OIKOS

Research article

Microclimate relationships of intraspecific trait variation in sub-Arctic plants

Julia Kemppinen and Pekka Niittynen

J. Kemppinen (https://orcid.org/0000-0001-7521-7229) ✉ (julia.kemppinen@oulu.fi), Geography Research Unit, Univ. of Oulu, Oulu, Finland. – P. Niittynen (https://orcid.org/0000-0002-7290-029X), Dept of Geosciences and Geography, Univ. of Helsinki, Helsinki, Finland.

Oikos
2022: e09507
doi: 10.1111/oik.09507
Subject Editor: Lonnie Aarssen
Editor-in-Chief: Dries Bonte
Accepted 1 August 2022

Within-species trait variation is a substantial part of plant functional diversity. However, this intraspecific trait variation (ITV) is rarely investigated in relation to a key characteristic of the Arctic and alpine ecosystems: fine-scale microclimatic heterogeneity. Here, we quantified the influence of microclimate (soil moisture, snow and local temperatures) on plant functional traits, specifically on ITV. We focused on six widespread northern latitude vascular plant species, and measured four traits: plant height, leaf area, leaf dry matter content (LDMC) and specific leaf area (SLA). We related ITV to field and remotely sensed microclimate data from 150 study plots within six study grids. The grids were located within a 76-m altitudinal belt in three environments: the tundra, tundra–forest ecotone and mountain birch forest in Kilpisjärvi, northwestern Finland. We compared the range of trait values between this local trait dataset (n = 5493) and global trait databases (n = 10 383). We found that information in the local dataset covers a relatively large portion of the trait ranges in global databases. The proportion varies among traits and species; the largest portion was 74% for variation in leaf area of *Vaccinium uliginosum*, and the lowest was 19% for LDMC of *Betula nana*. We found that ITV in height was mostly related to local temperatures, whereas SLA and LDMC were more related to soil moisture and snow conditions. However, species showed contrasting relationships with the microclimate drivers. We conclude that microclimate profoundly shapes ITV in northern latitude plants and that even a very compact geographic area can contain a large amount of ITV. The influence of the microclimatic conditions varies among functional traits and species, which indicates that plastic response or adaptive potential of the species to climate change may also vary across species, but that necessary variation may often be present within local plant populations.

Keywords: leaf area, leaf dry matter content, plant height, soil moisture, snow, specific leaf area

Introduction

In high-latitude ecosystems, a mosaic of contrasting habitats is created by soil moisture, snow and temperature conditions that often vary greatly over short spatial distances (Litaor et al. 2008, le Roux et al. 2013, Stewart et al. 2018, Dobbert et al.

© 2022 The Authors. Oikos 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.

2021). Microclimate , i.e. the local manifestation of atmospheric conditions, is regulated by the accumulation of water and snow, local input of solar radiation and air flow, which in turn, are all locally controlled, for instance by topographic heterogeneity (De Frenne et al. 2021). This microclimate heterogeneity is translated into fine-scale variation in plant community composition (Carlson et al. 2015, Kemppinen et al. 2021a, Thomson et al. 2021). Microclimatic heterogeneity may also be reflected on how individual species cope with local conditions, and thus it can be observed in functional traits of plant individuals (Henn et al. 2018, Andrew et al. 2022). Functional traits are chiefly related to size (e.g. plant height, leaf size) and resource acquisitiveness (e.g. leaf dry matter content (LDMC), specific leaf area (SLA)) and they inform about the abilities of a plant to survive, grow and reproduce in a given environment (Díaz et al. 2016, Funk et al. 2017). Broad-scale investigations show that plant functional traits show consistent trends along climate gradients (Bjorkman et al. 2018b, Bruelheide et al. 2018), but little is known about the very local within-species variation, its magnitude and drivers (Weemstra et al. 2021).

Community-level functional traits are strongly related to fine-scale soil moisture patterns in the tundra (Kemppinen et al. 2021b). Snowpack controls survival of plants for most of the year by regulating conditions at the soil surface, and thus snow depth can also be one the most influential factors for functional composition (Happonen et al. 2019). Temperatures are rapidly rising in the Arctic (Post et al. 2019), which has profound consequences on plant functional traits (Bjorkman et al. 2018b). In general, tundra plants grow taller in warmer conditions (Moles et al. 2009, Hudson et al. 2011); however, changes in their resource acquisitiveness depend also on available water resources (Bjorkman et al. 2018a). To fully understand the effects of climate change on cold climate ecosystems, it is important to quantify also the local variability and plasticity of plant functional traits to account for the potential for individual- and population-level adaptations (Dudley et al. 2019, Andrew et al. 2022).

In northern ecosystems, the focus on plant functional trait variation is often at the community level (Choler 2005, Niittynen et al. 2020a, Kemppinen et al. 2021a). However, trait variation within species (intraspecific trait variation, ITV) calls for more investigation, as it forms a large portion of the overall plant functional trait variation (Siefert et al. 2015, Thomas et al. 2020). Studying ITV within local plant populations might be especially relevant because plant species are not typically capable of following their shifting climatic niches at the pace of the current warming (Alexander et al. 2018), and thus local-scale variation in forms and functions of the species might be detrimental for the existence of local populations (Norberg et al. 2001). ITV is an important component of functional diversity, especially in harsh environments such as the tundra where overall species richness is typically low (Siefert et al. 2015, Niu et al. 2020, Thomas et al. 2020). In the tundra, ITV has been investigated in relation to increasing temperatures (Baruah et al. 2017, Bjorkman et al. 2018b) and along elevational and snow melt gradients (Kudo 1996, Kudo et al. 1999, Henn et al. 2018, Cruz-Maldonado et al. 2021, Weemstra et al. 2021, Rixen et al. 2022). However, from a tundra plant's perspective, soil moisture and snow are also highly relevant considerations when investigating plant trait variation (Happonen et al. 2019, Dobbert et al. 2021, Taseski et al. 2021).

Here, we investigate the local ITV of six widespread northern latitude plant species and we test if ITV is related to microclimatic conditions in a mountainous sub-Arctic region of northern Fennoscandia. Specifically, we ask: 1) How does local ITV compare to the global ITV of the species? 2) How does ITV relate to soil moisture, snow and local temperatures? To answer these questions, we measured plant functional traits and related them to field and remotely sensed data on microclimatic conditions. Given the high local heterogeneity in microclimatic conditions, we expect to find a relatively high amount of ITV and clear environmental controls of the within-species variation.

Material and methods

Study area

The study area was located in Kilpisjärvi, Finland (69°06′N, 20°81′E, 521–597 m a.s.l.). The mean annual air temperature is −1.4°C and total annual precipitation is 516 mm for the latest climatological normal period (1991–2020) as measured by the nearby meteorological station of Enontekiö Kilpisjärvi kyläkeskus, which is 1 km from the study area (Jokinen et al. 2021). The topography is heterogeneous across the area. The soils are a mixture of organic and mineral soils. The main vegetation type is dwarf shrub heath dominated by *Empetrum nigrum* subsp. *hermaphroditum*, *Betula nana* subsp. *nana* and *Vaccinium* spp. (Kemppinen et al. 2021b). *Betula pubescens* subsp. *czerepanovii* forms relatively sparse forests in valleys. Herb-rich meadows are present in moist and nutrient-rich habitats but are restricted mainly to topographic depressions and slopes fed by meltwater from late-melting snow patches. The study area is chiefly grazed by semi-domesticated reindeer *Rangifer tarandus tarandus*.

