

This is a self-archived version of an original article. This version may differ from the original in pagination and typographic details.

Author(s): Rissanen, Tuuli; Niittynen, Pekka; Soininen, Janne; Virkkala, Anna-Maria; Luoto, Miska

Title: Plant trait-environment relationships in tundra are consistent across spatial scales

Year: 2023

Version: Published version

Copyright: © 2023 The Authors. Ecography published by John Wiley & Sons Ltd on behalf of N

Rights: CC BY 3.0

Rights url: <https://creativecommons.org/licenses/by/3.0/>

Please cite the original version:

Rissanen, T., Niittynen, P., Soininen, J., Virkkala, A., & Luoto, M. (2023). Plant trait-environment relationships in tundra are consistent across spatial scales. *Ecography*, 2023(7), Article e06397. <https://doi.org/10.1111/ecog.06397>

ECOGRAPHY

Research article

Plant trait–environment relationships in tundra are consistent across spatial scales

Tuuli Rissanen¹✉, Pekka Niittynen², Janne Soininen¹, Anna-Maria Virkkala³ and Miska Luoto¹

¹Dept of Geosciences and Geography, Faculty of Science, Univ. of Helsinki, Helsinki, Finland

²Dept of Biological and Environmental Sciences, Univ. of Jyväskylä, Jyväskylä, Finland

³Woodwell Climate Research Centre, Falmouth, MA, USA

Correspondence: Tuuli Rissanen (tuuli.rissanen@helsinki.fi)

Ecography

2023: e06397

doi: [10.1111/ecog.06397](https://doi.org/10.1111/ecog.06397)

Subject Editor: Vigdis Vandvik

Editor-in-Chief: Miguel Araújo

Accepted 23 March 2023



Patterns and processes shaping ecosystems vary across spatiotemporal scales. As plant functional traits reflect ecosystem properties, investigating their relationships with environment provides an important tool to understand and predict ecosystem structure and functioning. This is particularly important in the tundra where a changing climate may trigger severe alterations in plant communities as both summer and winter conditions are changing. Here, we investigate the relationships between key environmental drivers including summer temperature, snow persistence, topographic position and soil pH, and species height, specific leaf area (SLA) and seed mass as plant traits. The study is carried out at three spatial extents in the arctic–alpine region of Fennoscandia, modelling the trait–environment relationships at each scale to investigate whether the relationships are scale dependent. Our results show that summer temperature and snow persistence are the most important variables explaining community trait composition. Temperature is important especially to vegetation height, which increased towards higher temperatures, whereas seed mass and SLA are related to snow persistence. Seed mass decreased towards longer snow persistence, while SLA responded in scale-dependent ways. Topographic position and soil pH affect community trait composition moderately. Overall, our study demonstrates that trait–environment relationships in the tundra are largely consistent across spatial scales. Our findings highlight the ecological relevance of snow for all three functional traits regardless of scale, showing that snow information could be particularly important to better understand large-scale trends in plant community composition and ecosystem functioning as seasonal snow cover is shrinking globally.

Keywords: arctic–alpine vegetation, functional traits, snow, summer temperature, vascular plants



www.ecography.org

© 2023 The Authors. Ecography published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Introduction

Scale is a fundamental issue in describing and understanding patterns and processes shaping ecosystems in space and time (Levin 1992). Across scales, environmental conditions drive plant species distributions (Guisan and Zimmermann 2000), functional properties, and community structure (Bruehlheide et al. 2018) as species coping well with prevailing biotic and abiotic conditions maintain viable populations if the species can disperse to the region. Therefore, plant communities and their relationships with environment have been widely studied to characterize and predict ecosystem structure and functioning on a broad range of scales and biomes (Bruehlheide et al. 2018, Bjorkman et al. 2018a, Rolhausser et al. 2021, Trujillo et al. 2022). However, different interpretations and conclusions regarding these relationships arise depending on the scale of the study and thereby available data. For example, it has been shown that large-scale climatological factors tend to drive species distributions and community patterns at a global or regional scale while locally soil resources and disturbances may be more decisive (Guisan and Zimmermann 2000, Bruehlheide et al. 2018). Yet, whether these relationships are constant over a range of scales remains poorly understood as multiscale approaches are scarce.

Plant functional traits provide an important tool to examine feedbacks of environmental conditions to ecosystem functioning (Reich 2014) as they can explain both individual plant responses to abiotic factors as well as effects of the species on ecosystems (Lavorel and Garnier 2002). Above-ground plant traits vary mainly on two axes. The first size-structural axis determines vegetation based on e.g. plant height and seed mass (Díaz et al. 2016) describing species light-competitiveness and reproductive ability which affect for instance shading, trapping of snow and biogeochemical cycling across landscapes (Lavorel and Garnier 2002, Myers-Smith et al. 2019, Sørensen et al. 2019). The second axis describes vegetation based on leaf economic spectrum i.e. leaf area and nutrient content (Wright et al. 2004) which in turn relate to species resource usage strategy (fast vs slow resource acquisition) influencing photosynthetic efficiency as well as water and nutrient cycles (Reich 2014). Additionally, seed traits can form a third axis depicting species dispersal and survival ability (Westoby 1998). Previous research has shown that variation in size traits has been related especially to limitation in water or energy whereas variation in economics traits is also explained by soil fertility (Ordoñez et al. 2009, Joswig et al. 2022). However, the significance of different environmental factors controlling community functioning may vary with scale (Bruehlheide et al. 2018).

Trait-environment relationships in environmentally extreme tundra are increasingly studied to better understand the effects of rapid warming on cold ecosystems (Myers-Smith et al. 2019, Kemppinen et al. 2021, Testolin et al. 2021). Alterations both in growing season and winter conditions trigger possible changes in plant communities (Bjorkman et al. 2018a), for example, due to shrubification of the tundra (Reichle et al. 2018) or as boreal species disperse to areas

currently dominated by arctic–alpine species (Niittynen et al. 2020). Consequently, changes in community traits affect ecosystem structure and functions (Reich 2014, Bruehlheide et al. 2018, Happonen et al. 2022). Previous research indicates that changes in snow cover might be particularly important for plant community structure in tundra (Niittynen et al. 2020). The uneven distribution of snow across the tundra landscapes drives variation in the availability of soil moisture and nutrients (Johansson et al. 2013, Semenchuk et al. 2015), determines the length of growing season, and provides shelter for species (Rixen et al. 2022, Rapacz et al. 2014). In addition to commonly used climatic and soil variables, snow information also provides a more process-based approach to characterize trait-environment relationships.

Environmental conditions and plant functional traits have consistent local-scale relationships over different tundra regions (Kemppinen et al. 2021) but whether consistent relationships also occur across spatial scales remains unclear. Traditionally, species data used in community trait calculations are based on in-situ species observations limiting the location and spatial extent of study regions. However, as species observation data come increasingly available e.g. in national and global databases, these data could be utilised to study species communities at larger extents. Examining trait-environment relationships from local to broader scales could expand our knowledge not only about the ecology of the sensitive tundra environments, but also about the effect of methodological choices (e.g. data and study setting) on modelling trait-environment relationships. Here, we aim to address these issues by combining vascular plant occurrences and global plant functional trait measurements with environmental data based both on local in-situ measurements as well as broader scale climate measurements and remote sensing products to investigate trait-environment relationships within the tundra biome at subcontinental, regional and local scale in Fennoscandia. We examine the effect of summer temperature, snow persistence, moisture conditions and nutrient status on functional traits representing plant growth, persistence and reproduction. More specifically, we aim to find out how plant height, seed mass and specific leaf area (SLA) vary over the studied scales and examine:

1. What is the relative importance of key environmental variables explaining variation in plant height, seed mass and SLA at subcontinental, regional, and local scales?
2. Are the observed trait-environment relationships consistent across the three scales?

Material and methods

Research area

Our study is located at the arctic–alpine region of Fennoscandia (ca 55–72° N, 5–32° E) at three geographical scales (Fig. 1). Study area at the subcontinental scale (SUB, Fig. 1a) covers the arctic–alpine region of Fennoscandia based on the

arctic and alpine biogeographical regions of Europe (European Environment Agency 2015, [Rissanen et al. 2021](#)). Two climatic gradients characterise the SUB area as climate shifts from oceanic in the east coast to continental in the western parts, and from temperate climate in the south to arctic conditions in the north ([Aalto et al. 2014](#)). Average annual temperature ranges from 7.8 in the south to -8.3°C in the northern parts of the study region, respectively ([Karger et al. 2017](#)). Variations in temperature and precipitation are also driven by the strong orographic effect of the Scandes mountains as elevation ranges from sea level to over 2400 m a.s.l. ([Tikkanen 2005](#)). The wide climatic and topographic gradients reflect also to snow persistence ranging from areas which are practically free of snow whole year to the coldest parts where snow may persist to late summer (Supporting information). Due to past orogenies and glaciations, the quality of bedrock varies within the area reflecting to variations in soil geochemical status ([Virtanen 2003](#), [Lidmar-Bergström and Näslund 2005](#)).

