96-107.