Study design

The study design (Fig. 1) consisted of 150 study plots (1 × 1 m) within six study grids (24 × 24 m). Each grid held 25 plots located at 6 m intervals. The study design followed a paired design where one grid pair was located in the tundra, one in tundra–forest ecotone (hereafter, ecotone) and one in mountain birch forest. We had two criteria for the locations. First, in each grid pair, one grid covered lush vegetation (likely indicating abundant soil moisture and nutrients; hereafter, rich) and one covered with more barren vegetation (limited resources; hereafter, poor). Second, all grids were on mesotopographical gradients (i.e. gradient from a small depression to a small ridge) where microclimatic conditions likely varied greatly over short distances. In the forest and ecotone, the

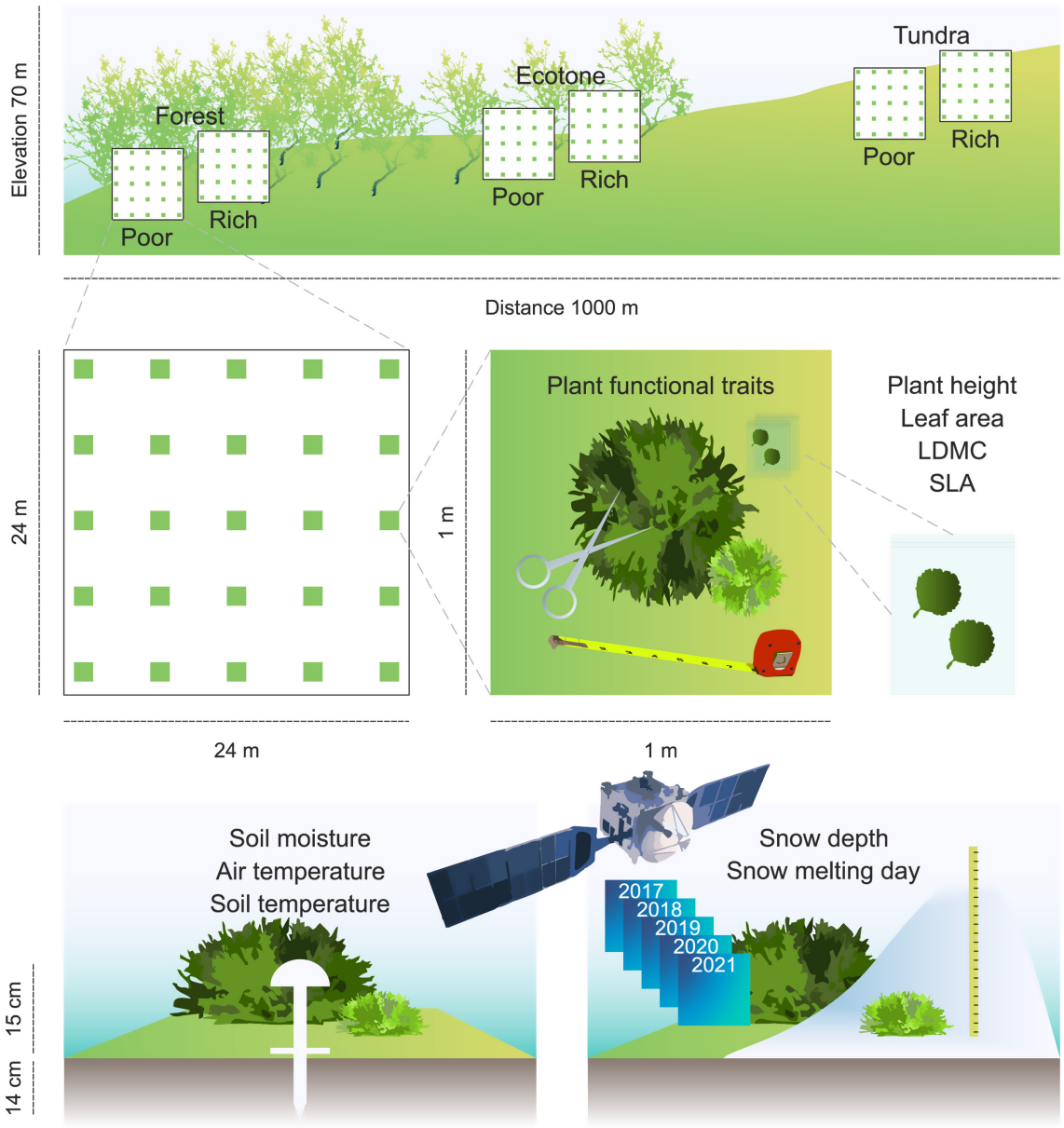

Figure 1. Study setting. We established 150 plots within six study grids in tundra, tundra–forest ecotone and mountain birch forest. We collected data on four plant functional traits from each plot for six plant species and up to four individuals per species. We related the trait data to microclimatic conditions of each plot by collecting data on soil moisture, snow and local temperatures. LDMC = leaf dry matter content. SLA = specific leaf area.

grid pairs were located ~50 m apart. In the tundra, the grid pairs were ~600 m from each other due to the absence of suitable topographic gradients and vegetation types closer to each other. The maximum elevational difference across the six grids was 76 m, and the maximum distance was 1000 m. We recorded the locations of each plot using a GPS receiver with centimetre accuracy (Emlid Reach RS2, Emlid Ltd).

Plant data

We selected six vascular plant species for trait measurements: *Bistorta vivipara*, *Solidago virgaurea*, *Betula nana*, *Vaccinium myrtillus*, *V. uliginosum* and *V. vitis-idaea*. These species are common in the area (Kemppinen et al. 2021b) and also widespread across the boreal and sub-Arctic zones. See a detailed description of the six study species in the Supporting information.

We collected data on plant height (cm), leaf area (cm^2), LDMC (dry weight/fresh weight; $g\ g^{-1}$) and SLA (leaf area/dry weight; $cm^2\ g^{-1}$). When any of the six study species were present at the plots, we measured and sampled them as close as possible to the centre of the plot, while also ensuring that we sampled separate individuals.

We collected the leaf samples on 20 July 2021 and processed them within the following 48 h before drying them. First, we

selected up to four plant individuals per species per plot and measured their heights from the soil surface to the highest photosynthetic part (i.e. excluding flowering part and stem) using rulers (mm precision). We also recorded whether the measured individuals were flowering/reproducing that summer. Second, we collected two leaf samples from the dwarf shrub species, and one from the forb species per individual. We sampled only mature leaves without marks of any kind of damage. For the forb species, we sampled rosette leaves because stem leaves are typically much smaller and stems are not present in sterile individuals. We pooled the sampled leaves together at plot level to reduce the amount of lab work and kept the samples moist in zip-lock bags with dampened paper towels. In the laboratory, we kept the samples in the zip-lock bags at 4°C between measurements. Third, we cut off the petioles and weighed the leaves using a Mettler AE 100 scale (0.0001 g precision) to measure their fresh weight. Fourth, we scanned the leaves using a Canon CanoScan LiDE 20 scanner (600 dpi resolution) to measure their area. We calculated leaf area from the scans using the ImageJ software via R with functions from the *LeafArea* R package (Katabuchi 2015). Finally, we dried the leaves at 70°C for 48 h using VWR VENTI-Line ovens, and then reweighed the dry leaves. The level of observations were plant individual for plant height, individual leaf for leaf area and plot-level means for LDMC and SLA. This resulted in a total of 5816 observations for the studied six species and four traits.

To compare the trait values and ranges in our locally collected data to the ITV of the species across the species' whole distributions, we gathered trait data from global trait databases, namely the TRY plant database (Kattge et al. 2020), Botanical Information and Ecological Network (Enquist et al. 2016, Maitner 2020) and Tundra Trait Team database (Bjorkman et al. 2018b). A full list of original data sources used in the study is provided in the Data sources section (Supporting information) and the spatial distribution of the database observations in the Supporting information. The same trait observations were clearly present in multiple datasets, and thus we divided the data into sub-datasets based on the reported original data provider, and cross-tabulated all sub-dataset pairs to calculate how many identical observations they shared. If the percentage of exact duplicates was over 20%, we merged the sub-datasets and removed the duplicates. This resulted in a total of 10 977 observations for the six species and four traits studied. However, histograms of the trait values indicated the presence of suspicious outliers that were likely errors in the heterogeneous data sources. Therefore, we excluded trait values falling outside the 95% percentiles (separately for trait*species) both in the data extracted from databases, and in our local data, before comparing the ranges of these data. This filtering was conducted only for these global–local comparisons, and the local data used in the rest of the analyses were not filtered.