The regional scale study area (REG, [Fig. 1b](#)) size of 195 km² is located in Finnmark, northern Norway ($70^{\circ}0' \text{N}$, $26^{\circ}14' \text{E}$) around two mountain massifs Rastigaisa and Geidnogaisa. From valley bottoms to mountain peaks elevation ranges from ca 100 to 1065 m a.s.l. and the average annual temperature varies between -0.3 and -5.7°C ([Niittynen and Luoto 2018](#)). Vegetation is dominated by tundra heath, though meadows

occur at moister and nutrient richer sites and mountain birch forest occurs in the southeast parts of the area. Snow is a fundamental feature of the area and persists to late summer in sheltered areas where redistributed snow by wind accumulates (day of year [DOY] for average snow melt ranging from 112 to 270, Supporting information). The bedrock of the area is mainly acidic crystalline rocks ([Ryvarden 1969](#)).

The local scale study area (LOC, [Fig. 1c](#)) size of 6 km² is located within the REG scale study area at the southeastern slope of Rastigaisa mountain (69.987°N , 26.345°E). Elevation within the area ranges from ca 400 to 764 m a.s.l. and the whole study area is located above forest line with the average annual temperature ranging from -2.5 to -4.5°C (gridded climate dataset 1981–2010, [Aalto et al. 2017](#)). Vegetation is dominated by dwarf shrubs, such as crowberry *Empetrum hermaphroditum*, dwarf birch *Betula nana* and dwarf willow *Salix herbacea*, like at the REG scale. There are several long-lasting snow patches around the area and the average DOY of snow melt ranges from 129 to 206 (Supporting information).

Species and functional trait data

Vascular plant species data included both field observations gathered by the authors (the LOC and REG scales) and

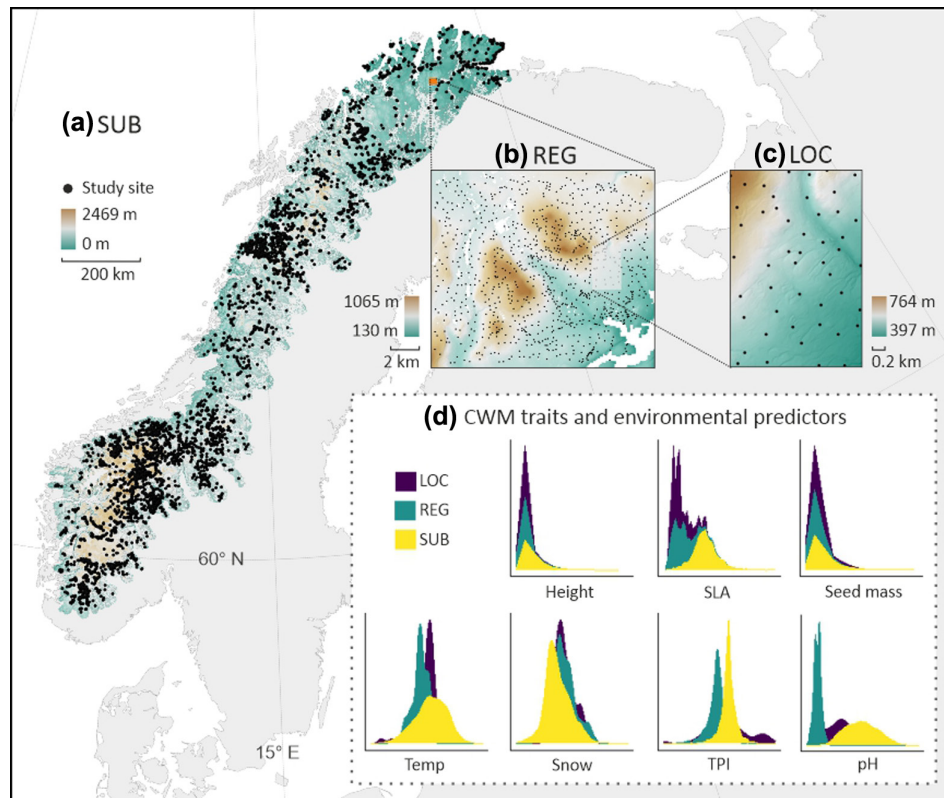


Figure 1. Research area at three geographical scales. The SUB scale (a) includes 4991 study sites, the REG scale (b) 968 sites and the LOC scale (c) 49 sites respectively. Forested areas at the SUB and REG scales are excluded. Density plots show the distributions of the investigated community weighted mean (CWM) plant functional traits (d) and environmental variables at the SUB, REG and LOC scale (e). SLA = specific leaf area, Temp = average July temperature, Snow = snow persistence, TPI = topographic position index.

occurrence data from databases (the SUB scale). At each scale, only species with at least three observations in unique study sites were considered in the plant community data to decrease the effect of single observations but to include as many species as possible (especially at the LOC scale). Similarly, at each scale, we used only sites with at least three species present to calculate community traits. Threshold of three species per site was chosen to include all LOC scale study sites in the analyses, as the minimum number of species present at a site in the LOC scale was three. Study sites and their species observations were independent at each scale as the sites from the finer scales were excluded from the broader scales.

Subcontinental community data were based on species occurrence observations gathered from the national databases of Finland (<https://laji.fi/en>), Sweden (www.artportalen.se) and Norway (www.artsdatabanken.no) as well as from GBIF (GBIF.org [25 February 2019] GBIF occurrence download <https://doi.org/10.15468/dl.4tfm4y>). Only occurrences within the defined arctic–alpine realm with a coordinate accuracy of at least 100 m (surveyed 1990–2019) were included. Occurrence observations were aggregated into a grid with a cell size of 1 km² and each grid cell was considered as a study site resulting in 12 041 study sites. Size of the SUB scale study sites was chosen to match the resolution of available environmental data and to decrease the possible effect of clustered sites.

Regional data comprised of 1102 study sites and the community data of each site consisted of four plots 1 m² of size located 5 m from the centre of the study site towards the principal compass directions. From all plots vascular plants were identified to species level (with few exceptions of ambiguous species, e.g. *Taraxacum* spp.) and their percentage cover was estimated. In the final site-level data the coverage of each species was averaged over the four plots on each site. The data were collected during summers 2014–2018 (Niittyinen et al. 2020).

Local data consisted of 49 study sites 1 m² of size from which the occurrence and coverage of vascular plants were surveyed as at the regional scale during summer 2019. The sites were located beforehand based on stratified sampling, with minimum distance of 50 m between sites, to make sure that main environmental gradients are represented in the data, but the final positioning of the sites was judged in the field (Supporting information). At the centre of each site, a TMS-4 microclimate logger (Wild et al. 2019) was installed to measure soil and air temperature. Originally 50 study sites with microclimatic loggers were founded, but one site had to be excluded due to a broken logger.

To focus the study to open tundra environments and to harmonize both species and environmental data across the three scales, we excluded all forested areas from the SUB and REG scales. We removed all study sites within areas that were classified as ‘broad-leaved forest’, ‘coniferous forest’ or ‘mixed forest’ in Corine Land Cover (CLC) data (European Environment Agency 2018). Additionally, we removed study sites that had any observations on tree species that form forests in Fennoscandia (species list in the Supporting information). In the final data, the SUB scale had 4991 study sites

and the REC scale 968 sites in total. Final data at all scales contain species with both arctic–alpine and boreal distributional background. We did not remove all boreal species as they (e.g. *Vaccinium* sp.) play a fundamental role in the Fennoscandian tundra communities. Forested areas were removed from the environmental raster layers, respectively, to prevent spatial predictions outside model calibration area.

Trait observations for three plant functional traits representing leaf-height-seed -scheme were derived from three international databases: Tundra Trait Team (Bjorkman et al. 2018b), TRY plant trait database (Kattge et al. 2011) and botanical information and ecology network (Maitner et al. 2018). Measurements of plant height, seed mass and SLA were chosen as they represent both species growth and reproduction, competitive ability as well as tolerance for stress and disturbances (Westoby 1998, Wright et al. 2004). We calculated community weighted mean (CWM) traits for each site using species’ median trait value. CWM traits were calculated utilising R-package ‘FD’ (Laliberté et al. 2014) for sites from which trait data was available for > 90% of species (cover-weighted at the LOC and REG scale). At the LOC and REG scales CWM traits were calculated using the abundances of the species, whereas at the SUB scale trait calculations were based on presence-absence data (and thus reflect the mean trait values across species) as abundance information was not derivable from the database occurrence observations. To include cryptogams in the community data, though they do not have seeds but spores instead, we used minimum seed mass (0.001 mg) found among other species to reflect their dispersal capability (Niittyinen et al. 2020). Species with no trait data available (56 species at the SUB, 7 species at the REG and 1 species at the LOC scale) as well as genus level taxa (two taxa at the SUB and REG scale and one taxon at the LOC scale) were excluded from the CWM trait calculations and further analyses. In the final CWM data, the SUB scale comprised 574 species, the REG scale 141 species and the LOC scale 55 species respectively. Distributions of CWM traits at three study scales are presented in Fig. 1d and descriptive statistics in the Supporting information.