Environmental data

We collected data on soil moisture, snow depth, snow melting day, air temperature and soil temperature for each of the 150 plots (Fig. 2). We collected the data in situ, except for the snow melting day, which was calculated from remotely sensed data.

We measured soil moisture, near surface temperature (hereafter expressed as air temperature) and soil temperature between 16 July and 31 August 2021 from the centre of each plot. We used TMS-4 dataloggers (TOMST Ltd, Prague, Czech Republic), which measure soil moisture to a depth of ca 14 cm, as well as soil temperature at –6 cm depth and air temperature at 15 cm above soil surface (Wild et al. 2019). The loggers measure with a 15-min interval and recorded 2 028 150 measurements. The loggers produce raw time-domain transmission data on soil moisture, which we calibrated into volumetric water content (VWC%) using a calibration function adopted from Kopecký et al. (2021). We plotted all soil moisture and temperature time series and inspected them visually (Supporting information). One logger fell down during the measurement period and for this logger we imputed the moisture and temperature time-series by using a Random forest-based method from the missForest R package (Stekhoven and Bühlmann 2012). The imputation was based on the microclimate data only; that is, the missing values in the one incomplete soil temperature time series were imputed based on all the other soil temperature time series from the rest of the loggers. Finally, we calculated mean soil moisture, air temperature and soil temperature for each logger for the whole study period. These mean values were used as predictors in the analyses.

We measured snow depth on 3 April 2022 (approximate date of the maximum snow depth) from the centre of each plot. We used a high-accuracy GPS device to navigate to the plots, and an aluminium probe to take measurements.

We calculated the snow melting day by utilising information from PlanetScope satellite images (3 × 3 m resolution) from years 2017–2021. See a detailed description of this method in the Supporting information.

Statistical analyses

We fitted hierarchical Bayesian linear models to relate the environmental variables to ITV. We fitted the models separately for each species and trait. We included soil moisture, snow depth, snow melting day, air temperature and soil temperature as predictors. All models were fitted in statistical software Stan (Carpenter et al. 2017, Stan Development Team 2019, 2020) via the functions of brms R library (Bürkner 2017). We used also tidybayes and bayesplot R libraries for model diagnostics.

We log-transformed all response variables (traits) to enchain the normality of the distributions of the variables and rescaled and centred all predictor variables. We used the default priors (i.e. noninformative priors for all slope parameters) of brms in the models. Four Markov chain Monte Carlo (MCMC) chains were used in all models with a minimum of 8000 iterations and a burn-in of 4000 iterations thinned by two. We checked the convergence of

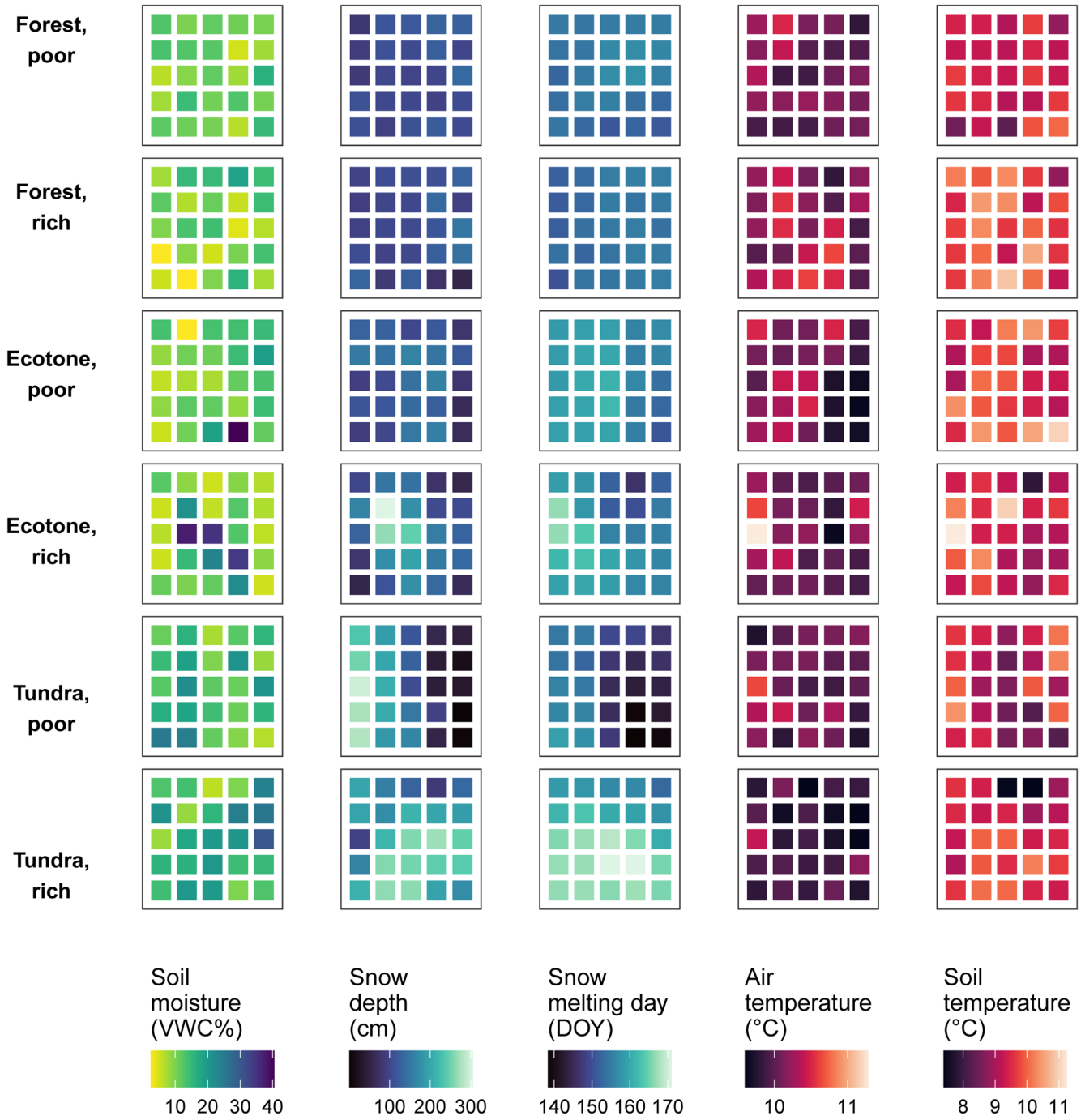

Figure 2. Fine-scale variation in soil moisture, snow conditions and local temperatures. The squares represent the study plots (n = 150) and the panels study grids (n = 6). The plot size is increased for visualisation purposes. VWC = volumetric water content. DOY = day of year.

the MCMC chains by visually evaluating MCMC trace plots, histograms of the sampled parameters and autocorrelation plots, and by comparing the distributions of the raw values of the response and the posterior predictions. We also checked Effective sample size and Rhat statistics for all model parameters (Effective sample size should preferably be > 1000 and Rhat < 1.1 (Bürkner 2017)) that help determine if the MCMC chains have mixed well (Gelman and Rubin 1992). Additionally, we calculated the k-pareto statistic for all observations with approximate leave one out (LOO) cross validation that indicates if there are especially problematic observations.

The level of observations were plant individual for plant height, individual leaf for leaf area and plot-level means for LDMC and SLA. The level of observations vary because we wanted to analyse the data at the finest possible level. LDMC

and SLA data were acquired only at the plot level (i.e. leaves pooled prior to the lab measurements) and thus individual level measurements were not available. Owing to these differences, the model structures were also slightly different for different traits.

For plant height and leaf area, which had multiple observations per plot, we included a nested random factor (plot within grid) to account for spatial structure and hierarchy of the study design.

Plant height OR *leaf area ~ soil moisture + snow depth + snow melting day + air temperature + soil temperature + (1|grid/id)*

Additionally, we included the binary information about whether the plant individual was reproductive in the plant height models of the two forbs (*Bistorta vivipara* and *S. virgaurea*) because this can have a strong impact on the height of the species, which grows a distinct above-ground stem only in the years when the individual is reproducing.

Plant height ~ soil moisture + snow depth + snow melting day + air temperature + soil temperature + flowers + (1|grid/id)

The model structure for LDMC and SLA was similar to the previous model structures (plant height, leaf area) but only the study grid was included as a random factor because the trait values were already at plot level. Another difference was that we weighted the plot level trait values by the number of individuals that were sampled, so that the model gives more weight for plots with more measurements (and, thus, likely less random variability).

LDMC OR *SLA | weights(n_inds) ~ soil moisture + snow depth + snow melting day + air temperature + soil temperature + (1|grid)*

LDMC and SLA models for *B. vivipara* were different from the above, however, because the species was recorded only in 13 plots. Owing to the low number of observations we simplified the model to avoid severe overfitting. We included only three predictors that we expected to be ecologically the most relevant ones and did not account for the structure of the study design. Thus, the *B. vivipara* models for LDMC and SLA should be interpreted with extra care. We stated this clearly in the results.

SLA OR *LDMC | weights(n_inds) ~ soil moisture + snow depth + air temperature*

The log-transformed response variables had approximately normal distributions, and so we first fitted Gaussian models. However, posterior predictive checks revealed that some of the models were not able to replicate the data distribution well. Additionally, we calculated the approximate LOO cross-validation, which showed that in many cases models predicted poorly multiple observations (k-pareto values > 0.7). Thus, we ran all models also with Student-t and skewed normal distributions. We decided the best model by calculating LOO-based model weight and selected the model with the highest weight score (i.e. lowest LOO SE). Parameter estimates were interpreted as being 'significant' when the 95% credible interval of the posterior distribution did not cross zero. We calculated Bayesian R^2 values for the models both with and without the effects of the random factors (Gelman et al. 2019).

Results

We investigated functional traits of six common northern latitude species that have large distributional extents both in geographic and climatic terms. Yet, our local dataset consists of a relatively large portion of the global ITV (Fig. 3). In this comparison, the largest portion was 74% for variation in leaf area of *V. uliginosum*, and the lowest 19% for LDMC of *B. nana* (Fig. 3). When averaged over the species, the highest variation in local dataset compared to global variation was in SLA (47.7%) followed by leaf area (47.0%), plant height (38.3%) and LDMC (32.2%). When averaged over traits, *V. vitis-idaea* holds the highest amount of relative variation in the local dataset (50.2%) followed by *B. nana* (48.5%), *V. uliginosum* (44.2%), *S. virgaurea* (37.5%), *B. vivipara* (35.5%) and *V. myrtillus* (32.0%).

In the local dataset, the range of variations in plant height was largest within the deciduous dwarf shrub species, particularly *B. nana*, and smallest within *B. vivipara* and *V. vitis-idaea* (Fig. 3). Regarding leaf area, a large range of variations was found within the two forb species, and a small range of variations within the dwarf shrub species (Fig. 3). The range of variation in LDMC was largest within *V. vitis-idaea* and smallest within *B. vivipara* (Fig. 3). Regarding SLA, *S. virgaurea* had a distinctly larger range of variation compared to the rest of the species (Fig. 3). See detailed trait distributions aggregated by study grid in the Supporting information.

High spatial and temporal variation in microclimate was found (Fig. 2, Supporting information). Plant height ITV of the species was chiefly related to the temperature variables, especially air temperature (Fig. 4, Supporting information). Plant height was positively associated with air temperature, whereas height and soil temperature had negative relationships. Soil moisture and snow depth showed no significant relationships with plant height. Regarding leaf area ITV, the models had very few significant predictors: soil moisture showed no significant relationships and the rest of the predictors were each a significant predictor to one of the six species (Fig. 4). SLA and LDMC, instead, were more related to soil moisture and snow than to the temperature variables. For example, soil moisture was a significant predictor for SLA for five out of six species and, similarly, snow depth for LDMC for five out of six species. Higher soil moisture was generally linked with higher SLA, but with *B. vivipara* soil moisture had the opposite effect. Bivariate trait–microclimate relationships for each species can be found in Supporting information and bivariate correlations in Supporting information.

The best performing models were those for *B. vivipara* (R^2 averaged over traits = 0.51) (Fig. 5, Supporting information); however, it must be noted that its sample size for all traits was low compared to the other species, and this affected the model performance when models are likely overfitting. For the rest, the highest average R^2 was for *B. nana* (0.25), *V. uliginosum* (0.22), *V. myrtillus* (0.15), *S. virgaurea* (0.14) and *V. vitis-idaea* (0.05) (Fig. 5). When averaged over species by trait, SLA models had the highest R^2 (0.28), followed by LDMC (0.26), plant height (0.19) and leaf area (0.14). If the

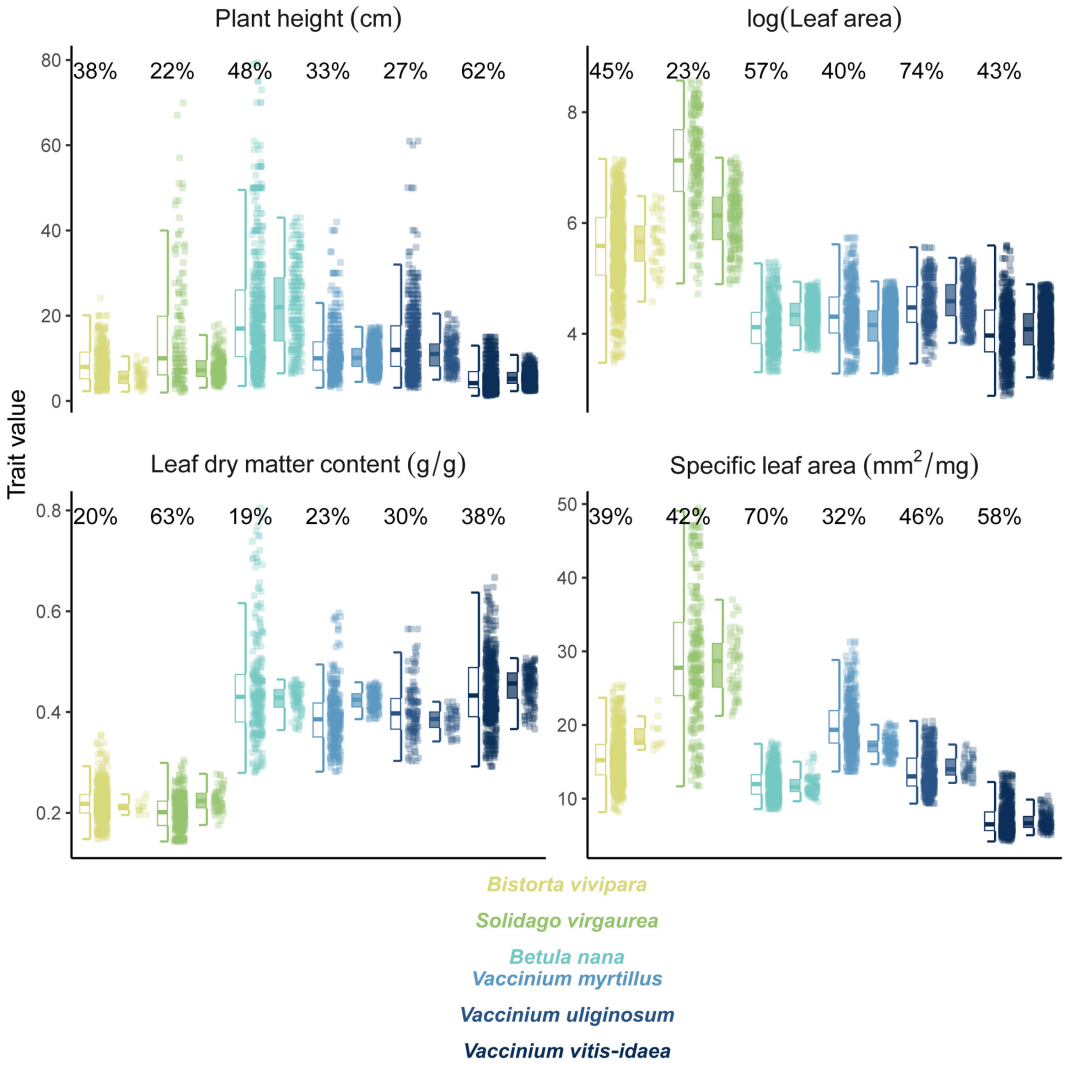

Figure 3. Intraspecific trait variation within the study species. The boxplots represent variation in global trait databases (boxes without fill) and in the local trait dataset collected for this study (coloured boxes). The points right to each box represent the individual measurements. The percentages indicate how large the range of the local trait values was in relation to the range of the global values.