Environmental data

To investigate trait-environment relationships we chose four key environmental variables (Fig. 1e, Supporting information) driving tundra ecosystem functioning representing growing season, snow cover, moisture conditions and soil pH (Bjorkman et al. 2018a, Myers-Smith et al. 2019). Moreover, we chose variables that were possible to acquire for each scale using as detailed information as possible to enable plausible comparison between scales. Hence, biotic factors and disturbances were not included in this study. July mean temperature (Temp) was chosen to account for growing season conditions, as it usually is the warmest summer month in northern regions and thus crucial for tundra vegetation. At the SUB scale Temp was derived from monthly average temperatures of CHELSA dataset (period 1979–2013, Karger et al. 2017) resampled to 1 km resolution. Temp at

the REG scale was based on a gridded climate dataset which was created utilising a digital elevation model (DEM) and the climate record (period 1981–2010) of 942 climate stations in Finland, Sweden and Norway (Aalto et al. 2017). Originally, climate surfaces were statistically modelled at 50 m resolution resampled here to 10 m resolution. At the LOC scale, Temp was calculated from monthly TMS-4 microclimate logger measurements averaging July temperature over three summers (2019–2021) based on measurements of T3 sensor (15 cm above ground) (for more detailed logger information see the Supporting information and Wild et al. 2019). A few measurement gaps in the temperature data (e.g. due to a fallen logger or detached radiation shield) were imputed using predictive mean matching based on temperature records from other years (van Buuren and Groothuis-Oudshoorn 2011). Additionally, to enable spatial predictions at the LOC scale, we modelled a spatially continuous Temp surface (at 2 m resolution) based on the logger data, geographical location, elevation, potential incoming solar radiation, slope and topographic position index (TPI, 10 m radius) utilising generalised additive model (gam, Hastie and Tibshirani 1986), generalised boosted regression (gbm, Ridgeway 1999) and random forest (rf, Breiman 2001) (Supporting information). Final Temp raster was the median of the three model predictions.

Snow persistence (Snow), defined using DOY of average snow melt, describes here the length of snow period. SUB scale snow persistence map (at ~ 400 m resolution) was constructed from two MODIS (moderate resolution imaging spectroradiometer) imagery-based snow cover products (MOD10A1 and MYD10A1) from January to September 2001–2018 (Hall et al. 2002). The snow melting DOY was determined per pixel from daily binary snow maps using binomial generalised linear model for each year and then averaging the melting DOY over the years (Niittyinen and Luoto 2018, Rissanen et al. 2021). At the REG scale, snow information was derived from Landsat TM 5, ETM 7 and OLI 8 images from March to October 1984–2016 following the procedure by Niittyinen and Luoto (2018) like at the SUB scale. LOC scale snow variable was derived from microclimate loggers using T2 sensor (2 cm above ground) surface temperature measurements from two winters (2019–2020 and 2020–2021). Snow persistence was calculated based on the days when the maximum T2 temperature remained below 1°C and the temperature range was below 10°C (calculated with a 10 day moving average). Different temperature ranges were tested manually to empirically find the range that best detected the snow cover period based on visual interpretation of the outcome. Final DOY of snow melt was averaged over the two hydrological years. For LOC scale spatial predictions, we modelled also a spatially continuous snow persistence map using the logger data, remotely sensed snow information, geographical location, elevation, slope, TPI (10 m radius) and wind index. Snow information for the spatial model was from 54 cloud-free PlanetScope satellite images (at 3 m resolution). We trained a RandomForest model to separate snowy pixels from melted ones resulting in two

predictions per satellite image: 1) binary classification (snow or no-snow) and 2) a probability (0–1) of the predicted classes. Next, we calculated the snow persistence pixel-wise by using a binomial generalised linear model where binary classification was treated as a response variable and the day of the year of the image as an explanatory variable. Additionally, the class probabilities of the snow classifications were included as weights in the models to give more weight to observations with high certainty. Then the model was used to predict snow probability to a sequence of days and the melting DOY was determined as they day when snow probability drops below 0.5. Snow persistence map was modelled similarly as Temp surface and the final snow map was the mean of gam, gbm and rf predictions (Supporting information).

Moisture conditions were accounted for using topographic position index as it was derivable for each scale respectively. TPI is the difference between the elevation of the focal location to the mean surrounding elevation within a given radius (Guisan et al. 1999, Wilson and Gallant 2000, Weiss 2001). Positive values indicate sites which are located higher than the mean elevation, negative values indicate depressions and values close to zero represent continuous slopes or flat areas. TPI was calculated for all scales using the Topographic Position Index Tool in SAGA-GIS (www.saga-gis.org/saga_tool_doc/7.6.2/ta_morphometry_18.html) with R-package ‘Rsagacmd’ (Pawley 2021). TPI was calculated from DEM of each study area with a 1000 m radius at the SUB scale, a 30 m radius at the REG scale and a 5 m radius at the LOC scale. As TPI is highly scale dependent, we calculated TPI using several radii at each scale and chose the one with highest Spearman correlations with the CWM traits (Supporting information). DEMs for each study area were based on combined national DEMs from the Land Surveys of Finland, Sweden and Norway (2 m resolution for the LOC and REG scales and 50 m resolution for the SUB scale [aggregated for 500 m resolution]).

Soil nutrient status was incorporated in our study using pH (Gough et al. 2000, Hobará et al. 2016, Happonen et al. 2019). At the SUB scale, pH was derived from global SoilGrids data (topsoil pH in water) at 1 km resolution (Hengl et al. 2014). REG scale pH was determined from soil samples collected in summer 2014 from 429 plots around the study area at 5–10 cm depth. pH was analysed from freeze dried soil samples using distilled water as a solution liquid following standard International Organization for Standardization 10 390 protocol. To derive pH information to all REG study sites we spatially modelled pH based on the in-situ measurements using geographic location, elevation, annual average temperature, slope, water balance, SAGA wetness index (Conrad et al. 2015) and soil conditions (soil quality and edaphic index, Niittyinen et al. 2020) as predictors. Final pH value derived for study sites, was median of three model predictions: gam, gbm and rf. At the LOC scale, pH was determined following the same ISO protocol as at REG scale from topsoil samples collected at the centre of each LOC study site during the vegetation survey in 2019. Additionally, pH was spatially modelled at the LOC scale to enable spatial

predictions of traits using measured pH, geographical location, elevation, water balance, SAGA wetness index, slope, soil class and edaphic index. Models were created similarly as for Temp and Snow and the final pH raster was the median of the three model predictions (Supporting information). Since pH was detected from topsoil samples, which often include both organic and mineral material depending on the organic and mineral layer depths as noticed from the REG and LOC scale samples, the values also reflect the organic vs mineral origins of the soil, with organic soils often having a lower pH.

To address comparability of differently derived environmental data across the three study scales, we extracted Temp, Snow and pH data from REG and SUB scale raster layers to LOC scale study points (TPI was not considered as it is scale-specific). Some variation occurred in the ranges of the coarser scale data compared to ground-truthed LOC scale data (Supporting information). However, the ranges of the environmental variables overlapped substantially across the datasets indicating that the data at each scale represent rather similar environmental conditions. Furthermore, the ranges of all variables at each scale are plausible considering the environmental conditions in the Fennoscandian tundra (Seppälä 2005). Hence, environmental data was considered representative at each scale.

Statistical analyses

All statistical analyses were carried out using R (ver. 4.0.4, www.r-project.org). Before model fitting, environmental predictors were tested for possible collinearity problems examining pairwise correlations at each study scale. The correlation coefficient did not exceed $|0.7|$ for any variable combination so the four predictors were kept for further analyses (Supporting information). To examine the relationship between plant functional traits and environmental conditions we used generalised linear models (glm, McCullagh and Nelder 1989). Glms were chosen as they allow non-linear relationships between response and predictor variables but are less prone to overfitting than more complex modelling methods and thus the responses are more easily interpreted (McCullagh and Nelder 1989, Elith et al. 2005). Glms were fitted with quadratic terms and without interactions using Gamma distribution and log-link. Gamma distribution was chosen as all three CWM traits were non-negative and positive-skewed at all study scales. Interactions between predictors were not included especially due to low number of study sites in the LOC scale to simplify model structure and hence increase the interpretability of the results.