likely overfitting *B. vivipara* models were excluded, the average R^2 values were slightly lower and the order of SLA and LDMC was flipped, but leaf area models remained with lowest average R^2 value. Apart from the *B. vivipara* models, the highest individual R^2 (0.42) was for the *Betula nana* LDMC model (Fig. 5).

Discussion

Generalisability of the results

We compared six widespread and common tundra/boreal species and their four functional traits. Our local dataset consisted of over 5000 trait observations, while the global trait databases consisted of over 10 000 observations collected around the globe. We found that the local trait variation at our study area constitutes a relatively high portion of the global trait variation for the six species, when we compared our local trait dataset to measurements from global trait databases. The range in the traits from our dataset corresponded to 19–74% of variation seen in the global databases. This comparison provides generalisability for our results, as these are high proportions considering our small study (< 1 km^2 with 76 m elevational difference). Tundra environments are known for high local-scale environmental heterogeneity (le Roux et al. 2013, Graae et al. 2018), and we were able to capture a wide range of this local microclimatic variability. For example, the snow depth gradient from 1 cm to 3 m depth is close to the maximum variability within the whole region (Kemppinen et al. 2021a). In this light, it is not surprising to find such a high amount of local trait variability even within the relatively small spatial extent.

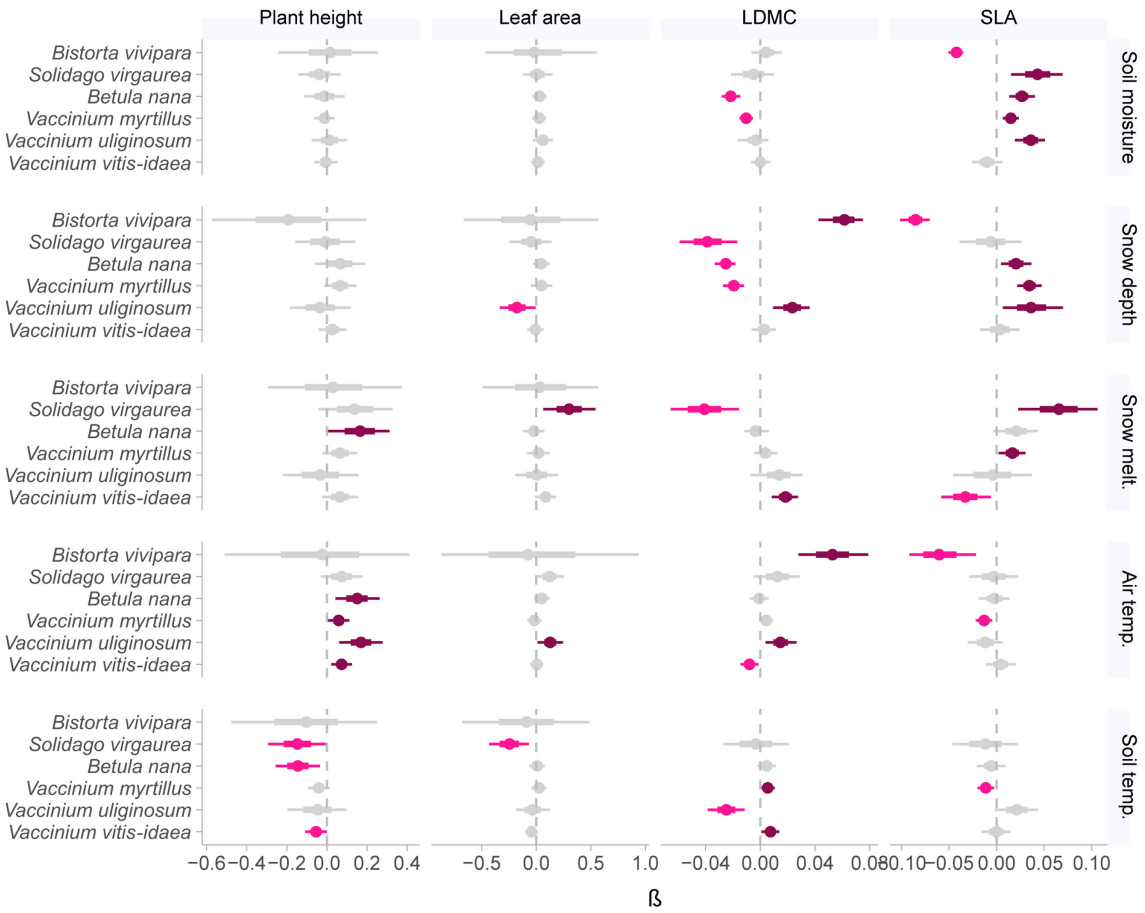

Figure 4. Slope (β) estimates for the predictors in hierarchical Bayesian linear models. Models were fitted separately for each species and trait. The points represent the posterior medians for the slope parameters, thickened lines the 66% credible intervals and the thin lines the 95% credible intervals. The coloured slope estimates were interpreted as 'significant', as their 95% credible intervals did not cross zero. LDMC = leaf dry matter content. SLA = specific leaf area.

Microclimate influences on intraspecific trait variation

Plant height was mainly explained by the local temperatures. This is in line with results from larger-scale studies where plant size has a strong latitudinal/elevational trend and was related to available energy (Kudo et al. 1999, Bjorkman et al. 2018a, Happonen et al. 2019, Pérez-Ramos et al. 2012). We found that air temperatures had a positive association with the height of all dwarf shrub species, whereas soil temperatures had negative associations with three species (Fig. 4). We want to note that interpreting the effect of soil temperature on plants might not be straightforward. We measured soil temperatures during the growing season when they are largely affected by vegetation volume and soil organic matter content, as moist peaty soils that are fully covered by rich vegetation can remain much cooler compared to exposed gravelly soils (Kemppinen et al. 2021a). Therefore, the negative effect of soil temperatures on heights of many species can also be due to these collinearily occurring aspects.