Glms were fitted separately for each trait at each study scale resulting in nine different models. To increase model parsimony and keep only the most significant predictor variables for each trait we selected final model structure based on AIC value (Akaike information criterion, Akaike 1973). Variable selection was done with function *stepAIC* in package 'MASS' (Venables and Ripley 2002). Further analyses and presented results are based on these trait-specific models and referred to as final models. Final model structures

for each trait at each scale are presented in the Supporting information.

From the final models we derived model fit, relative variable importance and response curves utilising all data from each scale. Model fit was expressed as mean explained deviance (D^2) calculated using ten times bootstrapping, i.e. fitting model ten times with sampled data. At each bootstrapping round we also calculated relative variable importance based on decrease in D^2 using variable shuffling (Mod et al. 2021). First, D^2 of the final model was recorded and then the model was re-fitted ten times by randomly shuffling one variable at time and recording D^2 of the model. At each round, the decrease in D^2 in comparison to the final model with non-shuffled variables was calculated (larger decrease in D^2 indicates higher variable importance). Mean decrease per variable was then proportioned to summed mean decrease of all environmental variables in the model and multiplied by 100 to present relative importance of each variable in percentages (Mod et al. 2021). To visualise the shapes of the relationship between traits and environmental variables i.e. response curves, we used the final model (fitted with non-sampled data) to predict values of environmental variables keeping other variables than that of interest constant in their median values (Elith et al. 2005). Response curves are projections of community trait variation in an environmental space where the predictor variable of interest varies whereas other predictors are kept constant. This enables to investigate the relationship between each trait and each environmental variable (Elith et al. 2005). In the visualisations, we set the range of the predictors to the shared minimum and maximum values over the three scales to enhance comparability of responses across the scales. However, as TPI values depend on scale-specific DEMs the range of TPI varies between scales also in the plotted response curves. The predictive power of the models was evaluated with repeated cross-validation (10 rounds with 70% calibration and 30% evaluation data) for the SUB and REG scale models. The LOC scale models were evaluated with leave-one-out cross-validation due to a small sample size. Predictive accuracy of the models across scales was expressed calculating root mean squared error (RMSE). In addition, the correlation between observed and predicted CWMs was calculated.

To visualise spatial variation in CWM traits across scales we produced spatial predictions of each trait at each scale. Spatial predictions were produced at each scale using the final model (fitted with all non-sampled data) of each trait and a raster stack of the predictor variables utilising 'raster' package (Hijmans 2020). The SUB scale predictions were produced at 1 km-resolution, the REG scale at 10 m and the LOC scale at 2 m resolution respectively.

Results

CWM trait values as well as the ranges of Temp, Snow, TPI and pH differed at the three geographical scales, with the

SUB scale covering the widest range of variation (Fig. 2). Differences were prominent in plant height, seed mass and SLA showing distinction between plant communities. Yet, the investigations indicated similar trends in the relationships between CWM traits and environmental predictors across scales. In the preliminary examinations, the scatterplots of plant height and seed mass showed similar responses to all predictors regardless of the study scale. For example, these trait values increased towards warmer summer temperatures (Fig. 2a). The scatterplots of SLA differed from the two other traits and also indicated more varying responses both between scales and environmental predictors. For example, at the LOC and REG scale, SLA showed a positive trend to increasing snow persistence, whereas at the SUB scale the trend was negative (Fig. 2b). According to the preliminary investigations, TPI and pH seemed to have somewhat weaker relationship with the studied traits than Temp and Snow (Fig. 2c–d).

Modelling results showed reasonable model fit for all traits at all scales, though for SLA at the SUB scale the fit was notably poorer (Fig. 3b). All presented modelling results concern the final trait-specific models (selected based on the AIC value). Over all three CWM traits and scales, model fit was best for SLA (mean D^2 0.31) even though at the LOC scale seed mass received almost as high values as SLA (mean D^2 0.35 and 0.38, respectively). At the SUB scale, model fit was highest for plant height (mean D^2 0.23) (Fig. 3b). Predictive performance of the models indicated similar results, suggesting higher predictability at the two finer scales (Supporting information). Correlation between the observed and predicted trait values was highest for SLA at the LOC and REG scale and for height at the SUB scale (Supporting information).

In the final trait-specific models, July temperature and snow persistence showed the highest relative variable importance values for the CWM traits, though there were some

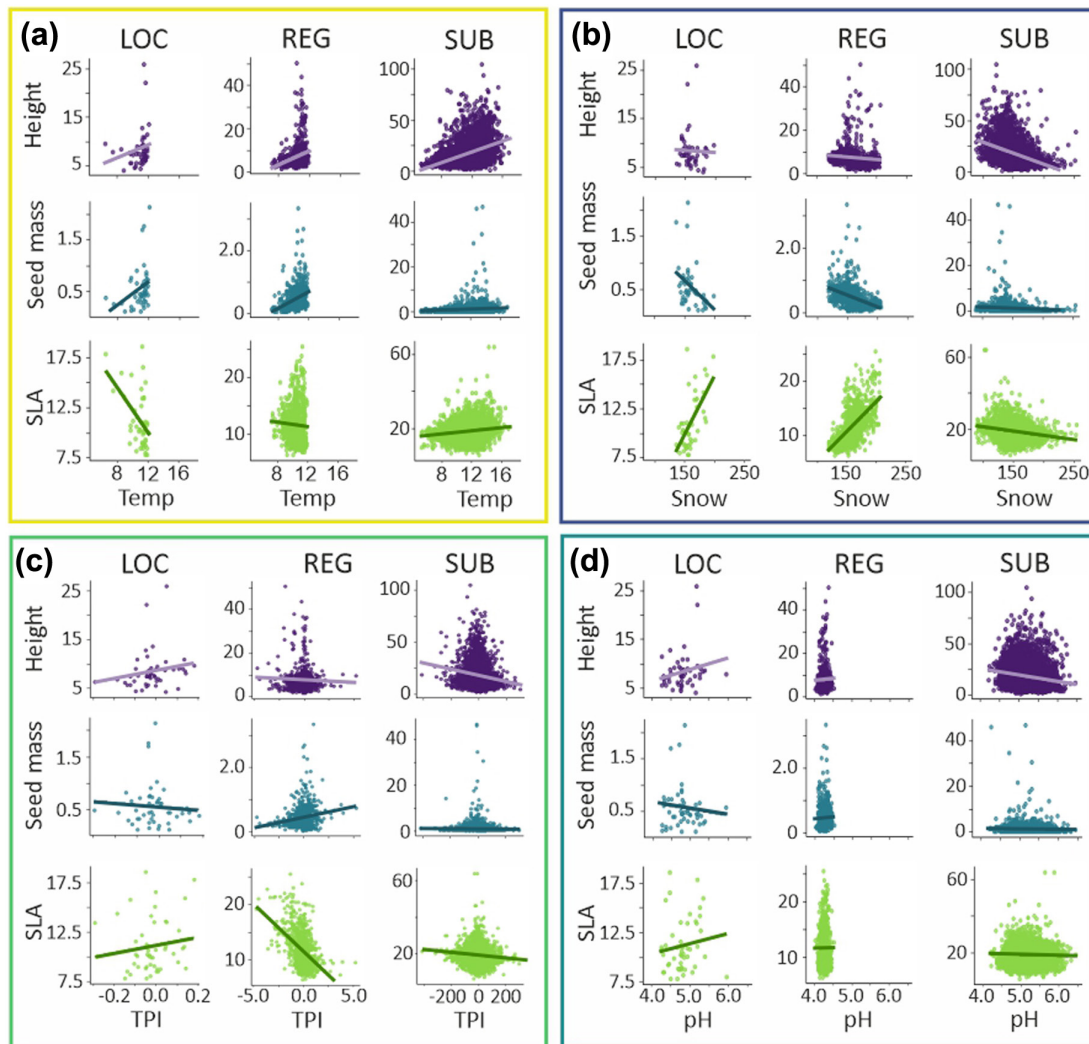


Figure 2. Relationships of CWM traits and environmental predictors at three study scales. Trend lines are based on a linear model between traits and environmental predictors. Temp = average July temperature (a), Snow = snow persistence (b), TPI = topographic position index (c), pH (d). Height: cm, Seed mass: mg, SLA: $\text{mm}^2 \text{mg}^{-1}$.

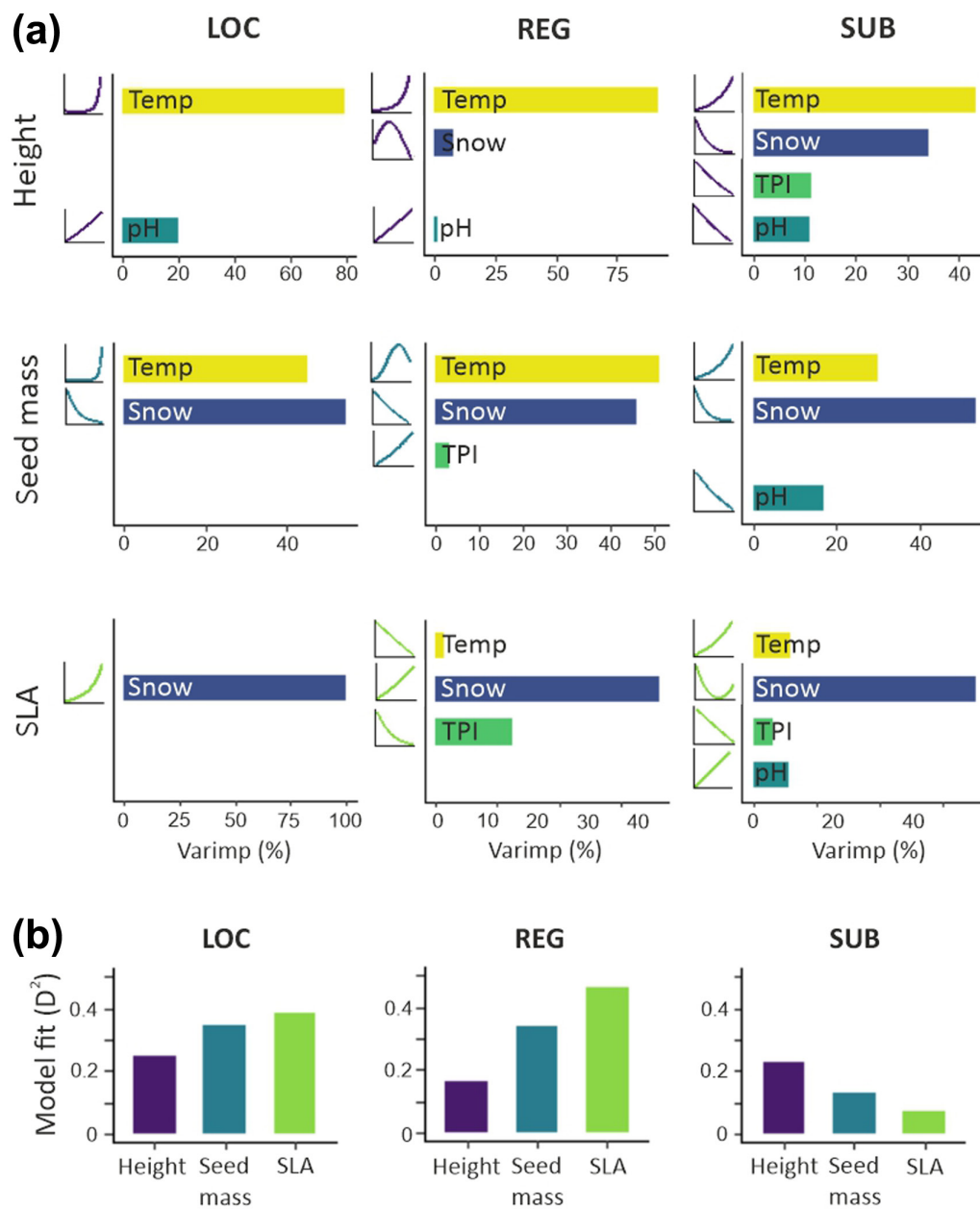


Figure 3. Response curves and relative variable importance for each trait and scale in the final models (a). Blanks show variables that were not included in the final models based on AIC-value. Lower panel (b) shows the fit of the final models at each scale. Both variable importance and explained deviance show the mean across ten modelling rounds. Larger figures of response curves showing the range of the response are presented in the Supporting information.

variation between the traits and scales (Fig. 3a). Temp had the highest variable importance for plant height at each scale with a mean of 71.7 over all three scales. The relationship between plant height and Temp was positive at all scales, though at the LOC scale the response was noticeable only for taller vegetation (Supporting information).

For seed mass, Temp was an important predictor at all three scales and its effect was primarily positive. At the REG and SUB scale Temp had some importance also for SLA, though, the response of SLA was contrary between the two

scales. Snow was highly important predictor for all CWM traits at the SUB scale (mean variable importance 52.7 over three traits) showing negative response with plant height, seed mass and SLA. At the REG scale Snow was the most important predictor for SLA (mean 72.5) and was of great importance for seed mass (mean 45.8) but its effect on plant height was minor (mean 7.3). SLA responded positively to longer snow persistence whereas seed mass and height showed negative or unimodal response. At the LOC scale, Snow was the only significant predictor for SLA with a positive effect

(variable importance 100.0) and the most important variable also for seed mass (mean 54.8), with a negative effect, however, snow did not affect plant height.

Soil pH and TPI had a minor effect on CWM traits at all three scales. At the LOC and REG scales, pH was included only in the models of plant height showing a positive response. The importance of pH was obvious (mean 20.3) at the LOC scale but negligible at the REG scale (mean 0.8). The effect of pH on community traits was modest also at the SUB scale (mean 13.1 over three traits) though for SLA it was nearly as important as Temp. Height and seed mass showed negative, whereas SLA had a positive response to pH, though the magnitude of the effect was minor (Supporting information). TPI was not included in the LOC scale models and at the REG scale, it notably affected only SLA (mean variable importance 24.8). At the SUB scale, TPI had a modest importance for plant height and SLA (mean 11.3 over the two traits). CWM traits had a negative response to TPI except seed mass at the REG scale, though the magnitude of that effect was small (Supporting information).

Spatial predictions (Fig. 4a–i) visualised the trends observed in variable importance and response curves. At the LOC and REG scales, the effect of Temp and Snow is evident as tallest plants as well as largest seeds are found in the southern and warmest parts of the study areas with shorter snow persistence (Fig. 4a, b, d and e). Additionally, at the LOC scale, the effect of pH on plant height (Fig. 4a) is more clearly observed in the spatial prediction when the prediction is compared with local pH raster (Supporting information). Furthermore, Snow was the only predictor of SLA at the LOC scale (Fig. 4c), and the spatial pattern of that trait follows the spatial variation in snow persistence (Supporting information). At the SUB scale, the spatial patterns look similar, as smallest trait values for all traits are found in the most central parts of the Fennoscandian arctic–alpine area (Fig. 4g–i).

Discussion

Our results showed that the trait–environment relationships are mostly consistent over the studied spatial scales in

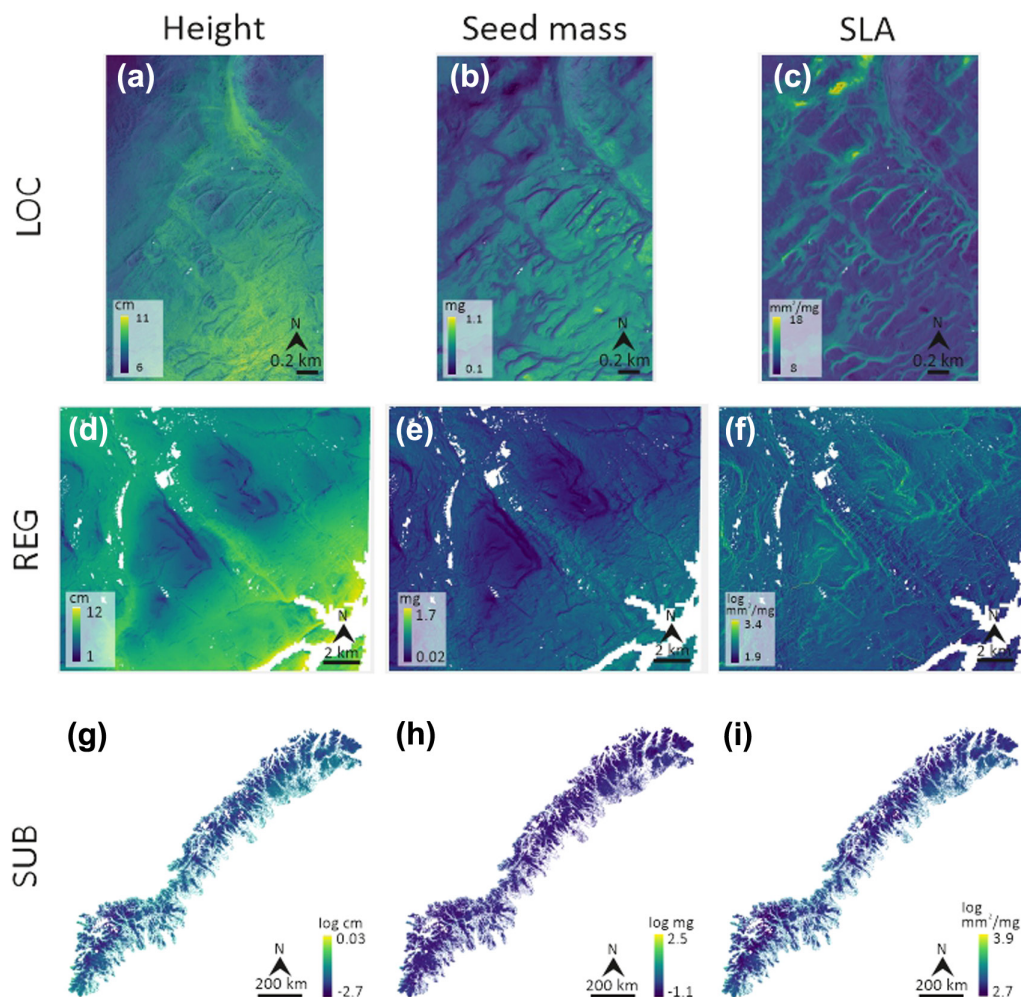


Figure 4. Spatial predictions of the CWM traits at three geographical scales. Predictions are based on the final model of each trait at each scale. Due to large range of predicted trait values at the SUB scale, the predictions are plotted using log-transformed values to better visualise spatial variation.