Leaf area had only a few relationships with the microclimatic predictors, and the models explained less variation than models for other traits (Fig. 4 and 5). This suggests that microclimate has less influence on plant adaptation that would manifest through leaf size, at least at this scale. Furthermore, Siefert et al. (2015) found that ITV is low in leaf area compared, for example, to that found in plant height. Midolo et al. (2019) also did not find clear ITV patterns in leaf area along elevations globally in their meta-analyses. However, Bjorkman et al. (2018b) found a significant positive relationship between leaf area ITV of tundra plants and coarse-scale summer temperatures across the Arctic, yet they did not find any indication of an increase in leaf area with warming over time. This indicates that even if there was adaptation through leaf size across populations over large extents, Arctic species may lack local plasticity in leaf area that could have readily responded to recent warming, or be visible along local microclimate gradients (Kudo 1996, Kudo et al. 1999). However, in our results, leaf area showed relatively large local variation compared to global. Therefore, a more plausible explanation to the lack of relationships could be that leaf area has also more within-individual variability causing noise in the models (e.g. leaves at different positions along the stems), and it may be more responsive to factors that we could not

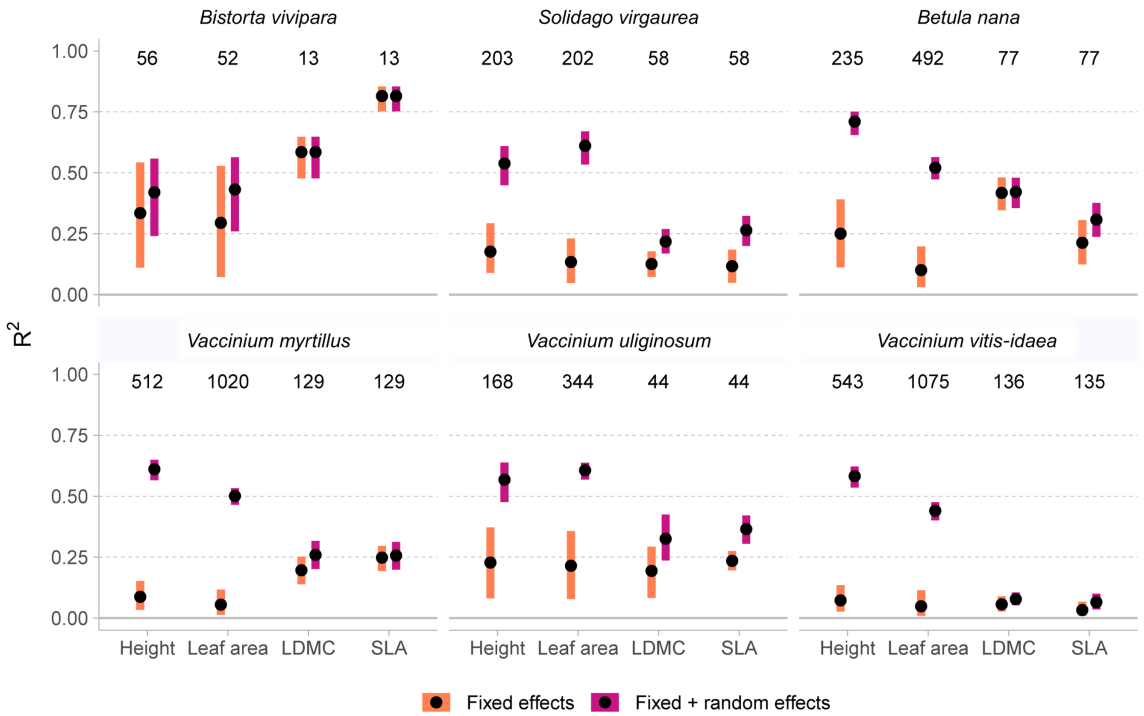

Figure 5. Model performance. Bayesian R^2 metrics with and without the effect of random factors. Plant height and leaf area models included nested study plots within study grids as random factors, whereas the LDMC and SLA models had only study grids as a random factor. The difference in model structure was because LDMC and SLA were measured at plot level and height and leaf area at individual/leaf level. The numbers represent the count of observations in a given model. LDMC and SLA models for *Bistorta vivipara* included only three instead of five predictors and no random factors due to low number of observations. LDMC = leaf dry matter content. SLA = specific leaf area.

test in our models (e.g. local light conditions affected by shadowing neighbour species).

LDMC and SLA were related to soil moisture. LDMC of *B. nana* and *V. myrtillus* had negative associations with soil moisture. For SLA, however, four species had positive associations with soil moisture, whereas *B. vivipara* had a negative relationship and *V. vitis-idaea* had no relationship (Fig. 4). Interestingly, we found that the size-structural traits were not explained by the fine-scale variation in soil moisture at all. It should be noted that our moisture gradient falls a bit short in the wettest extreme, and thus we can only speculate if plants growing on actual wetland sites would change the results. However, the studied species do not generally occur in the most waterlogged tundra wetlands, and so our moisture gradient likely sufficiently covers the moisture niches of the species within this ecosystem. The microclimate–trait relationships were in general similar to those found in Happonen et al. (2019) and Kemppinen et al. (2021a), which studied the traits at the community level. However, to the best of our knowledge, ITV patterns have not been related to soil moisture gradients in tundra, but their importance has been highlighted in studies in other ecosystems (Harzé et al. 2016, Roybal and Butterfield 2019, Westerband et al. 2021) and also for root traits (Taseski et al. 2021).

LDMC and SLA were also related to snow conditions, which is expected, as snow has multiple potential mechanisms controlling plant available resources and physiological stress (Kearney 2020). In general, thicker and more persisting snow cover hosts plants with faster leaf acquisition strategies; this has also been seen in studies that have looked at plant traits at community level (Kudo 1996, Kudo et al. 1999, Choler 2005, Happonen et al. 2019, Onipchenko et al. 2020). In particular, snow depth (measured at the peak snow season) explained LDMC of all species except for *V. vitis-idaea*. The LDMC of *B. vivipara* and *V. uliginosum* were positively associated with snow depth, whereas the rest of the species were negatively associated (Fig. 4). For SLA, all deciduous dwarf shrub species were positively related to snow depth, and *B. vivipara* was negatively related. Both the LDMC and SLA of *V. uliginosum* had positive associations with snow depth, although typically these traits are negatively correlated and so take opposite directions in their responses to environment (Díaz et al. 2016, Thomas et al. 2020). Regarding snow melting day, the species and their traits had less significant relationships, indicating that – at this scale and in these habitats – snow depth and its sheltering capacity might be a more important factor for plants than the (snow-limited) length of the growing season.

The highest proportion of variation in traits explained by microclimate was found for *B. nana* and *V. uliginosum* models, in addition to the likely overfitting *B. vivipara* models. Both species are deciduous dwarf shrubs with wide environmental niches in the tundra, which may explain why the trait–microclimate relationships were strongest for them.

Vaccinium myrtillus is also a deciduous dwarf shrub but our study site is relatively close to its cold range margin, and this may partly explain why it showed less defined trait variability compared to the other deciduous shrubs. *Bistorta vivipara* occurred only in a small number of our study plots, which is unfortunate because, based on our limited data on its trait trends along the microclimate gradients (see bivariate plots in the Supporting information), it seems that the species is very responsive to microclimatic differences (also documented in Opedal et al. (2015)). The models for *S. virgaurea* also explained a consistently low proportion of variation, which may be due to large variation in the species' ecomorphs (or differences between sterile and reproductive shoots) and perhaps because the species is often heavily grazed by *R. tarandus tarandus* (personal observation, no data). Last, out of all six species, *V. vitis-idaea* had clearly the lowest model performance and very few strong relationships with the microclimatic predictors. *Vaccinium vitis-idaea* also showed relatively little trait variation. We assume this indicates that the strategy of this evergreen species is conservative and it shows less plasticity compared to the deciduous species.

We found that in many cases species differ in their response directions along the microclimate gradients, as has been shown also along other environmental gradients (Kichenin et al. 2013, Bjorkman et al. 2018b, Roybal and Butterfield 2019, Onipchenko et al. 2020). A species might have unimodal trait–environment responses when the whole distribution of the species is covered, and so the response is different in certain parts of the gradients (Albert et al. 2010). However, unimodal responses have been rarely reported and the ITV patterns have been mostly linear (Kichenin et al. 2013, Bjorkman et al. 2018b). Another explanation is related to biotic interactions that affect species differently, and that biotic effects may even shift from competitive to facilitative along environmental gradients (Callaway et al. 2002, Adams et al. 2022).