the Fennoscandian tundra, but some contrasting effects also emerged. In previous research, climatic variables have often been shown to be strong drivers of community trait composition at broader spatial scales (Bjorkman et al. 2018a; Myers-Smith et al. 2019) whereas soil resources (e.g. nutrient status, moisture conditions) have played larger role locally (Bruelheide et al. 2018). Our study corroborates these former findings but also provides new insights into the trait-environment relationships. Across scales, summer temperature and snow persistence had consistently strong influence on plant functional traits, whereas topographic position and soil pH generally had lower effect. Snow cover duration and depth have been shown to be important drivers of functional traits at the local scale (Choler 2005, Venn et al. 2011) and our study expands on previous research by showing the fundamental importance of snow persistence also at regional to subcontinental scales. This is particularly interesting, as to our best knowledge, snow information has rarely been utilised in broader scale trait-environment studies.

Across three geographical scales summer temperature showed primarily a consistently positive effect on the community-level mean plant height and seed mass supporting earlier studies at local (Venn et al. 2011, Happonen et al. 2019) and global scales (Dubuis et al. 2013, Moles et al. 2014). Warmer summer temperatures often indicate longer growing season, which facilitates vegetative growth and investing in reproduction may be supported by increasing the mass of individual seeds. However, the strength of temperature's effect may depend on other environmental conditions such as available moisture (Bjorkman et al. 2018a) or snow cover duration (Niittynen et al. 2020). Even though summer temperature had strong influence on the community traits, its effect was often overridden by snow persistence, which caused varying responses depending on the specific trait and scale. A consistent negative influence on plant height and seed mass across the scales, as well as positive impact on SLA, support former findings from arctic-alpine landscapes (Choler 2005, Niittynen et al. 2020). Due to the short growing season in snowbed habitats species benefit from fast acquisition of resources leading to small seeds and low-cost leaves with short life span (Kudo et al. 2001). Additionally, shorter plants are better sheltered by the insulating effect of the snowpack especially in the beginning of the growing season decreasing possibility of frost damages, which also enables higher SLA leaves (Rapacz et al. 2014, Happonen et al. 2019). At the subcontinental scale, a somewhat negative response of SLA to snow persistence was observed, which might relate to a larger number of species with boreal distributional background in the community data, as similar negative trend was recorded by Niittynen et al. (2020) when they projected trait-environment relationships in possible future climate and snow cover conditions showing boreal species dispersion above current forest line. Even though forested areas were removed from the subcontinental scale data, it is possible that some forests remained due to the grid cell size increasing the number of boreal species, as the transition to treeless tundra may happen within short horizontal distance due to steep slopes e.g.

in the coastal regions of Norway (Seppälä 2005). It has been shown that different species groups with differing ecology and functional characteristics have varying responses to environmental processes such as snow persistence (Niittynen and Luoto 2018, Rissanen et al. 2021) and geomorphological disturbances (le Roux and Luoto 2014). Thus, a higher proportion of boreal species likely affected the trait-environment relationships in areas close to the tree line which are especially represented in the subcontinental dataset.

The dominating importance of snow for community functional trait composition in tundra, across the geographical scales, may be caused by several mechanisms. At finer scales, topography generates uneven distribution of snow creating a wide range of habitats from moist meltwater meadows to windblown ridges (Walker et al. 1993, French 2013). Overall, snow cover thickness and its duration affect both summer and overwintering conditions controlling growing season length, winter thermal conditions, and amount of incoming solar radiation at the ground level (Rixen et al. 2022). Our study shows that this ecologically relevant variation in environmental conditions seems to be captured also at broader spatial scales. As snow is connected with atmospheric conditions, topography and biosphere, it may characterise environmental heterogeneity more accurately than traditional macroclimatic, topographic or soil variables alone, thus overriding their effects when modelling vegetation patterns (Niittynen and Luoto 2018, Rissanen et al. 2021). It is also worth noting that the importance of snow persistence was high both for variables derived from remote sensing products (Landsat and MODIS) as well as for a variable based on microclimatic temperature measurements, highlighting the availability of useful snow information regardless of the scale.

Soil pH and TPI showed a weak relationship with the CWM traits at all scales and their effect was low also at the finer scales where nutrient status and moisture conditions have earlier shown to play large role (Bruelheide et al. 2018, Happonen et al. 2019, Kemppinen et al. 2021). However, TPI is only a proxy of moisture conditions which likely decreases its importance compared to in-situ soil moisture measurements (Kemppinen et al. 2019). TPI caused a consistent negative response for all traits, indicating the harsh growing conditions at ridges where available moisture is scarce (Kemppinen et al. 2018) and physical stress caused by wind and low temperatures is high, thus supporting only smaller-statured species with stress-tolerant (i.e. low-SLA) leaves (Dubuis et al. 2013). For soil pH, traits showed varying responses depending on the studied trait and scale. Higher soil pH might correlate positively with soil nutrient status (Gough et al. 2000, Hobara et al. 2016) and could therefore enhance taller plant growth and faster resource capturing providing an asset in light-competition (Lavorel and Garnier 2002). However, a negative relationship between soil pH and plant height was detected as well. This might indicate that in our data soil pH represents more the amount of organic matter in soil due to the topsoil sampling rather than calcareousness, which probably prevails more in deeper mineral soil samples. Consequently, the observed effects might indicate

for example environments with geomorphological disturbances mixing the soil thus supporting the occurrence of small-statured disturbance-tolerant arctic–alpine species (le Roux et al. 2013). An observed negative trend of seed mass with soil pH agreed with former research suggesting that more alkaline and consequently possibly nutrient richer soils enable faster production of numerous smaller seed instead of investing to the survival of few large ones (Westoby et al. 2002, Kemppinen et al. 2021).

We acknowledge that our results portray not only real ecological processes but also methodological choices and rely on the plausibility of the study setting, data, and methods. Even though we aimed to harmonise the used data across the scales as far as possible while also utilising as detailed information as possible, challenges remain. Firstly, the three study scales cover different amount of variation both in the utilised species data, and hence in the CWM traits, as well as in the environmental predictors. However, in order to characterize the trait–environment relationships as thoroughly as possible we wanted to use all data available for each scale after removing forested areas which represent a different habitat, and hence a large number of boreal species. This harmonized both trait and environmental data notably. Additionally, we wanted to create representative study settings at each scale following commonly utilised approaches, i.e. using in-situ measurements at the finest scale and global datasets at the broadest scale, instead of deriving exactly comparable variables at the cost of accuracy.

Secondly, regarding to the species observation data used to define plant communities, local and regional scale vegetation data were plot-based observations, whereas subcontinental scale data were derived from databases using single species observations aggregated to a grid cell. Therefore, subcontinental scale study sites do not cover all species occurring within each grid cell, and the observations might be biased towards rarer and easily identifiable species and to areas that are more easily reached. Due to the extent and resolution of the study area, subcontinental scale data holds more species with a boreal distributional background, even after removal of forested areas, compared to the two finer scales. This probably affected the scale-dependency of the trait–environment responses because areas close to the tree line were mostly represented in the subcontinental data whereas regional and local study areas were more strictly in tundra. However, boreal species often play a central role in the tundra communities as well, thus complete removal of boreal species was not considered. Moreover, the coarser resolution in the subcontinental data probably affected the trait–environment relationships as small-scale environmental heterogeneity and small habitat patches (such as snowbeds) are not as well captured as in the regional and local scale data. Additionally, in the subcontinental scale data, all species had the same weight in the CWM trait calculations due to the lack of abundance data, which decreases the weight of common species. However, the abundant species, such as crowberry and dwarf birch, had a high number of observations regardless of the scale suggesting that the plant communities in the subcontinental scale were also most affected by the most dominant species. Our

study indicates that such presence-only species observation data can be useful and informative for studies with functional approach, hence enabling investigations of trait–environment relationships at larger spatial grains and extents than available in traditional community-based sampling designs.

Thirdly, we acknowledge that even though our study areas were representative of the Fennoscandian tundra, the study design lacked replication as it contained only one study area at each scale. Hence, the results are not readily transferable to other tundra regions but need to be interpreted in the context of the current design. Thus, more multiscale studies across arctic–alpine regions are needed to make sound conclusions on the consistence of trait–environment relationships.

When it comes to the environmental data, microclimatic measurements represent habitat conditions at the plant scale, thus probably capturing the true effect of temperature better than variables derived from global climate data, which might explain the strong effect of summer temperature on vegetation height at the local scale. We trust that in the future as more global data sets on microclimatic conditions (Lembrechts et al. 2020) become available, these restrictions between scales could be overcome. In addition, soil nutrient status could be better captured by including also information of soil nutrient concentrations (Ordoñez et al. 2009) rather than using pH alone. Furthermore, soil properties might be better described by measuring organic and mineral layers separately (Happonen et al. 2022) which might increase the effect and ecological relevance of pH. We also acknowledge, that even though our models seemed to capture the variation in community traits relatively well, though depending on the scale and trait, correlative approaches cannot easily take e.g. species interactions and population dynamics into account, thus possibly decreasing the model accuracy (Guisan and Thuiller 2005). The number of predictors included in the final models also varied across the scales, with decreasing number of predictors especially at the local scale, most likely due to fewer observations in the dataset leading to lower statistical significance. Additionally, the inclusion of interactions between environmental variables might have increased model fit, ecological relevance, as well as predictability as the effect of environmental factors can depend on each other. This ecological context dependency can shape the observed vegetation–environment relationships like it has been shown in terms of temperature and soil moisture, for example (Bjorkman et al. 2018a, von Oppen et al. 2021). Therefore, considering interactions between environmental factors would benefit future studies. Moreover, predictive models of ecosystem structure could be further improved by accounting for intraspecific trait variability (Funk et al. 2017), disturbances (le Roux et al. 2013) and biotic interactions (Bruehlheide et al. 2018) across the scales.

Conclusions

Here, we demonstrated that arctic–alpine community trait composition has a strong relationship with summer

temperature and snow conditions across geographical scales in the Fennoscandian tundra. Specifically, our study pinpoints the importance of snow, not only at local and regional scales, but also at subcontinental scale in regulating plant functional traits. Utilising snow information could be particularly important to better understand large-scale trends in plant community composition as seasonal snow cover is shrinking globally (Hock et al. 2019). With a multi-scale study setting, we showed that trait-environment relationships are relatively consistent over different spatial scales, yet variability in these responses/contrasting relationships arise depending on the studied trait and environmental factor.

Acknowledgements – The authors thank Heli Kainulainen for her crucial assistance with fieldwork and Aino Aalto for her help in pH analyses. The authors also thank all current and former members of BioGeoClimate Modelling Lab for their assistance with collecting species observation data.

Funding – T. R. acknowledges funding from the Doctoral Programme in Geosciences (GeoDoc, Univ. of Helsinki). P. N. acknowledges funding from Finnish Cultural Foundation and Nessling foundation. A.-M. V. acknowledges funding from Gordon and Betty Moore Foundation (grant no. 8414). The authors thank Arctic Avenue (spearhead research project between the Univ. of Helsinki and Stockholm Univ.), The Finnish Foundation for Nature Conservation, The Finnish Society of Sciences and Letters (Sohlberg Foundation), Nordenskiöld-samfundet and Societas pro Fauna et Flora Fennica for fieldwork funding.

Author contributions

Tuuli Rissanen: Conceptualization (equal); Data curation (equal); Investigation-Lead, Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Pekka Niittynen:** Conceptualization (equal); Data curation (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Janne Soinen:** Conceptualization (equal); Investigation (equal); Methodology (equal); Supervision (equal); Writing – review and editing (equal). **Anna-Maria Virkkala:** Data curation (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Miska Luoto:** Conceptualization (equal); Investigation (equal); Methodology (equal); Supervision (lead); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at <https://publons.com/publon/10.1111/ecog.06397>.

Data availability statement

Data are available from the Zenodo Digital Repository: <https://doi.org/10.5281/zenodo.6119775> (Rissanen et al. 2023).

Supporting information

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

References

- Aalto, J., le Roux, P. C. and Luoto, M. 2014. The meso-scale drivers of temperature extremes in high-latitude Fennoscandia. – *Clim. Dyn.* 42: 237–252.
- 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.
- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. – In: Petrov, B. N. and Csaki, F. (eds), 2nd international symposium on information theory, Akademia Kiado, Budapest, pp. 267–281.
- 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.
- Breiman, L. 2001. Random forests. – *Mach. Learn.* 45: 5–32.
- Bruelheide, H. et al. 2018. Global trait–environment relationships of plant communities. – *Nat. Ecol. Evol.* 2: 1906–1917.
- Choler, P. 2005. Consistent shifts in alpine plant traits along a mesotopographical gradient. – *Arct. Antarct. Alp. Res.* 37: 444–453.
- Conrad, O., Bechtel, B., Bock, M., Dietrich, H., Fischer, E., Gerliz, L., Wehberg, J., Wichmann, V. and Böhner, J. 2015. System for automated geoscientific analyses (SAGA) ver. 2.1.4. – *Geosci. Model Dev.* 8: 1991–2007.
- Díaz, S. et al. 2016. The global spectrum of plant form and function. – *Nature* 529: 167–171.
- Dubuis, A., Rossier, L., Pottier, J., Pellissier, L., Vittoz, P. and Guisan, A. 2013. Predicting current and future spatial community patterns of plant functional traits. – *Ecography* 36: 1158–1168.
- Elith, J., Ferrier, S., Huettmann, F. and Leathwick, J. 2005. The evaluation strip: a new and robust method for plotting predicted responses from species distribution models. – *Ecol. Model.* 186: 280–289.
- European Environment Agency. 2015. BioGeoRegions2015.shp. – European Council. <https://www.eea.europa.eu/data-and-maps/data/biogeographical-regions-europe-2/zippped-shapefile-format-vector-polygon/zippped-shapefile-format-vector-polygon/view>.
- European Environment Agency. 2018. Corine land cover (CLC). – <https://land.copernicus.eu/pan-european/corine-land-cover/clc2018>.
- French, H. M. 2013. The periglacial environment, 3rd edn. – Wiley.
- Funk, J. L., Larson, J. E., Ames, G. M., Butterfield, B. J., Cavender-Bares, J., Firn, J., Laughlin, D. C., Sutton-Grier, A. E., Williams, L. and Wright, J. 2017. Revisiting the Holy Grail: using plant functional traits to understand ecological processes. – *Biol. Rev.* 92: 1156–1173.
- 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.
- Guisan, A. and Zimmermann, N. E. 2000. Predictive habitat distribution models in ecology. – *Ecol. Model.* 135: 147–186.
- Guisan, A., Weiss, S. B. and Weiss, A. D. 1999. GLM versus CCA spatial modeling of plant species distribution. – *Plant Ecol.* 143: 107–122.
- Guisan, A. and Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. – *Ecol. Lett.* 8: 993–1009.
- Hall, D. K., Riggs, G. A., Salomonson, V. V., DiGirolamo, N. E. and Bayr, K. J. 2002. MODIS snow-cover products. – *Remote Sens. Environ.* 83: 181–194.