Challenges for future investigations

Our results suggest that plant functional traits respond to local microclimates and vary greatly within species within small spatial extents. This local trait variability might be beneficial for the species' existence under changing environment and warming climate (Norberg et al. 2001), as our results indicate that local populations hold either notable capacity for plastic phenotypic responses to soil moisture, snow and thermal conditions, or a range of structural and morphological adaptations to the heterogeneous growing conditions. However, it should be noted that the studied species are widespread generalists with broad environmental niches, and more specialised or rare species might show less such trait variability (Violle and Jiang 2009). Furthermore, the high microclimatic heterogeneity documented here but also in many other tundra studies (Stewart et al. 2018, Niittynen et al. 2020b, Aalto et al. 2022) might serve as suitable microrefugia for cold-climate species even after the majority of the landscape has changed and become unsuitable (Hannah et al. 2014). It is known that microclimatic heterogeneity can increase the overall biodiversity across landscapes (Stewart et al. 2018, Niittynen et al. 2020b) but it seems evident that it also generates functional diversity through ITV. We encourage future studies to consider long-term monitoring of not only temperatures, but also soil moisture and snow patterns, as these seem to have as high relevance for local plant trait distributions as the direct effects of temperatures. However, a challenge for future investigations is to model and predict how microclimatic heterogeneity is influenced by climate change and how this is reflected in plant functional traits at both community and species level (Maclean 2020). Responses might not be straightforward if multiple environmental changes are happening simultaneously in communities with many species. Evidently, different species will have contrasting responses to changing climate, but also some traits might be more responsive. For instance, long-term monitoring across the tundra biome has shown that size-structural traits in particular have responded to warming, but leaf econometric traits have changed less (Bjorkman et al. 2018b).

Ultimately, a seminal question regarding the trait variation we measured is: how much of it is due to genetic differences or phenotypic plasticity (Pfennigwerth et al. 2017)? It is likely that at the spatial scale of our study, the plant individuals are genotypically relatively close to each other and no especially distinct sub-populations occur. Therefore, we assume that most of the variation here would be due to phenotypic plasticity. For example, *B. nana* individuals have been shown to be able to rapidly respond to altered growing conditions such as nutrient availability and warming by changing how the plants allocate their resources (Bret-Harte et al. 2001). Nevertheless, we recognise that the question of genetic and phenotypic variation is important to examine thoroughly in future trait–microclimate investigations on ITV.

The models were able to explain approximately one-fifth of the variation in the traits, which leaves a high amount of variation unexplained. It is likely that a large part of the unexplained variation may be related, for instance, to the status of the individual plant (e.g. phenology, damage), and potentially to sampling and measurement errors. However, we cannot exclude the possibility that some important environmental factors in the models may have been lacking (Mod et al. 2016), for instance the fine-scale variation in soil nutrients (Chapin et al. 1996). However, we did account for the overall fertility of the sites with the paired study design, in which one-half of the study grids were located with more nutrient-rich habitats and one-half in the more nutrient-poor habitats. When the effect of the study grid (as a random factor) was included in the R^2 calculations the variation explained increased by 0.06 (0.08 when *B. vivipara* models were excluded) in the LDMC and SLA models, in which the random factor consisted of only the grid. This means that there was not much variation that could have been explained by the plants' growing locations; namely, the tundra, ecotone or forest grids, or the poor or rich grids.

This study design enabled us to control for many potential sources for error related to practical aspects of field and

laboratory measurements. For example, all plants were measured and their leaves sampled within a couple of hours under equivalent weather conditions. In addition, the leaf measurements were carried out within two days after sampling. Plants were sampled in late July, thus phenological differences caused by the differences were likely largely levelled off. However, we were not exclusively able to control for the age of individual plants (Büntgen et al. 2018), although we avoided clearly juvenile individuals. Presumably, more individuals and leaves would have decreased noise in the data, and consequently, increased deviation explained by the models. However, as noise in data is by definition random, it should not affect the strongest relationships we found between the trait values and microclimate. Therefore, we are confident that potential error sources should not compromise our main findings and conclusions. We also want to highlight the size of the dataset, which for these species and traits is approximately one-half of the number of observations found in global trait databases (Fig. 3).

Conclusions

We conclude that microclimate is profoundly associated with ITV patterns in northern latitude plants. Our local-scale findings are largely in line with results from studies that consider larger environmental gradients, which suggests that the climatic processes filtering individual adaptations or driving plant plasticity are similar from one spatial scale to another. However, the relationship between ITV and microclimate varies among traits and species. Overall, water availability, snow conditions and local summer temperatures above and below ground can vary over short distances in sub-Arctic ecosystems, and local plant populations show capacity to shape their functional traits in relation to this mosaic of microclimatic conditions.

Acknowledgements – We thank the personnel at the Kilpisjärvi Biological Research Station for their support during fieldwork.
Funding – JK was funded by the Arctic Interactions at the University of Oulu and Academy of Finland (project number 318930, Profi 4). PN was funded by the Nessling Foundation. JK and PN acknowledge funding by the Finnish Cultural Foundation via the Foundations' Post Doc Pool and the Arctic Researchers' Network at the Thule Institute at the University of Oulu.
Permits – Permission to carry out fieldwork was granted by Metsähallitus.
Conflict of interest – The authors have no conflict of interest.

Author contributions

Julia Kemppinen: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Pekka Niittynen**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data and code are available at Zenodo digital repository: <https://doi.org/10.5281/zenodo.6965609>, (Niittynen and Kemppinen 2022).

Supporting information

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

References

Aalto, J. et al. 2022. Microclimate temperature variations from boreal forests to the tundra. – Agric. For. Meteorol. 323: 109037.
Adams, A. E. et al. 2022. A case for associational resistance: apparent support for the stress gradient hypothesis varies with study system. – Ecol. Lett. 25: 202–217.
Albert, C. H. et al. 2010. Intraspecific functional variability: extent, structure and sources of variation. – J. Ecol. 98: 604–613.
Alexander, J. M. et al. 2018. Lags in the response of mountain plant communities to climate change. – Global Change Biol. 24: 563–579.
Andrew, S. C. et al. 2022. Assessing the vulnerability of plant functional trait strategies to climate change. – Global Ecol. Biogeogr. 31: 1194–1206.
Baruah, G. et al. 2017. Community and species-specific responses of plant traits to 23 years of experimental warming across subarctic tundra plant communities. – Sci. Rep. 7: 2571.
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.
Bret-Harte, M. S. et al. 2001. Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment – Ecology. 82:18–32.
Bruelheide, H. et al. 2018. Global trait–environment relationships of plant communities. – Nat. Ecol. Evol. 2: 1906–1917.
Büntgen, U. et al. 2018. Long-term recruitment dynamics of arctic dwarf shrub communities in coastal east Greenland. – Dendrochronologia 50: 70–80.
Bürkner, P.-C. 2017. Brms: an R package for Bayesian multilevel models using Stan. – J. Stat. Softw. 80: 1–28.
Callaway, R. M. et al. 2002. Positive interactions among alpine plants increase with stress. – Nature 417: 844–848.
Carlson, B. Z. et al. 2015. Modelling snow cover duration improves predictions of functional and taxonomic diversity for alpine plant communities. – Ann. Bot. 116: 1023–1034.
Carpenter, B. et al. 2017. Stan: a probabilistic programming language. – J. Stat. Softw. 76: 1–32.