- Happonen, K., Aalto, J., Kemppinen, J., Niittynen, P., Virkkala, A.-M. and Luoto, M. 2019. Snow is an important control of plant community functional composition in oroarctic tundra. – *Oecologia* 191: 601–608.
- Happonen, K., Virkkala, A.-M., Kemppinen, J., Niittynen, P. and Luoto, M. 2022. Relationships between above-ground plant traits and carbon cycling in tundra plant communities. – *J. Ecol.* 110: 700–716.
- Hastie, T. and Tibshirani, R. 1986. Generalized additive models. – *Stat. Sci.* 1: 297–318.
- Hengl, T., De Jesus, J. M., MacMillan, R. A., Batjes, N. H., Heuvelink, G. N. M., Ribeiro, E., Samuel-Rosa, A., Kempen, B., Leenaars, J. G., Walsh, M. G. and Gonzalez, M. R. 2014. SoilGrids1km – global soil information based on automated mapping. – *PLoS One* 9: e105992.
- Hijmans, R. J. 2020. raster: geographic data analysis and modeling. – R package ver. 3.4-5. <https://CRAN.R-project.org/package=raster>.
- 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.
- Hock, R., Rasul, G., Adler, C., Cáceres, B., Gruber, S., Hirabayashi, Y., Jackson, M., Kääb, A., Kang, S., Kutuzov, S., Milner, A., Molau, U., Morin, S., Orlove, B. and Stelzer, H. 2019. High mountain areas. – In: Pörtner, H.-O., Roberts, D. C., Masson-Delmotte, V., Zhai, P., Tignor, M., Poloczanska, E., Mintenbeck, K., Alegria, A., Nicolai, M., Okem, A., Petzold, J., Rama, B. and Weyer, N. M. (eds), IPCC special report on the ocean and cryosphere in a changing climate. Intergovernmental Panel on Climate Change, pp. 131–202.
- Johansson, M., Callaghan, T. V., Bosiö, J., Åkerman, H. J., Jackowicz-Korczynski, M. and Christensen, T. R. 2013. Rapid responses of permafrost and vegetation to experimentally increased snow cover in sub-arctic Sweden. – *Environ. Res. Lett.* 8: 035025.
- Joswig, J. S. et al. 2022. Climatic and soil factors explain the two-dimensional spectrum of global plant trait variation. – *Nat. Ecol. Evol.* 6: 36–50.
- Karger, D. N., Conrad, O., Böhrer, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P. and Kessler, M. 2017. Climatologies at high resolution for the earth's land surface areas. – *Sci. Data* 4: 170122.
- Kattge, J. et al. 2011. TRY – a global database of plant traits. – *Global Change Biol.* 17: 2905–2935.
- 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. Process. 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., le Roux, P. C., Momberg, M., Happonen, K., Aalto, J., Rautakoski, H., Enquist, B. J., Vandvik, V., Halbritter, A. H. and Luoto, M. 2021. Consistent trait–environment relationships within and across tundra plant communities. – *Nat. Ecol. Evol.* 5: 458–467.
- Kudo, G., Molau, U. and Wada, N. 2001. Leaf-trait variation of Tundra plants along a climatic gradient: an integration of responses in evergreen and deciduous species. – *Arct. Antarct. Alp. Res.* 33: 181–190.
- Laliberté, E., Legendre, P. and Shipley, B. 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. – R package ver. 1.0-12.1, <https://cran.r-project.org/web/packages/FD/index.html>.
- 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 Roux, P. C., Virtanen, R. and Luoto, M. 2013. Geomorphological disturbance is necessary for predicting fine-scale species distributions. – *Ecography* 36: 800–808.
- le Roux, P. C. and Luoto, M. 2014. 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. J. et al. 2020. SoilTemp: a global database of near-surface temperature. – *Global Change Biol.* 26: 6616–6629.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. – *Ecology* 73: 1943–1967.
- Lidmar-Bergström, K. and Näslund, J.-O. 2005. Major landforms and bed-rock. – In: Seppälä, M. (ed.), *The physical geography of Fennoscandia*. Oxford Univ. Press, pp. 3–16.
- 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.
- McCullagh, P. and Nelder, J. A. 1989. *Generalized linear models*. Monographs on statistics and applied probability 37. – Chapman and Hall.
- Mod, H. K., Buri, A., Yashiro, E., Guex, N., Malard, L., Pinto-Figueroa, E., Pagni, M., Niculita-Hirzel, H., van der Meer, J. R. and Guisan, A. 2021. Predicting spatial patterns of soil bacteria under current and future environmental conditions. – *ISME J.* 15: 2547–2560.
- Moles, A. T. et al. 2014. Which is a better predictor of plant traits: temperature or precipitation? – *J. Veg. Sci.* 25: 1167–1180.
- Myers-Smith, I. H., Thomas, H. J. D. and Bjorkman, A. D. 2019. Plant traits inform predictions of tundra responses to global change. – *New Phytol.* 221: 1742–1748.
- 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. 2020. Decreasing snow cover alters functional composition and diversity of Arctic tundra. – *Proc. Natl Acad. Sci. USA* 117: 21480–21487.
- Ordoñez, J. C., Bodegom, P. M., Witte, J.-P. M., Wright, I. J., Reich, P. B. and Aerts, R. 2009. A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. – *Global Ecol. Biogeogr.* 18: 137–149.
- Pawley, S. 2021. Rsagacmd: linking R with the open-source ‘SAGA-GIS’ software. – R package ver. 0.1.2, <https://CRAN.R-project.org/package=Rsagacmd>.
- Rapacz, M., Ergon, Å., Höglind, M., Jørgensen, M., Jurczyk, B., Østrem, L., Rognli, O. A. and Tronsmo, A. M. 2014. Overwintering of herbaceous plants in a changing climate. Still more questions than answers. – *Plant Sci.* 225: 34–44.
- 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. and Luoto, M. 2021. Snow information is required in subcontinental scale predictions of mountain plant distributions. – *Global Ecol. Biogeogr.* 30: 1502–1513.

- Rissanen, T., Niittynen, P., Soinen, J., Virkkala, A.-M. and Luoto, M. 2023. Data from: Plant trait-environment relationships in tundra are consistent across spatial scales. – Zenodo Digital Repository, <https://doi.org/10.5281/zenodo.6119775>.
- Rixen, C. et al. 2022. Winters are changing: snow effects on Arctic and alpine tundra. – *Arct. Sci.* 8: 572–608.
- Rollhauser, A. G., Waller, D. M. and Tucker, C. M. 2021. Complex trait–environment relationships underlie the structure of forest plant communities. – *J. Ecol.* 109: 3794–3806.
- Ryvarden, L. 1969. The vascular plants of the Rastigaissa area (Finnmark, Northern Norway). – *Acta Boreal.* 26: 1–56.
- Semenchuk, P. R., Elberling, B., Amtorp, C., Winkler, J., Rumpf, S. Michelsen, A. and Cooper, E. J. 2015. Deeper snow alters soil nutrient availability and leaf nutrient status in high Arctic tundra. – *Biogeochemistry* 124: 81–94.
- Seppälä, M. 2005. The physical geography of Fennoscandia. – Oxford Univ. Press, p. 432.
- Sørensen, M. V., Graae, B. J., Classen, A., Enquist, B. J. and Strimbeck, R. 2019. Drivers of C cycling in three arctic-alpine plant communities. – *Arct. Antarct. Alp. Res.* 51: 128–147.
- Testolin, R. et al. 2021. Global functional variation in alpine vegetation. – *J. Veg. Sci.* 32: 1–14.
- Tikkanen, M. 2005. Climate. – In: Seppälä, M. (eds), *The physical geography of Fennoscandia*. Oxford Univ. Press.
- Trujillo, W., Rivera-Rondón, C. A., Jácome, J., Carcía, N., Eiserhardt, W. L. and Balslev, H. 2022. Palm functional trait responses to local environmental factors in the Colombian Amazon. – *J. Trop. Ecol.* 38: 39–47.
- van Buuren, S. and Groothuis-Oudshoorn, K. 2011. mice: multi-variate imputation by chained equations in R. – *J. Stat. Softw.* 45: 1–67.
- Venables, W. N. and Ripley, B. D. 2002. *Modern applied statistics with S*. 4th edn. – Springer.
- Venn, S. E., Green, K., Pickering, C. M. and Morgan, J. W. 2011. Using plant functional traits to explain community composition across a strong environmental filter in Australian alpine snowpatches. – *Plant Ecol.* 212: 1491–1499.
- Virtanen, R. 2003. The high mountain vegetation of the scandes. – In: Nagy, L., Grabherr, G., Körner, C., and Thompson, D. B. A. (eds), *Alpine biodiversity in Europe*, vol. 167. Springer, pp. 31–36.
- von Oppen, J., Normand, S., Bjorkman, A. D., Blach-Overgaard, A., Assmann, J. J., Forchhammer, M., Guéguen, M. and Nabe-Nielsen, J. 2021. Annual air temperature variability and biotic interactions explain tundra shrub species abundance. – *J. Veg. Sci.* 32: e13009.
- Walker, D. A., Halfpenny, J. C., Walker, M. D. and Wessmann, C. A. 1993. Long-term studies of snow–vegetation interactions. – *BioScience* 43: 287–301.
- Weiss AD. 2001. Topographic position and landforms analysis. – ESRI users conference: San Diego, CA.
- Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. – *Plant Soil* 199: 213–227.
- Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A. and Wright, I. J. 2002. Plant ecological strategies: some leading dimensions of variation between species. – *Annu. Rev. Ecol. Syst.* 33: 125–159.
- 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.
- Wilson, J. P. and Gallant, J. C. 2000. *Terrain analysis: principles and applications*. – Wiley.
- Wright, I. J. et al. 2004. The worldwide leaf economics spectrum. – *Nature* 428: 821–827.