Chapin III, F. S. et al. 1996. Plant functional types as predictors of transient responses of arctic vegetation to global change. – J. Veg. Sci. 7: 347–358.
Choler, P. 2005. Consistent shifts in alpine plant traits along a mesotopographical gradient. – Arct. Antarct. Alp. Res. 37: 444–453.
Cruz-Maldonado, N. et al. 2021. Aboveground-trait variations in 11 (sub)alpine plants along a 1000-m elevation gradient in tropical Mexico. – Alp. Bot. 131: 187–200.
De Frenne, P. et al. 2021. Forest microclimates and climate change: importance, drivers and future research agenda. – Global Change Biol. 27: 2279–2297.
Díaz, S. et al. 2016. The global spectrum of plant form and function. – Nature 529: 167–171.
Dobbert, S. et al. 2021. How does spatial heterogeneity affect inter- and intraspecific growth patterns in tundra shrubs? – J. Ecol. 109: 4115–4131.
Dudley, A. et al. 2019. Using traits to assess threatened plant species response to climate change. – Biodivers. Conserv. 28: 1905–1919.
Enquist, B. J. et al. 2016. Cyberinfrastructure for an integrated botanical information network to investigate the ecological impacts of global climate change on plant biodiversity. – PeerJ 4: e2615v2.
Funk, J. L. et al. 2017. Revisiting the Holy Grail: using plant functional traits to understand ecological processes. – Biol. Rev. Camb. Phil. Soc. 92: 1156–1173.
Gelman, A. and Rubin, D. B. 1992. Inference from iterative simulation using multiple sequences. – Stat. Sci. 7: 457–472.
Gelman, A. et al. 2019. R-squared for Bayesian regression models. – Am. Stat. 73: 307–309.
Graae, B. J. et al. 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.
Hannah, L. et al. 2014. Fine-grain modeling of species' response to climate change: holdouts, stepping-stones and microrefugia. – Trends Ecol. Evol. 29: 390–397.
Happonen, K. et al. 2019. Snow is an important control of plant community functional composition in oroarctic tundra. – Oecologia 191: 601–608.
Harzé, M. et al. 2016. Functional traits are more variable at the intra- than inter-population level: a study of four calcareous dry-grassland plant species. – Tuexenia 36: 321–336.
Henn, J. J. et al. 2018. Intraspecific trait variation and phenotypic plasticity mediate alpine plant species response to climate change. – Front. Plant Sci. 9: 1548.
Hudson, J. M. G. et al. 2011. Taller and larger: shifts in Arctic tundra leaf traits after 16 years of experimental warming. – Global Change Biol. 17: 1013–1021.
Jokinen, P. et al. 2021. Climatological and oceanographic statistics of Finland 1991–2020. – Finnish Meteorological Inst.
Katabuchi, M. 2015. LeafArea: an R package for rapid digital image analysis of leaf area. – Ecol. Res. 30: 1073–1077.
Kattge, J. et al. 2020. TRY plant trait database – enhanced coverage and open access. – Global Change Biol. 26: 119–188.
Kearney, M. R. 2020. How will snow alter exposure of organisms to cold stress under climate warming? – Global Ecol. Biogeogr. 29: 1246–1256.
Kemppinen, J. et al. 2021a. Consistent trait–environment relationships within and across tundra plant communities. – Nat. Ecol. Evol. 5: 458–467.
Kemppinen, J. et al. 2021b. Dwarf shrubs impact tundra soils: drier, colder and less organic carbon. – Ecosystems 24: 1378–1392.
Kichenin, E. et al. 2013. Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradient. – Funct. Ecol. 27: 1254–1261.
Kopecký, M. et al. 2021. Topographic wetness index calculation guidelines based on measured soil moisture and plant species composition. – Sci. Total Environ. 757: 143785.
Kudo, G. 1996. Intraspecific variation of leaf traits in several deciduous species in relation to length of growing season. – Ecoscience 3: 483–489.
Kudo, G. et al. 1999. Effects of snowmelt timing on leaf traits, leaf production and shoot growth of alpine plants: comparisons along a snowmelt gradient in northern Sweden. – Ecoscience 6: 439–450.
le Roux, P. C. et al. 2013. Soil moisture's underestimated role in climate change impact modelling in low-energy systems. – Global Change Biol. 19: 2965–2975.
Litaor, M. I. et al. 2008. Topographic controls on snow distribution, soil moisture and species diversity of herbaceous alpine vegetation, Niwot Ridge, Colorado. – J. Geophys. Res. 113.
Maclean, I. M. D. 2020. Predicting future climate at high spatial and temporal resolution. – Global Change Biol. 26: 1003–1011.
Maitner, B. 2020. BIEN: tools for accessing the botanical information and ecology network database. – R package ver. 1.2.4, <https://CRAN.R-project.org/package=BIEN>.
Midolo, G. et al. 2019. Global patterns of intraspecific leaf trait responses to elevation. – Global Change Biol. 25: 2485–2498.
Mod, H. K. et al. 2016. What we use is not what we know: environmental predictors in plant distribution models. – J. Veg. Sci. 27: 1308–1322.
Moles, A. T. et al. 2009. Global patterns in plant height. – J. Ecol. 97: 923–932.
Niittynen, P. and Kemppinen, J. 2022. poniitty/ITV_grids: data and code: Microclimate relationships of intraspecific trait variation in sub-Arctic plants (v1.0). – Zenodo, <https://doi.org/10.5281/zenodo.6965609>.
Niittynen, P. et al. 2020a.Decreasing snow cover alters functional composition and diversity of Arctic tundra. – Proc. Natl Acad. Sci. USA 117: 21480–21487.
Niittynen, P. et al. 2020b.Fine-scale tundra vegetation patterns are strongly related to winter thermal conditions. – Nat. Clim. Change 10: 1143–1148.
Niu, K. et al. 2020. Harsh environmental regimes increase the functional significance of intraspecific variation in plant communities. – Funct. Ecol. 34: 1666–1677.
Norberg, J. et al. 2001. Phenotypic diversity and ecosystem functioning in changing environments: a theoretical framework. – Proc. Natl Acad. Sci. USA 98: 11376–11381.
Onipchenko, V. G. et al. 2020. Do patterns of intra-specific variability and community weighted-means of leaf traits correspond? An example from alpine plants. – Bot. Pacif. 9: 53–62.
Opedal, Ø. H. et al. 2015. Linking small-scale topography with microclimate, plant species diversity and intra-specific trait variation in an alpine landscape. – Plant Ecol. Divers. 8: 305–315.
Pérez-Ramos, I. M. et al. 2012. Evidence for a 'plant community economics spectrum' driven by nutrient and water limitations in a Mediterranean rangeland of southern France. – J. Ecol. 100: 1315–1327.
Pfennigwerth, A. A. et al. 2017. Trait variation along elevation gradients in a dominant woody shrub is population-specific and driven by plasticity. – AoB Plants 9: lx027.

Post, E. et al. 2019. The polar regions in a 2°C warmer world. – Sci. Adv. 5: eaaw9883.
Rixen, C. et al. 2022. Intraspecific trait variation in alpine plants relates to their elevational distribution. – J. Ecol. 110: 860–875.
Roybal, C. M. and Butterfield, B. J. 2019. Species-specific trait–environment relationships among populations of widespread grass species. – Oecologia 189: 1017–1026.
Siefert, A. et al. 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. – Ecol. Lett. 18: 1406–1419.
Stan Development Team 2019. Stan modeling language users guide and reference manual, ver. 2.29. – <https://mc-stan.org>.
Stan Development Team 2020. RStan: the R interface to Stan. R package ver. 2.21.2. – <http://mc-stan.org/>.
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. 2018. Forecasted homogenization of high Arctic vegetation communities under climate change. – J. Biogeogr. 45: 2576–2587.
Taseski, G. M. et al. 2021. Shifts in fine root traits within and among species along a fine-scale hydrological gradient. – Ann. Bot. 127: 473–481.
Thomas, H. J. D. et al. 2020. Global plant trait relationships extend to the climatic extremes of the tundra biome. – Nat. Commun. 11: 1351.
Thomson, E. R. et al. 2021. Multiscale mapping of plant functional groups and plant traits in the High Arctic using field spectroscopy, UAV imagery and Sentinel-2A data. – Environ. Res. Lett. 16: 055006.
Violle, C. and Jiang, L. 2009. Towards a trait-based quantification of species niche. – J. Plant Ecol. 2: 87–93.
Weemstra, M. et al. 2021. Patterns in intraspecific variation in root traits are species-specific along an elevation gradient. – Funct. Ecol. 35: 342–356.
Westerband, A. C. et al. 2021. Intraspecific trait variation and reversals of trait strategies across key climate gradients in native Hawaiian plants and non-native invaders. – Ann. Bot. 127: 553–564.
Wild, J. et al. 2019. Climate at ecologically relevant scales: a new temperature and soil moisture logger for long-term microclimate measurement. – Agric. For. Meteorol. 268: 40–47.